Vijay Singh Meena *Editor*

Role of Rhizospheric Microbes in Soil

Volume 2: Nutrient Management and Crop Improvement

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Chapter 1
Towards Plant-Beneficiary Rhizobacteria and Agricultural Sustainability

Mahipal Choudhary, Prakash Chand Ghasal, Ram Prakash Yadav, Vijay Singh Meena, Tilak Mondal, and J. K. Bisht

Abstract The increasing demand for crop production, given worldwide increases in the human population, puts pressure on moving natural resources towards sustainable development. This creates a big challenge for the upcoming generation. If improvement is not successful, there exists the unfortunate consequence that global food production may soon become insufficient to feed all of the world's people. It is therefore essential that agricultural productivity be significantly increased in a more sustainable and environmentally friendly approach. Plant-beneficiary rhizobacteria (PBR) naturally activate microorganisms found in the soil. Because they are inexpensive, effective, and environmentally friendly, PBR are gaining importance for use in crop production by restoring the soil's natural fertility and protecting it against drought and soil diseases, thereby stimulating plant growth. PBR decrease the use of chemical fertilisers, pesticides, and artificial growth regulators; the intensive use of these inputs has led to severe health and environmental hazards, such as soil erosion, water contamination, pesticide poisoning, decreased groundwater table, water logging, surface crusting and depletion of biodiversity. The use of PBR has been proven to be an environmentally sound way of increasing crop yields by facilitating plant growth through either a direct or indirect mechanism with the aim of sustaining soil health over the long term.

Keywords PBR · IAA · Siderophore · Biofertilisers · Biocontrol agents · Biological nitrogen fixation · Nodulation

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1.1 Introduction

PBR are potential tools for creating sustainable agriculture as part of the environmentally friendly trend for the future. The benefits of PBR are globally accepted for sustainability in agriculture. The main benefits of PBR are that they increase and access nutrient availability in soil over the long term under adverse conditions, protect the environment (Das et al. 2013), and confer significant increases in the growth, yield and quality of agronomically important crops (Gray and Smith 2005; Silva et al. 2006; Figueiredo et al. 2008; Araujo 2008). PBR represent only 2–5% of total rhizospheric bacteria (Antoun and Kloepper 2001). The term "PBR" is used to refer to all beneficial bacteria living in the rhizosphere that play an important role in increasing soil fertility, promoting plant growth, and suppressing phytopathogens for the development of ecofriendly and sustainable agriculture (Gupta et al. 2015) through one or more mechanisms (Haghighi et al. 2011; Meena et al. 2013c; Kumar et al. 2016b).

However, PBR are also useful for crops needing high resistance to abiotic stresses, such as temperature extremes, pH, salinity, drought and heavy-metal and pesticide pollution (Gopalakrishnan et al. 2015). In India, the use of chemical fertilisers for crop production—which deteriorate soil quality (Choudhary et al. 2018a) and cause several types of environmental pollution that promote severe adverse effects on living beings—has increased to an alarming level (Das et al. 2013). Therefore, this is the right time to address concerns about sustainable agriculture development with use of PBR instead of using artificial substances in agriculture, such as chemical fertilisers, pesticides and growth regulators (Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015, 2016a; Jha and Subramanian 2016).

Plant-growth promotion by way of PBR can occur in two ways: direct and indirect. PBR work *directly* through atmospheric biological N_2 fixation (BNF), solubilisation, mobilisation and mineralisation of phosphorus (P); potassium (K) solubilisation; production of chelating agents, such as siderophores, which solubilise and increase the availability of iron (Fe) and zinc in soil; production of exopolysaccharides; and production of plant-growth hormones, such as indole acetic acid (IAA), gibberelins (GA), cytokinin (CK) and ethylene (Bhardwaj et al. 2014; Arora et al. 2012; Singh et al. 2016; Kaur et al. 2016). *Indirectly*, PBR work through antibiotic production (antibiosis), induced system resistance (ISR), hydrolytic enzymes, hydrogen cyanide, volatile-compound production, competition for nutrients and space, parasitism and predation, among others (Kaur et al. 2016).

Sustainable agricultural crops must possess disease resistance, salt (Na) tolerance, drought tolerance, heavy metal–stress tolerance, and better nutritional values. To accomplish the above-mentioned desired crop properties, one possibility is to use soil microorganisms (bacteria, fungi, algae, etc.) that increase nutrient-uptake capacity and water-use efficiency. Among these prospective soil microorganisms, bacteria known as PBR are the most promising.

In this sense, PBR may be used to enhance plant health and promote plant-growth rate without causing environmental contamination. In this chapter, we describe the different categories of PBR, their modes of action and their potential uses and benefits. The farming community faces many problems related to the high costs of chemical fertilisers, pesticides and other growth substances, which hamper sustainable agriculture development. Furthermore, the application of these chemicals causes harmful damage to the soil and the overall environment. Therefore, there is an immediate need to encourage farmers to adopt cost-effective, efficient and sustainable technologies, such as PBR, for better crop growth and a healthy environment (Ahmad et al. 2016a, b; Meena et al. 2016e; Parewa et al. 2014; Jaiswal et al. 2016).

1.2 What Is Rhizosphere?

The term "rhizosphere" was given by the German agronomist and plant physiologist, Lorenz Hiltner, in 1904. "Rhizosphere" is a Greek word: "Rhiza" means roots, and "sphere" means surrounding area. Rhizosphere is an area around the root surfaces where the biological activity of a microorganism is highest it is due to secretion of large quantity of metabolites from living root hairs or fibrous root systems. Rhizosphere is a unique vital ecological zone of soil that is highly enriched with nutrients obtained from plant roots by way of rhizodeposition with the help of rhizobacteria (Prashar et al. 2013).

Rhizosphere is categorised into the following three zones (Pinton et al. 2001) (Fig. 1.1):

1. *Endo-rhizosphere* is the intercellular space between the cortex and the endodermis, in which microbes and cations can occupy the "free space" between cells (apoplastic space) that do not form symbiotic structures (Bowen and Rovira 1999).
2. *Rhizoplane* is the medial zone directly adjacent to the root, including the root epidermis and mucilage. It consists of the epidermis, the cortex and the mucilaginous polysaccharide layer.
3. *Ecto-rhizosphere* is the outermost zone, which extends from the rhizoplane out into the bulk soil.

Algae or cynobacteria with fungus termed as "lichen," in vascular tissue of plants with fungi, have an association known as the mycorrhiza (Linderman 1988), whereas in some other plants another, a strongly adhering dense layer termed "rhizosheath" is found. It consists of root hairs, mucoid material, microbes and soil particles (Curl and Truelove 1986). The root itself is a part of the rhizosphere because endophytic microorganisms colonize the inner root tissues as well (Bowen and Rovira 1999). The volume of the soil that is not part of the rhizosphere, i.e., that is not influenced by the root, is known as "bulk soil" (Gobat et al. 2004). Thus, rhizosphere may be considered as a unique region distinct from bulk soil.

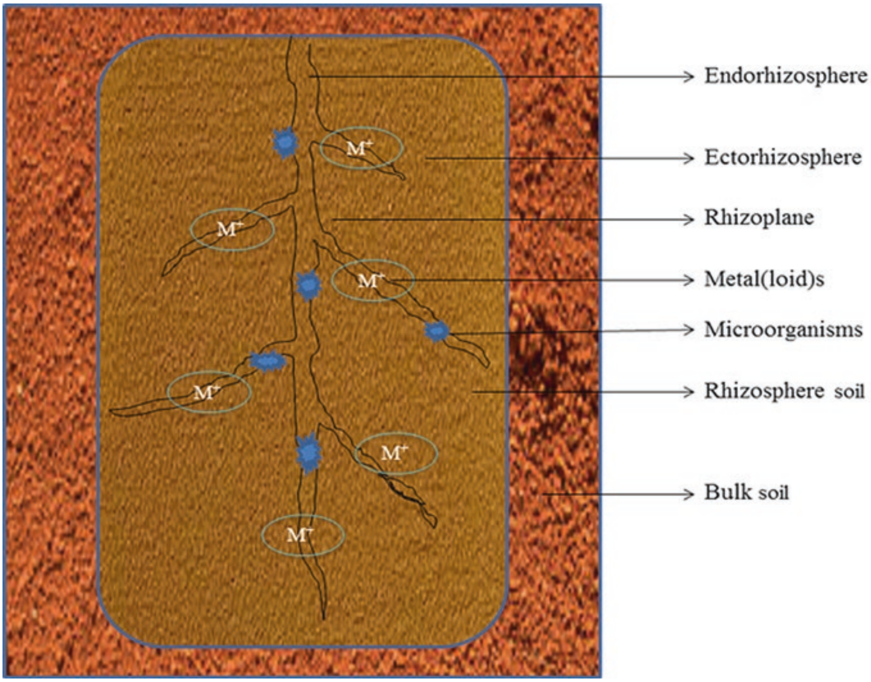

Fig. 1.1 Schematic of a root section showing the structure of the rhizosphere and their different zones

1.3 What Is the Rhizospheric Effect?

Rhizospheric effect is the enhanced growth of a soil microorganism resulting from physical and chemical alteration of the soil and the contribution of excretions and organic debris of roots exudation, secretion and deposition within a rhizosphere compared with the bulk soil. Micro-organism diversity is greater near the rhizoplane because plants typically exude a large fraction of their photosynthetically fixed carbon (C [estimated to generally be in the range of 5–30%]) through their roots. Roots exudates act as a bacterial food source, which is the main reason why the numbers of bacteria around the roots of plants (i.e., the rhizosphere) are 10–1000 times greater than those found in bulk soil. The microbial population decreases with an increase in distance from the rhizoplane (Chowdhury et al. 2009) (Table 1.1). Soil volume is affected by the secretion of exudates or metabolites, i.e., sugars, oligosaccharides, vitamins, nucleotides, flavones, auxins and stimulators, from roots that form a microclimate of the rhizosphere (Shukla et al. 2013; Dotaniya et al. 2013).

Compared with bulk soil, rhizospheric soil 1 has greater diversity of microbial population due to the secretion of organic compounds that attract and enhance microbes for the availability of C and energy in the rhizospheric zone (Aira et al.

Table 1.1 Microbial diversity with increasing distance from rhizoplane

Distance from root (mm)	CFU × 10^9 cm^{-3} soil
0–1	120
1–5	95
5–10	40
10–15	35
15–20	15

Table 1.2 Microorganism population in the rhizosphere of wheat (*Triticum aestivum* L.) and bulk soil and the R/S ratio

Microorganisms	Rhizospheric soil (CFU g^{-1} soil)	Bulk soil (CFU g^{-1} soil)	R/S ratio
Bacteria	1.2×10^9	5.3×10^7	23
Actinomycetes	4.6×10^7	7.0×10^6	7
Fungi	1.2×10^6	1.0×10^5	12
Protozoa	2.4×10^3	1.0×10^3	2
Algae	5.0×10^3	2.7×10^4	0.2
Ammonifiers	5.0×10^8	4.0×10^6	125
Denitrifies	1.26×10^8	1.0×10^5	1260

2010). The plant secretes 10–30% of photosynthates through the root system into the rhizosphere soil (Bowen and Rovira 1999).

The rhizosphere's effect on the soil microbial population can be measured by comparing the population density [colony-forming units (CFUs)] between the rhizosphere soil (R) and the bulk soil (S), for which the "R/S ratio" is employed (Atlas and Bartha 1997). The rhizosphere effect is greater for bacteria > fungi > actinomycetes > protozoa. In contrast, algae exhibit more population in bulk soil compared with rhizosphere soil. The type of associated plant can also affect the R/S ratio, which is directly related to the amount and type of root exudates (Rout and Katznelson 1961) (Table 1.2).

Various physicochemical changes and the biological activity in the surrounding rhizosphere are highly affected by plant-roots activity, and these processes are determined by nutrient availability, nutrients dynamics and solubility and mobility of toxic elements for plants and microorganisms, thereby creating a unique vital micro-climate of the rhizosphere, which can exhibit completely different properties compared with the bulk soil, which is not directly influenced by the activity of the roots (Neumann et al. 2009; Prakash and Verma 2016; Das and Pradhan 2016; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016; Meena et al. 2015d).

Organic-matter decomposition serves as energy source for the growth of microorganisms and supplies C for their cell synthesis (Rillig et al. 2007). Under aerobic conditions, microbes assimilate 20–40% of the substrate C, and the residual amount is released to the atmosphere as CO_2 (Zak et al. 2000; Rajendiran et al. 2012).

1.4 PBR

Rhizobacteria are the most plentiful microorganisms (~ 95% in the rhizosphere) because of their high growth rate and their ability to use different C and nitrogen (N) sources (Glick 2012), and a special class of bacteria—called "plant growth–promoting rhizobacteria—influences plant growth in a wide range of crops by way of a variety of direct and indirect mechanisms (Prashar et al. 2013). These group of bacteria is capable of actively colonising the plants' root surface system and can improve their growth and yield (Wu et al. 2005). Of the soil microbes, approximately 98% cannot be cultured.

Group of bacterial species—including *Pseudomonas, Azospirillum, Azotobacter, Klebsiella, Enterobacter, Alcaligens, Arthrobacter, Burkholderia, Bacillus* and *Serrati* —have been reported to enhance plant growth and yield (Saharan and Nehra 2011) (Table 1.3). *Agrobacterium, Bacillus, Escherichia coli, Pseudomonas, Rhizobium* and many fungi are capable of producing these Fe-chelating compounds (Meena et al. 2015e, 2016c; Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Zahir et al. 2004).

1.5 Mechanisms and Mode of Action of PBR

1.5.1 Direct Mechanism

The direct mechanism by PBR entails either providing the plant with plant growth–promoting substances that are synthesised by the bacterium or facilitating the uptake of certain plant nutrients from the environment. Biofertilisers contribute to plant nutrition both by facilitating nutrient uptake and by enhancing primary nutrient availability in the rhizosphere by direct mechanisms, such as fixing atmospheric N; solubilising mineral nutrients such as P, K, etc.; mineralising organic compounds; producing phytohormones; and production of siderophores which sequester micronutrients (Kaur et al. 2016; Bhardwaj et al. 2014; Arora et al. 2012) (Fig. 1.2).

1.5.1.1 PBR as Biofertiliser

Biofertiliser is a formulation that contains living cells of efficient strains of microorganisms. When applied to seeds, plant surfaces or soil, it colonises the rhizosphere and promotes growth by increasing the supply or availability of primary nutrients to the host plant or through the synthesis of growth-promoting substances by enhancing the decomposition of plant residues. Various sources of biofertilisers include biological-N fixers, phytostimulators, phosphate-solubilising bacteria (PSB), PBR, vesicular-arbuscular mycorrhiza (VAM), S-solubilising microorganisms, K-solubilising microorganisms (KSM), siderophores, etc. (Prathap and Ranjitha Kumari 2015). The use of biofertilisers and bioenhancers—such as N-fixing bacteria and beneficial

Table 1.3 Different PBR tested for various crop types

PBR	Host crop	Results addition the bacteria to crops	References
E. sakazaki 8MR5	–	Inoculation increased growth parameters	Babalola et al. (2003)
Rhizobium; Pseudomonas sp.	*Medicago sativa, Trigonella foenumgraecum, Vigna radiata*	BNF	Maheshwari et al. (2010), Zhao et al. (2012) and Choudhary et al. (2017a)
P. fluorescens C7	*Arabidopsis thaliana*	Iron pyoverdin synthesised and increased Fe levels inside plants and improved their growth	Vansuyt et al. (2007)
Xanthomonas sp. RJ3, *Pseudomonas* sp. RJ10, *Bacillus* RJ31, *Azomonas* sp. RJ4	*Brassica napus*	Stimulated plant growth and increased cadmium accumulation	Sheng and Xia (2006)
Bradyrhizobium MRM6	*T. aestivum*	Enhanced growth parameters in green gram at all tested herbicide concentrations	Ahemad and Khan (2011)
Pseudomonas sp. PS1	*Vigna radiate*	Significantly increased plant dry weight, nodule numbers, total chlorophyll content, leghaemoglobin, root N, shoot N, root P, shoot P, seed yield and seed protein	Ahemad and Khan (2012a, b, c)
Bradyhizobium sp. 750	*Lupinus luteus*	Increased both biomass and N content and accumulation of metals	Dary et al. (2010)
Pseudomonas sp., *Ochrobactrum cytisi*			
Coccus DIM7, *streptococcus* PIM6 *Bacillus* sp. PIS7	*Zea mays*	Achieved RP mineralisation in soil and improved all growth parameters including shoot (~ 56%), root yield (~ 52%), height (~ 41%), N (~ 80%) and P (~ 91%) uptake by maize plants compared with the control	Wahid et al. (2016)
Pseudomonas sp.	*Z. mays*	Significantly increased soil-enzyme activities, total productivity and nutrient uptake	Sharma et al. (2011) and Phi et al. (2010)
P. polymyxa	*Piper nigrum*	Significantly increased the biomass of plants and elicited ISR against bacterial-spot pathogen in untreated *X. axonopodis* pv. Vesicatoria plants	

(continued)

Table 1.3 (continued)

PBR	Host crop	Results addition the bacteria to crops	References
Pseudomonas, Azospirillum	*P. nigrum* L.	Increased P solubilisation and availability	Ramachandran et al. (2007)
AM fungi, *A. brasilense, Azotobacter, Pseudomomas* sp.	*Pinus sabiniana, Solanum lycopersicum, Lactuca sativa, T. aestivum, Z. mays*	Stimulated root colonisation, increases biomass, limited soil salinity stress and affected plant yield	Kohler et al. (2010)
Acinetobacter sp.	*Oryza sativa*	Significantly increased rice growth and yield parameters and increased Zn solubility from Zn sources, such as ZnO and $ZnCO_3$, with inoculation	Gandhi and Muralidharan (2016)
Bacillus sp.	*Glycine max*	Increased P solubilisation and availability	Wahyudi et al. (2011)
B. polymyxa	*Lycopersicon esculentum*	Proline accumulation improved the physiological and biochemical parameters of plants	Shintu and Jayaram (2015)
B. subtilis	*S. lycopersicum*	Dry biomass increased ~ 31% for tomato, ~ 36% for okra and ~ 83% for African spinach	Adesemoye et al. (2008)
P. aeruginosa	*Abelmoschus esculentus*		
	Amaranthus		
P. fluorescens BAM-4, *B. cepacia* BAM-12 and *Glomus etunicatum*	*T. aestivum*	Significantly improved plant growth and nutrient uptake, showed significant increase in wheat grain yield and increased P availability from insoluble-P sources	Minaxi et al. (2013)
Azotobacter and *Bacillus*	*Tr. aestivum*	Wheat inoculation with *Azotobacter* and *Bacillus* increased seed yield by ~ 30% and 43%, respectively. This increase was due to the production of certain growth hormones, such as IAA	Kloepper et al. (1991)
Enterobacter strain CIK-521R and *Klebsiella* strain CIK-518	*Z. mays*	Showed great tolerance to Cd and thus could be deployed to manage Cd-contaminated soil. Both strains could be effective inoculants to obtain greater maize production in normal and Cd-contaminated soils.	Ahmad et al. (2016a, b)

RP Rock phosphate

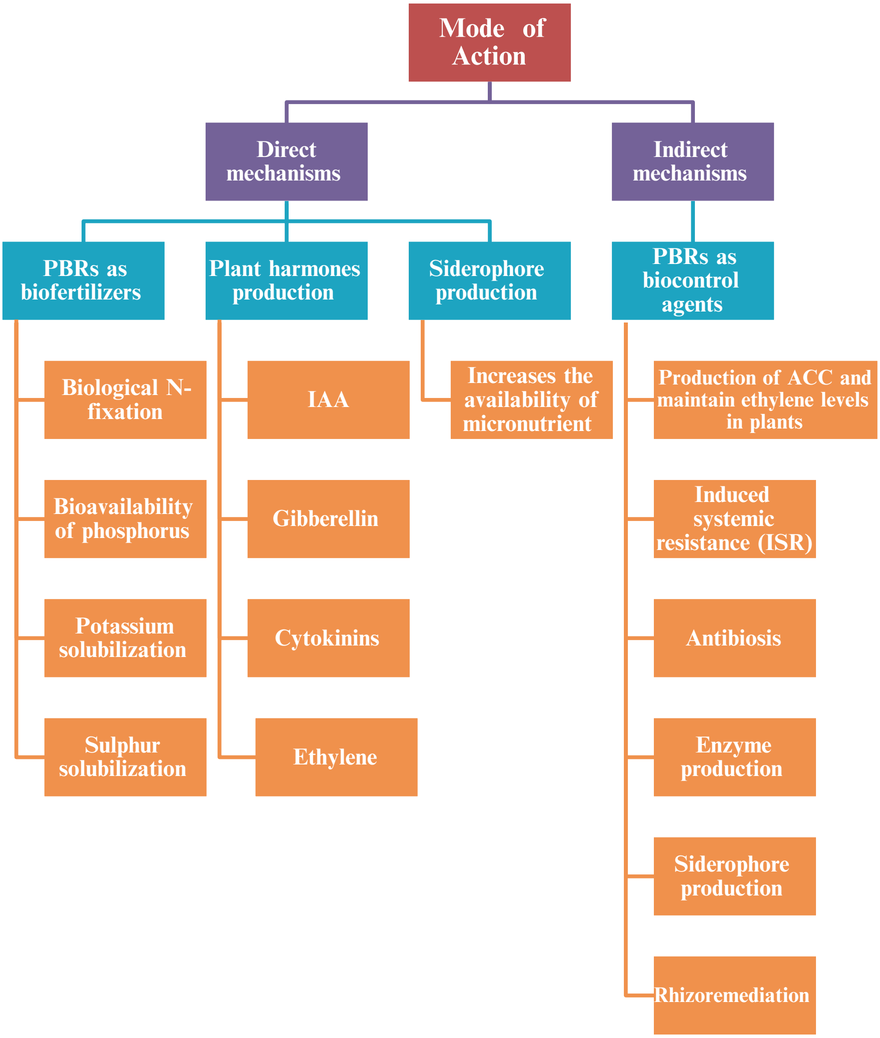

Fig. 1.2 Direct and indirect mechanisms stimulating plant growth for enhancing productivity

microorganisms—can decrease chemical fertiliser applications (Raghavendra et al. 2016; Zahedi 2016; Meena et al. 2015b, 2016d; Teotia et al. 2016; Bahadur et al. 2016b) and consequently decrease production cost; foster soil enrichment with nutrient, which is compatible with long-term soil sustainability; poses no danger to the environment; is ecofriendly and promotes more sustainable agricultural production (Mohapatra et al. 2013; Ashrafuzzaman et al. 2009). BNF is a vital characteristic of ecofriendly food production for long-term soil sustainability and crop productivity. Biofertilisers increases crop yield ≤10–40% and fixes N ≤ 40–50 kg ha^{-1}, and parental inoculums are sufficient for the growth and multiplication of organisms in

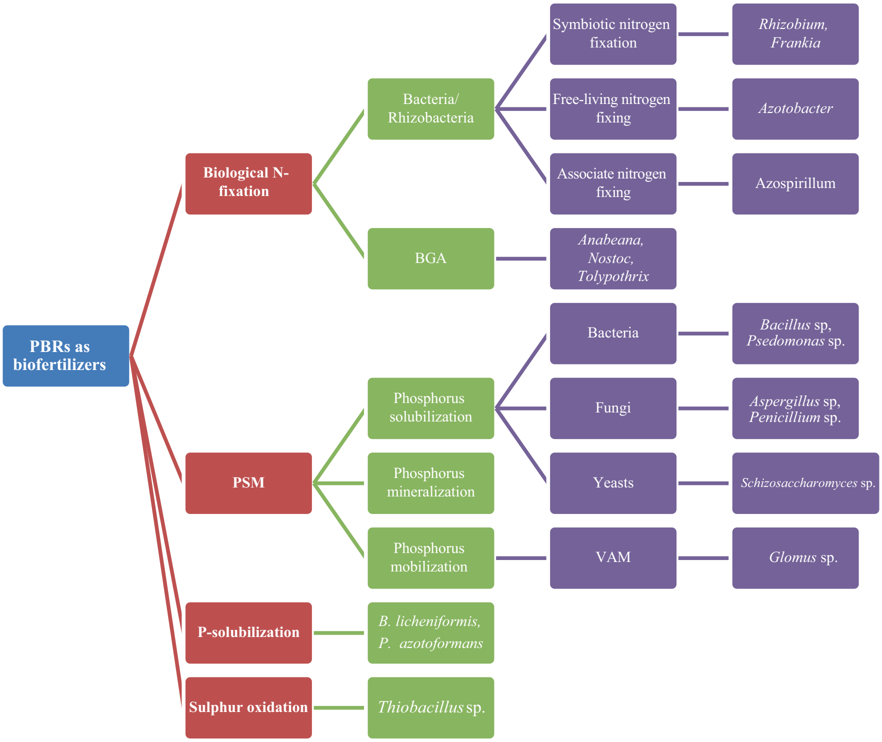

Fig. 1.3 Outlined diagram showing classification of biofertilisers

subsequent years. They improve soil texture, pH, water holding capacity (WHC) and other properties of soil (Mohapatra et al. 2013) (Fig. 1.3).

1.5.1.2 BNF

BNF is the biochemical process in which atmospheric N is reduced or converted into ammonia (plants can only use reduced forms of this element) in the presence of nitrogenase enzyme and legheamoglobin pigment. Nitrogenase is a biological catalyst found naturally only in certain microorganisms, such as the symbiotic *Rhizobium* and *Franki,* or the free-living *Azospirillum* and *Azotobacter* (Franche et al. 2009; Suhag 2016).

Mechanism of BNF

nitrogenase

N_2(a) ------------------------- > NH_3 – – > – – – > – – – > amino acids --------- > proteins
+ ATP
+ H +
low oxygen tension

1.5.1.2.1 Symbiotic N Fixation by *Rhizobium*–Legume Plant

Rhizobium associated with leguminous plants (e.g., various members of the pea family). The symbiotic N-fixing bacteria invade the root hairs of host plants where they multiply and stimulate the formation of root nodules, enlarge plant cells, and confer bacteria in intimate association. Within the nodules, the bacteria convert free N to ammonia, which the host plant uses for its development (Fig. 1.4), e.g., alfalfa, beans, clovers, peas, soybeans, and seeds are usually inoculated with commercial cultures of appropriate *Rhizobium* species, especially in poor soils or those lacking in the required bacterium. Rhizobium–legume symbiosis could have important agronomic implications and enable the use of N fertiliser applications to be decreased or even avoided. Indeed, in the short term, improved understanding could lead to more sustainable exploitation of the biodiversity of N-fixing organisms (Santi et al. 2013). Several genera have been outlined by Sahgal and Johri (2003)—including *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Methylobacterium*, *Rhizobium* and *Sinorhizobium*—as being the most important (Table 1.4).

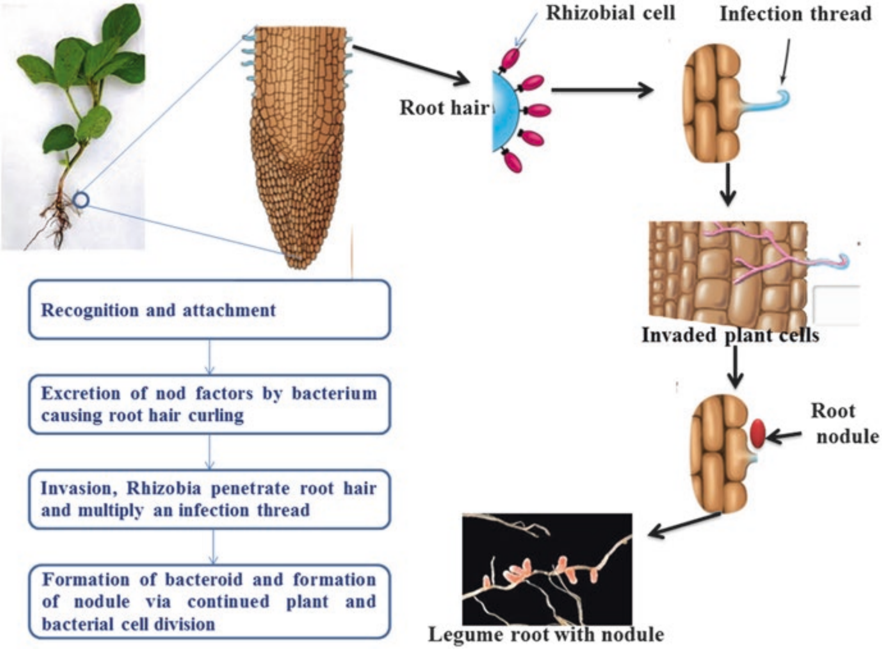

Fig. 1.4 Schematic diagram showing mechanism of BNF in soybean crop

Table 1.4 Major legume crop inoculated with different bacterial groups

Crop	Nodulating bacteria	Biological N_2 fixed (kg ha^{-1} $year^{-1}$)
Alfalfa	*Rhizobium meliloti, S. melilotii*	150–300
Beans	*R. legumninosarum biovar phaseoli*	25–150
	R. tropici	
Clover	*R. leguminosarum biovar trifolii*	120
Lotus	*M. loti*	20–25
Peas	*R. leguminosarum biovar viceae*	25–150
Pigeon pea	*Rhizobium* sp.	140–280
Sesbania	*A. caulinodans*	20–25
Soybean	*B. japonicum*, *B. elkanii*,	30–250
	R. fredii	

1.5.1.2.1.1 Symbiotic N Fixation by Non-legume Plant

Frankia belong to the genus of soil actinomycetes in the family Frankiaceae that fix N both under symbiotic and free-living aerobic conditions. *Frankia* is associated with certain dicotyledonous species of woody plants (actinorhizal plants), i.e., Alnus (alder) and Casuarina (beef wood) (Dawson 2008) (Fig. 1.5).

1.5.1.2.1.2 Anabaena–Azollae Symbiotic Association

Azolla pinnata is a floating aquatic fern and a microscopic filamentous blue-green algae or cyanobacterium *(Anabaena–azollae)* are symbiotically associated with each other. The merits of the *Azolla–anabaena* association lie in its ability to fix atmospheric N and photosynthesise and increases rice yields by 10–20%. It can also be used as "green manure," particularly in flooded rice fields. The use of *Azolla* as a green manure has also been reported to improve soil porosity (3.7–4.2%) and decrease the bulk density of soils. *Aulosira fertilissima* is the most active N fixer in rice fields, whereas *Cylindrospermum* is active in sugarcane and maize fields. They add 20–30 kg N_2 ha^{-1} $annum^{-1}$. A. *fertilissima* has been used as a biofertiliser for rice cultivation and animal feed in China (Carrapiço 2001; Mazid and Khan 2014; Kollah et al. 2016). *Azolla* contributes to maintaining soil health by providing nutrient-rich humus through its decomposition and improving physico-chemical conditions and soil structure (Choudhary et al. 2017b; Singh et al. 2016a, b; Meena et al. 2015f; Rawat et al. 2016; Bahadur et al. 2016a; Masood and Bano 2016).

1.5.1.2.1.3 Associative N Fixation

Azospirillum is an associative symbiotic and non-nodule forming aerobic bacteria that occurs in the roots of dicots and monocot plants, i.e., corn, sorghum, wheat and sugarcane (Bashan and De-Bashan 2010; Babalola and Glick 2012; Duca et al. 2014; Glick 2014). It is considered important that PBR worldwide increase the growth, yield and phytohormones (Vurukonda et al. 2016) of many cereals. Two

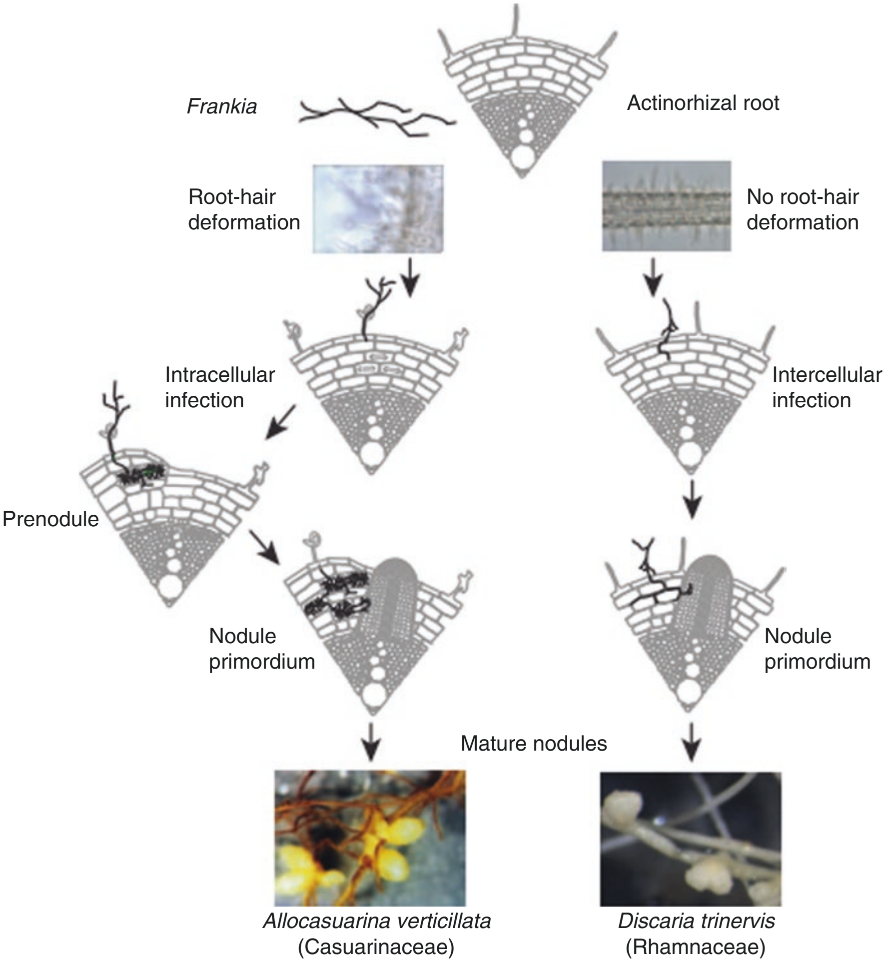

Fig. 1.5 Schematic representation of actinorhizal root infection by Frankia (Source: Franche and Bogusz 2011)

important species of *Azosirillum*, identified *A. brasilense* and *A. lipoferum,* exist. These are isolated from wheat seed and cause an increase in seed germination, plant growth, plumule and radicle length and rice crop, respectively. Other free-living diazotrophs have been repeatedly detected in association with plant roots, including *Acetobacter diazotrophicus, Herbaspirillum seropedicae, Azoarcus spp.* and *Azotobacter*. According to Dimkpa et al. (2009), *Azospirillum* enhanced plant tolerance to drought stress by the production of IAA) *A. lipoferum* decreased drought stress in maize by the synthesis of abscisic acid (ABA) and GA (Cohen et al. 2009). *Azospirillum* has been found to be very effective in increasing the yield of cereal crops by 10–15% and fixing N ≤20–40 kg ha^{-1}. It also produces growth promoters

(IAA, GA, CK) and enhances root development and the uptake of plant nutrients (N, P and K) (Mohapatra et al. 2013; Mazid and Khan 2014).

1.5.1.2.2 Non-symbiotic or Free-Living N-Fixing Bacteria

Non-symbiotic or free-living N-fixing bacteria have great importance for sustainable agricultural production. They (bacteria/rhizobacteria) perform N fixation freely or without association, but there is a deficiency of C and energy by moving closer to the root rhizosphere. Some important non-symbiotic N-fixing bacteria include *Gluconacetobacter diazotrophicus, Azotobacter* sp.*, Achromobacter*, *Alcaligenes*, *Arthrobacter*, *Azomonas*, *Bacillus*, *Beijerinckia*, *Clostridium*, *Corynebacterium*, *Derxia*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Rhodo-spirillum*, *Rhodopseudomonas* and *Xanthobacter* (Vessey 2003; Barriuso and Solano 2008). *Azotobacter Beijerinckia* and *Clostridium* (anaerobic) are saprophytic (both are aerobic). *Desulphovibrio* is a chemotrophic N-fixing bacterium. *Rhodopseudomonas, Rhodospirillum* and *Chromatium* are N-fixing photoautotrophic bacteria. These bacteria fixed ≤10–25 kg of N_2 ha^{-1}/annum. *Bacillus* sp., WhIr-15 and *B. subtilis* WhIr-12, have potential at field level to improve the yield of wheat crop and may be helpful in the formulation of an effective biofertiliser for wheat (Ahemad and Kibret 2014; Baghaeeravari and Heidarzadeh 2014). *Ba. amyloliquefaciens* is an important bacterium for soybean that enhanced growth, yield and quality of soybean (Kumar et al. 2017; Mazid and Khan 2014).

1.5.1.3 P Bioavailability

P is the second most important essential element in the nutrition of crops after N. It governs all major metabolic processes in plants, including photosynthesis, energy transfer, signal transduction, macromolecular biosynthesis and respiration (Khan et al. 2010). It is copiously available in soils in both organic and inorganic forms. Most of the P after application in soil as chemical fertiliser (~ 70–90%) precipitates into stable, insoluble compounds, such as calcium phosphate (calcareous and alkaline soils), aluminum phosphate, and Fe phosphate (acid soils) (Chen et al. 2008). The remaining P is present in organic form, which is unavailable to the plant: Only 0.1% of total soil P exists in a soluble form for plant uptake (Meena et al. 2013c, 2016c; Yasin et al. 2016). This occurs due to the fixation and low solubility of P in soil (Pereira and Castro 2014). Plants absorb phosphate in two soluble forms only: monobasic ($H_2PO_4^-$) and diabasic (HPO_4^{2-}) ions (Bhattacharyya and Jha 2012; Pandey and Maheshwari 2007) (Fig. 1.6).

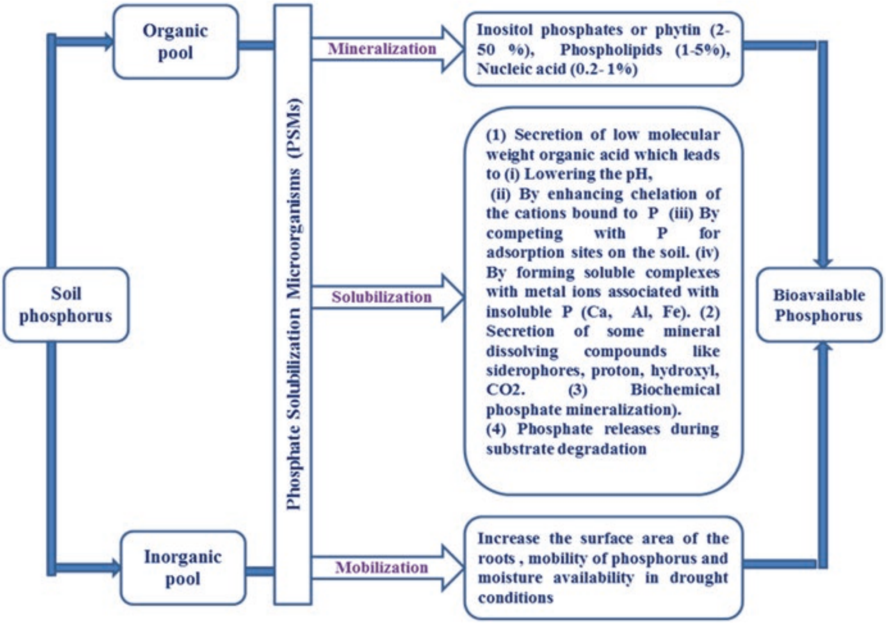

Fig. 1.6 Different organic/inorganic compounds synthesised by P-solubilising microorganisms (PSM) responsible for P solubilisation, mineralisation and mobilisation in soils

1.5.1.3.1 P Solubilization

These efficient PBR are amply present in the rhizosphere, i.e., PSB. They play an important role in P nutrition by enhancing its availability through the conversion of insoluble or bounded P into available form with the help of certain mechanisms (Khan et al. 2009; Sundaram et al. 2016) (Fig. 1.6).

Locked inorganic and organic P are made available to plants in an eco-friendly manner through solubilization and mineralization with PSB (Kumar 2016; Sharma et al. 2013). Seed inoculation with PSB decreases 30 kg P_2O_5 ha^{-1} or 50% phosphatic fertilisers. Thus, PSB culture increases the efficiency of P in soil and thus increases uptake by plants. They have capability to solubilize insoluble inorganic phosphate (mineral phosphate) compounds, such as tricalcium phosphate, dicalcium phosphate, hydroxyl apatite and RP (Rodríguez and Fraga 1999; Rodríguez et al. 2006; Sureshbabu et al. 2016; Saha et al. 2016b; Yadav and Sidhu 2016; Singh et al. 2015).

1.5.1.3.1.1 Mechanism of P Solubilization by PSM

1. Secretion of low molecular–weight organic acid, i.e., malic, succinic, fumaric, citric, tartaric, 2-ketogluconic, gluconic and acetic acid, which leads to:
    - (i) Decreasing pH;
    - (ii) Enhancing chelation of cations bound to P;
    - (iii) Competing with P for adsorption sites on soil; or
    - (iv) Forming soluble complexes with metal ions associated with insoluble P (Ca, Al, Fe)
2. Secretion of some mineral dissolving compounds, such as siderophores, protons, hydroxyls, CO_2
3. Discharge of extracellular enzymes (biochemical phosphate mineralization)
4. Phosphate release during substrate degradation (biological phosphate mineralization)

1.5.1.3.2 P Mineralization

Organic P solubilization is also called "P mineralization." Mineralization of soil organic P plays a vital role in the P cycling of a cultivation system. Organic P may constitute 4–90% of the total soil P (Khan et al. 2009). Soil P can be mineralised from different organic compounds, such as inositol phosphates or phytin (2–50%), phospholipids (1–5%), nucleic acid (0.2–1%), etc., with the help of enzymes that are secreted from P-solubilizing microorganisms (Table 1.5), i.e., phosphatase produced by the *Bacillus* sp. NG7 (Saravanan et al. 2016). In this process, mainly three categories of enzymes—i.e., phosphatases, phytases and phosphonatases—are involved (Behera et al. 2013).

1.5.1.3.3 P Mobilization

Mycorrhizae arise from a mutualistic symbiotic relationship between soil fungi and the roots of vascular plants. This is an important bidirectional nutrient transfer between fungi and roots, and it is ubiquitous in nature. The plant supplies the fungi with sugars produced by photosynthesis, whereas the hyphae network improves the plant capacity to absorb water and nutrients (Smith et al. 2003; Plenchette et al. 2005; Smith and Read 2008). The arbuscular mycorrhizal (AM) fungi are a group of endophytes that constitute the phylum Glomeromycota. However, these efficient AM fungi form a symbiosis with the roots including approximately 80% of all vascular plant species, such as many important crop species like maize, wheat, rice and potato (Smith and Read 2008; Meena et al. 2016a; Saha et al. 2016a; Verma et al. 2015a). Endomycorrhizae (forms arbuscules or vesicles) and ectomycorrhizae (forms harting net) are the two main types of mycorrhizae and are categorised according to the penetration of mycelia into the root tissue (Fig. 1.7).

Table 1.5 Important PSM

Microorganism	Related species	References
Bacteria	*Alcaligenes* sp., *Aerobactor aerogenes, Achromobacter* sp., *Actinomadura oligospora, Agrobacterium* sp., *A. brasilense, Bacillus* sp., *B. megaterium, B. circulans, B. cereus, B. fusiformis, B. pumils, B. mycoides, B. polymyxa, B. coagulans B. chitinolyticus, B. subtilis, B.* sp., *Brevibacterium* sp., *Citrobacter* sp., *Pseudomonas* sp., *P. putida, P. striata, P. fluorescens, P. calcis, Flavobacterium* sp., *Nitrosomonas* sp., *Erwinia* sp., *Micrococcus* sp., *E. intermedia, Serratia phosphoticum, Nitrobacter* sp., *Thiobacillus ferroxidans, T. thioxidans, R. meliloti, Xanthomonas* sp., *Gluconacetobacter* sp., *Burkholderia* sp.	Vazquez et al. (2000), Kumar et al. (2001), Chung et al. (2005), Chen et al. (2006), Saharan and Nehra (2011), Sharma et al. (2013), Nehra and Choudhary (2015), Stephen et al. (2015) and Sureshbabu et al. (2016)
Fungi	*Aspergillus awamori, A. niger, A. tereus, A. flavus, A. nidulans, A. foetidus, A. wentii. Fusarium oxysporum, Alternaria teneius, Achrothcium* sp., *Penicillium digitatum, P lilacinium, P balaji, P. funicolosum, Cephalosporium sp., Cladosprium* sp., *Curvularia lunata, Cunnighamella, Candida* sp., *Chaetomium globosum, Humicola inslens, H. lanuginosa, Helminthosporium* sp., *Paecilomyces fusisporous, Pythium* sp., *Phoma* sp., *Populospora mytilina, Myrothecium roridum, Morteirella* sp., *Micromonospora* sp., *Oideodendron* sp., *Rhizoctonia solani, Rhizopus* sp., *Mucor* sp., *Trichoderma viridae, Torula thermophila,Schwanniomyces occidentalis, Sclerotium rolfsii*	Fenice et al. (2000), Khan and Khan (2002), Reyes et al. (1999, 2002) and Duponnois et al. (2006)
Yeast	*Yarrowia lipolytica, Schizosaccharomyces pombe* and *Pichiafermentans*	Vassilev et al. (2001)
Actinobacteria	*Actinobispora yunnanensis, Actinomodura citrea, Microtetrospora astidiosa, Micromonospora echinospora, Sacchromonospora viridis, Saccharopolyspora hirsute, Streptomyces albus, Streptoverticillium album, Streptomyces cyaneus, Thermonospora mesophila*	Araujo et al. (2001) and Adhya et al. (2015)
Algae	*Cyanobacterium* sp., *Chlorella* sp., *Lyngbya* sp., *Anabena* sp., *Calothrix braunii, Nostoc* sp., *Scytonema* sp.	Mukherjee et al. (2015)
VAM	*Glomus fasciculatum, G. etunicatum, G. mosseae, Funneliformis, Rhizophagus, Sclerocystis, Claroideoglomus, Gigaspora, Scutellospora, Racocetra, Acaulospora, Entrophospora, Pacispora, Diversispora, Otospora, Paraglomus, Geosiphon, Ambispora, Archaeospora* sp.	Al-Karaki et al. (2004) and Mahanta et al. (2014)
Endophytes	*Achromobacter, Acinetobacter, E. cloacae, Pantoea agglomerans, Pseudomonas* sp., *Piriformospora indica,* dark septate endophytes belonging to *Ascomycota*	Jumpponen (2001), Buch et al. (2009), Varma et al. (2012) and Adhya et al. (2015)

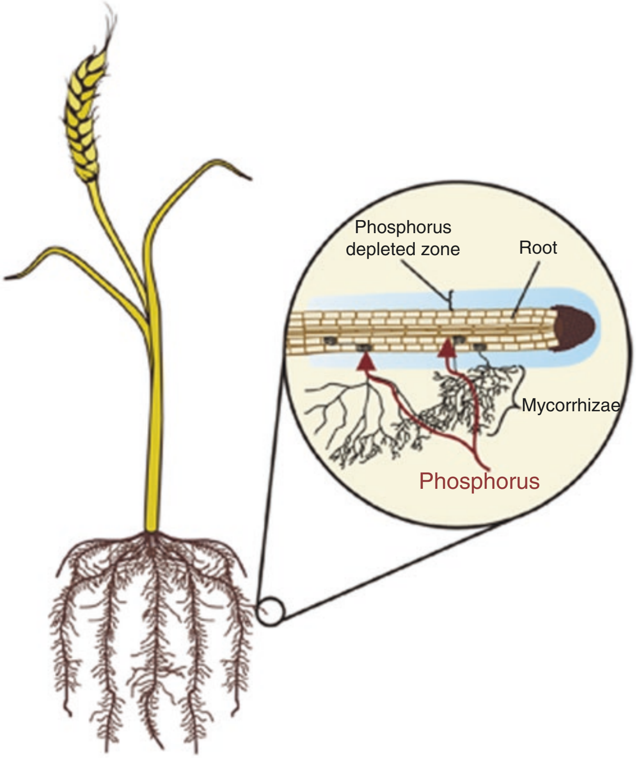

Fig. 1.7 Wheat-root colonization with mycorrhizae, which enhances mobilization of P from the spare zone to the scarce zone. The hyphae of arbuscular mycorrhizal fungi produce the glycoprotein glomalin, which may be one of the major stores of C in the soil, i.e., *Glomus, Bolutus, Amanita*, etc

1.5.1.3.3.1 Mode of Action

(i) Increase the surface area of the roots and form a network in the rhizosphere
(ii) Increase the mobility of highly immobile nutrient, such as P, Zn, etc. (Roy-Bolduc and Hijri 2011)
(iii) Increase the moisture availability under drought conditions
(iv) Function of AM fungi with rhizosphere microorganisms (PSB) enhances P availability and uptake (Barea et al. 2002; Lecomte et al. 2011, Minaxi et al. 2013, Wahid et al. 2016); many secrete phosphate-solubilising enzymes (Smith and Read 2008)

The inoculation with AM fungi led to significant enhancement of plant growth, yield, nutrient and water uptake, disease resistance and drought tolerance (Dwivedi et al. 2015). According to Wahid et al. (2016), application of indigenous AM fungi inoculated with PSB strains significantly enhanced AMF root colonization in maize. Mycorrhizal association is vital for P mobilization and increase the uptake in plants

(Roy-Bolduc and Hijri 2011). Mycorrhizal fungus increases the yield of crops by 30–40% (Meena et al. 2014b, 2015a; Mohapatra et al. 2013; Verma et al. 2014; Singh et al. 2016a, b).

1.5.1.3.4 P-Solubolising Microorganisms

K is the third major plant-essential macronutrient. The amount of plant-available K in soil is very low (0.1–0.2%), and approximately 98% of K in soil exists in the form of fixed mineral and rocks, i.e., muscovite, orthoclase, biotite, feldspar, illite, mica. PBR are a rhizospheric microorganism that solubilises insoluble K, i.e., minerals, to soluble forms or the plant-available form of K for plant growth and enhanced yield (Meena et al. 2013a, b, c). KSM solubilize fixed forms or minerals of K to plant-available K by various mechanisms, including acidolysis, chelation, exchange reactions, complexolysis and production of organic acids. A large number of saprophytic bacteria (*Agrobacterium tumefaciens*, *B. mucilaginosus*, *B. licheniformis, B. edaphicus, B. circulans, Acidothiobacillus ferrooxidans, Pseudomonas azotoformans, Paenibacillus* sp., *Rh. pusense and Flavobacterium anhuiense*) and fungal strains (*Aspergillus* sp. *and A. terreus*) are useful for solubilising K from waste mica and increasing K availability in soil (Mazid and Khan 2014; Meena et al. 2015a, b, c, d, e, f; Saha et al. 2016a, b).

1.5.1.3.5 Sulphur-Oxidising Microorganisms

Sulphur (S) is a macronutrient; however, it is required by crops in much smaller quantities than N and K. It is important to ensure adequate S nutrition for crops with high S demand. In the soil, S is mostly present in the organic form (>90%) (S-containing amino acids, such as cystine, methionine, proteins, polypeptides, biotin, thiamine, etc.), which is metabolised by soil microorganisms to make it available in an inorganic form (SO_4^{-2}) for plant nutrition. Various transformations of the S in soil result mainly from microbial activity (Vidyalakshmi et al. 2009; Mazid and Khan 2014), although some chemical transformations are also possible (e.g., oxidation of Fe sulphide). The major types of transformations involved in the cycling of S include the following:

1. *Mineralization*: This is the disintegration of large organic S compounds to smaller units and their further conversion into inorganic compounds (sulphates) by microorganisms.
2. *Immobilization*: This is the microbial conversion of inorganic S compounds to organic S compounds.
3. *Oxidation*: This is the oxidation of elemental S and inorganic S compounds (such as H_2S, sulphite and thiosulphate) to sulphate (SO_4) brought about by chemoautotrophic and photosynthetic bacteria.

Proteins (amino acids) → Degradation → Sulphur released → oxidized into Sulphate (inaerobic condition) or reduced under anaerobic condition (water logged soils) into H_2S.

(a)

$$2S + 3O_2 + \underset{\text{Light}}{2H_2O} \rightarrow 2H_2SO_4 \overset{\text{Ionization}}{\rightarrow} 2H(+) + SO_4\,(\text{Aerobic})$$

(b)

$$CO_2 + 2H_2S \rightarrow \underset{\text{Light}}{(CH_2O)} + H_2O + 2S$$

or

(c)

$$H_2 + S + 2CO_2 + H_2O \rightarrow H_2SO_4 + 2(CH_2O)(\text{anaerobic})$$

The members of genus *Thiobacillus* (obligate chemolithotrophic, non-photosynthetic), e.g., *T. ferrooxidans*, *T. denitrificans, T. thiooxidans* and *T. thioparus*, are the main organisms involved in the oxidation of elemental S to sulphates. Other than *Thiobacillus,* heterotrophic bacteria (Paracoccus; occurring in diverse habitats; *Xanthobacter, Alcaligens*, *Bacillus*, *Pseudomonas* and *Arthrobacter* are the only species), fungi (*Aspergillus* and *Penicillium*) and some actinomycetes are also reported to oxidize S compounds. Green and purple bacteria (Photolithotrophs) of genera *Chlorbium, Chromatiu* and *Rhodopseudomonas* have also been reported to oxidize S in the aquatic environment (Vidyalakshmi et al. 2009).

The formation of S/sulphuric acid is beneficial in agriculture in different ways: (1) Because it is the anion of strong mineral acid (H_2SO_4), it can render alkali soils fit for cultivation by correcting the soil PH; and (2) it solubise inorganic Na–containing plant nutrients and thereby increases the level of soluble P, K, calcium, magnesium, etc., for plant nutrition.

4. *Reduction of S*: Sulphate (SO_4^{-2}) in the soil is assimilated by plants and microorganisms and incorporated into proteins. This is known as “assimilatory S reduction.” SO_4^{-2} can be reduced to hydrogen sulphide (H_2S) by S-reducing bacteria (e.g., *Desulfovibrio* and *Desulfatomaculum*) and may diminish the availability of S for plant nutrition. This is called “dissimilatory S reduction,” which is not at all desirable from the point of view of soil fertility and agricultural productivity.

1.5.1.4 Plant-Hormone Production

Plant-growth regulators (PGR) or phytohormones are organic compounds that influence the physiological processes in plants at extremely low concentrations. These are synthesised by plants as well as PBR (Lincoln and Kotasthane 2014; Porcel et al. 2014; Jha and Saraf 2015), which are important for promoting growth, allowing plants to survive stressful conditions (Skirycz and Inze 2010; Fahad et al. 2015) and improving soil fertility (Teale et al. 2006; Egamberdieva 2013; Ambawade and Pathade 2013; Sharma et al. 2016; Verma et al. 2015b; Meena et al. 2013a). Important PGR include IAA, GAs, ethylene, ABA and CK. Important PBR known to produce plant hormones are listed in Table 1.6.

Auxin is an IAA that stimulates cell division, cell elongation, differentiation, and extension in plants (Das et al. 2013; Kundan et al. 2015). IAA is a phytohormone produced in young leaves, stems (Kaur et al. 2016) and seeds from transamination and a decarboxylation reaction of tryptophan (found in root exudates, which is a main precursor molecule for biosynthesis of IAA in bacteria) (Etesami et al. 2009). Auxins are quantitatively the most abundant phytohormones secreted by Azospirillum (Kaur et al. 2016). The most common species for the biosynthesis of IAA by plant growth–promoting rhizobacteria (PGPR), such as *Acinetobacter* sp., *Pseudomonas, Rhizobium, Azospirillum, Bacillus* sp. and *Klebsiella*, produce indole-3- pyruvic acid and indole-3-acetic aldehyde (Shilev 2013) in the rhizosphere of different crops. According to Sharma and Rai (2015), the production of IAA from *Pseudomonas sp*. significantly increases plant growth and yield of tomato (*Lycopersicum esculentum).*

GA affects the processes of seed germination and emergence, floral induction, flower and fruit development, and steam and leaf growth and shoot elongation (Bottini et al. 2004; Spaepen and Vanderleyden 2011). Khan et al. (2014) showed that tomato plants inoculated with the GA-producing *Sphingomonas sp*. LK11 strain have a significant increase in various growth parameters.

CK stimulate plant-cell division and control root development by inhibiting primary root elongation and lateral root formation and promoting root hair formation (Werner et al. 2003; Riefler et al. 2006). Important CK-producing bacteria are *B. subtilis* in Chinese arborvitae (Liu et al. 2013); *Azobacter* sp. in cucumber (Sokolova et al. 2011; Aloni et al. 2006) and wheat (Timmusk et al. 1999); *Ps. fluorescens* in soybean (de Salamone et al. 2001); and *R. leguminosarum* in rape and lettuce (Noel et al. 1996).

Ethylene plays important role initiating root development, inhibiting root elongation, promoting fruit ripening, promoting less wilting, stimulating seed germination, promoting leaf abscission and activating the synthesis of other plant hormones. The enzyme 1-aminocyclopropane-1 carboxylic acid (ACC) is a pre-requisite for ethylene production, which is catalysed by ACC oxidase. Sometimes ethylene is produced under stress conditions, such as heavy-metal stress, phytopathogens, flooding, drought and high Na concentration, which exacerbate the effect of general stress. Thus, one way to decrease the damage to plants caused by a wide range of phytopathogens is to lower the plant's ethylene response. To deal with this problem in crops, ACC deaminase containing PBR is used. PBR—such as *Acinetobacter,*

Table 1.6 Different strains of PBR that produce plant hormones in several crop types

Plant hormones	PBR	Host plant	References
IAA	*Acinetobacter* sp.	Rice	Gandhi and Muralidharan (2016)
	Azospirillum sp., *Bacillus* sp.,	Wheat, potato	Prathap and Ranjitha Kumari (2015), Ahemad and Kibret (2014), Baghaeeravari and Heidarzadeh (2014) and Arzanesh et al. (2011)
	B. thuringiensis	Lavender (*Lavandula dentate*)	Armada et al. (2014)
	Bacillus sp.	*Asparagus racemosus*	Mitra et al. (2016)
	R. leguminosarum (LR-30), *Mesorhizobium ciceri* (CR-30 and CR-39) and *Rh. phaseoli* (MR-2)	Wheat	Hussain et al. (2014)
	A. brasilense, *B. subtilis* LK14, *Psedomonas sp*	Tomato	Kumar et al. (2016a, b), Khan et al. (2016), Sharma and Rai (2015) and Molina-Favero et al.(2008)
	Pseudomonas putida, Pseudomonas aeruginosa	Mustard	Ahemad and Khan (2012)
	Pseudomonas sp., *bacillus sp*	Maize	Zahid et al. (2015)
	Rhizobium sp.	Pepper, tomato, lettuce, carrot	Garcia-Fraile et al. (2012) and Flores-Felix et al. (2013)
GA	*Pseudomonas* sp.	Apple and pear	Kapoor et al. (2016)
	Psedomonas putida H-2–3 Secretion of GA	Soybean	Sang-Mo et al. (2014)
	A. lipoferum	Maize	Cohen et al. (2009)
	Sphingomonas sp.	Tomato	Khan et al. (2014)
	Bacillus sp.	Pepper	Joo et al. (2005)
CK	*B. subtilis*	Chinese arborvitae *(Platycladus orientalis)*	Liu et al. (2013)
	Azobacter sp., *bacillus* sp.	Cucumber	Sokolova et al. (2011) and Aloni et al. (2006)
ABA	*Phyllobacterium brassicacearum* strain STM196	*Arabidopsis*	Bresson et al. (2013)
ACC deaminase	*B. thuringiensis AZP2*	Wheat	Timmusk et al. (2014)
	P. fluorescens biotype G *(ACC-5)*	Pea	Zahir et al. (2008)
	Alcaligenes sp.	Rape	Belimov et al. (2001)
	Pseudomonas cepacia	Soybean	Cattelan et al. (1999)
	Pseudomonas putida	Mung bean	Mayak et al. (1999)

ACC 1-aminocyclopropane-1-carboxylate

Achromobacter, Agrobacterium, Alcaligenes, Azospirillum, Bacillus, Burkholderia, Enterobacter, Pseudomonas, Ralstonia, Serratia and *Rhizobium*, etc.—are able to produce ethylene (Glick 2012; Das et al. 2013).

1.5.1.5 Siderophore Production to Increase Micronutrient Availability

Siderophores (Greek: "Fe carrier") are small, high-affinity organic chelating molecules secreted by microorganisms, such as bacteria, fungi and grasses (Neilands 1995). Siderophores are low molecular–weight compounds (~ 400–1500 Da) with an exceptionally high affinity for Fe^{+3} (*KKaa* ranging from 1023 to 1052) and other micronutrients as well as membrane receptors. Membrane receptors can fix the Fe/micronutrient–siderophore complex, thereby facilitating the mobilization of micronutrients in soil and their uptake by microorganisms and thereby stimulating plant growth by increasing Fe-uptake efficiency by the plant (Leong 1986). PBR may increase the mobility and availability of micronutrients by the formation of high-affinity siderophores. Currently there are >500 known siderophores; the chemical structures of 270 of these compounds have been determined (Cornelis 2010). Siderophores are usually classified by the ligands used to chelate the ferric Fe. The major groups of siderophores include the catecholates (phenolates), hydroxamates and carboxylates (e.g., derivatives of citric acid) (Table 1.7).

Table 1.7 Different siderophores produced by rhizobacteria

Ligand group	Siderophore	Organism
Hydroxamates	Ferrichrome	*Ustilagosphaerogena*
	Desferrioxamine B (deferoxamine)	*Streptomyces pilosus and S. coelicolor*
	Desferrioxamine E	*S. coelicolor*
	Fusarinine C	*F. roseum*
	Ornibactin	*Burkholderia cepacia*
	Ferribactin	*Ps. fluorescens*
	Gonobactin and nocobactin	*Neisseria gonorrhoeae*
Catecholates (phenolates)	Enterobactin	*E. coli*
	Bacillibactin	*B. subtilis and B. anthracis*
	Vibriobactin	*Vibrio cholera*
	Parabactin	*Paracoccus denitrificans*
	Agrobactin	*Agrobacterium tumefaciens*
Carboxylate (complexones)	Rhizobactin	*R. meliloti* strain DM4
	Staphyloferrin A	*Staphylococcus hyicus*
Mixed ligands	Azotobactin	*Azotobacter vinelandii*
	Pseudobactin	*Pseudomonas putida*
	Pyoverdine	*Pseudomonas aeruginosa*
	Yersiniabactin	*Yersinia pestis*

Source: Saharan and Nehra (2011)

Organisms as diverse as *Bacillus, Rhizobium, Pseudomonas, Agrobacterium, E. coli*, and many fungi produce a wide range of Fe-chelating compounds (Zahir et al. 2004).

The direct benefits of siderophores on the growth of plants are as follows: (1) Several studies using radiolabeled ferric-siderophores as a sole source of Fe showed that plants are able to take up the labeled Fen; (2) mung bean plants, inoculated with the siderophore-producing *Pseudomonas* strain GRP3 and grown under Fe-limiting conditions, showed decreased chlorotic symptoms and an enhanced chlorophyll level compared with uninoculated plants; (3) the Fe–pyoverdine complex synthesised by *Ps. fluorescens* C7 was taken up by *A. thaliana* plants, leading to an increase of Fe inside plant tissues and improved plant growth (Noumavo et al. 2016)

1.5.2 Indirect Mechanism

The indirect mechanism of plant growth occurs when PBR prevent the deleterious effects of one or more phytopathogenic microorganisms. This involves synthesising lytic enzymes, including chitinases, cellulases, 1, 3-glucanases, proteases, and lipases, which can lyse a portion of the cell walls of many pathogenic fungi; cause the formation of enzymes; form siderophores, which cause micronutrient deficiency in pathogens; and form other volatile compounds and antibiotics produced in response to the proliferation of plant pathogens (Glick 2012; Kundan et al. 2015; Shrivastava et al. 2016; Velazquez et al. 2016).

PBR as Biocontrol Agent

Phytopathogenic microorganisms are the most important and chronic threat to sustainable agriculture and ecosystem stability. Continuous use of pesticides and fungicides has led to environmental concerns and has even caused pathogen resistance. The use of PBR promotes plant growth and suppresses plant disease by colonising plant roots, decreasing plant pathogen populations in the soil, and maintaining a beneficial effect on plant growth (Qi et al. 2016). Fluorescent *Pseudomonads* are most suitable for application as biological control agents due to their abundant population in natural soils and plant root systems and their capability to use many plant exudates as nutrient (Panpatte et al. 2016). In soybean, PBR were successfully tested against *Macrophomina phaseolina* (Simonetti et al. 2015) and *Pythium ultimum* (León et al. 2009). Biocontrol PBR are able to antagonize phytopathogenic fungi by different mechanisms (Siddiqui 2006), including antibiosis, competition, mycoparasitism, degrading enzymes or induced resistance (Ahmad et al. 2008; Punja and Utkhede 2003). *Trichoderma* sp. are a very effective biocontrol agent in a sustainable disease-management system. The following rhizospheric environment and bacterial antagonistic activities are highlighted: (1) synthesis of hydrolytic enzymes—such as chitinases, glucanases, proteases, and lipases—which can lyse pathogenic fungal cells; (2) competition for nutrients and suitable colonization of niches at the root surface; (3) control of plant ethylene levels through the

ACC-deaminase enzyme, which can act to modulate the level of ethylene in a plant in response to stress imposed by the infection; and (4) production of siderophores and antibiotics. PBR have been successfully used for the biocontrol of nematode, fungal, bacterial, and viral diseases of plants in different parts of the world (Table 1.8).

Table 1.8 Biocontrol of fungal plant pathogens in crops with applicaton of PBR

Biocontrol agent	Plant pathogen	Crop	Mode of action	References
Actinobacteria, Pseudomonas, Bacillus, Staphylococcus, Enterobacter, Pantoae, Alcallgenes	*A. niger, P. chrysogenum, Microsporum gypseum, Fusarium* sp., *Pythium ultimum, A. alternate, Botrytis cinerea, Phytophtoracryptogea*	Wheat	Antagonism and growth promotion	Jog et al. (2014) Egamberdieva et al. (2008)
B. cereus, Brevibacterium laterosporus, P. fluorescens, S. marcescens	*Pythium ultimum*	Sorghum	Antibiotic production, siderophores, induction of systemic resistance	Idris et al. (2008)
Bacillus sp.	*F. oxysporum* f. sp. *Cubense*	Banana	Antagonism, IAA and siderophore production	Anusuya and Manimekalai (2016)
Bacillus spp., *Pseudomonas fluorescens*	*G. graminis, R. solani, R. oryzae, P. ultimum*	Wheat	Not specified	Cook (1992)
B. stearothermophilus, B. cereus, B. licheniformis, B. circulans, Chromobacterium violaceum	*F. oxysporum*	Sorghum	Antibiotic production, chitinolytic enzymes, efficient root colonization	Idris et al. (2007)
B. subtilis CE1	*F. verticilloides*	Maize	Not specified	Cavaglieri et al. (2005)
B. thuringiensis	*F. oxysporum*	Tomato	Produces the proteins cry and Cyt, which are highly toxic to insects	Qi et al. (2016)
P. chlororaphis	*Macrophomina phaseolina* (charcoal rot of sorghum)	Sorghum	Extracellular antibiotics, production of volatiles, siderophores, effective root colonization	Das et al. (2008)

(continued)

Table 1.8 (continued)

Biocontrol agent	Plant pathogen	Crop	Mode of action	References
P. fluorescens	*Micronidium nivale/F. nivale, F. culmorum*	Wheat and rye	Growth promotion, siderophore production, in vitro antibiosis	Amein et al. (2008)
P. fluorescens MKB 100 and MKB 249, *P. frederiksbergensis* 202, *P.* spp. MKB 158	*F. culmorum*	Wheat and barley	Induced resistance, antibiotic production, PR-related proteins (induced resistance) in wheat	Khan et al. (2006)

1.5.2.1 Production of ACC and Maintenance of Ethylene Levels in Plants

PBR use different mechanisms to promote the growth of plants. Arguably, the key bacterial trait in facilitating plant growth is possession of the enzyme ACC deaminase (Jalili et al. 2009; Glick 2012; Farajzadeh et al. 2012) (Fig. 1.8). This enzyme is responsible for cleavage of the plant ACC into ammonia and α-ketobutyrate (Arshad and Frankenberger 1998; Saleem et al. 2007) (Fig. 1.7). ACC deaminase activity is found in a wide range of bacterial isolates, including *Alcaligenes* sp., *B. pumilus, B. cepacia, E. cloacae, Methylobacterium fujisawaense, Ralstonia solanacearum, Pseudomonas* spp. and *Variovorax paradoxus* (Noumavo et al. 2016) Here, PBR, which have the action to degrade ACC in the rhizosphere, could shorten the deterioration cycle and reconstruct a healthy root system that could withstand environmental stress.

Furthermore, Glick (2014) has illustrated how ACC-producing, plant growth–promoting bacteria produce ACC deaminase and synthesize IAA, which may facilitate plant growth. ACC deaminase, involved in the primary mechanism of rhizobacteria, is used to degrade ethylene (Glick 2014; Souza et al. 2015). Ahmad et al. (2013) proved that *Rhizobium* and *Pseudomonas* strains that produce ACC deaminase can improve the growth, physiology, and quality of mung beans in Na-affected environments. *P. fluorescens, Alcaligenes* sp., *Bacillus* sp. and *Ochrobactrum* sp., which exhibit ACC deaminase activity, induce Na tolerance and consequently improve the growth of rice plants under Na-stress conditions (Bal et al. 2013; Ali et al. 2014).

1.5.2.2 ISR

ISR emerged as an important mechanism by which selected PBR and fungi in the rhizosphere prime the whole plant body for enhanced defence mechanisms against a broad range of pathogens and insect herbivores, including *Pseudomonas, Bacillus, Trichoderma*, and *mycorrhizae* species. ISR sensitises the plant immune system for

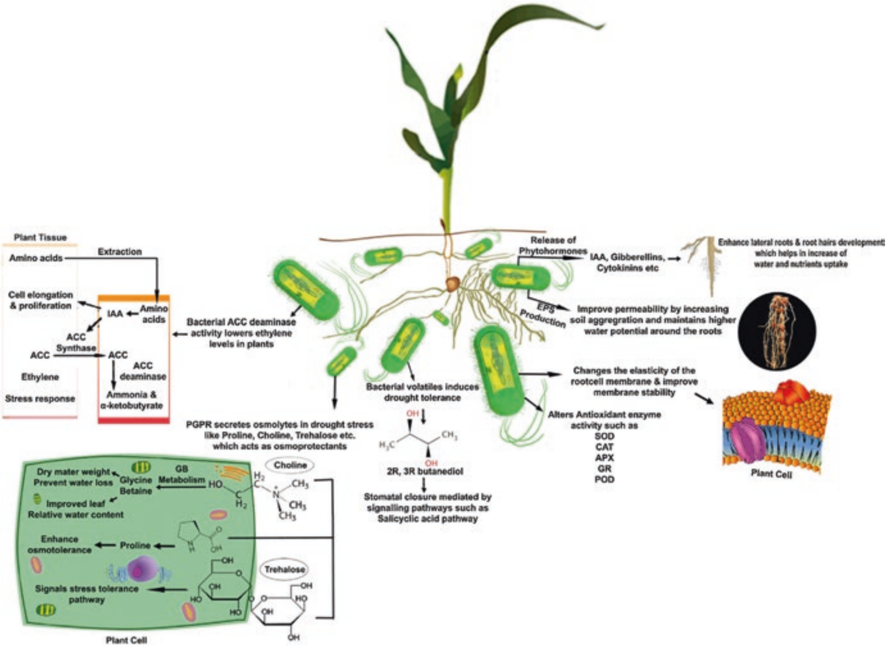

Fig. 1.8 Schematic representation of inhibition of ethylene production by ACC deaminase production and plant drought tolerance induced by PBR (Vurukonda et al. 2016)

enhanced defence without directly activating costly defences (Pieterse et al. 2014). ISR-eliciting microorganisms may modulate the defence responses of plant for their own benefit (Zamioudis and Pieterse 2012).

PBR bring about ISR through improving the physical and mechanical strength of the cell wall and changing the physiological and biochemical reaction of the host, thus leading to the synthesis of defence chemicals, the accumulation of pathogenesis-related (PR) proteins or acids (e.g., jasmonic, salicylic acid and malic acid), the synthesis of phytoalexin, and the production hydrolytic enzymes (e.g., chitinases and *β*-1,3 glucanases) and other secondary metabolites against the challenge pathogen. The success of a plant in evading invading pathogens relies primarily on its ability to rapidly build a line of defence for protecting cell walls against the spread of a pathogen (Benhamou et al. 1996a; Meena et al. 2014a, 2015c; Sindhu et al. 2016;). It is well known that PBR induce cell-wall structural modification in response to pathogenic attack (Benhamou et al. 1996b). PBR mediate ISR through lignification of cell wall, formation of structural barriers, viz., cell-wall apposition (papillae) and deposition of newly formed callose and accumulation of phenolic compounds at the site of penetration of invading hyphae of pathogens. Such a rapid defense reaction at sites of fungal entry delays the infection process and allows sufficient time for the host to build up other defense reactions to restrict pathogen growth to the outermost layers of root tissue. Thus, priming is a cost-effective way

Table 1.9 Mechanism of ISR by rhizobacteria to control pathogens

PBR	Mechanism	Pathogen	References
Bacillus sp.	Strengthening of cell wall	*F. oxysporum* f. sp. *Radices-lycopersici*	Kloepper et al. (2004) and Jourdan et al. (2009)
Pseudomonas sp. *Pseudomonas fluorescens WCS417r*	Cell-wall thickening, deposition of callose and accumulation of phenolic compounds Accumulation of PR proteins, namely, β-1,3 glucanases and endochitinases	*Pythium ultimum* and *F. oxysporum* f. sp. *pisi*	Bakker et al. (2007) and Pieterse et al. (2014)
Serratia spp.	Jasmonic acid and ethylene singnaling	*Colletotrichum orbiculare*	Schuhegger et al. (2006)
Trichoderma spp.	Jasmonic acid and ethylene singnaling	*Pythium ultimum, F. oxysporum*	Koike et al. (2001) and Segarra et al. (2009)
P. indica, AM fungi, P. simplicissimum, Phoma sp.	Secretion of salicylic acid and malic acid	*F. oxysporum, Pythium ultimum*	Pozo et al. (2009), Sultana et al. (2009), Shoresh et al. (2010) and Elsharkawy et al. (2012)
Micromonospora	Jasmonic acid singnaling	*Botrytis cinerea*	Martínez-Hidalgo et al. (2015)
B. subtilis strain FB17	Secretion of increased levels of malic acid	*P. syringae* pv. tomato	Rudrappa et al. (2008)
Psedomonas sp.	Production of 2,4-diacetylphloroglucinol and phenazines	*G. graminis* var. tritici, *R. solani*	Mavrodi et al. (2012)

DAPG 2,4-diacetylphloroglucinol

of increasing plant resistance (Conrath et al. 2006; Pastor et al. 2013). Some important examples of ISR mediated by PBR are listed in Table 1.9

Fluorescent *Pseudomonas* and *Trichoderma* species are important groups of plant growth–beneficiary microorganism reported to protect plants against pathogens by evolving various mechanisms, such as antagonism, competition and ISR (Vinale et al. 2008). ISR enhanced by plant growth–promoting fungi and plant growth–beneficiary rhizobacteria confers a broad-spectrum resistance that is effective against different types of pathogens.

1.5.2.3 Antibiosis

Synthesis of antibiosis compounds by PBR is the most effective and powerful mechanism to prevent the proliferation of phytopathogens (Shilev 2013). Different metabolites—such as amphisin, butyrolactones, diacetylphloroglucinol (DAPG), cyclic lipopeptide, (hydrogen cyanide (HCN), kanosamine, oligomycin A, oomycin

A, phenazine-1-carboxylic acid (PCA), pyoluterin, pyrrolnitrin, tensin, tropolone, viscosinamide, xanthobaccin and zwittermycin—are produced by rhizobacteria (Akhtar and Siddiqui 2010). Significantly, both 2-4, diacetylphloroglucinol (Phl) and PCA have been isolated from wheat rhizosphere after the introduction of biocontrol strains of *Pseudomonas*, thus confirming that such antibiotics are produced in vivo. Furthermore, Ph1 production in wheat rhizosphere was strongly related to the density of the bacterial population present and the ability to colonize roots (Raaijmakers et al. 1999).

PCA from *P. aureofaciens* has even been used as a direct field treatment for the control of *Sclerotinia homeocarpa* on creeping bent grass. The first antibiotics clearly implicated in biocontrol by *fluorescent pseudomonads* were the phenazine derivatives. *P. fluorescens* strain 2–79 and *P. aureofaciens* strain 30–84 contribute to disease suppression of take-all of wheat (Brisbane and Rovira 1988).

1.5.2.4 Enzyme Production

The mechanism of enzyme production involves the production of hydrolytic enzymes, of which two examples are chitinase and glucanase. Major fungal cell-wall components are made up of chitin and beta-glucan; thus, chitinases and beta-glucanase–producing bacteria inhibit fungal growth. *Sinorhizobium fredii* KCC5 and *P. fluorescens* LPK2 produce chitinase and beta-glucanases and dictate the fusarium wilt produced by *F. udum* (Kumar et al. 2010). Apart from exhibiting the production of chitinase and beta-glucanases, *Pseudomonas* spp. inhibits *Rhizoctonia solani* and *Phytophthora capsici,* two of the most destructive crop pathogens in the world (Arora et al. 2008)

1.5.2.5 Siderophore Production

PBR can prevent the proliferation of fungal and other pathogens by producing siderophores that bind most of the Fe^{3+} in the area around the plant root (Martinez-Viveros et al. 2010). The resulting lack of Fe prevents pathogens from proliferating in this immediate vicinity. Siderophore synthesis in bacteria is generally regulated by Fe-sensitive fur proteins, global regulators (GasS and GasA), sigma factors (RpoS, PvdS and Fpv1), quorum-sensitive autoinducers (N-acyl homoserine lactone) and many site-specific recombinases. Suppression of soil-borne plant pathogens by siderophore-producing pseudomonads has been observed, and the wild-type siderophore–producing strain was more effective in suppressing disease compared with the non–siderophore-producing mutants (Akhtar and Siddiqui 2010).

Siderophore production is an important feature for the suppression of plant pathogens and promotion of plant growth. The antagonism depends on the amount of Fe available in the medium: Siderophores produced by a biocontrol agent and the sensitivity of target pathogens. Production of ALS 84 and siderophores contributed to the biocontrol of crown gall by *Agrobacterium rhizogenes* K84 especially under conditions of Fe limitation (Penyalver et al. 2001). Notably, in rice roots isolates belonging to genera *Enterobacter* and *Burkholderia* produced the highest levels of siderophores (Souza et al. 2013, 2014). Plant-beneficiary characteristics—such as siderophore production from *Bacillus* genus—showed the most efficiency against the growth of *F. verticillioides*, *Colletotrichum graminicola, Bipolarismaydis*, and *Cercospora zea-maydis* fungi (Szilagyi-Zecchin et al. 2014). Siderophores produced by *A. brasilense* (REC2, REC3) showed in vitro anti-fungal activity against *Colletotrichum acutatum* (the causal agent of anthracnose). Also, a decrease of disease symptoms was observed in strawberry (*Fragaria vesca*) plants previously inoculated with *A. brasilense* (Tortora et al. 2011).

1.5.2.6 Rhizoremediation

It is important to develop methods, such as remediation, for the removal or extraction of heavy metal from contamination sites of crop rhizosphere with the help of microorganisms (Glick 2010; Sessitsch et al. 2013; Cabello-Conejo et al. 2014). Several microorganisms have gained attention for being able to extract heavy metals from polluted soil or contaminated sites through plant–microbe interaction (Khan and Lee 2013). Ahmad et al. (2016a, b) showed that bacteria could play an important role in determining metal uptake and toxicity to plants. Bacterial strains *Bacillus* (CIK-517, CIK-519), *Klebsiella* (CIK-518), *Leifsonia* (CIK-521) and *Enterobacter* (CIK-521R) significantly increased shoot/root growth and dry biomass in normal and Cd-contaminated soil compared with their respective controls. Durand et al. (2016) showed that inoculation of PBR *Variovorax paradoxus* in two different plant associations (*Bornmuellera tymphaea/Noccaea tymphaea*) (NB) and *Bornmuellera tymphaea/Alyssum murale* (AB) increased Ni amounts in roots by 105.8% and 66.4%, respectively, in ABi and NBi covers and by 39.9% and 79.6% in shoots.

1.6 Future Strategies for Sustainable Agriculture

In our present agriculture practices, due to copious use of chemical fertilisers and pesticides on crops, the sustainability of agriculture systems has collapsed; the cost of cultivation has increased at a high rate; the income of farmers stagnated; and the provision of food security and safety has become a daunting challenge (Panday et al. 2018). Indiscriminate and imbalanced use of chemical fertilisers, especially urea, along with chemical pesticides and the unavailability of organic manures has led to a considerable decrease of soil health (Choudhary et al. 2018b). Thus, there is an important need to adopt eco-friendly, easy-to-apply, non-toxic and cost-effective nature techniques that can sustain crop production and avoid creating negative environment impacts (Mazid and Khan 2014). For these reasons, PBR—organic substances that make use of microorganisms to increase the fertility of soil—have been identified as helpful harmless input in safeguarding soil health and the quality of crop products (Suhag 2016). PBR add nutrients through the natural processes of fixing biological N, solubilising and mobilising P, solubising K, oxidising S, producing siderophores, providing biocontrol of various plant diseases and stimulating plant growth through the synthesis of growth-promoting substances. The use of PBR is a relevant strategy for the efficient and rational use of agricultural resources with minimal generation of adverse environmental impacts that may affect water resources, ecosystems, or the quality of human life. In addition, PBR provide a wide range of possibilities for the development of conservative agriculture in different geographic, economic, and cultural areas (Choudhary et al. 2016).

Limitations of PBR require future research focused on identifying the options available to tackle the issues and offering valid frameworks for the development of worldwide environmentally friendly practices that allow improvements of the efficiency and consequent supply of product for the industry in the global economy. Although several options for biofertiliser application are available, feasibility studies should be carried out by producers and farmers to effectively select the best option that offers the best results and allows minmising environmental impacts. Integrated nutrient management with PBR, i.e. biosolids (sewage sludge, crop residue), animal manures, green manures, composting, microbial inoculants and seaweeds extracts are techniques that should be used in today's agriculture, however, their implementation still requires research, investment and technological development to fully understand their impacts on the soil, flora, fauna and, ultimately, on human health. Nano-encapsulation technology could be used as a versatile tool to protect PBR by enhancing their service life and dispersion in fertiliser formulation and allowing controlled release of PBR.

1.7 Conclusions

Due to the pressure of an increasing human population, the world will have to withstand the increasing demand for food, fuel and fodder. Adoption of an intensive crop-production system causes much harmful effect on environment: It degrades land, soil quality, and soil health. PGPR are excellent model systems that can provide the biotechnologist with novel genetic constituents and bioactive chemicals having diverse uses in agriculture and environmental sustainability. Considering the good impact of PBR, i.e. exerting a positive influence on crop productivity and ecosystem functioning, encouragement should be given to their implementation in sustainable agriculture. Hoping for the betterment of technology in creating successful research and development, the use of PBR will surely become a reality and will be instrumental to crucial processes that ensure the stability and productivity of agroecosystems, thus leading us towards an ideal sustainable agricultural and environmental system.

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Chapter 2
Microbes: A Sustainable Approach for Enhancing Nutrient Availability in Agricultural Soils

Asha Sahu, Sudeshna Bhattacharjya, A. Mandal, J. K. Thakur, Nagwanti Atoliya, Nisha Sahu, M. C. Manna, and A. K. Patra

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 CO_2 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).

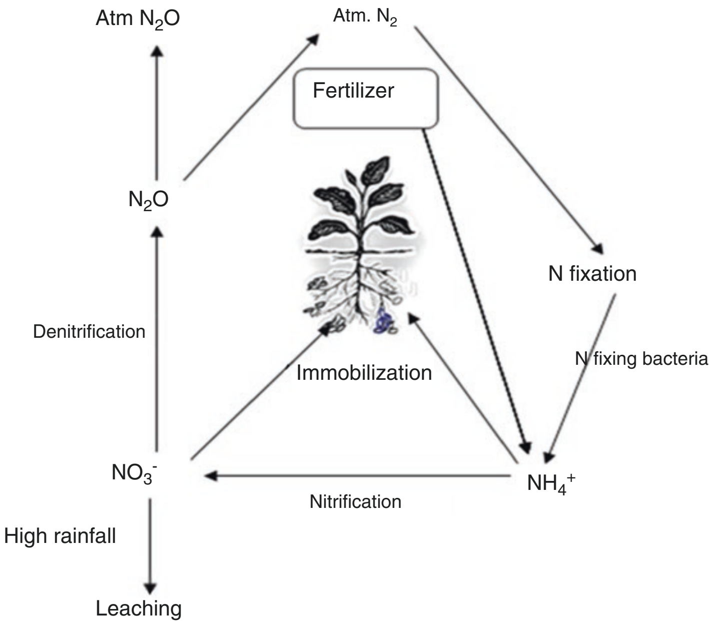

Fig. 2.1 Nitrogen cycle in the agroecosystem

Nitrogen fixation

$$N_2 \xrightarrow{\text{Nitrogenase}} NH_3 \longrightarrow NH_4^+ \xrightarrow{\text{Plants/Microbes}} \text{Aminoacid} \longrightarrow \text{Protein}$$

Ammonification

$$\text{Protein} \longrightarrow \text{Peptide} \xrightarrow{\text{Aminisation}} \text{Amino acids} \xrightarrow{\text{Ammonification}} NH_3$$

Nitrification

$$NH_4^+ \xrightarrow{\textit{Nitrosomonas}} NO_2^- \xrightarrow{\textit{Nitrobacter}} NO_3^-$$

Denitrification (*Pseudomonas*, *Bacillus*, *Paracoccus*, *Thiobacillus*)

$$NO_3 \longrightarrow NO_2 \longrightarrow NO \longrightarrow N_2O \longrightarrow N_2$$

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

Source: Sharma et al. (2013)

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

PSMs	Organic acid produced	References
Aspergillus niger, *Penicillium* sp., *Bacillus megaterium*, *Pseudomonas* sp., *Bacillus subtilis*, *Arthrobacter* sp.	Lactic, malic, citric, gluconic	Bajpai and Sundara Rao (1971), Fankem et al. (2006), Vyas and Gulati (2009), and Gaind (2016)
Aspergillus japonicus, *A. foetidus*, *B. pumilus*, *Citrobacter* 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)
Bacillus amyloliquefaciens, *B. licheniformis*, *Vibrio proteolyticus*, *Xanthobacter agilis*, *Enterobacter aerogenes*, *Pseudomonas aerogenes*	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 O_2/CO_2 gaseous exchange) (Nenwani et al. 2010; Stevenson

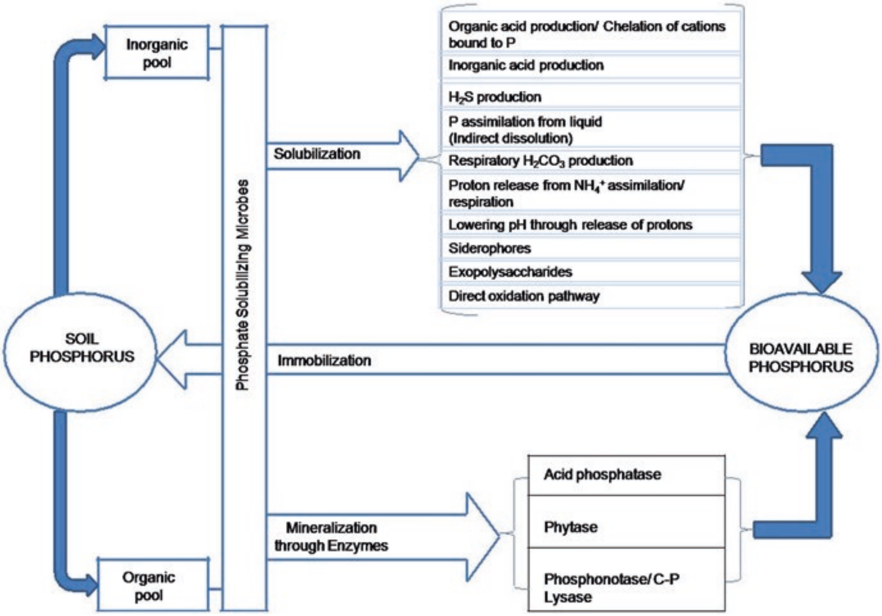

Fig. 2.2 Schematic representation of mechanism of soil P solubilization/mineralization and immobilization by PSMs

2005; He et al. 2002). Figure 2.2 shows the schematic representation of mechanism of soil P solubilization/mineralization and immobilization by PSMs. Wyciszkiewicz 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 $Ca_3\ (PO_4)_2$ 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 (Kpomblekou 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

	Import (Mt)		Consumption (Mt)	
Name of fertilizer	2013–2014	2014–2015	2013–2014	2014–2015
Muriate of potash (60% K_2O)	3.180	4.197	2.280	2.853
Sulphate of potash (50% K_2O)	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 Si_4^+ 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
Bacillus mucilaginosus	Zhao et al. (2008), Basak and Biswas (2009), Sugumaran and Janarthanam (2007), and Zarjani et al. (2013)
Bacillus circulans	Lian et al. (2002)
Bacillus edaphicus	Zhao et al. (2008), Basak and Biswas (2009), Sugumaran and Janarthanam (2007), and Zarjani et al. (2013)
Burkholderia sp.	Sheng and Huang (2002) and Sheng and He (2006)
Acidithiobacillus ferrooxidans	Sheng and Huang (2002) and Sheng and He (2006)
Arthrobacter sp.	Zarjani et al. (2013)
Enterobacter hormaechei (KSB-8)	Prajapati et al. (2013)
Paenibacillus mucilaginosus	Liu et al. (2012) and Hu et al. (2006)
Paenibacillus frequentans	Argelis et al. (1993)
Cladosporium sp.	Argelis et al. (1993)
Aminobacter sp.	Uroz et al. (2007)
Sphingomonas sp.	Uroz et al. (2007)
Paenibacillus glucanolyticus	Sangeeth et al. (2012)
Agrobacterium tumefaciens	Meena et al. (2015a)
Fungi	
Aspergillus niger	Prajapati and Modi (2012)
Aspergillus terreus	Prajapati and Modi (2012)
Penicillium sp.	Sangeeth et al. (2012)
Glomus intraradices, *Glomus mosseae*	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.

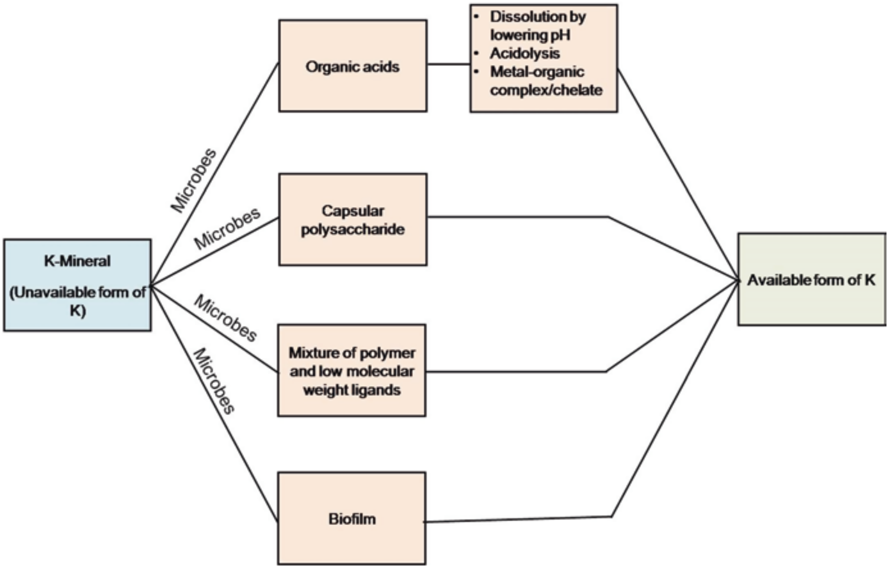

Fig. 2.3 Mechanisms involved in potassium solubilization by soil microbes

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.

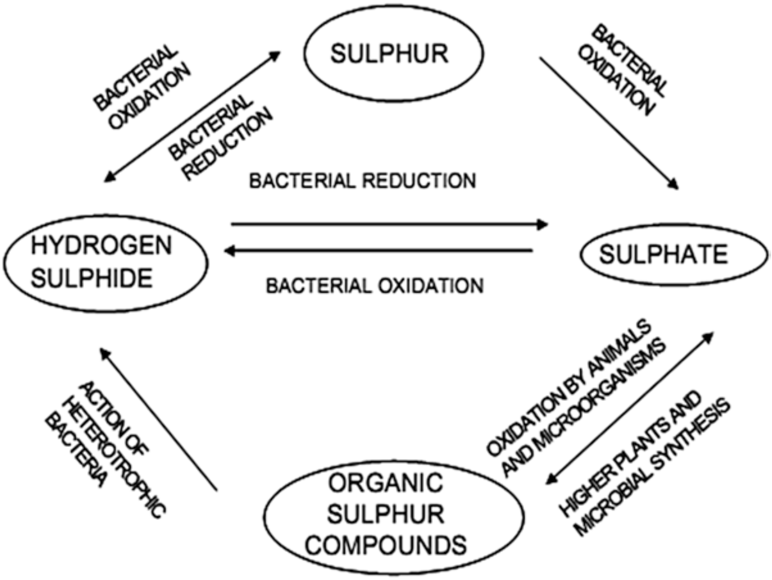

Fig. 2.4 The oxidation of sulphur in soils (Burns 1967)

Table 2.5 List of sulphur-oxidizing microbes (SOMs)

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

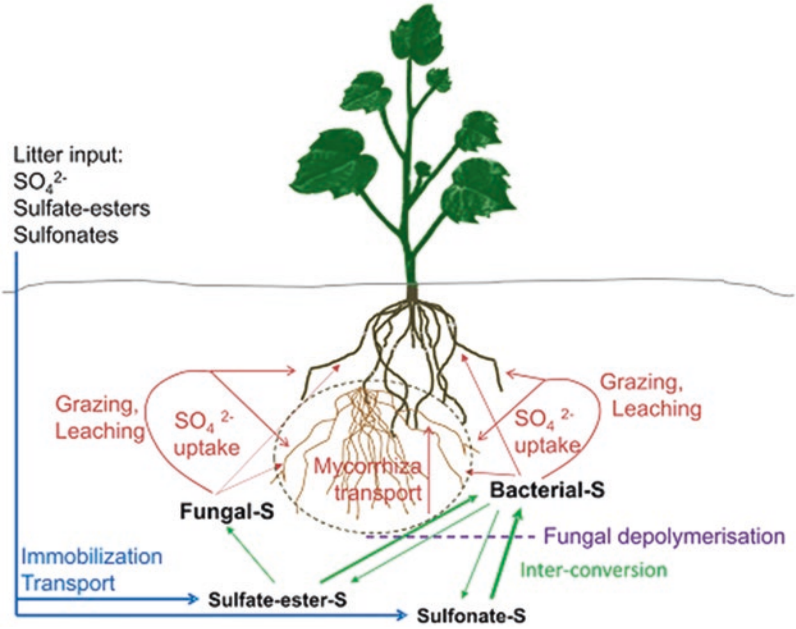

Fig. 2.5 The sulphur cycle in soil and plant sulphate uptake (Autry and Fitzgerald 1990; Kertesz and Mirleau 2004)

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 Koornhuyse 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

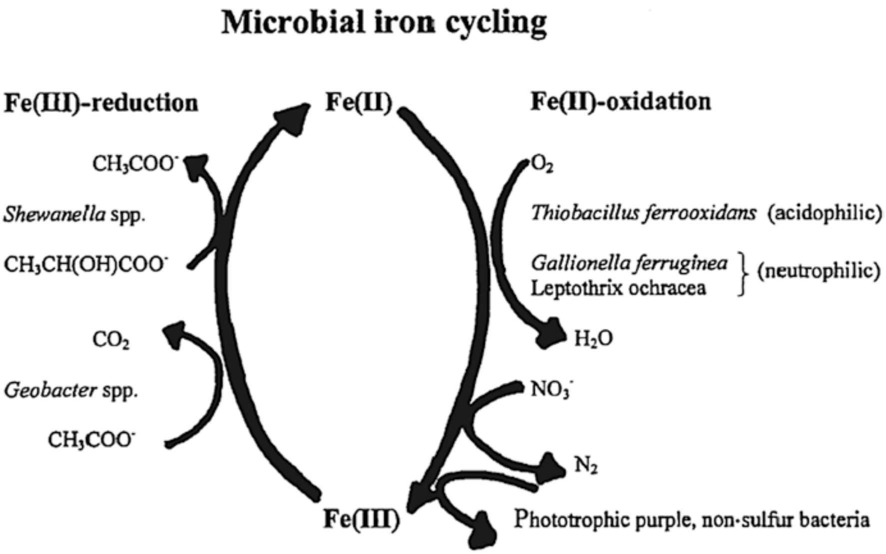

Fig. 2.6 The microbial iron cycle (Erbs and Spain 2002)

conversion of Fe(II) to Fe(III) can be carried out by microbes including *Crenothrix*, *Gallionella*, *Leptothrix*, *Metallogenium*, *Sphaerotilus*, etc. without any energy generation (Coyne 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	*Thiobacillus ferrooxidans* and *Sulfobacillus acidophilus*
Neutral, aerobic	No energy generation	*Gallionella* and *Leptothrix*
Anaerobic Fe(II)-oxidizing phototrophic bacteria		Purple sulphur bacteria (*Halothiobacillus* sp.), purple non-S bacteria (*Rhodomicrobium* sp., *Rhodobacter* sp., *Rhodopseudomonas* sp.) Green bacteria (*Chlorobium ferrooxidans*)
Acidophilic Fe(III)-reducing microorganisms		*Acidiphilium* sp.
Reduction of Fe(III) at neutral pH		*Shewanella putrefaciens* and *Geothrix fermentans*

whereas the facultatively anaerobic *Shewanella* sp. belongs to the ϒ-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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Chapter 3
Microbial Transformation of Sulphur: An Approach to Combat the Sulphur Deficiencies in Agricultural Soils

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Abstract Sulphur, an essential component for plant as well as animals, is present in soils in both organic and inorganic forms, with organic form particularly sulphate esters and carbon-bonded sulphur contributing ~75–90% of the total. The major sources of sulphur in soils are sulphur-containing minerals, plant and elemental residue and external addition including atmospheric deposition. Sulphur deficiency in plants results in poor nitrogen metabolism thus protein biosynthesis, chlorosis, low oil percentage and ultimately low yield. The conversion of organic sulphur in organic matter to inorganic form and vice versa is dominantly a microbiological process. In well-aerated soil, organic sulphur is mineralized to sulphate and taken up by plants. Concurrently inorganic sulphur is immobilized to organic form and incorporated in microbial tissue. The rate of these processes obviously depends on soil reaction, temperature, moisture and addition of crop residue and many other factors that ultimately affect the activity of microorganism. Several enzymes in soil, viz. arylsulphatase, play a major role in sulphur mineralization process though very little information is available till now towards the pathway of decomposition. In addition to this process, inorganic sulphur in soil undergoes various oxidation and reduction process, modulated by microorganisms. Various reduced inorganic sulphur compounds are oxidized by a group of bacteria in suitable condition and utilize the energy. The wide range of stable redox states and their interconversion affect sulphur cycle, fate of applied fertilizer and ultimately its availability to plants and microbes. In this chapter we reviewed the sulphur cycle and its transformation by various microbial processes.

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3.1 Introduction

Besides carbon and nitrogen which are important constituents of plants, microorganisms are also known to influence the availability of sulphur (S) as well as phosphorus and certain trace elements in soil for absorption by plants. Sulphur is the tenth most abundant and widely distributed element in the nature. Sulphur is an essential element for plant as well as animals and found in nature in combined form, viz. gypsum ($CaSO_4.2H_2O$) and pyrite (FeS_2), and in elemental form (S^0). The sulphur is considered as 'secondary' nutrient as only because their requirement by plant is quantitatively less as compared to the primary nutrients. In spite of the essentiality, very less importance was given to S addition in field in the past mainly due to restricted area and crops that response with the fertilizer and contribution through major fertilizer or from natural sources (Tandon 2011; Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015).

The S is added in soil through fertilizer, pesticides, irrigation water and adsorption of SO_2 gases from atmosphere. An amount of 5–250 kg/ha/year of sulphur is added in soil through rainfall depending on industrial activity and burning of fossil fuel. Highly weathered soils away from sea and industrial activity are generally prone to sulphur deficiency. In earth, the lithosphere is the major sink of sulphur (24.3×10^{18} kg) followed by the hydrosphere (1.3×10^{18} kg), pedosphere (2.7×10^{14} kg) and atmosphere (4.8×10^{9} kg), respectively (Stevenson 1982). Sulphur, with atomic weight 32.064, exists in various oxidation states. This is indicated by the oxidation number in several compounds, viz. sulphides (−2), polysulphide (−1), elemental sulphur (0), thiosulphate [(−2) and (+6)], sulphite (+4) and sulphate (+6) (Rao 1999).

3.2 Major Sources of Sulphur in Soil and Its Various Pools

Organic matter is the major source of S in soil in most of the cases. Of the total sulphur present in soil, only 10–15% is in inorganic form (sulphate), and ~75–90% is in organic form. Thus inorganic component of soil sulphur constitutes only a minor portion of the total sulphur content of soils. However, the inorganic sulphur released from mineral in the form of sulphate (SO_4^{2-}) due to weathering is consumed by plants and converted to various organic forms (Fig. 3.1). Upon addition to soil, the bulk of sulphur in the organic form is metabolized by soil microorganisms to make a major part available in an inorganic state (sulphur, sulphates, sulphite, thiosulphate, etc.) for plant nutrition and a small amount converted to humus (Gharmakher et al. 2012).

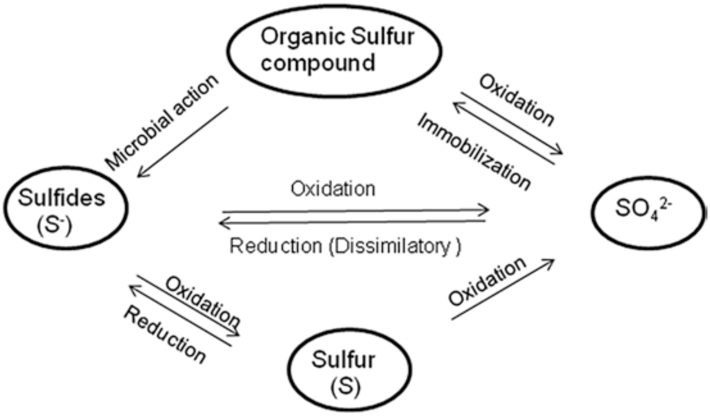


Fig. 3.1 Contribution of microorganism in S cycle

Sulphur is bound in organic state in proteins of vegetable and animal origin and in the protoplasm of microorganisms in the form of sulphur-containing amino acids (cysteine, cystine, methionine), lipid, proteins, polypeptides, biotin, thiamine, etc. These organic sulphur compounds can broadly be divided in two groups, namely, ester sulphates, which have C-O-SO_3 linkages, and carbon-bonded S, which has direct C-S linkages. Other organic forms also exist, but they are of minor importance. Ester sulphates include compounds such as choline sulphate, phenolic sulphates and sulphated polysaccharides. Carbon-bonded S is comprised principally of amino acids such as methionine and cysteine and sulpholipids (Tabatabai and Bremner 1970). Ester sulphate mineralized faster than C-bonded S and acts as readily available S stores for plant and microbes (Kovar and Grant 2011).

In temperate condition even more than 95% of the total sulphur may present as organic form in soil (Stevenson 1982). Inorganic sulphur also present in appreciable amount in arid or semiarid region. Minerals that supply sulphur to soil are mainly pyrites (FeS_2), sphalerite (ZnS), chalcopyrite ($CuFeS_2$), gypsum, epsomite ($MgSO_{4,}6H_2O$), etc. Sulphur in soil is found more in fine texture soil as compare to coarse texture sandy soil and in subsurface soil as compare to surface due to difference in distribution of organic carbon. Sulphur released from mineral in the form of sulphate (SO_4^{2-}) due to weathering is consumed by plants and converted to various organic forms (Fig. 3.1).

3.3 Functions of Sulphur

Concentration of sulphur in healthy plants ranges from 0.1 to 0.4% on dry weight basis. Sulphur has several important functions in plant metabolism such as synthesis of glucosides and glucosinolates (in mustard oils) and activation of enzymes and sulphydryl (-SH) linkages that are the source of pungency in oils and is also involved in formation of chlorophyll. Ferredoxin, being a component of Fe-S cluster protein, plays an important role in photosynthetic electron transport system. Sulphur is required for the synthesis of sulphur-containing amino acids methionine (21%), cysteine (26%) and cystine (27%), which are essential components of protein. Approximately 90% of plant sulphur is present in these amino acids (Tandon and Messick 2002). It is also needed for the synthesis of metabolites such as coenzyme A, biotin, thiamin or vitamin B and glutathione. The sulphur requirement of oilseed crops was found to be the highest followed by pulses and cereals. Therefore, sulphur deficiency results in low photosynthetic activity, growth retardation, yellowing of young leaves and ultimately poor yield. Sulphur deficiency also retards nitrogen fixation as both are constituent of protein. Thus the desired N:S ratio is necessary for optimum N metabolism. The optimum N:S ratio should be maintained for obtaining good yield. The desired N:S ratio for legumes has been identified as 15–16:1 and 11–12:1 for cereals (Pasricha and Sarkar 2002).

Sulphur deficiency is reported from larger areas all over the world soils and in many crops too. The reason being the nutrient management strategies mainly depended on application of NPK fertilizers, ignoring the replenishment of other nutrients through fertilizers or organic sources (Sahrawat et al. 2009). Apart from that, progressively higher removal of sulphur owing to high production level led to appearance of sulphur deficiency (Tandon 2011). The availability of sulphur for plant uptake largely depends on the dynamic sulphur cycle and the rate of conversion of organic sulphur to inorganic sulphate which is plant usable form. Such conversion in soil is typically termed as mineralization, and it is strictly a microbial process. Especially in the rhizosphere zone, microbes play a vital role in converting the organic sulphur in to plant available inorganic form. This chapter will consider the microbial processes that influence sulphur cycling in the soil and will summarize what is known about the organisms that catalyse these processes.

3.4 Cycling of Sulphur in Soils

Cycling of sulphur is similar to that of nitrogen. Transformation/cycling of sulphur between organic and elemental states and between oxidized and reduced states is brought about by various microorganisms, specially bacteria. Thus the conversion of organically bound sulphur to the inorganic state by microorganisms is termed as mineralization of sulphur. The sulphur/sulphate, thus released, is either absorbed by the plants or escapes to the atmosphere in the form of oxides (Ahmad et al. 2016; Meena et al. 2016a, b; Parewa et al. 2014; Prakash and Verma 2016; Jaiswal et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a, b). In the absence of oxygen, certain microorganisms produce hydrogen sulphide from organic sulphur substrates especially in waterlogged soils. Chemical and spectroscopic studies have shown that in agricultural soils, most of the soil sulphur (~ 95%) is present as sulphate esters or as carbon-bonded sulphur (sulphonates or amino acid sulphur), rather than inorganic sulphate (Kertesz and Mirleau 2004; Wang et al. 2006).

Plant sulphur nutrition depends primarily on the uptake of inorganic sulphate. However, recent research has demonstrated that the sulphate ester and sulphonate pools of soil sulphur are also plant-bioavailable, probably due to interconversion of carbon-bonded sulphur and sulphate ester sulphur to inorganic sulphate by soil microbes. In addition to this mineralization of bound forms of sulphur, soil microbes are also responsible for the rapid immobilization of sulphate, first to sulphate esters and subsequently to carbon-bound sulphur. The rate of sulphur cycling depends on the microbial community present, and on its metabolic activity, though it is not yet known if specific microbial species or genera control this process (Kertesz and Mirleau 2004). The genes involved in the mobilization of sulphonate and sulphate ester sulphur by one common rhizosphere bacterium, *Pseudomonas putida*, have also been investigated by Kertesz and Mirleau (2004). Mutants of this species that are unable to transform sulphate esters show reduced survival in the soil, indicating that sulphate esters are important for bacterial S nutrition in this environment. *P. putida* S-313 mutants that cannot metabolize sulphonate-sulphur do not promote the growth of tomato plants as the wild-type strain does, suggesting that the ability to mobilize bound sulphur for plant nutrition is an important role of this species (Fig. 3.1).

Thus the sulphur pools in soils are dynamic in nature. Inorganic sulphur compounds are immobilized to organic sulphur, different organic forms interconverted, and immobilized sulphur is simultaneously mineralized to yield plant available inorganic sulphur. Most of the processes are linked to the microbial biomass present in the soils. Especially in the rhizosphere, microbes play a vital role in allowing plants to access soil organosulphur (Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Meena et al. 2015a, b, f; Raghavendra et al. 2016; Zahedi 2016; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016).

3.5 Sulphur Transformations in Soil

The various transformations of sulphur in the biosphere can be summed up as a cyclic reaction involving (i) decomposition of organic sulphur compounds into subunits which are, in turn, converted into inorganic compounds through a process of mineralization; (ii) assimilation of sulphur into the protoplasm of microorganisms, a process referred to as immobilization; (iii) oxidation of inorganic sulphur compounds into elemental sulphur; and (iv) reduction of sulphate. Both aerobic and anaerobic microorganisms take part in organic S formation, though only 1–3% of microbial biomass is composed of S (Strick and Nakas 1984; Chapman 1987). The short life cycles of microorganisms, however, result in rapid turnover and S recycling (Smith and Paul 1990). Microbial biomass has been described as the most active and readily available form of soil organic S, and much of the mineralized S seen in short-term incubation experiments may originate from microbial biomass (McLaren et al. 1985; Gharmakher et al. 2012). Various transformations of the sulphur in soil result mainly due to microbial activity, although some biogeochemical transformations (Lamers et al. 2012) are also possible (e.g. oxidation of iron sulphide). The major types of transformations involved in the cycling of sulphur which are mineralization, immobilization, oxidation and reduction are briefly described below.

3.5.1 Mineralization of Soil Sulphur

Sulphur is taken up by the plant root system largely as the sulphate ion although several amino acids may be assimilated without prior degradation. Since agricultural crops and other vegetation require for growth the sulphate found in their rooting medium, the mineralization of organic sulphur plays an important part in the microbiological reactions required for higher life. The breakdown and/or decomposition of large organic sulphur compounds to smaller units and their conversion into inorganic compounds (sulphates) by the microorganisms. The rate of sulphur mineralization is about 1.0–10.0 percent/year. A diverse group of organic compounds containing sulphur are presented as substrates to the microflora. The elements occur in plant, animal and microbial proteins; in the amino acids, cystine and methionine; and in the B vitamins, thiamine, biotin and thioctic acid. It is also found in the tissues and excretory products of animals as free sulphate, as taurine and, to some extent, as thiosulphate and thiocyanate (Rajvaidya and Markandey 2006).

Upon the addition of plant or animal remains to soil, the sulphur contained therein is mineralized due to microbial activities in soils. A portion of the inorganic products so released is utilized by the microflora for cell synthesis, and the remainder is escaped into the environment. Aerobically, the terminal, inorganic product is sulphate, while in the absence of atmospheric O_2, particularly during the putrefaction of proteinaceous matter, H_2S and the odoriferous mercaptans are accumulated in soils. Many soil bacteria have the ability to form H_2S from partially degraded proteins, and as such it is likely that sulphides are among the major inorganic substances released during the decomposition of proteinaceous substrates (Jez 2008).

The sulphur in cystine and cysteine is recovered quantitatively as sulphate when either of these amino acids is applied to well-aerated soils. The conversion is rapid because many microorganisms attack the two compounds. The decomposition may proceed by any one of several known mechanisms. In soil, cystine can be formed by a chemical oxidation of added cysteine. The sulphur of the molecule in turn is oxidized to sulphate (Solomon et al. 2010) with cystine disulphoxide and possibly cysteine sulphinic acid as intermediates, a reaction sequence not involving H_2S (Rawat et al. 2016; Yasin et al. 2016; Meena et al. 2015e, 2016c; Saha et al. 2016a; Yadav and Sidhu 2016; Meena et al. 2016d; Teotia et al. 2016; Bahadur et al. 2016b; Das and Pradhan 2016).

Alternatively, fungi such as *Microsporum gypseum* convert cysteine sulphur to sulphate by a mechanism possibly involving the consecutive formation of cystine, sulphenic and sulphinic acids, sulphite and sulphate (Stahl et al. 1949). In the process of ammonification of organic nitrogen, the extent of mineral sulphur formation is influenced by the sulphur content and the C:S ratio of the decomposing substrate. Sulphate accumulates only when the sulphur level in the organic matter exceeds the microbial needs. Thus, it is likely that the percentage of sulphur mineralized per annum is similar to the figure for nitrogen mineralization, i.e. 1–3% of the total supply in soils of the humid-temperate zone. It is also likely that environmental factors that govern microbial growth in general would affect the rate of sulphur mineralization in soils.

3.5.2 Immobilization of Sulphur

Immobilization of sulphur represents the microbial conversion of inorganic sulphur compounds to organic sulphur compounds. The major sulphur-containing compounds are sulphate, hyposulfite, sulphoxylate, thiosulphate, persulphate, sulphide, elemental sulphur, sulphite, tetrathionate and thiocyanate among the inorganic substances and cysteine, cystine, methionine, taurine and undecomposed proteins of the organic group. Sulphate immobilization is a reductive process and is performed by both aerobic and anaerobic chemotrophs and phototrophs. However, certain anaerobic microbes (e.g. the phototrophic green S bacteria) are only capable of sulphide immobilization for their needs which requires less energy than sulphate assimilation (Bauld 1986).

The C:S ratio of microbial tissue is in the range 57–85 in bacteria and 180–230 for fungus. The sulphur content of most microorganisms lies between 0.1 and 1.0% of the dry weight, and the most conspicuous cellular constituents containing the element are the amino acids, cystine and methionine. Immobilized sulphur is assimilated into organic matter generally by covalent bonding (Strickland et al. 1987). Sulphate added to soil can be adsorbed quickly or transformed to low molecular weight organic S compounds (Jez 2008), especially ester sulphates as fulvic acids (Saggar et al. 1981), which later can be polymerized to larger insoluble organic compounds (Strickland et al. 1986). Sulphur, immobilized by microbes, can be estimated by measuring inorganic sulphate released in chloroform fumigation technique. Though less quantity of sulphur is actually sequestered in microbial biomass, the fraction is extremely labile (Balota et al. 2003) and an important indicator of plant availability.

The addition of starch to a sulphur-poor soil depresses crop yields, but the reduction in yield is prevented if sulphates are applied. The detrimental effect is probably a result of microbial utilization of the available sulphur during the decomposition of the starch, leading to an immobilization of the nutrient. The critical C:S ratio in carbonaceous materials above which immobilization is dominant to mineralization is reported to be approximately 50:1. Critical C:S ratio of the substrate, diversity within microbes present in soil and environmental factors, viz. temperature, moisture, organic matter, atmospheric deposition inputs and other factors, influence immobilization rates.

3.5.3 Oxidation of Inorganic Sulphur

Oxidation of elemental sulphur and inorganic sulphur compounds (such as H_2S, sulphite and thiosulphate) to sulphate (SO_4) is brought about by chemoautotrophic and photosynthetic bacteria. When plant and animal proteins are degraded, the sulphur is released from the amino acids and accumulates in the soil which is then oxidized to sulphates in the presence of oxygen and under anaerobic condition (waterlogged soils); organic sulphur is decomposed to produce hydrogen sulphide (H_2S). H_2S can also accumulate during the reduction of sulphates under anaerobic conditions which is further oxidized to sulphates if aerobic conditions prevail in soils (Behera et al. 2014).

(a)

$$2\mathrm{S} + 3\mathrm{O}_2 + 2\mathrm{H}_2\mathrm{O} \rightarrow 2\mathrm{H}_2\mathrm{SO}_4 \overset{\text{Ionization}}{\rightarrow} 2\mathrm{H}^+ + \mathrm{SO}_4\,(\text{Aerobic})$$

(b)

$$\mathrm{CO}_2 + 2\mathrm{H}_2\mathrm{S} \overset{\text{Light}}{\rightarrow} (\mathrm{CH}_2\mathrm{O}) + \mathrm{H}_2\mathrm{O} + 2\mathrm{S}$$

Or

$$\mathrm{H}_2 + \mathrm{S} + 2\mathrm{CO}_2 + \mathrm{H}_2\mathrm{O} \overset{\text{Light}}{\rightarrow} \mathrm{H}_2\mathrm{SO}_4 + 2(\mathrm{CH}_2\mathrm{O})(\text{Anaerobic})$$

3.5.3.1 Bacteria of Genus *Thiobacillus*

The members of genus *Thiobacillus* (obligate chemolithotrophic, non-photosynthetic), e.g. *T. ferrooxidans* and *T. thiooxidans*, are the main organisms involved in the oxidation of elemental sulphur to sulphates. These are aerobic, non-filamentous, chemosynthetic autotrophs.

3.5.3.2 Green and Purple Sulphur Bacteria

Green and purple bacteria (photolithotrophs) of genera *Chlorobium*, *Chromatium* and *Rhodopseudomonas* are also reported to oxidize sulphur in aquatic environment (Madigan and Martinko 2006). They are classified within the families *Thiorhodaceae* and *Chlorobacteriaceae*. The green and purple bacteria, developed anaerobically, meet their energy requirements from light, with carbon dioxide as their only source of carbon, and oxidizing reduced sulphur materials. They are most commonly found in the bottom of water body containing sulphur material.

3.5.3.3 Colourless Filamentous Sulphur Bacteria

These bacteria of species *Thiothrix*, *Beggiatoa*, *Thiospirillopsis* and *Thioploca* are found in sulphide-containing waters and oxidize sulphide to sulphate with accumulation of elemental sulphur in cells (Starkey 1950). Besides, heterotrophic bacteria (*Bacillus*, *Pseudomonas* and *Arthrobacter*) and fungi (*Aspergillus*, *Penicillium*) and some actinomycetes are also reported to oxidize sulphur compounds.

Sulphuric acid produced during oxidation of sulphur and H_2S is of great significance in reducing the pH of alkaline soils and in controlling potato scab and rot diseases caused by *Streptomyces* bacteria. The formation of sulphate/sulphuric acid is beneficial in agriculture in different ways: (i) as it is the anion of strong mineral acid (H_2SO_4), it can render alkali soils fit for cultivation by correcting soil pH and (ii) solubilize inorganic salts containing plant nutrients and thereby increase the level of soluble phosphate, potassium, calcium, magnesium, etc. for plant nutrition (Chien et al. 2011; Karimizarchi et al. 2014).

3.5.4 Reduction of Sulphate

Sulphate in soil is taken up by plants and microorganisms and assimilated into proteins. This is known as ‘assimilatory sulphate reduction’. Sulphate can also be reduced to hydrogen sulphide (H_2S) by sulphate-reducing bacteria (e.g. *Desulfovibrio* and *Desulfotomaculum*) and may render the availability of sulphur for plant nutrition. Such conversion of sulphate to H_2S is termed as ‘dissimilatory sulphate reduction’ which is not at all desirable from soil fertility and agricultural productivity view point. The favourable environment for dissimilatory sulphate reduction is alkaline and anaerobic condition of soil.

For example, calcium sulphate is attacked under anaerobic condition by the members of the genus *Desulfovibrio* and *Desulfotomaculum* to release H_2S.

$$\mathrm{CaSO_4 + 4H_2 \rightarrow Ca\left(OH\right)_2 + H_2S + H_2O}$$

Hydrogen sulphide produced by the reduction of sulphate and decomposition of sulphur-containing amino acids is further oxidized by some species of green and purple phototrophic bacteria (e.g. *Chlorobium*, *Chromatium*) to release elemental sulphur.

$$\mathrm{CO_2 + 2H_2 + H_2S \xrightarrow{Light} \left(CH_2O\right) + H_2O + 2S}$$

The predominant sulphate-reducing bacterial genera in soil are *Desulfovibrio*, *Desulfotomaculum* and *Desulfomonas* (all obligate anaerobes) although *Desulfovibrio desulfuricans* are most ubiquitous in soils. It is a non-spore forming, obligate anaerobe that reduces sulphates at rapid rate in waterlogged/flooded soils, while species of *Desulfotomaculum* are spore-forming, thermophilic, obligate anaerobes that reduce sulphates in dry land soils. All these sulphate-reducing bacteria excrete an enzyme called ‘desulphurases’ or ‘bisulphate reductase’ which is responsible for reduction of sulphur. The rate of sulphate reduction in nature is accentuated with increasing water levels (flooding), organic matter content and increased temperature.

3.6 Enzyme Reactions in Soil Involving Sulphur Compounds

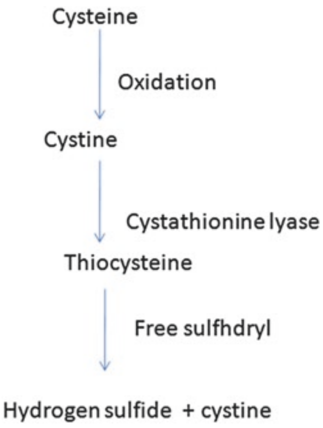
A. Sulphatases

Since much of the soil organic sulphur is present as sulphate esters, aryl and alkylsulphatase enzymes are thought to play a key role in sulphur mineralization. The overall reaction can be written as

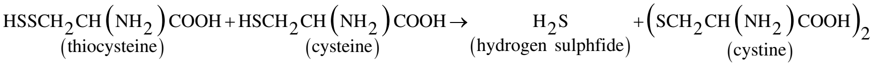
$$R-OSO_3^{-}+H_2O\rightarrow R-OH+H^{+}+SO_4^{2-}$$

Sulphatases are classified according to the nature of substrate over which it works and mainly categorized into arylsulphatases, alkylsulphatases, glucosulphatases, mycosulphatases (Roy and Trudinger 1970), etc. Arylsulphatases or phenol sulphatases are most widely distributed (Wyszkowska et al. 2016) among other sulphatase enzymes and found in soils of cultivable land, forest, sediment, marshes, etc. (Fitzgerald 1978). The major sources of this enzyme in soils are bacteria and fungi. Arylsulphatases, first reported by Tabatabai and Bremner (1970), are assayed in soil by measuring the amount of p-nitrophenol released from p-nitrophenyl sulphate added to soil and incubating for 1–2 h.

Cysteine and methionine, the two major sulphur amino acids, also undergo enzyme-catalysed transformations in soil. First, however, oxidation of cysteine to cystine (the disulphide form of the amino acid) rapidly occurs in soil as this reaction can be catalysed by trace amounts of a number of metal ions. An enzyme called cystathionine lyase acts upon cystine to form a disulphide called thiocysteine. Thiocysteine can then react with a free sulfhydryl group to form hydrogen sulphide (H_2S).



Inspection of the chemical structures of cysteine and thiocysteine illustrates how the hydrogen sulphide may be formed during the sequence of reactions as follows:



$$\underset{\text{(thiocysteine)}}{HSSCH_2CH(NH_2)COOH} + \underset{\text{(cysteine)}}{HSCH_2CH(NH_2)COOH} \rightarrow \underset{\text{(hydrogen sulphfide)}}{H_2S} + \underset{\text{(cystine)}}{(SCH_2CH(NH_2)COOH)_2}$$

In environments that are neither highly aerobic nor anaerobic, both cysteine and cystine (which contains a free sulphydryl) may be present. Field experiments have shown that losses of hydrogen sulphide are more likely to occur during the initial period waterlogging than after a more strongly anaerobic condition has developed.

The activity of arylsulphatase varies according to soil type, soil depth, organic matter content, season and climate. Maximum activity of this enzyme is observed in surface soils with optimum pH 5.5–6.2 (Tabatabai and Bremner 1970). Factors affecting microbial biomass are also known to influence the activity of the enzyme. Arylsulphatase activity in soil is significantly correlated with clay content, moisture percentage, organic carbon, nitrogen content, etc. The different types of vegetation and their rhizospheric effect have also significant influence on arylsulphatase activity in soils. Repeated application of S^0 fertilizer in soil declines the enzyme activity due to decline in microbial population and inhibitory effect of large quantities of SO_4^{2-} in this fertilized soil (Gupta et al. 1988). The enzyme activity is measured by pretreating the soils with toluene followed by incubation with buffered $S_2O_3^{2-}$ and CN^- solution, and the SCN^- thus produced is measured calorimetrically (Saha et al. 2016b; Verma et al. 2014; Verma et al. 2015b; Meena et al. 2013c, 2014a, 2016e; Singh et al. 2015; Bahadur et al. 2016a; Masood and Bano 2016).

B. Rhodanese

One other enzyme involved in the sulphur cycle has been detected and characterized in soil. This enzyme is called rhodanese (thiosulphate cyanide sulfotransferase) and belongs to the transferase class of enzymes. It catalyses the formation of thiocyanate from thiosulphate and cyanide according to the following reaction.

$$S_2O_3^{2-} + CN^- \rightarrow SCN^- + SO_3^{2-}$$

The enzyme is found in animal, plant tissue, bacteria and soils. Rhodanese activity is found in a large number and variety of soils. Both thiosulphate and tetrathionate are formed as intermediates during the oxidation of elemental sulphur to sulphate, and the rhodanese-catalysed reaction may be involved in the further metabolism of these compounds in soil.

3.7 Groups of Microorganisms Involved in Sulphur Transformation

Efficient microbes play important roles in releasing S from elemental S and sulphide minerals in the earth surface to soil. Only from sulphate minerals, S becomes readily available in soil and to plants, since plants take up sulphur only as $SO_4^=$ form preferentially. Bacteria, archaea as well as fungi are involved in the oxidation of sulphur; however, the major role is played by the bacteria, *Thiobacillus* sp. Among the archaea, aerobic oxidation of sulphur is restricted to the members of the Sulfolobales only (Setter et al. 1990). Fungi like *Alternaria tenuis*, *Aureobasidium pullulans* and *Epicoccum nigrum* and a range of *Penicillium* sp., *Scolecobasidium constrictum*, *Myrothesium circutum* and *Aspergillus* sp. are reported to be involved in the oxidation of elemental S and thiosulphate (Wainwright 1978; Shinde et al. 1996). Bacteria involved in the oxidation of sulphur can be broadly classified into three groups as chemolithoautotrophs, chemolithoheterotrophs and chemolithomesotrophs (Aragono 1991; Vidyalakshmi et al. 2009).

3.7.1 Chemolithoautotrophs

These bacteria obtain energy from oxidation of sulphur and carbon from carbon dioxide for their growth and development. The examples are *Thiobacillus thioparus*, *T. neapolitanus*, *T. denitrificans*, *T. thiooxidans*, *T. ferrooxidans*, *T. halophilus* and some species of *Thiomicrospira*.

3.7.2 Chemolithoheterotrophs

These bacteria obtain energy from oxidation of sulphur and carbon from organic molecules for their growth and development. The examples are *Thiobacillus novellus*, *T. acidophilus*, *T. aquaesulis*, *Paracoccus denitrificans*, *P. versutus*, *Xanthobacter tagetidis*, *Thiosphaera pantotroph* and *Thiomicrospira thasirae* (Prasad and Shivay 2016).

3.7.3 Chemolithomesotrophs

These bacteria obtain energy from oxidation of sulphur and carbon from inorganic as well as organic molecules for their growth and development. The examples include *Thiobacillus denitrificans* and *T. ferrooxidans*. There are a number of enzymes involved in sulphur oxidation. These include thiosulphate dehydrogenase, tetrathionate hydrolase, trithionate hydrolase and sulphur oxygenase (Friedrich et al. 2001;

Keppler et al. 2000). On the contrary, sulphates are reduced to H_2S by S-reducing organisms under anaerobic conditions such as those obtained in lowland rice paddies. H_2S is responsible for the bad odour from paddy fields. Sulphate-reducing bacteria reduce sulphate to obtain energy. Sixty genera containing 220 species of sulphate-reducing bacteria are known (Barton and Fauque 2009). The largest group (about 23 genera) includes *Desulfobacterales*, *Desulfovibrionales* and *Syntrophobacterales* (Muzer and Stams 2008). The second largest group includes genera *Desulfotomaculum*, *Desulfosporomusa* and *Desulfosporosinus* (Prasad and Shivay 2016).

Bacteria capable of oxidizing organic sulphur compounds could be either aerobic or anaerobic. Their morphology varies from nonfilamentous (*Thiobacillus*) to filamentous forms (*Beggiatoa*, *Thiothrix* and *Thioploca*). Several fungi and actinomycetes have also been reported to be sulphur oxidizers (*Aspergillus*, *Penicillium*, *Microsporum*). Among these microorganisms, *Thiobacillus* deserves special mention as it produces sulphuric acid when elemental sulphur is added to soil with the result that the pH of soil may fall as low as 2.0 after prolonged incubation with the bacterium. The possible role of *Thiobacillus* in controlling plant diseases in sulphur-amended soils has been demonstrated with regard to potato scab caused by *Streptomyces scabies* and the rot of sweet potatoes caused by *S. ipomoea*. Under acidic soil conditions (below pH 5.0), inoculation of soil with *Thiobacillus* after addition of sulphur effectively minimizes losses of sulphur in soils. The application of sulphur coupled with *Thiobacillus* inoculation has also the potentiality of rendering alkali soils fit for cultivation of crops. The formation of H_2SO_4 in soil following additions of elemental sulphur augments nutrient mobilization by increasing the level of soluble phosphate, potassium, calcium, manganese, aluminium and magnesium (Chien et al. 2011; Karimizarchi et al. 2014). In fact, manganese deficiency in soils can be corrected by sulphur applications.

Sulphate-reducing bacteria, i.e. those bacteria which reduce inorganic sulphate into hydrogen sulphide, may diminish the availability of sulphur for plant nutrition and thus influence agricultural production. *Desulfovibrio desulfuricans* is a species belonging to this class of bacteria which is an obligate anaerobe capable of producing hydrogen sulphide at a rapid rate. Other species of *Desulfovibrio* are also active in inorganic sulphate reduction, but the exact pathway is not yet clearly understood.

3.8 Role of Mycorrhizal Association in Plant Sulphur Supply

Several fungi in soil are capable of mineralizing S from sulphate esters (Klose et al. 1999). In contrast, an exclusively bacterial multicomponent monooxygenase enzyme complex is necessary to mobilize sulfonates, the dominant organo-S source in soil (Vermeij et al. 1999; Kertesz and Mirleau 2004). In fact, soil S cycling may involve complex interactions between several free-living and symbiotic root-associated microbial populations. Arbuscular mycorrhizal (AM) fungi form symbiosis with 80% of land plant species which depend upon them for growth (Wang and Qiu 2006). AM fungal symbiosis is characterized by fungal penetration of root cortical cells forming microscopic branched structures called arbuscules that increase efficiency of plant-fungus metabolite exchange. Extraradicular AM hyphae provide surfaces for functional bacterial populations to colonize. A number of studies have reported interactions between AM fungi and phosphorus (P) and nitrogen (N) mobilizing bacteria (Hodge and Storer 2015). Like S, both N and P exist predominantly inaccessible to plants which rely on interactions with mycorrhizal fungi and associated microbes to facilitate their mobilization (Richardson et al. 2009). The rhizosphere is regarded as a hot spot for microbial activity, and recent studies indicate that this is also the case for the mycorrhizosphere where bacteria may attach to the fungal hyphae capable of mobilizing organo-S (Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b, 2015c; Shrivastava et al. 2016; Velazquez et al. 2016). While current evidence is not showing sulphatase and sulphonate activity in arbuscular mycorrhiza, their effect on the expression of plant host sulphate transporters is documented (Gahan and Schmalenberger 2014).

3.9 Sulphur Management for Sustainable Crop Production

Sulphur has become more important as a limiting nutrient in crop production in recent years for several reasons. These include higher crop yields that require more S, less S impurities in modern fertilizers, less use of S-containing pesticides, reduced industrial S emissions to the atmosphere and a greater awareness of S needs. The crop's need for S is closely associated with N. The relationship between S and N is not surprising since both are components of protein and are involved in chlorophyll formation. They are also linked by the role of S in the conversion of nitrate to amino acids. Crops having high N need will usually also have high S needs. The majority of S in most soils is contained in organic matter. Organic S must be mineralized to the inorganic sulphate anion before it can be taken up by crops. Organic matter decomposition and the resulting S release are affected by temperature and moisture, and generally conditions that favour crop growth also favour mineralization and release of S, although this may be less likely with cool season crops. Sulphate, like most anions, is somewhat mobile in soils and therefore subject to leaching. Soil conditions where S is most likely to be deficient are low organic matter levels, coarse (sandy) texture with good drainage and high rainfall conditions. But, these are generalizations and S can be deficient under other conditions as well. Several factors should be taken into account when making S fertilization decisions. Among these are crop and yield goal, soil and plant analysis, organic matter content, soil texture and contribution from other sources such as irrigation water and manure. High-yielding forage crops such as alfalfa and hybrid Bermuda grass remove more S than most grain crops and tend to be relatively responsive. Soil test S is usually a measure of sulphate-S, and as with nitrate-N samples should be taken deeper than normal (0–2 ft) because of sulphate mobility in the soil. Soils containing less than 2% organic matter are most commonly S deficient; however, deficiencies do occur in soils with higher organic matter.

Coarse-textured soils are more apt to need S, but finer-textured soils can also be deficient. Sulphur content of irrigation water should be determined since in some cases it can deliver significant amounts of S. There are several S fertilizer sources available. Most soluble S fertilizer contains sulphate, but others such as bisulphites, thiosulphates and polysulphides are also available. The most common insoluble S fertilizer is elemental S, which must be oxidized to sulphate before plants can use it. This is a biological process and is affected by temperature, moisture, aeration and particle size. This process also produces acidity, and elemental S can be used in some instances specifically to acidify soils. Sulphur is an important component of complete and balanced crop nutrition and has justifiably gained more attention in recent years (Sindhu et al. 2016; Meena et al. 2014b, 2015d; Singh et al. 2016). Several factors should be considered to make the best decision regarding S need and fertilization.

3.10 Concluding Remark and Future Prospective

Wide application of sulphur-free fertilizer costs spreading of sulphur deficiency in agriculture soils of humid and semi-humid region, and it has become a deterrent towards achieving optimum production. Plants can able to synthesize sulphur-containing amino acids only in the presence of sufficient amount sulphur in available form in soil. It has been elucidated that there is an active interconversion of organic and inorganic sulphur forms in the soil, controlled largely by the group of microorganism, and this cycle determines the sulphur nutrition of plants and others. The future study should look upon composition of soil microbial communities responsible for sulphur transformation, detection of changes in their activity in different microclimate and the detail pathway of the same.

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Chapter 4
Towards the Bioavailability of Zinc in Agricultural Soils

Rashmi Baruah

Abstract The micronutrient availability in the rhizosphere soil is controlled by crop species, plant properties and interactions of roots with rhizospheric microorganisms and the surrounding bulk soils. Zinc (Zn) is an established micronutrient required for normal growth and functioning of plants. It is deficient in plants mostly not due to low Zn content of soil but to poor bioavailability. Approximately 50% of agricultural lands of India are deficient of Zn. The bioavailability of Zn in soil is also strongly influenced by the calcareousness of soil, i.e. with increase of pH, bioavailability of Zn decreases by many folds. Apart from soil pH, moisture content, soil temperature, root morphology, etc. also have visible effect on Zn bioavailability. Zinc is transported to root by diffusion, and this transport process is mostly enhanced by microbes present in the root rhizosphere. Plants exude a variety of organic and inorganic compounds as well as ions (protons, phosphate, etc.) to change the chemistry and biology of the rhizosphere, and this change becomes the driving force for micronutrient bioavailability. Zinc availability can be improved instantly by application of inorganic fertilizers or chelated Zn, but due to global awareness of soil health, the use of organic amendments or bioinoculants is gaining importance. Moreover, micronutrient-efficient crops and genotypes are also getting good response and becoming prevalent, but further research is needed. Our understanding of the physiological processes governing exudation and the soil-plant-microbe interactions in the rhizosphere is currently inadequate. In this chapter, focus was given on zinc, and the reason of poor bioavailability along with a comprehensively discussion of all possible strategies which can promote Zn availability to plants has been tried to be covered up.

Keywords Zinc · Rhizosphere · Exudation · Bacteria · Fungi · Mycorrhiza

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4.1 Introduction

The essential nature of zinc to life processes among all terrestrial organisms is certainly related to its bioavailability at the time of the origin of life. The whole living system runs on the spontaneous biochemical reactions, and enzymes act as driving force for almost all reactions. Zinc has been an imperative component of many enzymes such as oxidoreductases, transferases, hydrolases, isomerases, lyases and ligases, which indicates its importance for normal growth and functioning within plants along with various physiological roles (Imran et al. 2014), for example, carbohydrate metabolism, stabilization of ribosomal fractions and synthesis of cytochrome, maintenance of the integrity of cellular membranes, protein synthesis, regulation of auxin synthesis and pollen formation, etc.

However, Zn is a trace element found in varying concentrations in all soils, plants and animals, and it is essential for the normal healthy growth of higher plants, animals and humans. All living systems need Zn in small but critical concentrations (Goteti et al. 2013), and if the amount available is not adequate, plants and/or animals will suffer from physiological stress brought about by the dysfunction of several enzyme systems and other metabolic functions in which Zn plays a part (Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015, 2016b; Ahmad et al. 2016). The concept of bioavailability is driven by the organisms or solution phase used for the measurement of the metal availability. For example, the bioavailability of metal is often defined as the fraction of metal extractable in a chemical reagent based on correlation with the total nutrient uptake by plants (Fairbrother et al. 2007). In these cases bioavailability is largely a measure of metal solubility (Degryse et al. 2009).

Metal bioavailability has been linked to metal ion activity in soil solution, the exchangeable metal fraction and more recently to the concentration of metals that causes ecotoxicity (Antunes and Kreager 2009; Smolders et al. 2009). However, there is still no general consensus among the scientific community on the components involved in determining bioavailability. This may be due to the many inconsistencies between the bioavailable fraction measured and the uptake of metals by plants and the largely undescribed processes that may influence bioavailability occurring in the rhizosphere (Basar 2009).

Metal bioavailability in soils is largely dependent on the partition of the metals between the solid and solution phases (Alloway 2009). The importance of the metal content of soil solution as a major controlling factor in the bioavailability of metals is widely acknowledged (Rieuwerts et al. 1998). The movement of metals from unavailable forms to available forms mostly depends on chemical conditions of soil and time, and it is well understood from Fig. 4.1.

Zinc is an essential element for crops and Zn deficiency is an ubiquitous problem (Hotz and Brown 2004; Welch and Graham 2004). Low availability of Zn in soils is one of the most widely distributed abiotic stresses in world agriculture, particularly in Turkey, Australia, China and India (Brennan and Bolland 2006). In southern Australia more than 18 million hectares of agricultural land are Zn-deficient

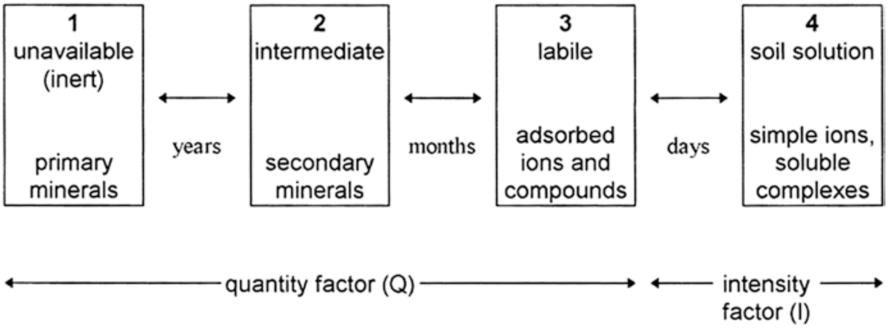

Fig. 4.1 Simplified presentation of forms of metals in soils and rates of change. The first three categories represent the soil's potential to supply trace elements. Typically the equilibria between compartments 1 and 2 occur over a period of years, between 2 and 3 over a period of months and between 3 and 4 over a period of days. Compartment 4 therefore represents the soil's trace element 'intensity factor'

(Brennan and Bolland 2006). Similarly, in India alone more than 50% of the agricultural lands are deficient of Zn (Singh et al. 2005), out of which ~85% of cereal growing area is mostly affected by low Zn (Regmi et al. 2010) status. Bell et al. (2004) reported that high-yielding cereals can remove 25 g/ha/yr of Zn in grains. Zublena (1991) summarized the nutrient removal by crops in North Carolina and reported that the removal rate of Zn varies within grain crops, and it ranged from 1.4 to 136 g Zn/ha/yr. Sakal (2001) in a field experiment on rice-wheat-sorghum sequence in calcareous soil after ten cropping cycles observed an average removal of Zn which ranged from 148 to 186 g Zn/ha/yr. Therefore, there is a wide gap between Zn availability and Zn removal which result in various Zn deficiency symptoms along with poor yield (Meena et al. 2016a, b; Parewa et al. 2014; Prakash and Verma 2016; Priyadharsini and Muthukumar 2016; Jaiswal et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a).

4.2 Causes of Poor Zn Bioavailability to Crops

Zinc availability to plants can be affected by factors such as total soil zinc contents, soil pH, organic matter, soil temperature and moisture regimes, root distribution and rhizosphere effects.

4.2.1 Total Zinc Contents

Low amount of total zinc content in soil (e.g. sandy soil) produces Zn-deficient crops (Sadeghzadeh and Rengel 2011). Some soils, despite having fair quantity of Zn (e.g. vertisols), cannot support plant growth because of precipitation or adsorption to the soil constituents which make it poorly bioavailable. A negative correlation between DTPA-extractable Zn and clay content of the soil was reported by Sidhu and Sharma (2010). They stated that heavy-textured soils had shown more retention of Zn on their adsorptive sites than light-textured soils. Over the soil texture, the form of Zn in soil also affects its availability to plant. Mandal et al. (1988) have reported that ~90% of the total soil Zn exists in residual fraction, having no relevance to bioavailable fraction.

4.2.2 Soil pH

The soil pH (soil reaction) is correlated with various biological and other chemical soil properties, and it is dynamic in nature with significant spatial (Behera and Shukla 2015) and temporal differences (Kariuki et al. 2010). Zinc becomes unavailable to plant at $pH > 7.0$ due to precipitation or adsorption to various soil constituents. The rhizosphere pH is usually lower than the bulk soil in 1–2 units. Several mechanisms are responsible of this effect: (1) production of CO_2 by respiration processes, (2) pump of H^+ in nutrient uptake by plant and microbes, (3) release of organic acids by roots and microbes, (4) organic matter decomposition, etc. (Vega 2007).

The bioavailability of Zn in soil is also strongly influenced by the calcareousness of soil. Sorption on surface of $CaCO_3$ reduces soil Zn bio-availability due to its poor rate of desorption (Kiekens 1995). Not only sorption to carbonates and clays contributes to poor Zn bioavailability, but co-precipitation with carbonates and formation of calcium zincate are also very much important in calcareous soils. Yang et al. (2011) investigated the effect of $CaCO_3$ on Zn availability in soil, using wheat as a test crop. They found a decrease in availability of Zn with increase of rate of $CaCO_3$ in soil. Most of the added Zn was transformed into an unavailable form as only 1.3% of the applied Zn was taken up by the plants. Sidhu and Sharma (2010) observed a negative correlation with soil $CaCO_3$ content and DTPA-extractable Zn content. Yoo and James (2002) also found a decrease in water-soluble Zn with an increase in soil pH from 4.0 to 7.0. The authors suggested that the decrease in water-soluble Zn occurred due to adsorption on exchangeable as well as at nonexchangeable sites. Zhao and Selim (2010) compared the sorption and desorption capacity of acidic and neutral soils. They found that sorption was less in acidic soils compared to neutral soil. Only 9–11% of sorbed Zn was released in neutral soils over time, while it was 42–51% in acidic soils. Ghosh et al. (2009) reported a negative relation between soil pH and DTPA-extractable Zn.

4.2.3 Organic Matter

Soil organic matter increases solubility of Zn and reduces fixation, which results in its more uptake by plant roots (Obrador et al. 2003; Cakmak 2009). According to Hodgson (1963), the production of complexing agent from organic matter is responsible for enhanced Zn solubility and extractability. Yoo and James (2002) in a laboratory study determined the extractability of added Zn as a function of organic matter. They noted that organic matter amendment increased the solubility of Zn in soils. Katyal and Sharma (1991) found a significant positive correlation between organic carbon and DTPA-extractable Zn. Similarly, Sidhu and Sharma (2010) observed an increase in DTPA-extractable Zn with soil organic carbon. Behera (2011) determined the correlation between soil organic carbon and extractable Zn of Hariharpur, Debatoli, Rajpora and Neeleswarm having organic carbon 0.12–1.07, 0.11–0.85, 0.52–2.79 and 0.39–3.46, respectively. They found that with an increase in organic carbon, extractable Zn was also increased.

4.2.4 Soil Water Content

Water content in soil is a very important factor, which determines the availability of Zn to plants (Patnaik et al. 2008). Usually, flooding of soil reduces Zn availability most probably due to dissolution of indigenous P (Neue and Lantin 1994) and formation of insoluble compounds with manganese, iron, carbonate and sulfide under strictly anaerobic conditions (Alloway 2004). Flooding also affects Zn availability through pH changes (Beebout-Johnson et al. 2009). Gao et al. (2012) documented a reduction in DTPA-extractable Zn under submerged conditions and reported that this reduction occurred due to formation of insoluble Zn compounds such as hydroxides, carbonates and sulfides. According to Mandal and Hazra (1997), a high concentration of Fe^{2+} under submerged conditions contributed to reduced Zn availability in soils. Yoo and Jame (2003) compared the Zn extractability and uptake by rice (*Oryza sativa*), wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*) on flooded and non-flooded soils. They observed that flooding resulted in a significant reduction in Zn concentration in the leaves of all plants. Beebout-Johnson et al. (2009) determined DTPA-extractable Zn from oxidized and reduced soils cultivated with rice. They have done extraction of field-moist soil and air dry soil and found ~60% reduction in DTPA-extractable Zn in case of field-moist soil.

4.2.5 Soil Temperature

Zinc deficiency is generally observed in early growing season due to low temperature and gradually diminishes as temperature rises. Both incidence and severity of zinc deficiency symptoms are exacerbated by low soil temperature (Zhu and Cheng 2011). It was suggested that a colder root zone temperature decreases root colonization with arbuscular mycorrhizae, root growth, zinc uptake and its translocation into the shoots (Zhu and Cheng 2011). In case of barley, shoot zinc uptake was ~82% higher in plants grown in solution at 20 °C compared with 10 °C (Schwartz et al. 1987).

4.2.6 Root Morphology and Distribution

Widespread Zn deficiency problems have motivated breeders to develop Zn-efficient genotypes (Sadeghzadeh 2013) which not only can help in improving yield but also reduce land degradation by limiting the use of machinery and minimizing fertilizer inputs on agricultural lands. Research efforts over the last two decades have resulted in considerable genotypic variation and a better understanding of underlying mechanisms of Zn efficiency in cereals. Some studies attributed Zn efficiency to better internal Zn utilization (Hacisalihoglu and Kochian 2003), while others attributed it to greater Zn uptake by the root (Wissuwa et al. 2006). During the last decades, studies in wheat (Genc et al. 2006) and rice (Gao et al. 2005) suggested that among numerous other mechanisms, Zn uptake is the most important. However, there has been little critical appraisal of root morphological traits such as length, diameter and surface area and their relationships to plant growth and Zn uptake in crop species. It is already established that thin roots with large surfaces and root systems exploiting large soil volumes enable high Zn uptake (Rengel and Graham 1995). Genc et al. (2007) have studied the importance of root morphological traits, especially root hairs in Zn uptake in case of barley using genotype Pallas and its root-hairless mutant, brb (Gahoonia et al. 2001), under two growth conditions, i.e. soil culture and solution culture. They have reported that plants grown at deficient and moderate Zn supply developed longer roots than those grown at adequate Zn supply (Fig. 4.2) (on average 10% and 5% longer roots at deficient and moderate Zn supply, respectively). Moreover, compared with soil culture, root hairs were considerably shorter and thinner in solution culture, but their length and density did not appear to be affected by Zn supply (Fig. 4.3). Similar results were reported by Chen et al. (2009). They found that total root length along with total fine root and root tips increases for Zn-efficient genotype (IR8192) at medium Zn-deficient condition than Zn-inefficient genotype (Erjiufeng) (Fig. 4.4).

The term root architecture is used to represent the shape of root system, i.e. the spatial configuration of the root system. Since soil resources are distributed unevenly, spatial coverage or distribution of the root system will determine the ability of plants to exploit the unevenly distributed soil resources effectively. Hence, it is highly desirable to breed cereal species with root systems (finer and longer roots) that are capable of mobilizing Zn on low Zn soils (Singh et al. 2005; Kumar et al. 2017; Meena et al. 2015a, b, f; Raghavendra et al. 2016; Zahedi 2016; Rawat et al. 2016; Yasin et al. 2016; Dotaniya et al. 2016).

As zinc is mostly absorbed by roots, primarily as Zn^{2+} or as $Zn(OH)_2$ from soil solution, therefore, either mass flow or diffusion may be the driving force for Zn towards the rhizosphere. But due to low concentration (3×10^{-8}–5×10^{-7} M) of Zn in soil solution, diffusion takes over the mass flow in supply of Zn to root. It is found that Zn uptake is mainly by direct root contact and is metabolically controlled. As per findings of Kochian (2000), the transport of zinc across the plasma membrane was towards a large negative electrical potential, and to maintain neutrality at root surface, plant releases OH^- or HCO_3^- ions. To understand the concept of Zn transport to root, we have to understand the concept of rhizosphere.

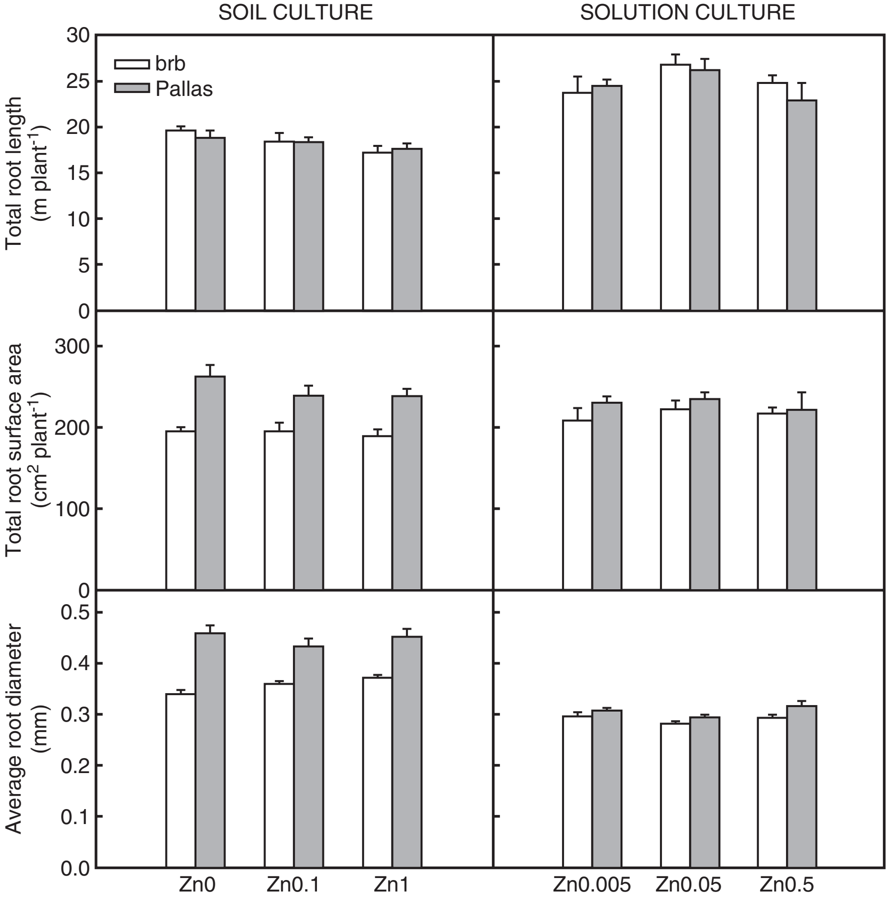

Fig. 4.2 Total root length, root surface area and average root diameter in brb and Pallas grown in a Zn-deficient soil (left) and a nutrient solution (right) supplied with different levels of Zn. The vertical bars represent standard errors based on five and four replicates in soil and solution culture, respectively

4.3 Concept of Rhizosphere

Rhizosphere is the narrow zone of soil around roots that is directly influenced by root secretions (Kennedy et al. 2004) and is considered a hot spot of microflora, having manifold increase in microbial population than bulk soil (Hiltner 1904). Rhizosphere is variable both in extent and composition, and from root surface to the bulk soil, there is gradient of many chemical, physical and biological properties (Meena et al. 2017). To accommodate this gradient, microbiologists have proposed some terms such as 'outer/ecto-rhizosphere', 'inner/endo-rhizosphere' and 'rhizoplane' (soil which is obtained when the roots are transferred to a fresh sterile solution and shaken vigorously). Ecto-rhizosphere is the area surrounding the root

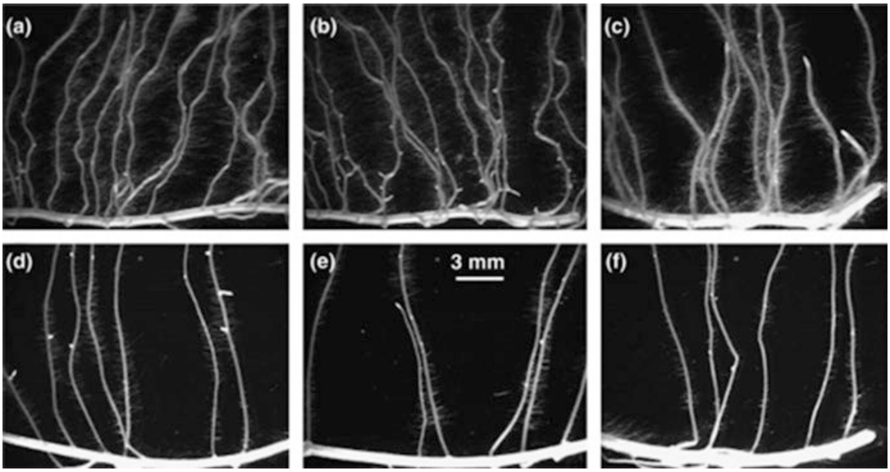

Fig. 4.3 Root hair growth on primary and lateral roots of Pallas grown at different Zn levels in soil [(**a**) Zn0, (**b**) Zn0.1 and (**c**) Zn1] and solution culture [(**d**) Zn0.005, (**e**) Zn0.05 and (**f**) Zn0.5]. Root sections of primary roots were observed under a microscope [Leica MZFL III (103)]

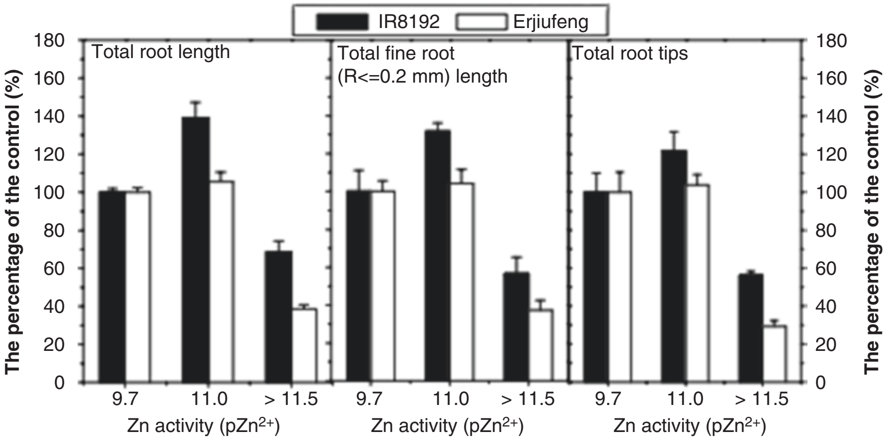

Fig. 4.4 The total root length, total fine root length and total root tips of Zn-efficient genotype IR8192 and Zn-inefficient genotype Erjiufeng under different Zn^{2+} activity conditions

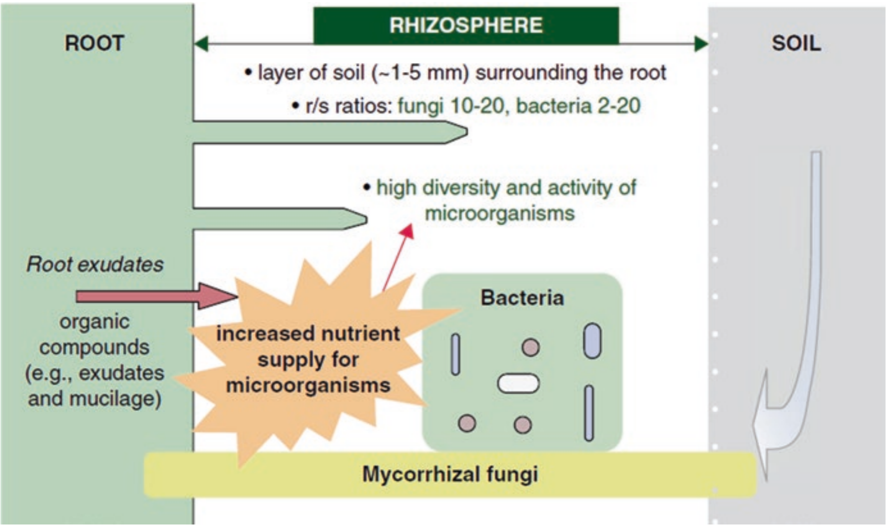

Fig. 4.5 Rhizosphere microorganisms as a critical link between plants and soil. (Adapted from Richardson et al. 2009)

which is inhabited by microorganisms, and endo-rhizosphere is the various cell layers of the root tissue including the endodermis and cortical layers colonized or potentially colonized by microorganisms (Morgan et al. 2005). Although the physical extent of the rhizosphere soil may not be easily defined, because of the complex root-soil interface, in most cases, rhizosphere soil is considered to extend only a few millimetres from the root surface (Gregory 2006). The use of eelworms to measure the extent of the rhizosphere is a cheap and effective method as they are highly specific in responding to stimulants produced by plants, but this may not be very accurate especially for light-textured soil, as movement of water is impeded (Meena et al. 2014a, 2016c, d Saha et al. 2016a, b; Yadav and Sidhu 2016; Verma et al. 2015b; Verma et al. 2014; Dominguez-Nunez et al. 2016).

As plant roots grow through soil, they release water-soluble compounds such as amino acids, sugars and organic acids that act as food for the microorganisms, and this food supply is the reason of higher microbiological activity in the rhizosphere than in soil away from plant roots. Therefore, we can say that rhizosphere microorganisms provide a critical link between plants and soil (Lynch 1990) (Fig. 4.5), and due to this link, plant can grow on soil. The highest portions of microorganisms which inhabit the rhizosphere are fungi and bacteria. When considering the rhizosphere effect on their abundance, the fungal abundance is 10–20 times higher, and the bacterial abundance is 2–20 times higher in the rhizosphere than in the bulk soil (Morgan et al. 2005). Competition for nutrient sources in the rhizosphere is very high; therefore, different microorganisms have developed distinct strategies, giving rise to a range of antagonistic to synergistic interactions, both among themselves and with the plant (Perotto and Bonfante 1997).

4.4 Sources of Energy in Rhizosphere

Living roots exude a wide range of compounds into the rhizosphere soil. These compounds can be classified into two groups based on their subsequent utilization as microbial substrates (Table 4.1), viz (1) low molecular weight organic compounds (such as sugars, amino acids, organic anions (OAs), phenolics and various other secondary metabolites) that can be readily assimilated by soil microorganisms and (2) high molecular weight organic exudates (such as proteins, pigments, mucilage and other miscellaneous substances) that require extracellular enzymic activity to break them down before they can be assimilated (Meharg 1994; Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b, 2015e; Shrivastava et al. 2016; Velazquez et al. 2016; Teotia et al. 2016; Bahadur et al. 2016b; Das and Pradhan 2016). In addition, inorganic compounds (e.g. inorganic ions, H^+, water and electrons) are also released by plant roots into rhizosphere soils (Bertin et al. 2003). Low molecular weight organic compounds account for the majority of the compounds exuded by plant roots (Bais et al. 2006). These compounds serve some specific rhizosphere functions (Table 4.3) and promote healthy plant growth.

Table 4.1 Organic compound released by plant roots

Amino acids	A-Alanine, β-alanine, α-amino adipic, γ-amino butyric, arginine, asparagines, aspartic, citrulline, cystathionine, cysteine, cystine, deoxymugineic, 3-epihydroxymugineic, glutamine, glutamic, glycine, homoserine, histidine, isoleucine, leucine, lysine, methionine, mugineic, ornithine, phenylalanine, proline, serine, threonine, tryptophan, tyrosine, valine
Enzymes	Amylase, invertase, peroxidase, phenolase, phosphatases, polygalacturonase, protease
Fatty acids	Linoleic, linolenic, oleic, palmitic, stearic
Flavanones and nucleotides	Adenine, flavanone, guanine, uridine or cytidine
Growth factors	P-Amino benzoic acid, biotin, choline, n-methyl nicotinic, niacin, pantothenic, vitamins B3 (thiamine), B2 (riboflavin) and B6 (pyridoxine)
Miscellaneous	Auxins, p-benzoquinone, scopoletin, hydrocyanic acid, 8-hydroxyquinoline, glucosides, hydroxamic acid, luteolin, unidentified ninhydrin-positive compounds, unidentified soluble proteins, reducing compounds, ethanol, glycinebetaine, inositol- and myo-inositol-like compounds, Al-induced polypeptides, dihydroquinone, quercetin, quercitrin, sorgoleone
Organic acids	Acetic, aconitic, aldonic, ascorbic, benzoic, butyric, caffeic, citric, ρ-hydroxyl benzoic, ρ-coumaric, erythonic, ferulic, formic, fumaric, glutaric, glycolic, glyoxilic, lactic, malic, malonic, oxalacetic, oxalic, benzoic, piscidic, propionic, pyruvic, succinic, syringic, tartaric, tetronic, valeric, vanillic
Sterols	Campesterol, cholesterol, sitosterol, stigmasterol
Sugar and polysaccharides	Arabinose, desoxyribose, fructose, galactose, glucose, maltose, mannose, mucilages of various compositions, oligosaccharides, raffinose, ribose, sucrose, xylose

Modified from Neumann and Römheld, 2007.

Table 4.2 Possible functional role of root exudate components in rhizosphere

Components	Rhizosphere function
Phenolics	Nutrient source
	Chemoattractant signals to microbes
	Microbial growth promoters
	Nod gene inducers in rhizobia
	Nod gene inhibitors in rhizobia
	Resistance inducers against phytoalexins
	Act as chelaters
	Phytoalexin against soil pathogens
Organic acids	Nutrient source
	Chemoattractant signals to microbes
	Chelaters of poorly soluble mineral nutrients
	Acidifiers of soils
	Detoxifiers of AI
	Nod gene inducers
Amino acids and phytosiderophores	Nutrient source
	Chemoattractant signals to microbes
	Chelaters of poorly soluble mineral nutrients
Vitamins	Promoters of plant and microbial growth
	Nutrient source
Purines	Nutrient source
Enzymes	Catalyst for nutrient release from organic molecules
	Biocatalyst for organic matter transformation in soil
Root border cell	Produces signal that controls mitosis
	Produces signal controlling gene expression
	Stimulates microbial growth
	Releases chemoattractants
	Synthesizes defence molecules for rhizosphere
	Acts as decoy that keeps root cap infection free
	Releases mucilages and proteins
Sugar	Nutrient source
	Promoters of microbial growth

Adapted from Paul, E. A. and Clark, F. E., *Soil Microbiology and Biochemistry*, Academic Press, CA, 1996, 2nd edn

Root exudates broadly called as root product can be again classified based on their functional roles (Table 4.2). Brief notes on various types of root products are furnished below:

Exudates The chemicals secreted into the soil by roots which are of low molecular weight (low-M_r) organic compound. The ability to secrete a vast array of compounds into the rhizosphere is one of the most remarkable metabolic features of plant roots,

Table 4.3 Influence of environmental factors of root exudation

Factors	Effect	References
Light intensity	High light intensity increases	Hodge et al. (1997)
	Exudation	
Microorganism	Presence of microorganisms increases exudation; however, microorganisms could also utilize exudates	Meharg and Killham (1995)
Nutrient availability	Nutrient deficiencies (e.g. P, iron) increase exudation	Lambers et al. (2002)
Oxygen status	Composition is different under aerobic and anaerobic conditions	Whipps and Lynch (1986)
Plant growth stage	Roots in the early growth stage secrete exudates more frequently	Gransee and (Wittenmayer 2000)
Plant species	Different plants and cultivars have different exudate compositions	Brimecombe et al. (2007)
Root locations	Different parts of root release different types of exudate compounds	Thornton et al. (2004)
Soil moisture	Relieving drought stress increases exudation	Rivoal and Hanson (1994)
Soil pH	Acidification changes composition of exudates	Meharg and Killham (1990)
Soil texture/plant culturing media	Mechanical impedance changes root morphology; sandy substrate produces greater amounts of exudates	Kamilova et al. (2006)
Stress condition (toxic metals)	Stress changes the composition of exudates	Donnelly et al. (2004)
Temperature	High temperature stimulates exudation	Bekkara et al. (1998)

Modified from Koo et al. (2005)

with ~5–21% of all photosynthetically fixed carbon being transferred to the rhizosphere through root exudates (Marschner 1995). Low-M_r compounds such as amino acids, organic acids, sugars, phenolics and various other secondary metabolites are believed to comprise the majority of root exudates (Meena et al. 2014b, 2015c, d, 2016e; Sindhu et al. 2016; Singh et al. 2016; Masood and Bano 2016),

Secretion Chemical compound released through plant metabolic processes. These compounds are of both low and high molecular weight.

Mucilages and Mucigels Mucilage is a polymeric gel that is capable of holding large volumes of water. Four sources of plant mucilages which contribute to the organic materials in the rhizosphere are as follows:

1. Mucilage originating in the root cap and secreted by Golgi vesicles.
2. Hydrolysates of polysaccharides of the primary cell wall between the epidermal cells and sloughed root cap cell.
3. Mucilage secreted by epidermal cells which still only have primary walls. This includes mucilage secreted by root hair. The development of secondary walls in those cells further from the tip means that no further secretion or mucilages are released, only exudates. This part of root the primary plant mucilages is confined to intercellular grooves where bacteria are unable to enter.
4. Mucilage produced by bacteria degradation of the outer multilamellated primary cell wall of old, dead epidermal cell.

When released into the soil, mucilage remains in the vicinity of roots due to its relatively high viscosity and reduced surface tension. As mucilages are mainly made of water and have very high surface tension, therefore, it penetrates into the soil very slowly and has low hydraulic conductivity compared to nearby bulk soil. Mucilage released by plant roots can help the permeation of roots through soil, improve soil aggregate structure and maintain hydraulic conductivity between roots and soil (Uren 2007; Singh et al. 2015; Meena et al. 2013c; Bahadur et al. 2016a).

On the other hand, when mucilages enter the nearby soil matrix and are enclosed with soil particles, they then form mucigels.

Lysates A large percentage of carbon releases in root rhizosphere is a result of cuticle of root being lysed or ruptured by mechanical abrasion. The primary wall of the plant root is initially bounded externally by a thin cuticle; mechanical action of roots forcing a passage through the soil causes mineral particles to rupture the cuticle. The compounds released from root cells through such degradation of root are called lysates.

4.5 Factors Affecting Root Exudates

Many factors can affect the quantity and/or composition of root exudates (Neumann and Römheld 2007) (Table 4.3). According to Bowen and Rovira (1999), plants can release between 10% and 30% of photosynthates through the root system. Whipps and Lynch (1986) reviewed this subject and found that a same factor (e.g. water stress, low soil pH, chemical applied to foliage) produced increase or decrease in the release of organic compounds in different plants. Gransee and Wittenmayer (2000) reported that maize plants released higher amounts of carboxylic acids and less sugar than pea plants. Grayston and Campbell (1996) compared root exudate composition from several tree species and found considerable variations between tree species, even for closely related species of pine trees. Different plants use different methods to take up zinc from soil solution. Kochian (2000) showed that

Poaceae family secretes nonprotein amino acids known as 'phytosiderophores' which form a complex with zinc and transport it to the outer face of the root-cell plasma membrane and then transported to leaves via a transporter protein. These phytosiderophores are released from the roots as a result of zinc deficiency.

According to the research of Suzuki et al. (2006), barley can release a very specific type of phytosiderophore called mugineic acid (MA) which can't be found in Zn-deficient rice. However, rice plants can secrete LMWOA (low molecular weight organic anion) compounds which can grant tolerance against Zn deficiency (Hoffland et al. 2006). On the other hand, Arnold et al. (2010) found that lowland rice can secrete deoxymugineic acid (DMA) which helps in solubilization and uptake of Zn by rice. Zn-efficient genotypes of wheat (Daneshbakhsh et al. 2013) and rice (Widodo et al. 2010) released greater amounts of phytosiderophores and also took up more Zn than Zn-inefficient genotypes (Erenoglu et al. 1999). However, a positive correlation between phytosiderophore exudation and Zn efficiency was not always found in wheat genotypes (Cakmak et al. 1998), indicating a complexity of the Zn efficiency syndrome in wheat. It is well known that in rice seedlings, translocation of zinc from roots increases with manganese application. However, during recent decades, research progress has shown the existence of transport proteins in some plant species is responsible for zinc translocation within rice plants (Ishimaru et al. 2011). These proteins are known as ZIPs (zinc-regulated, iron-regulated proteins), and those in rice (*Oryza sativa*,'Os') are known as OsZIPs. Their investigations showed that OsZIP-4 was highly expressed under conditions of zinc deficiency in shoots and roots especially in phloem cells.

Plant growth stage can also influence root exudates (Singh and Mukerji 2006). For instance, Keith et al. (1986) measured the relative amount of ^{14}C-labelled photosynthate released from wheat roots to the rhizosphere during different developmental stages when wheat plants were pulse-labelled with $^{14}CO_2$ and grown in the field. At the seedling stage, 8% of ^{14}C was released from roots to the soil, while at the growth stage, the percentage went down to 5%, and at the flowering stage, only 1% of ^{14}C was released by roots. Gransee and Wittenmayer (2000) also reported that younger (four-leaf stage) maize plants exuded considerably higher amounts of ^{14}C-labelled organic substances per g root dry matter than older ones (six- and eight-leaf stages). The release of exudates is not homogenous along the roots in many cases (Bringhurst et al. 2001). Jaeger et al. (1999) demonstrated that the efflux of tryptophan was associated with branched roots of *Avena barbata*, while sucrose was released around the apical region of primary roots of *A. barbata*.

The amount and composition of root exudates released by plants are also strongly affected by the physico-chemical environment (e.g. soil pH, moisture, nutrient availability, soil temperature, soil texture or plant growth media) in the surrounding rhizosphere soils (Hartmann et al. 2009). For example, the concentration of organic acids (OAs), especially oxalate, malate and citrate in root exudates of *Pinus sylvestris*, significantly increased in soils containing toxic metals such as aluminium (Al) (Ahonen-Jonnarth et al. 2000). Lipton et al. (1987) showed that alfalfa (*Medicago sativa*) released 80% more citrate under P-stress condition than was exuded by a plant receiving a complete nutrient solution.

As per findings of Fan et al. (1997), all major compounds (OAs, amino acids, mugineic acid, phytosiderophores) secreted by barley (*Hordeum vulgare*) under moderate iron and zinc deficiency revealed a sevenfold increase in total exudation in comparison with plants grown in complete nutrient solution, and among these compounds, 3-epihydroxymugineic acid (one kind of phytosiderophore) comprises ~22% of the exudate. As iron or zinc deficiency increased, total quantities of exudate per gram of root remained unchanged, but the relative quantity of phytosiderophore increased to approximately 50% of the total exudate in response to severe iron deficiency.

Soil Zn availability and the plant Zn status influence the composition and abundance of microbial communities in the rhizosphere (Dotaniya and Meena 2015). Some microbial species may be instrumental in increasing Zn availability in the rhizosphere (Muhammad et al. 2014) because soil microflora was not Zn-deficient in low Zn soil (Khan and Joergensen 2010). Moreover, bacteria isolated from Zn hyperaccumulator *Sedum alfredii* increased DTPA-extractable Zn in the rice rhizosphere and enhanced Zn uptake and biofortification of rice grain (Wang et al. 2014a). It was reported by Rengel and Römheld (2000) that wheat genotypes differing in Zn efficiency may differentially influence microbial populations in the rhizosphere. Zinc deficiency increased abundance of fluorescent pseudomonads in the rhizosphere of all wheat genotypes tested so far, but the effect was particularly obvious for Zn-efficient genotypes (Rengel 1995). Hence, the use of specific bacterial strains may be helpful in enhancing soil Zn availability as well as plant uptake and accumulation in grain (biofortification) (Muhammad et al. 2014) in a range of crops, including wheat and soybean (Aketi et al. 2014). Further work on a possible causal relationship between composition and abundance of rhizosphere bacteria and an increased capacity of crop genotypes to acquire Zn under deficient conditions is warranted. Apart from bacteria and fungi, there are few diazotrophs isolated by Sarathambal et al. (2015) from the rice rhizosphere that have the capacity to solubilize Zn-containing compounds.

4.6 Potential Strategies to Enhance Zn Bioavailability to Plants

Various strategies both chemical such as application of chemical fertilizers and chelated Zn and biological such as organic amendments and bioinoculants (Tariq et al. 2007) can be used to increase Zn concentration in the rhizosphere. But due to increase concern of environmental factor, biological approach is becoming popular. It is crucial to increase bioavailability of Zn to plants by solubilizing fixed Zn and/or by reducing fixation of the applied Zn fertilizers for better sustainable yield. This can be achieved either by using organic amendments or potential Zn-solubilizing bioinoculants.

4.6.1 Agronomic Approach

Agronomic measures to improve the Zn concentration in crop plants rely on either application of mineral Zn fertilizer or various soil treatments. The goal of all these measures is to raise bioavailable Zn in soil (White and Broadley 2005).

1. *Mineral Zn fertilization*

The most direct way to raise Zn concentrations in food crops is application of mineral Zn fertilizer (Schulin et al. 2009). Zinc sulfate ($ZnSO_4$) is the most widely applied inorganic Zn fertilizer, because of its high solubility and comparatively low price (Cakmak et al. 2010b). Zinc sulfate can be used for either soil or foliar application. Foliar application of soluble mineral Zn fertilizer is recommended when the Zn would otherwise immediately be immobilized in soil or not translocated to the edible parts of crop plants (White and Broadley 2009).

2. *Soil application*

Grain Zn concentrations in cereal crops may increase up to two to three times, depending on species and cultivar after application of Zn fertilizers to soil (Rengel et al. 1999). However, the efficiency with which mineral Zn fertilizers increase crop Zn concentration depends on the soil type (Rengel et al. 1999).

3. *Foliar application*

The advantage of foliar over soil Zn application is that the Zn directly reaches the plant. Zinc uptake via leaf surfaces and redistribution within the plants circumvent the often growth- and yield-limiting step of Zn uptake from soil. There are several convincing examples of successful foliar Zn application, which demonstrate that crop yields and qualities can be increased. When the agronomic measures succeed with increasing the Zn concentrations in the harvested crop part, the process is termed Zn biofortification (Cakmak et al. 2010b; Zou et al. 2012). The success of Zn biofortification via foliar Zn fertilization depends, however, on the timing of the application, with later applications found to be more effective than earlier ones (Cakmak et al. 2010a).

4. *Seed priming*

Covering seeds with Zn prior to sowing is much easier and less expensive than applying Zn fertilizer to soil or leaves (Schulin et al. 2009). The amount of Zn applied to seeds must, however, be well balanced not to inhibit germination. Grain yields were found to increase more after treating seeds with Zn than after foliar Zn application. The treatment of the seeds with Zn did, however, not significantly raise grain Zn concentration in comparison to foliar and soil Zn application (Yilmaz et al. 1997). It was assumed that increased plant growth may have diluted the tissue Zn concentration (Rengel et al. 1999).

However, the fertilizer-use efficiency of inorganic Zn sources is very low; therefore, alternately, we can use chelated Zn compounds. But despite the fact that synthetic chelated Zn compounds are a source of readily available Zn (Mortvedt 2000), their application is limited because they are expensive and pose a socio-economic constraint to farmers, particularly in developing countries. Therefore, it is advised to make use of soil microflora having good potential to improve availability of nutrients and reduce fixation of applied Zn in soil. This can be achieved by using organic amendments which can enhance activities of indigenous microflora and exogenous application of potential bioinoculants in soil. The detailed role of organic amendments and various rhizospheric microbes in zinc solubilization is furnished below.

4.6.2 Organic Amendment

Soil organic matter is considered a very crucial factor in nutrient mobility in soil. Various organic amendments, such as compost, farmyard manure (FYM), poultry manure, olive husk, etc., are applied to soil to improve soil health, fertility and crop yields. The organic material can improve the availability of Zn by releasing Zn with time and through changes in physico-chemical properties of soil. These properties may increase soluble/available fraction of Zn in soil for plant uptake. Moreover, application of organic amendments also improves biological properties of soil (Tejada et al. 2006). For instance, microbial biomass and soil enzyme activities are substantially increased with application of organic amendments (Liang et al. 2003). This increase in microbial population and activities is an important indicator of soil health and soil productivity.

Soils having more microbial biomass and microbial activities are supposed to be productive soils as they have good nutrient mobility and availability to plants. Organic amendments improve soil microbial biomass carbon (Cmic) (Fließbach and Mäder 2000) and the Zn content in soil and plant tissues (Saviozzi et al. 1999). For instance, Garcia-Gil et al. (2000) observed 29% and 39% increase in soil Cmic and soil Zn content with the application of manure compared to control. Likewise, substantial increase in Cmic and Zn content in soil was recorded with application of FYM and compost (Leita et al. 1999). Application of olive husk was also found to increase Zn concentration in soil and tissues of *B. vulgaris* and *B. maritime* plants (Clemente et al. 2007). The quality of organic amendments is variable, which has high importance (Tu et al. 2006). More proliferation of microflora prevails in soils treated with organic substrates having easily decomposable carbon. While comparing different organic sources, Chowdhury et al. (2000) found highest Cmic in soils treated with manure compost than those soils treated with sawdust and rice husk. Das and Dkhar (2011) also observed a significant increase in Cmic after the addition of plant compost and integrated plant compost. Tu et al. (2006) found maximum Cmic by the addition of cotton grain trash compared to animal manure and rye/vetch green manure. Cmic represents the active fraction of soil organic matter and serves as a source of nutrients to soil microbial community, which in turn releases plant-available nutrients by the decomposition of organic materials, hence increasing nutrient availability in the rhizosphere.

Improvement in Cmic and microbial activity in soil with the addition of organic amendments ensures better soil quality and also has a beneficial impact on soil fertility. By mineralization process, these organic amendments also ensure the availability of those macro- and micronutrients (including Zn), which are generally ignored by the farmers. As microbial activity in soil is associated with organic matter decomposition, release of chelating agents and organic ligands improves Zn availability by forming soluble complexes with inorganic Zn.

No doubt organic matter is a good source for improving soil health and level of Zn in plant tissues, but these results are dependent on the type, nature and composition of organic amendment. Some organic amendments, like poultry manure, sewage sludge, municipal solid waste compost, etc., contain substantial amount of heavy metals, which may pose a risk of metal contamination of agricultural soils and underground water (McBride 1995). Since these metals are highly toxic to biological system, the application of organic amendments contaminated with metals may disturb biological transformations in soil by suppressing the activities of various enzymes like urease, phosphatase, etc. (Garcıa-Gil et al. 2000). Furthermore, from the soil these metals will enter into the plant tissues and from there, ultimately, they will reach the human body causing serious disturbance in human systems. It has been documented that organic matter may also reduce available Zn concentration in soil (Mora et al. 2005). According to Harter and Naidu (1995), organic matter may form insoluble complexes with metals (Zn) and is a major cause of Zn deficiency in organic soils (Stevenson 1991). Likewise, organic amendments can increase the population of microbes, but not the specific group (Zn solubilizers). Therefore, exogenous application of some potential Zn-solubilizing microbes enhances Zn content in the rhizosphere and ultimately in the plants. Thus, application of organic amendments along with potential bioinoculants is a dire need of the hour to overcome health problems associated with Zn deficiency in food.

4.6.3 Reduction in pH

Soil pH has a dominant effect on solubility and therefore availability of Zn (Clark and Baligar 2000) in soil. Usually, low pH shifts the equilibrium towards free metal cations and protonated anions, and higher pH favours carbonate or hydroxyl complexes. Therefore, availability of Zn and other metal ions present in soil solution as cations (e.g. Al^{3+}, Mn^{2+} and Fe^{2+}) increases with increasing soil acidity (Khabaz-Saberi and Rengel 2010), whereas availability of those present as anions [MoO_4^{2-} CrO_4^{2-}, SeO_4^-, SeO_3^- and $B(OH)^{4-}$] increases with increasing pH (Rengel 2015).

It has been reported that availability of Zn decreases 100 times with one unit increase in pH (Havlin et al. 2005). Thus by decreasing the pH of alkaline soil, bioavailable fraction of Zn can be enhanced to an appreciable level. Rhizosphere microflora has been reported to lower the soil pH to a good extent (Wu et al. 2005), which may occur due to secretion of some organic acids and proton extrusion (Fasim et al. 2002). For instance, *Pseudomonas fluorescens* secreted gluconic acid and 2-ketogluconic acid in the culture during solubilization of Zn phosphate. In addition, concentration of protons was also found higher in the culture after incubation period (Di Simine et al. 1998). Likewise, Fasim et al. (2002) observed that solubilization of Zn oxide and phosphate was accompanied by proton extrusion and production of 2-ketogluconic acid. Martino et al. (2003) documented that ericoid mycorrhizal fungi secreted organic acid to solubilize Zn from insoluble ZnO and Zn_3 $(PO_4)_2$. A change in pH was observed when *Pseudomonas* and *Bacillus* spp. were used to solubilize ZnS, ZnO and $ZnCO_3$ in broth culture (Saravanan et al. 2004). Koide and Kabir (2000) proposed that mycorrhizal plants facilitate Zn availability by lowering the pH of soil by the release of some organic acids. Subramanian et al. (2009) also stated that microbial activity and acid phosphatase activity in arbuscular mycorrhizal (AM) inoculated soil would have reduced the rhizospheric pH and contributed the release of Zn from mineral fraction. However, the extent of reduction in rhizosphere pH varies among microorganisms as Giri et al. (2005) observed a 1.1 unit reduction in pH of rhizosphere soil with mycorrhizal inoculation, while Wu et al. (2006) observed a decrease in pH up to 0.47 unit with bacterial inoculation. Thus, pH goes down due to the release of organic acids and H^+, which facilitates Zn solubilization and uptake by plants.

4.6.4 Zn Chelation

Zinc ions have high interaction with the soil constituent because its persistency in the soil solution is very low (Alloway 2009). Due to low persistency/high reactivity of Zn in soil solution, plant-available fraction of Zn in the soil is poor. However, bioavailability of Zn could be increased by means of Zn-chelating compounds (Obrador et al. 2003). These compounds are either synthetic or synthesized and released by the plant roots and potential rhizosphere microflora into the rhizosphere to chelate the Zn and improve its bioavailability. The chelates of microflora are the metabolites, which form complexes with metal cations like Zn^{2+} (Tarkalson et al. 1998), which reduces their reaction with the soil. These Zn chelates subsequently move towards the roots and release chelating ligand (Zn^{2+}) at the root surface, making them free to chelate another Zn ion from the soil solution. In some microorganisms, chelation has been observed as a dominant phenomenon to improve bioavailability and uptake by plant roots. For instance, Whiting et al. (2001) suggested that a possible mechanism used by bacteria (*Microbacterium saperdae*, *Pseudomonas monteilii* and *Enterobacter cancerogenus*) for increasing water-soluble Zn (bioavailable) in soil was the production of Zn-chelating metallophores. In another report, Tariq et al. (2007) found that *Azospirillum lipoferum* (JCM-1270, ER- 20), *Pseudomonas* sp. and *Agrobacterium* sp. mobilized Zn and made it bioavailable for longer period of time when they were applied as a biofertilizer to rice by producing chelating agent like ethylenediaminetetraacetic acid (EDTA). According to the reports of Kucey (1988), inoculation of *Penicillium bilaji* increased Zn solubilization and uptake in plant to a greater extent which might occur through chelating mechanism.

4.6.5 Changes in Root Architecture

Root morphology and rhizodeposition root growth and surface area are important for Zn uptake by plants, because Zn bioavailability is mainly limited by poor mobility, which makes active foraging necessary (Havlin et al. 2005). Due to poor native bioavailable Zn and low exogenous supply, depletion zones are formed around roots. Therefore, to improve Zn uptake, it should be in close proximity with roots. This can be achieved either by application of more Zn or improving root growth and surface area so that roots can take nutrients beyond the depletion zone. A rhizosphere microflora especially mycorrhizal fungus is widely known for its impact on root architecture. Mycorrhizal plants uptake Zn over more distances, crossing the depletion zone (see Sect. 4.7.2). Sofo et al. (2013) observed that the Zn-induced changes in root morphology of *Arabidopsis* were caused by a hormonal imbalance, mainly controlled by the auxin/cytokinin ratio. It has been indicated that Zn deficiency depends on plant species and growth stage of the crop. Apart from the above-mentioned factors, genetic improvement for better root system also can prove to be promising towards development of Zn-efficient genotypes of different crops. Fathi et al. (2016) have selected four (4) different traits of wheat and found that Zn-efficient genotypes expressed more root diameter, surface area density and shoot and root dry weight compared to Zn-inefficient genotypes. Furthermore, shoot and root dry weight also showed a significant correlation with root fineness, diameter and surface area density at 30 and 60 DAPs (days after planting) and concluded that roots have a major role in Zn efficiency.

4.7 Role of Rhizosphere Microorganisms in the Improvement of Zn Bioavailability

4.7.1 Rhizosphere Microflora

Rhizosphere is the narrow zone of soil around roots that is directly influenced by root secretions and is considered a hot spot of microflora, having manifold increase in microbial population than bulk soil. All the microbial communities residing in this region constitute the rhizosphere microflora (Miransari 2013). The rhizosphere microflora may benefit plants through multifarious mechanisms including fixation of atmospheric nitrogen, mobilization of nutrients, production of phytohormones, alteration of indigenous level of phytohormones and improvement of plant stress tolerance to salinity, toxicity, drought, metal and pesticide load and also acts as a biocontrol agent (Khalid et al. 2009). Although each and every mechanism has its own significance, mobilization of nutrients by microflora has been considered the most crucial function they perform in order to improve nutrient content in plant tissues.

There is a good deal of research on mobilization of phosphorus in the rhizosphere through these tiny creatures, but increase in Zn bioavailable fraction in the rhizosphere due to the activities of rhizosphere microbes has not been well explored yet. However, there are sufficient reports indicating substantial potential of these microbes in improving Zn bioavailable fraction in the rhizosphere of plants and Zn content in plant tissues (Subramanian et al. 2009). Since these microbes play an important role in improving food quality, therefore, they would be given prime importance in the future while devising strategies to mitigate Zn malnutrition in humans through food, especially in developing countries where diverse food is not available to common people and food supplements are not affordable.

Among microbes, both bacteria and fungi have shown tremendous ability to improve plant-available Zn in the rhizosphere and also increase Zn in plant parts (Biari et al. 2008; Subramanian et al. 2009). The ways through which rhizosphere microflora may cause mobilization/solubilization of Zn include reduction in soil pH (Subramanian et al. 2009), chelation (Whiting et al. 2001) and through improving root growth and root absorptive area (Burkert and Robson 1994). These mechanisms vary from one microorganism to the other. Some organisms may use one of them, while others may use more than one mechanism to improve Zn in soil and ultimately improve Zn acquisition/uptake in plant tissues. Importance and examples of these mechanisms have been discussed in detail here.

4.7.2 Bioinoculants

Bioinoculants are products containing living cells of different types of microorganisms which, when applied to seed, plant surface or soil, colonize the rhizosphere or the interior of the plant and promote growth and yield. In case of Zn, many bacterial and fungal strains have been found with the capacity to solubilize fixed Zn and consequently increase its uptake by plants (Table 4.4). Several studies have revealed that bioinoculants help in mitigation of Zn deficiency in plants through improving mobilization of Zn in soil. The role of fungal and bacterial inoculants in improving availability of Zn to plants is comprehensively discussed below.

1. *Fungal Inoculants*

Among the fungal inoculants, AM fungus is considered highly effective in improving the availability and absorption of immobile nutrients by higher plants (Liu et al. 2000). AM fungi are well known in improving the availability of phosphorus to plant roots. It has also been reported that mycorrhizal symbiosis is also very effective in improving availability of Zn to plants (Subramanian et al. 2009). A substantial increase in soil bioavailable content of Zn has been reported in fungal-inoculated soils compared to uninoculated soils (Table 4.3). This bioavailable Zn is taken up by the plant root and accumulates in root or translocated to other plant parts. Thus, concentration of Zn in plant tissues is directly dependent on its availability in soil. There are good reports about increase in Zn uptake by the application of bioinoculants (Subramanian et al. 2009), which might have occurred through increase in bioavailable Zn in soil. For instance, Swaminathan and Verma (1979)

Table 4.4 Potential of bioinoculants in improving soil bioavailable Zn (mg kg^{-1} soil)

			Soil bioavailable Zn		
Bioinoculants	Crop	Extraction method	Exenic control	Inoculation	References
Glomus intraradices	*Z. mays*	DTAP-Zn	1.08	1.43	Subramanian et al. (2009)
Consortium of five strains (*Azospirillum lipoferum* JCM-1270, *Azospirillum lipoferum* ER-20, *Pseudomonas* sp. K-1, *Pseudomonas* sp.96-51 and *Agrobacterium* sp. Ca-18)	*O. sativa*		0.3	1.7	Tariq et al. (2007)
Consortium of three strains (*Microbacterium saperdae, Pseudomonas monteilii and Enterobacter cancerogenus*)	*Thlaspi Caerulescens*	WE-Zn	50.68	73.85	Whiting et al. (2001)
Glomus macrocarpus	*Z. mays*	Zn-L	1.33	2.85	Swaminathan and Verma (1979)
	T. aestivum		0.96	2.03	
	S. tuberosum		1.86	3.17	

Source Imran et al. (2014)

observed a great improvement in bioavailable Zn fraction in soil through fungal (*Glomus macrocarpus*) treatment which subsequently increased the Zn concentration in the leaves of wheat, maize and potato grown on Zn-deficient soils. Likewise, Subramanian et al. (2009) found that inoculation of *Glomus intraradices* caused an overall increase of 43% in bioavailable Zn in soil after 75 days compared to uninoculated soils at various Zn levels. This increase in available Zn resulted in more acquisition of Zn and its partitioning to maize grain. Similar enhancement impact of mycorrhizal inoculation on grain Zn acquisition was observed by Jensen (1982) and Purakayastha and Chhonkar (2001) in barley, wheat and rice, respectively. Like grain, other plant parts like root, shoot and leaves also accumulated more Zn due to mycorrhizal infection.

About 23 fungal isolates were studied by Sutjaritvorakul et al. (2013) for their ability to solubilize and transform insoluble zinc compounds (Table 4.5) and found that *Phomopsis* spp. (HM1), *Aspergillus* sp.1 (HM3), *Aspergillus niger* (HM4) and *Aspergillus* sp.2 (SS1) showed the highest efficiency for solubilizing all the different insoluble zinc compounds (halo diameters >40 mm). Moreover, they have reported of the presence of mycogenic crystals in the agar medium after growth of *Aspergillus* sp.1 on zinc oxide. These crystals were purified and analysed by XRPD and SEM-EDS and revealed that zinc oxalate was produced by *Aspergillus* sp.1 with zinc oxide. Similar findings were reported by Martino et al. (2003) where they found that ericoid mycorrhizal fungi *Oidiodendron maius* Cd8 could also transform zinc oxide into zinc oxalate.

However, response of AM fungi on Zn acquisition is comparatively low when Zn is applied at higher rate to soil. It is generally more effective under low Zn supply.

Table 4.5 Clear halo zone diameters produced by fungi grown on insoluble zinc compounds

Isolate origin	Isolate	Insoluble zinc compounds 0.5% (w/v)		
		ZnO	$Zn_3(PO)_4$	$ZnCO_3$
Hemimorphite	HM1	+++	+++	+++
	HM2	+	–	–
	HM3	+++	+++	+++
	HM4	+++	+++	+++
	HM5	+++	++	++
	HM6	+++	–	++
Zinc silicate	ZS1	–	–	–
	ZS2	+++	++	++
	ZS3	+++	++	+++
	ZS4	–	–	–
Smithsonite	SS1	+++	+++	+++
	SS2	+++	++	++
	SS3	+++	–	++
	SS4	++	–	–
Mining soil	MS1	+	–	–
	MS2	+++	++	++
	MS3	+++	–	++
	MS4	++	–	–
	MS5	+	–	–
	MS6	+++	++	+++
	MS7	+++	++	++
	MS8	–	–	–
	MS9	+++	++	++

(–) = no clear zone, (+) 7–20 mm, (++) 20–40 mm, (+++) > 40 mm

For instance, Purakayastha and Chhonkar (2001) found low response of AM fungi inoculation when Zn was applied compared to no application. Even when Zn supply is abundant, impact of AM inoculation becomes negative as Chen et al. (2003) observed more Zn in shoots of red clover plants having mycorrhizal symbiosis with 0 and 50 mg kg^{-1} soil Zn application, but when Zn was applied at the rate of 100 and 300 mg kg^{-1}, Zn concentration was recorded even less in inoculated plants. This is fortunate, because in most of the developing countries, either no Zn is applied to soil or applied at very lower rate. So under such circumstance, AM fungi inoculations are very useful in improving the Zn content in plant tissues. Like AM fungi, free-living fungi are also capable to convert insoluble Zn compounds into soluble compounds and improve Zn concentration in plant tissues. These include fungi belonging to genera *Aspergillus* and *Penicillium* (Sayer et al. 1995). Kucey (1988) reported that inoculation with *Penicillium bilaji* resulted in a significant increase in Zn uptake by wheat plants. It increased from 161 (uninoculated control) to 232 μg pot^{-1} under greenhouse conditions while from 9.61 to 10.7 mg plot^{-1} in field study with fungal bioinoculant. These studies clearly demonstrated that fungal inoculants could be effectively used to increase Zn availability to plants.

2. *Bacterial Inoculants*

One another possible way to increase crop productivity as well as food quality without creating environmental issues along with fungal inoculants is by the use of plant growth-promoting rhizobacteria (PGPR). The PGPR were capable of colonizing the rhizosphere, root surface and internal tissues in plants. The main microbial mechanisms by which PGPR improved plant growth include N fixation, inorganic P solubilization, siderophore production, phytohormone synthesis and controlling plant pathogens (Verma et al. 2015a). Different plant growth-promoting bacteria including free living and associative such as *Azospirillum*, *Azotobacter*, *Bacillus* and *Pseudomonas* have been used in agricultural systems as biofertilizers for their beneficial effects on plant growth (Tilak et al. 1982). Trân Van et al. (2000) have reported the beneficial effects of *Burkholderia vietnamiensis* inoculation on rice plants. Recently, Sharma et al. (2014) have also reported the positive inoculation effect of PGPRs isolated from rice rhizosphere on growth promotion of different rice genotypes. According to the research of Vaid et al. (2014), bacterial consortium such as *Burkholderia* sp. and *Acinetobacter* sp. can effectively increase the growth attributes and yield of rice. They found that rice plants inoculated with suitable combination of Zn-solubilizing bacterial strains were found more efficient in acquiring Zn from Zn-deficient soil as compared to non-inoculated plants. In an in vitro study, Saravanan et al. (2004) found that *Pseudomonas* and *Bacillus* can solubilize various Zn compounds like ZnS, ZnO and $ZnCO_3$ to a good extent in liquid medium. Likewise, in another study, Saravanan et al. (2007) demonstrated Zn-solubilizing potential of *Glomus diazotrophicus* PA15 through inoculation, and results showed 41, 15.7 and 60 times increase in soluble Zn content in case of ZnO, $ZnCO_3$ and $Zn_3(PO_4)_2$, respectively, after 48 h of incubation compared to uninoculated control. Similarly, Fasim et al. (2002) found a high potential of *Pseudomonas aeruginosa* to solubilize ZnO in liquid medium. Bacteria have also shown high mobilization of soil Zn as Tariq et al. (2007) observed almost 5.6 times higher bioavailable Zn in inoculated soil compared to uninoculated soil. Whiting et al. (2001) have also documented about 0.45-fold increase in bioavailable Zn in rhizosphere soil through bacterial inoculation.

As we know that bacterial inoculation improves plant Zn content, Whiting et al. (2001) observed a twofold more Zn concentration in the shoot of *T. caerulescens* compared to control while uptake was increased up to fourfold. Eleiwa (2005) reported that under no Zn application, inoculation of *Azotobacter* and *Azospirillum* was helpful in controlling Zn deficiency in wheat as up to 18% increase in Zn uptake in response to inoculation was measured compared to uninoculated control. Sunithakumari et al. (2016) have found that bacteria called *P. aeruginosa* (ZSB-22) extracted from soil have a potential to solubilize the insoluble forms of zinc and can be used as a bioinoculant to overcome Zn deficiency in plants. Similarly, inoculation of corn with *Azotobacter* and *Azospirillum* caused a significant increase in grain Zn content (Biari et al. 2008). They observed up to 107, 85, 95 and 107% increase in Zn content in seed with *Azospirillum* sp. strain 21, *Azospirillum brasilense* DSM2286, *Azotobacter* sp. strain 5 and *Azotobacter chrooccoccum DSM2286*, respectively, as compared to uninoculated control. Mishra et al. (2012) found consortium of *Pseudomonas* spp. and *Rhizobiu*m leguminosarum-pr-1 improved the shoot Zn content to a greater extent. While conducting experiment on rice, Tariq et al. (2007) observed 133% increases in Zn concentration in grain of rice by inoculation. The bacterial application also alleviated the deficiency symptoms of Zn in plant. Canbolat et al. (2006) and Sadaghiani et al. (2008) also found a substantial increase in Zn acquisition in wheat and barley with *Bacillus* M-13 and *Pseudomonas aeruginosa* 7NSK2, respectively. Thus such inoculants could be useful to increase solubilization of Zn in soil and its consequent availability to plants.

3. *Root Mycorrhiza*

Zinc is immobile in soil and is taken up by plant mainly by diffusion (Havlin et al. 2005). Due to poor native bioavailable Zn and low exogenous supply, depletion zones are formed around roots. Therefore, to improve Zn uptake, it should be in close proximity with roots. This can be achieved either by application of more Zn or improving root growth and surface area so that roots can take nutrients beyond the depletion zone. A rhizosphere microflora especially mycorrhizal fungus is widely known for its impact on root architecture. Mycorrhizal plants uptake Zn over more distances, crossing the depletion zone. According to Burkert and Robson (1994), arbuscular mycorrhizae can acquire Zn from a distance of 40 mm from the root surface. Subramanian et al. (2009) observed that mycorrhizal fungus significantly increased root length, spread and volume of roots compared to the plants without fungal inoculation, and this increased the Zn concentration in the grain up to 4%. Again, according to the study of Hajiboland et al. (2009), the effect of inoculation of lowland rice with arbuscular mycorrhizal fungi (AMF) under Zn-deficient condition revealed that Zn uptake of Zn-efficient genotype (Shafagh) increased by about twofold ($P < 0.01$), but a reduction of 52% ($P < 0.05$) was observed in the Zn-inefficient genotype (Fajr) upon mycorrhization (Fig. 4.6). Likewise, Tariq et al. (2007) observed a substantial increase in root weight, length and volume and Zn uptake in straw and grain with bacterial inoculation in rice. According to the study of Giri et al. (2005), about 15 times more Zn accumulation in shoots of +AM compared to −AM plants which was in accordance with results of Chen et al. (2003) support increase in shoot Zn concentration through fungal inoculation.

4.8 Conclusion and Future Research

Zinc bioavailability is controlled by several factors, but soil pH and zinc chelation by root exudates primarily affect the uptake efficiency of crops. Increase or decrease of pH by one unit can change Zn status in soil by many folds (Yang et al. 2010), and this change of pH also can change composition of exudates (Meharg and Killham 1990). Apart from manipulation of various soil factors (e.g. soil pH, organic matter,

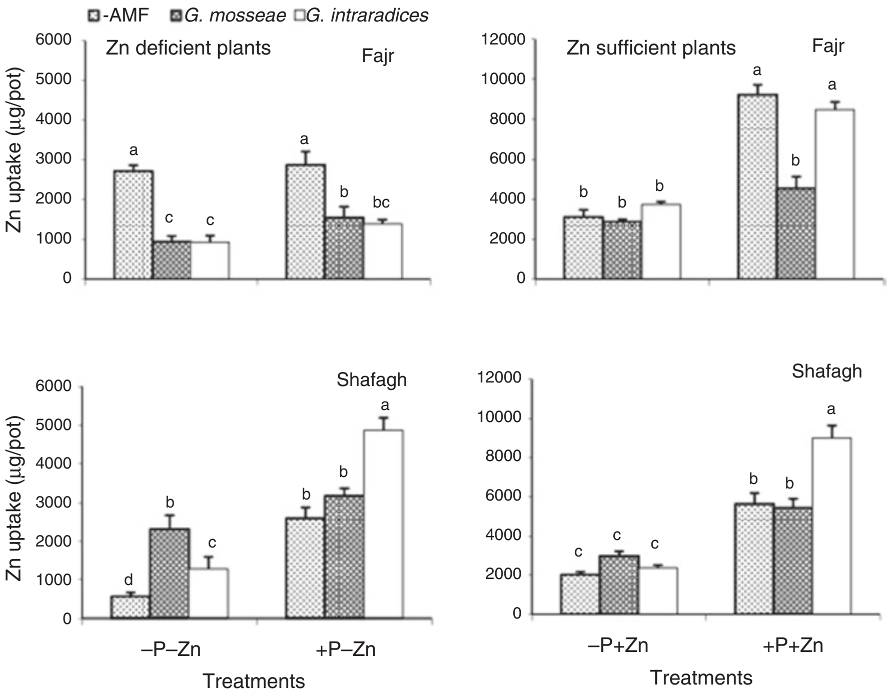

Fig. 4.6 Uptake of Zn by rice (*Oryza sativa* L. cv. Fajr and Shafagh) without (–AMF) and with inoculation by *Glomus mosseae* or *Glomus intraradices* at different Zn nutritional status. Columns indicated by the same letter are not different significantly ($P < 0.05$)

etc.), breeding as well as selection for improved biosynthesis of phytosiderophore can prove to be a promising technology to impose Zn efficiency in crops (Gahoonia et al. 2001). Exogenous application of chemical zinc fertilizers, no doubt, can improve zinc content instantly, but it has environment- and soil health-related limitations. Therefore, we should look more in depth into the potential of microbial biotechnology to improve the indigenous Zn availability which not only eliminates zinc deficiency but also improves soil health. It is already proved by various researchers that (Subramanian et al. 2009; Sharma et al. 2014) application of various fungal and bacterial bioinoculants to soil can improve Zn content in soil as well as in plant tissues which ultimately improve yield. Despite the fact that work related to impact of these bioinoculants for increasing Zn in soil and plant tissues is limited, even then there are reasonably good reports about the importance of these bioinoculants in improving bioavailable Zn fraction in soil and mitigating Zn malnutrition in plants and ultimately reducing the use of chemical fertilizers. Therefore, the concept of the use of biofertilizers with potential Zn-solubilizing microbes should be made popular with high priority. In addition, identifying genes involved in the Zn-solubilizing activity is imperative for development of Zn-efficient mutants, and crossing them with local crop varieties will defiantly be highly helpful in addressing the problem of poor Zn bioavailability in rhizosphere soil as well as uptake efficiency of crops.

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Chapter 5
Phosphate-Solubilizing Microbes: Diversity and Phosphates Solubilization Mechanism

Manoj Shrivastava, P. C. Srivastava, and S. F. D'Souza

Abstract Phosphorus (P) is an essential plant nutrient second after nitrogen. Soil phosphorus, especially in soils of high P-fixing capacity, remains unavailable to plants. Soil microorganisms belonging to diverse genera having ability to transform insoluble P into soluble and plant accessible forms are collectively referred as phosphate-solubilizing microorganisms (PSM). The strains of *Pseudomonas*, *Bacillus*, *Aspergillus*, *Penicillium*, etc. are some known phosphate solubilizers. These microorganisms in addition to supplying soluble P to plants also facilitate the growth of plants by several other mechanisms, for instance, improving the uptake of other nutrients and stimulating the production of some phytohormones and protecting the plant from biotic and abiotic stresses. Even though several bacterial, fungal, and actinomycetal strains have been identified as PSM, the mechanism through which they make P available to plants is poorly understood. This chapter focuses on the biochemical and molecular mechanisms exhibited by PSM for phosphate solubilization from inorganic and organic P sources. A short overview of the phosphate-solubilizing microbes and their effect on P uptake and crop growth is also presented herein. Phosphorus dynamics in soils and its availability to plants, metabolic pathways effecting the release of organic acids by PSM, are covered. The aspects of immobilization of PSM for the ease of application and the role of VAM in P mobilization in soil plant system have been also explored.

Keywords Glucose dehydrogenase (GDH) · Immobilization · Mycorrhiza · Organic acids · Phosphate-solubilizing microorganisms · PQQ synthase gene · Phosphatase

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5.1 Introduction

Phosphorus (P) is a primary essential nutrient which plays both structural and metabolic functions in plants. It is structural constituent of several biomolecules including nucleic acids, both DNA and RNA. It is also a structural constituent of phospholipids present in biomembranes. Phosphorus is also involved in energy transfer mechanism in the biological systems. The energy released during respiration or tapped in the light reaction of photosynthesis is used in synthesis of adenosine triphosphate (ATP) from adenosine diphosphate (ADP) with the formation of an energy-rich pyrophosphate bond. It also has a role in photosynthesis and remobilization of starch. In leguminous plants, P has a role in early stage of nodule initiation and development and also nitrogenase activity of nodules (Israel 1990). In rice culture, P application increases biological N fixation of *Azolla* (Watanabe and Cholitkul 1990).

5.2 Phosphorus Dynamics in Soil and Availability to Plants

The content of P in earth lithosphere is around 0.12%. In surface soils, the total content of P varies from 0.02 to 0.15% with an average of 0.06% (Lindsay 1979). In mineral soils, about 20–80% of total soil P is in organic form, while the rest amount is in inorganic form. Inorganic soil P may exist as non-occluded P (in soil solution, as exchangeable and adsorbed form and P present in minerals) and occluded P (held by Fe and Al oxides and oxyhydroxides).

The phosphorus released from primary and secondary P minerals enters in soil solution from where it can be either absorbed by plants or adsorbed by inorganic soil colloids or precipitated as secondary P minerals or used by soil microorganisms or lost due to leaching or runoff (Fig. 5.1). Leaching losses of P are significant in very sandy soil, in organic soils, and also in soils receiving high doses of organic manures (Sharpley et al. 1999; Sharma 1992).

5.2.1 Chemical Pools of P in Soils

5.2.1.1 Soil Solution P

Phosphorus in soil solution may vary from 0.02 to 5.46 mg PL^{-1} (Morel and Plenchette 1994) with an average value around 0.05 mg P L^{-1}. In soil solution, inorganic P may exist as $H_2PO_4^-$, HPO_4^{-2}, or PO_4^{-3} depending upon pH conditions. At pH 7.2, both $H_2PO_4^-$ and HPO_4^{-2} forms are nearly equal, and further increase in pH increases the proportion of HPO_4^{-2} form, a less preferred form by plant for absorption in comparison to $H_2PO_4^-$. Traces of some low molecular weight organic P compounds may also be present in soil solution.

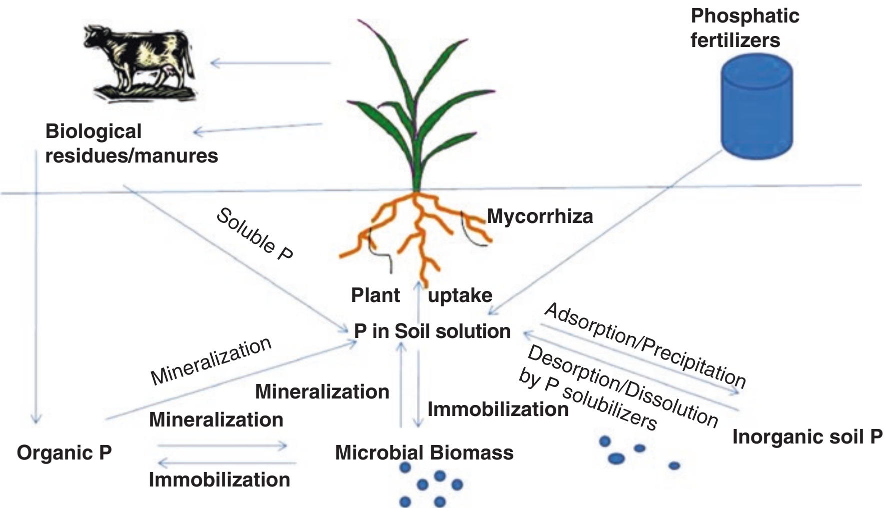


Fig. 5.1 An overview of phosphorus cycle in nature

5.2.1.2 Inorganic Solid-Phase P

In acidic soils, variscite (Al PO_4: $2H_2O$) and strengite (Fe PO_4. $2H_2O$) are dominant, while dicalcium phosphate dihydrate ($CaHPO_4$. $2H_2O$) (brushite), dicalcium phosphate ($CaHPO_4$) (monetite), octacalcium phosphate (Ca_8H_2 $(PO_4)_6$. $5H_2O$), tricalcium phosphate ($Ca_3(PO_4)_2$), and hydroxyapatite ($Ca_{10}(PO_4)_6$ F_2) are mainly present in neutral and calcareous soils. Inorganic solid-phase P exists either as adsorbed P or precipitated secondary phosphates. Adsorption-desorption phenomenon dominantly governs P supply at low P concentration, while precipitation starts when the soil solution becomes saturated with the constituents of a particular phosphate mineral. In acidic soils (ultisols and oxisols), P is mainly adsorbed onto the surface of sesquioxides and soil clays.

Aluminosilicate clays retain P by anion exchange on positively charged broken edges at low pH values and also through cation bridging at higher pH values. In acidic soils, sesquioxides play the most important role in the retention of P. Being amphoteric in nature, iron and aluminum oxides and hydroxides maintain +ve or –ve charges on their surface depending upon equilibrium pH condition. Phosphate anions retained by sesquioxides in this manner are in rapid equilibrium with P present in soil solution and therefore, called as labile P or nonspecific adsorption. However, when two metal ions of oxides bind with $H_2PO_4^-$ through ligand exchange of OH group making its release difficult, phosphorus retained in this manner is said to be “non-labile” or specifically adsorbed P.

In calcareous soils, P at low concentrations is retained by $CaCO_3$ surface through replacement of CO_3^{-2} by phosphate. At higher P concentration, surface precipitation of calcium phosphate occurs on the surface of $CaCO_3$ (Yin et al. 1989). Initially, the

Ca-phosphate formed is amorphous but gradually changes to a crystalline structure of low solubility (Parfitt, 1978). Besides $CaCO_3$, sesquioxides present in calcareous soils also retain P.

5.2.1.3 Organic Soil P

Organic soil P constitutes about 15–50% of total soil P and ranges from 654 to 1942 mg P kg^{-1} soil. It is generally higher in fine-textured soils compared to coarse-textured soils. Organic soil P decreases with rainfall and mean annual temperature and has an inverse relationship with the degree of polymerization of humic substances. The nature and pattern of land use also influence the composition of organic P in soils (Ruback et al. 1999; Cheesman et al. 2014). In the soil profile, like organic matter, organic P also decreases with depth. It is present as inositol phosphate (12.1–32.3%), phospholipids (1.9–5.8%), and nucleic acid (0.7–3.7%) (Hon and Yuan 1990). Sumann et al. (1998) reported that monoester P dominated in clay particles, while diester P concentrated in coarser soil particles. An increase in the mean annual rainfall and temperature increases the proportion of diester P in clay fraction as well as the whole soil. Inositol hexaphosphate is the most common form produced in the microbial degradation of plant residues which reacts with clays and sesquioxides. It also forms complexes with proteins and insoluble salts of Fe and Al in acidic soils and with Ca in calcareous and alkaline soils. These complexes are resistant to microbial enzyme and justify its predominance over other organic P compound in the soil. Recently, ^{31}P nuclear magnetic resonance spectroscopic characterization of organic P in soil extracts revealed the existence of both low (<10 kDa) and high (>10 kDa) molecular weight fractions (McLaren et al. 2015). The latter fraction had P bound by phosphomonoester linkages in supra-/macromolecular structures and accounted for 61–73% of soil organic P.

Phospholipids, another group of organic P compounds in soil, are readily utilized by soil microorganisms. Organic P present as nucleic acids (RNA and DNA) is released from dead cells and can be easily degraded by soil microorganisms. Therefore, the organic P present as nucleic acid P in soil at a given time remains invariably much lower than inositol phosphates. Some fraction of soil organic P may also be present as P bound to bacterial cell walls.

5.2.2 Factors Affecting P Retention and Availability in Soils

5.2.2.1 Clay Content and Clay Minerals

In general, fine-textured soils retain more P than coarse-textured soils. Among clay minerals, kaolinite (1:1 clay) retains more P than montmorillonite (2: 1 clay) due to the presence of large number of exposed OH group on the edge surfaces and also due to higher pH-dependent charge in the former.

5.2.2.2 Sesquioxides

Iron and Al oxides adsorb large amount P in soils. High P fixation capacity of oxisols and ultisols is ascribed to dominance of sesquioxides in these soils. Aluminum oxide has greater effect on P adsorption than Fe oxides (Agbenin and Tiessen 1994).

5.2.2.3 Calcium Carbonate

Phosphorus is adsorbed by $CaCO_3$ particles with large surface area. Coatings of Fe oxides on $CaCO_3$ particles further increase the P sorption capacity of $CaCO_3$. Hamad et al. (1992) reported that the maximum sorption of P by calcite increased from 18.2 to 160 mg P kg^{-1} as oxide coatings increased from 0 to 16.0 g $Fe_2O_3kg^{-1}$ $CaCO_3$.

5.2.2.4 Soil Organic Matter

Organic matter has a favorable effect on the availability of P in soils (Iyamuremye et al. 1996a) unless the C:P ratio is >300 which causes immobilization of P in soils. Organic matter improves the availability of P in soils through the following ways:

1. Carbon dioxide evolved during the decomposition of organic matter produces $H_2CO^-{}_3$which solubilizes Ca-phosphate minerals of low solubility (O'Conner et al. 1986).
2. Organic compounds formed during the decomposition of organic matter reduce P fixation capacity by reacting with potential adsorption sites on Fe and Al oxides. These compounds also help in replacing $H_2PO_4^-$ from adsorption sites and prevent precipitation of Fe and Ca-phosphate (Iyamuremye et al. 1996b).
3. Labile organic P compounds present in organic matter also release P upon their mineralization.

According to an estimate done in a tropical sandy clay loam soil (Haplustox), on an average 5.1% of total soil organic P exists in the labile, while 44.4% is in the moderately labile, and the remaining 50.5% is in the non-labile fractions (Braos et al. 2015).

5.2.2.5 Soil pH

Higher solubility of P is noted in the soil pH range of 6.0–6.5. In acidic soils, higher pH values decrease the concentration of soluble Fe and Al to reduce P adsorption and precipitation. In calcareous soil, pH values above 7.0 leads to precipitation of P as Ca-phosphates. In sodic soils, high pH values ensure an increased availability of P due to dissolution of Ca-phosphates.

5.2.2.6 Effect of Cations

Divalent cations present on soil exchange complex encourage the retention of P more than monovalent ions such as Na. The highest P adsorption in the presence of Ca^{2+} ions on the soil exchange complex is possible by making positively charged edge sites more accessible to phosphate ion. This phenomenon operates below pH 6.5. Curtin et al. (1993) considered that the observed cation-induced differences in P retention were due to a rapid decrease in potential at measured pH values in the case of Na^+ than Ca^{2+}. Cations like Ca^{2+} and Al^{+3} on exchange complex also encourage adsorption or precipitation of P after hydrolyses.

5.2.2.7 Effect of Anions

Anions like NO_3^- or Cl^- have little competitive effect on the adsorption of P, but OH^-, SO_4^{2-}, $HSiO^-_3$, and MoO_4^{2-} effectively compete with P anion for retention on soil adsorption sites. The resultant effect depends upon their bonding strength. Organic acids formed during decomposition of organic matter or added to soil system through sewage or waste water also maintain higher content of soluble P by reducing P adsorption.

5.2.2.8 Temperature and Bulk Density

Low-temperature conditions reduce the availability of P to plants by restricting growth of plant roots (Buhse et al. 1992). An increase in temperature up to the optimum level (25–30 °C) increases the mineralization of organic P compounds in soil by enhancing microbial activity in soil. Soil temperature also influences dissolution of P from added P fertilizers and its subsequent reaction with different soil components to decrease soil extractable P in P fertilized soils. With soil compaction, root growth and P uptake by crops are reduced. Soil compaction also limits the mobilization of P to growing roots by decreasing the thickness of water films around soil particles.

5.2.2.9 Soil Submergence

In most soils, flooding enhances the availability of P due to reduction of insoluble ferric phosphates present in Al-Fe oxide skins into soluble ferrous phosphate and hydrolysis of Al-phosphate. Besides this, increased solubility of Ca-phosphate, mineralization of organic P, and greater diffusion of P in soil also enhance the availability of P is flooded soils. Under anaerobic condition, the decomposition of O.M. transforms crystalline Fe compounds into amorphous Fe and increases P sorption and occlusion of P in rice soils (Sah and Mikkelsen 1986).

5.2.2.10 Crop Residue Burning

The burning of crop residues increases P adsorption and inorganic P concentration in soil due to high content of exchangeable Ca^{2+} and addition of CO_3^- and OH^- ions present in ash. The increase in P sorption reduces the concentration of P in soil solution and P availability to young seedlings of maize (Kwari and Batey 1991).

5.2.2.11 Liming

The liming of acid soils results in the formation of polynuclear complexes of Al which strongly adsorb P to decrease the availability of P in limed soil. Besides this, an increase in pH due to liming dissociates $H_2PO_4^-$ to form HPO_4^- which is more strongly adsorbed by soil. Low rates of lime used to slightly raise soil pH with considerable reduction in soil exchangeable Al improves P availability to crops.

As regards the availability of soil P to crop plants, the contribution of mass flow for P mobilization is minor due to low concentration of P in soil solution. Since the concentration of P in soil at the root surface decreases rapidly, the diffusion process is the main mechanism of P mobilization to plant roots. The zone P depletion extends progressively with time. The degree of depletion and the extent of depletion zone depend upon soil texture which is more for a coarse-textured soil but less for a fine-textured soil. Root hair length decides the feeding volume of a unit root; therefore, P flux increases with the length of root hairs (Jungk 1987). Phosphorus uptake by corn genotypes is very closely related to root surface area (Barber and Mackay 1986). Jungk and Classen (1987) noted that the product of P influx per unit of root length and root length/unit of shoot weight correlated well with P concentration of shoots.

5.3 Phosphate-Solubilizing Microbes

Phosphate-solubilizing microbes are abundant in the soil and may be readily isolated from a plant's rhizosphere (Sperber 1958; Kucey 1983).

5.3.1 Diversity of PSM

Phosphorus solubilization by the rhizospheric microbes dates back to 1903 (Khan et al. 2007). Among soil microorganisms, several bacteria belonging to genera *Pseudomonas*, *Bacillus*, *Rhizobium*, and *Enterobacter* and also some fungi like *Penicillium* and *Aspergillus* are capable of solubilizing P (Whitelaw 2000). The bacteria like *Bacillus megaterium*, *B. circulans*, *B. subtilis*, *B. polymyxa*, *B. sircalmous*, *Pseudomonas striata*, and *Enterobacter* are often most referred PSM

Table 5.1 Microorganisms having P solubilization potential

Microorganism	Examples
Bacteria	*Alcaligenes* sp., *Aerobactor aerogenes*, *Achromobacter* sp., *Actinomadura oligospora*, *Agrobacterium* sp., *Azospirillum brasilense*, *Bacillus* sp., *Bacillus circulans*, *B. cereus*, *B. fusiformis*, *B. pumilus*, *B. megaterium*, *B. mycoides*, *B. polymyxa*, *B. coagulans*, *B. chitinolyticus*, *B. subtilis*, *Bradyrhizobium* sp., *Brevibacterium* sp., *Citrobacter* sp., *Pseudomonas* sp., *P putida*, *P. striata*, *P. fluorescens*, *P. calcis*, *Flavobacterium* sp., *Nitrosomonas* sp., *Erwinia* sp., *Micrococcus* sp., *Escherichia intermedia*, *Enterobacter asburiae*, *Serratia phosphoticum*, *Nitrobacter* sp., *Thiobacillus ferrooxidans*, *T. thiooxidans*, *Rhizobium meliloti*, *Xanthomonas* sp.
Fungi	*Aspergillus awamori*, *A. niger*, *A. tereus*, *A. flavus*, *A. nidulans*, *A. foetidus*, *A. wentii*, *Fusarium oxysporum*, *Alternaria tenuis*, *Achrothcium* sp., *Penicillium digitatum*, *P. lilacinium*, *P balaji*, *P. funiculosum*, *Cephalosporium* sp., *Cladosporium* sp., *Curvularia lunata*, *Cunninghamella*, *Candida* sp., *Chaetomium globosum*, *Humicola insolens*, *Humicola lanuginosa*, *Helminthosporium* sp., *Paecilomyces fusisporous*, *Pythium* sp., *Phoma* sp., *Populospora mytilina*, *Myrothecium roridum*, *Mortierella* sp., *Micromonospora* sp., *Oidiodendron* sp., *Rhizoctonia solani*, *Rhizopus* sp., *Mucor* sp., *Trichoderma viride*, *Torula thermophila*, *Schwanniomyces occidentalis*, *Sclerotium rolfsii*
Vesicular arbuscular mycorrhiza (VAM)	*Glomus fasciculatum*
Actinomycetes	*Actinomyces*, *Streptomyces*
Cyanobacteria	*Anabaena* sp., *Calothrix braunii*, *Nostoc* sp., *Scytonema* sp.

(Subbarao 1988; Kucey et al. 1989). Duponnois et al. (2006) also reported an nematofungus (*Arthrobotrys oligospora*) which has the ability to solubilize rock phosphate (Meena et al. 2013a, 2016a, 2017; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015; Ahmad et al. 2016; Parewa et al. 2014; Prakash and Verma 2016). Other microorganisms playing an important role in P acquisition by plants include mycorrhizal fungi (Fankem et al. 2006) and endosymbiotic rhizobia (Igual et al. 2001). The microorganisms having P solubilization activity are listed in Tables 5.1 and 5.2.

5.3.2 Plant Growth Promotion by PSM

Phosphate-solubilizing microorganisms improve the supply of P to plants by their capability to solubilize inorganic or organic P and consequently result in an improvement in plant growth (Richardson 1994).The P-solubilizing microorganisms have been used as inoculants with or without insoluble P source like rock phosphates for improving plant growth (Mishustin and Naumova 1962; Laheurte and Berthelin 1988; Illmer et al. 1995). In a growth chamber studies, *B. circulans* and

Table 5.2 Microbes solubilizing P from specific insoluble P sources

Sr. No.	Microorganism	Source of isolation	Insoluble P source	References
A. Bacteria				
1.	*Pseudomonas* sp. (PI18/89)	Forest soil	Hydroxyapatite [$Ca_5(PO_4)_3OH$] and brushite [$CaHPO_4.2H_2O$], $AlPO_4$	Illmer and Schinner (1995) and Illmer et al. (1995)
2.	*Streptosporangium* sp. (actinomycete)	Casts of tropical earthworm (*Eudrilus eugeniae*)	Rock phosphate	Mba (1996)
3.	*Bacillus megaterium*, *B. sphaericus*, *B. polymyxa*, *B. brevis*, *B. thuringiensis*, and *Xanthomonas maltophilia*	Rhizosphere of wheat, barley, and pea	Rock phosphate	de Freitas et al. (1997)
4.	*Bacillus amyloliquefaciens*, *Bacillus licheniformis*, *Bacillus atrophaeus*, *Paenibacillus macerans*, *Vibrio proteolyticus*, *Xanthobacter agilis*, *Enterobacter aerogenes*, *Enterobacter taylorae*, *Enterobacter asburiae*, *Kluyvera cryocrescens*, *Pseudomonas stutzeri*, and *Chryseomonas luteola*	Rhizosphere of mangroves	Tricalcium phosphate	Vazquez et al. (2000)
5.	*Mesorhizobium mediterraneum*, *Mesorhizobium ciceri*	Root nodules of *Cicer arietinum*	Tricalcium phosphate	Peix et al. (2001a, b)
6.	*Azospirillum brasilense*, *Azospirillum lipoferum*	Rhizosphere of sugarcane	$Ca_3(PO_4)_2$	Rodriguez et al. (2004)
7.	*Xanthomonas maltophilia* and *Enterobacter cloacae*	Crop rhizosphere	Pikovskaya medium with $Ca_3(PO_4)_2$	Martínez and Martínez (2007)
8.	*Acinetobacter lwoffii*, *Pseudomonas aeruginosa*, *Bacillus thuringiensis*	Soil	Zinc phosphate	Shahab and Ahmed (2008)
9.	*Bacillus licheniformis*, *Staphylococcus epidermis*, *Acinetobacter calcoaceticus*, *Bacillus cereus*, *Bacillus thuringiensis*	Rhizospheric soil of different plants	$Ca_3(PO_4)_2$ and rock phosphate	Shrivastava (2008)
10.	*Burkholderia vietnamiensis* M6	Ginseng rhizospheric soil	$Ca_3(PO_4)_2$, $CaHPO_4$, and hydroxyapatite	Park et al. (2010)

(continued)

Table 5.2 (continued)

Sr. No.	Microorganism	Source of isolation	Insoluble P source	References
11.	*Proteus mirabilis*, *Pseudomonas oleovorans*, *Burkholderia cepacia* *Pantoea agglomerans* *Enterobacter hormaechei*	Rhizospheric soil of different plants	$Ca_3(PO_4)_2$	Shrivastava et al. (2010)
12.	Halophilic archaea *Natrinema* sp. strain IARI-WRAB2, *Halococcus hamelinensis* strain IARI-SNS2	Hyper-saline soil	Haloarchaea P solubilization (HPS) medium containing $Ca_3(PO_4)_2$	Yadav et al. (2015)
13.	*Enterobacter asburiae* PSI3	Soil	Rock phosphate	Kumar et al. (2016c)
B. Fungi				
1.	*Penicillium aurantiogriseum*	Forest soil	Hydroxyapatite [ca,$(PO_4)_3$OH and brushite [$CaHPO_4.2H_2O$], $AlPO_4$	Illmer and Schinner (1995) and Illmer et al. (1995)
2.	*Penicillium radicum*	Rhizosphere of wheat	$CaHPO_4$	Hocking et al. (1998)
3.	*Trichoderma harzianum* Rifai 1295-22 (T-22)	Soil	Rock phosphate	Altomare et al. (1999)
4.	*Aspergillus aculeatus*	Rhizosphere of gram (*Cicer arietinum*)	Rock phosphate	Narsian and Patel (2000)
5.	*Penicillium variabile* P16	Soil	Rock phosphate	Fenice et al. (2000)
6.	*Yarrowia lipolytica* (Yeast)	Unknown	Rock phosphate	Vassileva et al. (2000)
7.	*Penicillium rugulosum*	Soil	Hydroxyapatite, $FePO_4$, $AlPO_4$, and variscite	Reyes et al. (1999a, b) Reyes et al. (2001)
8.	*Aspergillus tubingensis* and *Aspergillus niger*	Rhizospheric soils of the Eucalyptus	Rock phosphates	Reddy et al. (2002)
9.	*Fomitopsis* sp. PS 102	Soil	Tricalcium phosphate, rock phosphate, aluminum phosphate	Kang et al. (2002)
10.	*Paecilomyces marquandii AA1*	Soil	Rock phosphate	Ahuja et al. (2007)
11.	*Penicillium pinophilum*, *Penicillium oxalicum*	Rhizospheric soil of different plants	Rock phosphate	Shrivastava (2008)
12.	*Trichoderma* sp.	Soil	Ferric phosphate and tricalcium phosphate	Rawat and Tewari (2011)

Table 5.3 Plant growth promotion by phosphate-solubilizing microbes (PSM)

Sr. No.	PSM	Crop	References
A. Phosphate-solubilizing bacteria			
1.	*Rhizobium leguminosarum* bv. phaseoli	Maize and lettuce	Chabot et al. (1996)
2.	*Bacillus megaterium*, *B. sphaericus*, *B. polymyxa*, *B. brevis*, *B. thuringiensis*, and *Xanthomonas maltophilia*	Canola (*Brassica napus* L.)	de Freitas et al. (1997)
3.	*Pseudomonas fluorescens* and *Bacillus megaterium*	*Cicer arietinum*	Sharma et al. (2007)
4.	*Mesorhizobium mediterraneum*	Chickpea and barley	Peix et al. (2001a, b)
5.	*Burkholderia cepacia*	Common bean (*Phaseolus vulgaris*)	Peix et al. (2001a)
6.	*Bacillus megaterium* var. phosphaticum	Sugarcane	Sundara et al. (2002)
7.	*Xanthomonas maltophilia* and *Enterobacter cloacae*	Sugarcane	Martínez and Martínez (2007)
B. Phosphate-solubilizing fungus			
1.	*Penicillium radicum*	Wheat	Whitelaw et al. (1997)
2.	*Penicillium bilaii*	Field pea	Gulden and Vessey (2000)
3.	*Aspergillus ustus*	Fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.)	Barrow and Osunaw (2002)
4.	*Penicillium rugulosum*	Maize	Reyes et al. (2002)
5.	*Chaetomium globosum*	Wheat and pearl millet	Tarafdar and Gharu (2006)
6.	*Aspergillus niger* TMPS1	Wheat	Shrivastava and D'Souza (2014)

B. megaterium var. *phosphaticum* inoculants increased plant weight and P uptake of millet and pea, respectively (Saber et al. 1977; Raj et al. 1981; Meena et al. 2015a, b, 2016b; Priyadharsini and Muthukumar 2016; Kumar et al. 2016b, 2017; Raghavendra et al. 2016; Zahedi 2016; Rawat et al. 2016; Yasin et al. 2016). Similarly, Gaind and Gaur (1991) reported that a *B. subtilis* inoculant increased biomass, grain yield, and P and N uptake of mung bean grown in a P-deficient field soil amended with rock phosphate. In another field study, Datta et al. (1982) found that *B. firmus*, a P-solubilizing and indole-3-acetic acid-producing strain, increased the grain yield and P uptake of rice in a P-deficient soil amended with rock phosphate. de Freitas et al. (1997) reported that P-solubilizing rhizobacteria increased the growth of canola and P solubilization was not the main mechanism responsible for positive growth response. Furthermore, recently several examples of simultaneous growth promotion and increase in P uptake by plants as the result of phosphate-solubilizing microbial inoculations have been reported (Table 5.3).

5.3.3 Role of VAM in Phosphate Mobilization and Uptake by Plants

Mycorrhizal roots are capable of absorbing sufficient amount of P from even P-deficient soils. Phosphorus-deficient plants are easily colonized by mycorrhizal fungus due to higher carbohydrate content in roots (Jasper et al. 1979) and increased exudation of sugars and amino acids (Graham et al. 1981). Mycorrhizal, especially endomycorrhizal, roots have higher P absorption rate per unit root length (Sanders and Tinker 1973; Meena et al. 2014a, 2016c, d; Saha et al. 2016a, b; Yadav and Sidhu 2016; Verma et al. 2014, 2015a, b; Sharma et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a) due to increased absorption surface as extended extra-matricular hyphae traverse up to 7 cm distance away from the roots to feed from a larger area as compared to non-mycorrhizal roots (Rhodes and Gerdemann 1975) or have an apparent greater affinity (km) for P (Cress et al. 1979).

Mycorrhizal roots also maintain higher phosphatase activity than their non-mycorrhizal counter parts. In mycorrhizal Norway spruce (*Picea abies* L., Karst) trees, acid phosphatase activity was recorded to be 2.0–2.5 times greater in rhizoplane soil than in the bulk soil (Haussling and Marschner 1989). New acid and alkaline phosphatase isoenzymes with significantly higher activities appear in VAM colonized of *Phaseolus vulgaris* cv, Mexico-309, a cultivar more responsive to VAM colonization (Pacovsky et al. 1991). The activity of polyphosphate hydrolase is also elevated in VAM-infected roots for enhancing the P utilization capacity of plant. Mycorrhizal roots are also able to utilize organic P sources. Tarafdar and Marschner (1994) reported that mycorrhizal wheat plants could absorb 24–33% extra P from sodium phytate than non-mycorrhizal plants (Meena et al. 2013b, 2014b, 2015c, f; Shrivastava et al. 2016; Velazquez et al. 2016; Sindhu et al. 2016; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016; Jaiswal et al. 2016).

Mycorrhizal fungi having a symbiotic association with plant roots also interact directly with other microorganisms present in the soil or indirectly through their effect on the physiology of host plants. Some microorganisms such as *Aspergillus niger*, *Penicillium* sp., and *Pseudomonas* sp. are capable of releasing organic acids and chelating agents and improve the availability of P from soil and also from applied P source. A synergistic interaction between phosphate-solubilizing bacteria and mycorrhizal fungi has been suggested as mycorrhizal fungi could assist the plant in taking up phosphate solubilized by phosphate solubilizers (Barea et al. 1983; Piccini and Azcon 1987). A similar synergistic interaction has been reported between *Glomus mosseae* and *Aspergillus fumigatus*, a phosphatase-producing fungus for utilization of organic P sources (Tarafdar and Marschner 1995). Ectomycorrhizae also assist plant to utilize P from insoluble phytates.

5.3.4 Immobilization of PSM for Soil Application

Immobilization refers to the process of associating the desired enzyme(s)/microbe(s) (biocatalyst) with an insoluble matrix, to restrict their gross movement and to retain them in proper reactor geometry for their economic reuse under stabilized conditions (D'Souza 2002). The process of immobilization separates the enzyme or cells into a distinct phase, which is different from the bulk substrate-containing phase. This not only helps in the reuse of the biocatalyst but also results in an enzyme or cell-free product. Immobilization of cells is desirable for an efficient and economically attractive bioprocess. Immobilized living cells offer general advantages such as the ability to synthesize various useful chemicals using multienzyme reactions (Singh et al. 2016; Meena et al. 2013c, 2015d; Singh et al. 2015; Bahadur et al. 2016a; Das and Pradhan 2016) and regeneration activity to prolong their catalytic life, avoid washout of cells under fermentation conditions, ensure higher cell concentration in small volumes, provide easy product separation, and provide excellent protection of cells against adverse environmental effects (Vassilev et al. 2001). Various studies for immobilization of PSM for insoluble P solubilization are presented in Table 5.3. Immobilized PSM produced relatively higher amount of organic acids compared to the free suspended cells of PSM, which in turn enhanced rock phosphate solubilization, and the immobilized cultures have higher stability and catalytic longevity. Immobilized PSM could be used to substitute mineral acids for chemical RP solubilization as currently used in superphosphate production industry. Ultimately, such immobilized cell system could be applied as biofertilizer for soil application (Vassilev et al. 2001). Some of the immobilized PSM used for insoluble P solubilization are presented in Table 5.4.

5.4 Mechanism of P Solubilization by PSM

The major processes involved in the release of soil solid P into soil solution are (1) dissolution-precipitation, (2) sorption-desorption, and (3) mineralization-immobilization (Sims and Pierzynski 2005). Soil microorganisms effect solubilization of P through the (1) release of complexing or mineral dissolving compounds, e.g., organic acid anions, siderophores, H^+, OH^-, and CO_2, (2) release of extracellular enzymes like phosphatases, and (3) release of P during organic matter decomposition (McGill and Cole 1981).

5.4.1 Solubilization of Mineral P

This mechanism is operative through organic acid production by microorganisms which lead to (1) lowering the pH in rhizosphere or (2) chelation of the cations responsible for precipitation of P, (3) competing with P for sorption sites on the soil, and (4) forming soluble complexes with the metal ions associated with insoluble P compounds (phosphates of Ca, Al, Fe). The lowering of pH in the rhizosphere is effected by the release of organic acids (Whitelaw 2000; Maliha et al. 2004) which occurs through the direct oxidation respiratory pathway operative on the outer face of the cytoplasmic membrane (Zaidi et al. 2009). The produced organic acids directly dissolve the mineral P as a result of anion exchange of phosphate by acid anion or can complex/chelate cations like Fe, Al, and Ca in the rhizosphere (Omar

Table 5.4 Immobilized PSM used for insoluble P solubilization

PSM	Carrier material	System	P source	P solubilized	References
Aspergillus niger	Polyurethane foam (PUF)	Solid-state fermentation process	Rock phosphate (RP)	2.8 g P L^{-1} of 5.0 g RP L^{-1}	Vassilev et al. (1997a)
Penicillium variable P16	Polyurethane foam (PUF)	Repeated batch cultivation	Rock phosphate (RP)	0.3 g P L^{-1} of 14.0 g RP L^{-1}	Vassilev et al. (1996)
Aspergillus niger	Agar and *k*-carrageenan	Repeated batch cultivation	Rock phosphate (RP)	0.29 and 0.21 g L^{-1}, respectively, for agar and *k*-carrageenan of 3.0 g RP L^{-1}	Vassileva et al. (1998)
Penicillium variable	Agar	Repeated batch cultivation	Rock phosphate (RP)	0.226 g P L^{-1} of 14.0 g RP L^{-1}	Fenice et al. (2000)
Yarrowia lipolytica	Agar	Repeated batch-shake-flask fermentation	Rock phosphate (RP)	0.165 g P L^{-1} of 3.5 g RP L^{-1}	Vassileva et al. (2000)
Enterobacter	Agar	Repeated batch-shake-flask fermentation	Rock phosphate (RP)	70 mg P L^{-1}	Vassilev et al. (1997b)
Bacillus megaterium	Alginate	Liquid culture and maize cultivated soil	Tricalcium phosphate	124 mg P L^{-1} in liquid culture study and 89.4 mg P/plant	Zayed (1997)
Pseudomonas striata and Bacillus polymyxa	Alginate	*Lactuca sativa* cultivated soil	Rock phosphate	2.57 mg P/plant	Vassileva et al. (1999)
Co-inoculation of Glomus deserticola and *Yarrowia lipolytica*	Ca-alginate	*Tomato* cultivated soil	Native insoluble soil P	P uptake by tomato plants 3.2 mg P/pot	Vassilev et al. (2001)
Paecilomyces marquandii AA1	Polyurethane foam (PUF)	Shake flask repeated batch cultivations	Rock phosphate	0.440 g P L^{-1} of 8 g RP L^{-1}	Ahuja and D'Souza (2009)

1998). The common organic acids released by PSM are gluconic acid (Di-Simine et al. 1998; Bar-Yosef et al. 1999), oxalic acid, citric acid (Kim et al. 1997), lactic acid, tartaric acid, and aspartic acid (Venkateswarlu et al. 1984).

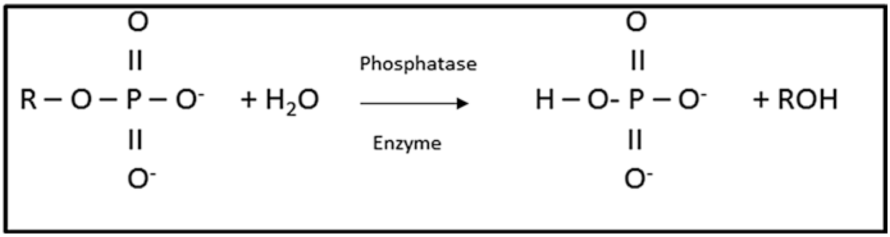
However, acidification alone does not seem to be the universal mechanism of solubilization. Altomare et al. (1999) noted that a fungus *T. harzianum* (T-22) solubilized insoluble rock phosphate P in vitro cultures and no organic acids were detected in the culture filtrates. The phosphate-solubilizing activity of *T. harzianum* (T-22) was attributed to both chelation and reduction processes. Some bacteria like *Nitrosomonas* and *Thiobacillus* species producing nitric and sulfuric acids can also effect solubilization of insoluble phosphate compounds (Azam and Memon 1996; Masood and Bano 2016; Meena et al. 2015e, 2016e; Teotia et al. 2016; Bahadur et al. 2016b). The reduction of ferric phosphate to yield ferrous sulfate results in a concomitant release of phosphate (Swaby and Sperber 1959). Other indirect processes like the assimilation of NH_4^+ resulting in the excretion of H^+ (Parks et al. 1990) or stimulation of plant metabolism promoting proton efflux and release of organic acids from plant roots (Carrillo et al. 2002) have also been implicated in release of P.

5.4.2 Solubilization Organic P

Mineralization of soil organic P which constitutes 4–90% of the total soil P (Khan et al. 2009b) plays an important role in the cycling of P in a farming system. The mineralization of organic phosphorous compounds depends mainly on the physico-chemical and biochemical properties of the organic P compounds, e.g., nucleic acids, phospholipids, and sugar phosphates are easily mineralized than phytic acid, polyphosphates, and phosphonates. Soil organic P compounds mainly associated with clay particles are easily mineralized as a fraction of them is easily accessible for rapid microbial utilization (Ruback et al. 1999). The enzymes which cause the release of P from organic compounds are as follows.

5.4.2.1 Nonspecific Acid Phosphatases

Many soil microorganisms like *Aspergillus*, *Penicillium*, *Mucor*, *Rhizopus*, *Bacillus*, *Pseudomonas*, and mycorrhizal hyphae produce phosphatases which cause the dephosphorylation of soil organic P compounds by breaking phosphoester or phosphoanhydride bonds.



$$R-O-\underset{\underset{\displaystyle O^-}{\|}}{\overset{\overset{\displaystyle O}{\|}}{P}}-O^- \quad + H_2O \xrightarrow[\text{Enzyme}]{\text{Phosphatase}} H-O-\underset{\underset{\displaystyle O^-}{\|}}{\overset{\overset{\displaystyle O}{\|}}{P}}-O^- \quad + ROH$$

Among the variety of phosphatase enzyme classes produced by PSM, both acidic and alkaline phosphatases are most abundant in nature (Nannipieri et al. 2011). Acid phosphatases are dominant in acid soils, while alkaline phosphatases are more abundant in neutral and alkaline soils (Eivazi and Tabatabai 1977; Juma and Tabatabai 1998; Renella et al. 2006). In contrast to phosphatases produced by plants, the phosphatase of microbial origin possesses a greater affinity for organic P compounds (Tarafdar et al. 2001). The phosphatase activity in soils also increases with soil organic matter content, P content in soil, soil pH, and moisture and temperature conditions.

5.4.2.2 Phytases

Richardson (2001) observed that *Arabidopsis* plants which were genetically transformed with the phytase gene (phyA) derived from *Aspergillus niger* were able to utilize P from phytates. This hint that such microorganisms in the rhizosphere can mineralize phytates present in soil organic P and can help the plants to derive P directly from organic P compounds (Richardson and Simpson 2011).

5.4.2.3 Phosphonatases and C-P Lyases

These enzymes break the C-P bond of organophosphonates (Rodriguez et al. 2006).

5.4.2.4 Role of Microbial Siderophores in P Solubilization

Siderophores are the complexing agents produced by almost all microorganisms in response to iron deficiency. These siderophores can solubilize Fe from minerals or organic compounds. There are approximately 500 known siderophores, and the majority of them are being used by a wide range of microorganisms and plants, while some of them are being exclusively used by the microbial species and strains producing them (Crowley 2007). The release of siderophores from different PSM has been reported by many researchers (Vassilev et al. 2006; Caballero-Mellado et al. 2007; Hamdali et al. 2008); however, siderophore production has not been widely implicated as a P solubilization mechanism. In view of the dominance of mineral dissolution over ligand exchange by organic acid anions as a P solubilization mechanism (Parker et al. 2005), a potential role of siderophores in enhancing P availability in the rhizosphere can be anticipated.

5.4.2.5 Role of EPS in P Solubilization

The role of polysaccharides in the microbial-mediated solubilization of P was assessed by Yi et al. (2008). Microbial exopolysaccharides (EPSs) are polymers consisting mainly of carbohydrates excreted by some bacteria and fungi and are deposited on the outsider side of their cell walls. These may be homo- or heteropolysaccharides with both organic and inorganic substituents (Sutherland 2001).

Yi et al. (2008) examined four bacterial strains involving *Enterobacter* sp. (EnHy-401), *Arthrobacter* sp. (ArHy-505), *Azotobacter* sp. (AzHy-510), and *Enterobacter* sp. (EnHy-402) to evaluate the role of exopolysaccharide (EPS) for the solubilization of tricalcium phosphate. Their results revealed that bacteria producing significant amount of EPS had a strong ability for P solubilization.

5.5 Biochemical and Molecular Mechanism of Phosphate-Solubilizing Microbes

The mineral phosphate solubilization (MPS) by bacteria is mainly associated with the production of low molecular weight organic acids (Goldstein 1986). Outer perimeter of gram-negative bacteria is composed of two membranes separated by a porous gel-like material. The direct oxidation metabolic pathway is essential for insoluble P solubilization and therefore for the MPS phenotype. This pathway is also known as the “nonphosphorylating oxidation” pathway. The direct oxidation pathway involves the enzymatic conversion of glucose to gluconic acid and/or 2-ketogluconic acid on the outer face of the inner membrane. It is important to note that acid production actually occurs in the periplasmic space. Glucose can enter and move freely through the periplasmic space. Likewise, gluconic acid and 2-ketogluconic acid can move freely out of the periplasmic space to the outer surface. Glucose dehydrogenase (GDH) is the enzyme that oxidizes glucose to gluconic acid (pKa ~ 3.6). This enzyme is anchored in the inner membrane, but the catalytic surface is in the periplasmic space.

The production of gluconic acid occurs functionally at the cell surface because the catalytic surface of glucose dehydrogenase lies in the periplasmic space and glucose is freely diffusible from the external solution to the catalytic surface. Gluconic acid produced from glucose oxidation will freely diffuse out of the periplasmic space and contact the insoluble P source. Gluconic acid dehydrogenase (a.k.a. gluconate dehydrogenase; GADH) is the second enzyme in the direct oxidation pathway. GADH converts gluconic acid to 2-ketogluconic acid (pKa ~ 2.4). Like glucose dehydrogenase, this enzyme is anchored in the inner membrane, but the catalytic surface is in the periplasmic space. As a result, 2-ketogluconic acid will also freely diffuse out of the periplasmic space and make direct contact with the insoluble P source. Gluconic acid (pKa ~ 3.4) and 2-ketogluconic acid (pKa ~ 2.6) are two of the strongest naturally occurring organic acids and the first two products in the direct oxidation pathway (Duine 1991).

In addition, both gluconic acid and 2-ketogluconic acid are capable of acting as Ca^{++} chelators under appropriate physicochemical conditions. Liu et al. (1992) identified the metabolic and genetic bases for high efficiency solubilization of poorly soluble phosphates. These workers have shown that solubilization is the result of acidification of the periplasmic space (and ultimately the external medium) by the direct oxidation of glucose (nonphosphorylating oxidation) or other aldose sugars by the quinoprotein glucose dehydrogenase. Glucose-derived gluconic acid often undergoes one or two additional periplasmic oxidations to 2-ketogluconic or 2,5-diketogluconic acid (Anderson et al. 1985).

The enzymes of the direct oxidative pathway are oriented in the outer face of the cytoplasmic membrane so that they oxidize their substrates in the periplasmic space (Duine 1991). The products of direct periplasmic oxidation are taken up by specific phosphotransferase or other transport systems. GDH oxidizes a broad range of aldose sugars. Little is known about the regulation of the genes coding for quinoproteins or how quinoprotein-mediated oxidative metabolism is regulated. Non-phosphorylating oxidation is one of the four major metabolic pathways for glucose (aldose) utilization by bacteria (Gottschalk 1986). Most species have at least two of these pathways. The quinoprotein GDH controls the unique step in direct oxidation. GDH transfers electrons from aldose sugars to the electron transport chain via two electrons, two proton oxidations mediated by the cofactor pyrroloquinoline quinone (PQQ) (Duine 1991).

The molecular mechanism(s) whereby periplasmic oxidation is coupled to respiratory electron transport vary between genera and even species. The biochemical or genetic regulatory mechanisms by which a given species switches between the direct phosphorylative and periplasmic oxidative mode remain unknown. The complexity of the direct oxidation phenotype is reflected in the molecular genetics of GDH and related quinoprotein dehydrogenases. There is no information on the genetic or biochemical mechanisms that regulate the synthesis or assembly of the GDH/PQQ holoenzyme. *Acinetobacter lwoffii*, *Azotobacter vinelandii*, *Agrobacterium*, and *Rhizobium* species contain quinoprotein glucose dehydrogenase apoenzyme (EC 1.1.99.17). In addition to whole cells of pyrroloquinoline quinone (PQQ), the prosthetic group of this enzyme resulted in the production of gluconic acid from glucose (Vanschie et al. 1987).

The *gabY* gene could play an alternative role in the expression and/or regulation of the direct oxidation pathway in *Pseudomonas cepacia*, thus acting as a functional mineral phosphate solubilization gene in vivo (Babu-Khan et al. 1995). Many bacteria confer an incomplete system for MPS activity. For example, the *Escherichia coli* genome encodes apo-glucose dehydrogenase but not PQQ synthase (Blattner et al. 1997), while some bacteria, including *Deinococcus radiodurans*, encode PQQ synthase and lack apo-glucose dehydrogenase (White et al. 1999), making them MPS (−) (Khairnar et al. 2003). MPS+ phenotype in bacteria is regarded as an indicator of the presence of both PQQ synthase and apo-glucose dehydrogenase. The presence of PQQ in MPS (+) bacteria could have a role beyond mineral phosphate solubilization (Shrivastava et al. 2010).

The principal mechanism for phosphatases production for organic phosphorus solubilization is the regulation by inorganic phosphate (Pi) concentration (i.e., phosphate-repressible phosphatases). This mechanism has been best studied in the alkaline phosphatase (gene *phoA*) of *E. coli*, which is suddenly and fully induced when the Pi concentration decreases from 100 mM to 0.16 mM (Rosenberg 1987). The mechanism involves a Pi transport operon as a regulatory element, in addition to the sensor-activator operon. The genes controlled by Pi and activated by PhoB constitute the PHO regulon (Torriani-Gorini 1994).

5.6 Concluding Remarks and Future Perspectives

Phosphate-solubilizing microbes (PSM) play an important role in P supply to plants. Their use as a biofertilizer can help in reducing dependence on phosphatic fertilizers and economizing crop production besides ensuring environmental safety. In order to harness the potential of PSM, future research should focus on the stability and performance of the phosphate solubilization ability for both natural and genetically modified strains applied to soil. The detailed biochemical and molecular mechanisms of P solubilization operative in PSM are poorly understood. Mineral phosphate-solubilizing ability of microbes could be linked to specific genes. The rhizosphere competence is a major determinant for the success of the inoculants. Understanding the genetic basis of P solubilization could help in transforming more rhizosphere-competent bacteria into PSMs. Future studies on chromosomal insertion of the PQQ synthase gene would be advantageous, both to avoid horizontal transfer risk and to increase the stability of the new trait. Future research should also focus on the microbial solubilization of phosphates bound to iron (Fe) and aluminum (Al) compounds and organic P present in the soils.

AM fungi together with PSMs could be much more effective in the utilization of native soil P. Understanding AM-PSM symbiosis and attempts to develop AM fungi which could be cultured in vitro may help realize their potential as phosphate biofertilizers. Immobilization of PSM for use in agriculture, so far, is limited to entrapment in gels or passive immobilization only. Immobilization by adsorption on inert materials may offer minimal mass transfer limitations and supports which are cheap, nontoxic to the microbes, and mechanically stable. There is a necessity to explore other suitable natural or synthetic polymers with controlled characteristics as immobilizer for PSM.

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Chapter 6
Role of Phosphate-Solubilizing Microbes in the Enhancement of Fertilizer Value of Rock Phosphate Through Composting Technology

P. C. Moharana, M. D. Meena, and D. R. Biswas

Abstract Preparation and use of enriched compost has become an important component of sustainable agriculture and received much interest in recent years as a means of alternative utilization of crop residues and low-grade minerals like rock phosphate (RP) by composting technology, thus reducing the ill effects of residue burning as well as improving the P content. The process has many advantages including sanitation, mass and bulk reduction, and decrease in carbon-to-nitrogen (C/N) ratio of crop residues. The performance of compost depends on the quality of the substrate. However, composts prepared from farm wastes have low nutrient content, particularly phosphorus (P) and potassium (K), and are considered poor suppliers of nutrients to crops. A possible means of improving the nutrient content, after prepare enriched compost by addition of low-grade RP and microbial techniques for RP solubilization. It will not only help farmers in supplying plant nutrients at a very low investment but also keep the environment pollution-free. The mineralization of insoluble forms of P present in RP by organic acids released during decomposition of organic matter is the major advantage of preparation of enriched compost. Organic acids released from the various organic materials used in the composting help in breaking down the RP faster during the composting period by pushing the dissolution reaction to the forward direction. The availability of P also increases due to inoculation with PSM, which are also known to produce organic acids. These acids are able to dissolve the mineral phosphate and make it available for the plant. The composting of organic wastes with RP has been demonstrated to be an effective method for producing end-products which are ensuring their maximum benefit for

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agriculture. Here, we emphasize pre-application techniques, especially the co-composting of RP with various organic by-product materials that include crop residues. A range of laboratory incubations have demonstrated the underlying mechanisms involved with solubilization. The significance of microbial induced production of organic acids and acidity during composting is particularly important in this respect. Inoculation with *Aspergillus awamori* into the composting mass increased the content of total P (2.35%) as well as water-soluble P (0.05% P) and citrate-soluble P (0.85% P) significantly. While co-composting with RP offers a great potential that could be developed for use at the individual farm scale, the key controlling factors and underlying mechanisms are far from being fully understood. Studies on synchronization of nutrient mineralization and crop demand will provide information on the efficient use of RP-enriched compost in a more integrated manner with inorganic fertilizers for achieving sustainable higher crop productivity.

Keywords Rock phosphate · Solubilization · Compost · Crop residues · Phosphate-solubilizing microorganisms

Abbreviations

N	Nitrogen
P	Phosphorus
PSB	Phosphate-solubilizing bacteria
PSF	Phosphate-solubilizing fungi
PSM	Phosphate-solubilizing microorganisms
RP	Rock phosphate
WSP	Water-soluble P
CSP	Citrate-soluble P

6.1 Introduction

Phosphorus (P) is the second major essential plant nutrients, required for crop growth and productivity. Phosphorus is quite abundant in many soils of the world, but due to least mobility and availability to plants in most soil conditions, therefore, it is one of the major plant nutrients limiting plant growth. The P deficiency is widespread on soils throughout the world that P fertilizer represents a major cost for increasing agricultural production. The importance of diammonium phosphate (DAP) and single superphosphate (SSP) as efficient P fertilizer is well established, but these are very expensive and need to be imported. For manufacturing of conventional P fertilizers, India imports large amounts of premium-grade (high-grade) rock phosphate (RP) containing ~30% P_2O_5 and sulfur from other countries which involve a considerable amount of foreign exchange (Biswas and Narayanasamy 2006). Furthermore, P is receiving more attention as a nonrenewable resource, and, based on current rate of use, it is expected that the world's known reserves of high-quality RP will be depleted within the current century (Isherwood 2000). Beyond this time, the production of phosphate-based fertilizers will require the processing of lower-grade RP at significantly higher cost. This imposes heavy burden on Govt. exchequer. Therefore, research priorities have been directed toward finding alternative sources of P fertilizers for crop production. Alternatively, the direct use of RP as fertilizers will require an effective means for solubilization (Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015, 2016b; Ahmad et al. 2016). These issues are particularly relevant to soils throughout developing countries and on acidic soils in tropical and subtropical regions (Bolan et al. 1990). In view of environmental concerns and current developments in sustainability, research efforts are concentrated on elaboration of agro-techniques that involve the use of less expensive, though less bioavailable, sources of plant nutrients such as RP. Several alternative approaches have been used or proposed to increase P availability in RP including (1) incorporation of additives into RP, (2) partial acidulation of RP, (3) compaction of RP with water-soluble P fertilizers, and (4) microbial methods. Composting manure and/or biological waste with RP has been shown to enhance the dissolution of the RP (Singh and Amberger 1998) and is practiced widely as a low-input technology to improve the fertilizer value of manure (Biswas et al. 2009; Moharana and Biswas 2016). For these reasons, various strategies for RP solubilization have been recently proposed with an increasing emphasis on application of PSMs (Rodriguez and Fraga 1999; Vassilev et al. 2001; Whitelaw 2000). Recently, the efficient PSMs have attracted the attention of agriculturists as inoculums to improve the solubilization of RP (Biswas et al. 2009; Meena and Biswas 2014). The availability of P from these low-grade resources could be improved through composting technology using agricultural wastes and crop residues. In India, ~600–700 Mt. of agricultural waste is available including ~272 Mt. of crop residues every year (Pathak et al. 2010). However, the rice straw is the major component of crop residues, a substantial portion of which is disposed from the field by burning in order to clean the field to sow the next crop. Burning of these crop residues is common practices in India, particularly in northern India as well as other developing countries. As a result decline in soil organic matter (SOM) levels, lowering of biological activity, and destroying soil structure are very common (Biswas 2011). This potent source of organic matter and nutrients, however, could be recycled back to agricultural field, if converted them into quality compost like enriched compost using low-grade RP for crop production as well as maintaining soil fertility (Meena et al. 2016a, b; Parewa et al. 2014; Prakash and Verma 2016; Priyadharsini and Muthukumar 2016; Kumar et al. 2016a, 2017; Jaiswal et al. 2016; Jha and Subramanian 2016). The purpose of this paper is to review recent developments in microbial solubilization of RP with emphasis on composting techniques that utilize farm wastes, aimed at the enhancement of the fertilizer value of the final products.

6.2 Rock Phosphate (RP) as Low-Cost P Source

6.2.1 Availability of Rock Phosphate (RP)

Worldwide demand of P is met essentially from RP, a finite mineral resource, which is the only economic source for production of P fertilizers like single super phosphate, diammonium phosphate, nitro phosphates, etc. in the earth. ~150 minerals containing >1% P_2O_5 occur in nature, but minerals belonging to two groups, namely, "apatites" and "aluminous phosphates," are of commercial importance. According to available data (van Kauwenbergh 2010), the recoverable global phosphate reserves of all types and grades are estimated to be ~60,000 Mt. The commercial RP occurs in nature as deposits of apatites (P-bearing minerals) along with other accessory minerals such as quartz, silicates, carbonates, sulfates, sesquioxides, etc. Four types of RP minerals are carbonate apatite [$3Ca_3(PO_4)_2.CaCO_3$], fluorapatite [$3Ca_3(PO_4)_2.CaF_2$], hydroxyapatite [$3Ca_3(PO_4)_2.Ca(OH)_2$], and sulpho apatite [$3Ca_3(PO_4)_2.CaSO_4$]. The apatites of igneous and metamorphic origin are generally regarded as less reactive because of their well-developed crystalline form. However, the apatites of sedimentary rock deposits are soft minerals possessing microcrystalline structure and are of major commercial importance for direct application in the soil (Narayanasamy and Biswas 1998). There is a general consensus that the quality and accessibility of RP reserves are decreasing, while the demand for additional P and low P-use efficiency (PUE) created a doomsday scenario worldwide. The estimated lifetime of reserves of RP ranged from ~60 to 400 years (van Kauwenbergh 2010). In another estimate, it is reported that the world RP reserves may be exhausted within next 70–175 years (Cordell et al. 2009). The deposits of RP have been discovered in many parts of the world. However, most of world production of RP is confined to some countries, namely, Morocco and other African countries, the USA, Near East, and China. Meanwhile, the ~90% of the total RP that is mined at present is used for fertilizers production (Cordell et al. 2009). The classification of reserves of indigenous RP as done by Indian Bureau of Mines and the purpose for which each grade can be used is given in Table 6.1.

Table 6.1 Classification of indigenous rock phosphate (RP) found in India

Grade	P_2O_5 (%)	Reserve (Mt)	Generalized remarks
High	>30	15.27	Could be considered for wet process production of fertilizers
Medium	25–30	18.95	Could be considered mainly for partially acidulated RP and for processed phosphates after less benefication
Low	11–25	55.22	About 20% P_2O_5 grade and relatively more reactive material may be considered for partially acidulated RP production and others for direct application
Unclassified		170.04	
Total		259.48	

The total phosphate resource in India is estimated to be ~260 Mt., and the recoverable phosphate reserves are of the order of ~142 Mt. (FAI 2013). Most of the deposits of Indian RPs are low-grade and unsuitable for manufacturing of commercial P fertilizers because of their low P content and low reactivity (Narayanasamy and Biswas 1998). Although there have been many developments in the field of P-fertilizer production in the recent years, ammonium phosphates, namely, diammonium phosphate (DAP) and monoammonium phosphate (MAP), dominate worldwide (in terms of P-fertilizer consumption) followed by single superphosphate (SSP) and triple superphosphate (TSP). For manufacturing P fertilizers, India imports large amounts of high-grade RP (>30% P_2O_5) from the countries like Egypt, Peru, Jordan, and Morocco. It is estimated that the consumption of P_2O_5 was ~8 Mt. in India, while the total production was in the order of only 4.36 Mt. during the year 2011–2012 (FAI 2013). In order to bridge the wide gap between production and consumption, enhancing use efficiency of fertilizer P is highly desirable (Meena et al. 2015a, b, f, 2016c; Raghavendra et al. 2016; Zahedi 2016; Rawat et al. 2016; Yasin et al. 2016; Saha et al. 2016a; Das and Pradhan 2016; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016). Under such circumstances, utilization of the large reserves of low-grade RP through improved fertilizer production technology, use of non-apatite or nonconventional source of RP, and maximization of applied P recovery through development of new fertilizer materials of higher P-use efficiency are of prime importance across the globe and India in particular.

6.2.2 Properties of Rock Phosphate (RP)

Rate of dissolution of RP is determined by its chemical composition which includes apatite lattice composition, the type of accessory minerals and particle size. It has been well established that increasing substitution of CO_3^{2-} for PO_4^{3-} in the lattice structure increases the solubility of carbonate apatites. This occurs due to decreased a-dimension of the unit cell and crystal instability on increased incorporation of planar CO_3^{2-} and F^- for PO_4^{3-} tetrahedral (Basak and Biswas 2016). As the RPs are relatively insoluble materials, their geometric surface area is having an important bearing on their rate of dissolution in soil. Bolan and Hedley (1990) reported that the finer particles of RP (100 mesh) resulted in higher values of dissolution than relatively coarser particles (60 mesh). This might be due to the fact that the finer the particle size, the greater the degree of contact between RP and soil and, therefore, greater the rate of dissolution. Solvents such as citric acid and formic acid are used in conjunction with X-ray diffraction, infrared spectroscopy, or electron microscopy to evaluate solubility (Chien and Menon 1995). Different sources of RP can thus be compared using relative solubility indexes. Hammond et al. (1986) ranked the relative agronomic potential of RP sources from throughout the world based on ranges of percent soluble P. Citrate-soluble P fraction is correlated to plant P uptake during the cropping season (Biswas and Narayanasamy 2006).

6.2.3 Soil Properties Affecting Dissolution of Rock Phosphate (RP)

Soil properties can affect the suitability of RP for direct application. Figure 6.1 shows the factors influencing the dissolution of RP in soil. Rock phosphates are less effective in soils with high Ca content and low SOM, resulting in decreased dissolution (Bolan et al. 1990). The low-grade RP is considered as a suitable alternative to costly water-soluble P fertilizer in acid soils. However, the feasibility or the agronomic effectiveness of low-grade RPs for direct use as source of P in neutral to alkaline soils is less effective than that of SSP or TSP (Narayanasamy and Biswas 1998). The efficiency of RP also depends on its reaction and retention in the soil and on the chemical properties and type of soil to which it is applied; however, Anderson et al. (1985) reported that no single soil characteristic has a consistent and predominant effect on P release. Studies indicated that the amount of RP-P dissolved decreases either exponentially or linearly with the increasing soil pH (Rajan et al. 1991; Meena et al. 2017). Following the law of mass action, the dissolution of RPs is favored as long as Ca concentration in the soil solution is maintained at a lower level. The rate of dissolution of RP is highly sensitive to Ca^{2+} activity in the soil solution. A linear relationship between the log of Ca^{2+} activity and log of P in soil solution has been reported by Robinson and Syers (1990). Capacity of the soil to

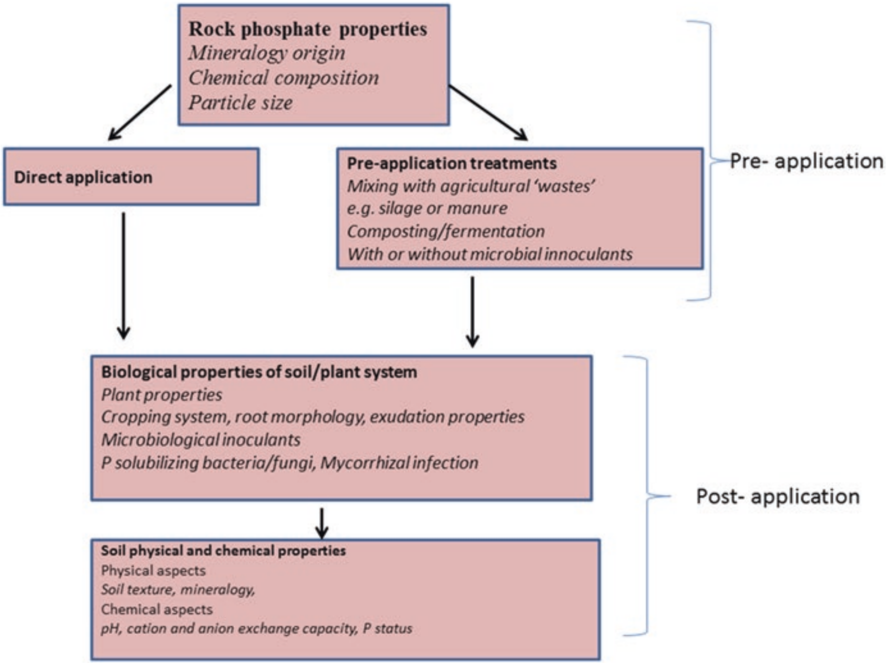

Fig. 6.1 Schematic plan of the factors significantly influencing the dissolution, reactivity, and uptake of P derived from RP. A major distinction is made between those factors which are likely to apply to either pre- or post-application situations

retain P and soil moisture is also important soil parameters affecting RP dissolution. Dissolution of RP is considerably enhanced by the soil if it remains sufficiently wet to allow the dissolution products to be transported away from the surface of the RP particles (Yadav and Sidhu 2016; Meena et al. 2014a, 2016d; Saha et al. 2016b; Verma et al. 2014, 2015b; Bahadur et al. 2016b).

The water retained at field capacity is sufficient to support near potential maximum dissolution. The positive influence of organic matter on RP dissolution has also been recognized which is due to its high cation exchange capacity (CEC) and organic acids produced as a result of microbial and chemical transformation of organic debris (Biswas and Narayanasamy 2006). The CEC of organic matter which exceeds even 200 cmol kg^{-1} soils enhances RP dissolution by increasing the Ca-buffering capacity of the soil (Helling et al. 1964). Numerous organic acids (e.g., oxalic, citric, tartaric, gluconic) have been reported to be produced in the soil as a result of microbial and chemical transformation of organic debris. Thus, dissolution of RP in soil, according to law of mass action, could be favored under conditions of low (a) soil pH, (b) soil exchangeable Ca, and (c) P concentration in soil solution. The above reaction has led to the view that soil acidity or proton (H^+) supply is the single most important factor influencing the dissolution of a RP in soil. However, some studies indicate that the slow dissolution of RP in soils with high P-sorption capacities actually improves its efficiency because it is taken up as it dissolves, rather than being transformed into unavailable forms as can occur with excess P from soluble sources (Medhi and De Datta 1997). Slow dissolution rates may also be an advantage over soluble fertilizers in soils with very low P-fixing capabilities, as P is less likely to be lost to leaching (Sanyal and De Datta 1991). High soil organic matter can promote dissolution of RP by forming complexes with Ca^{2+} ions (Basak and Biswas 2016).

The dissolution reaction of fluorapatite RP in acid soils is as follows:

$$\mathrm{Ca_{10}\left(PO_4\right)_6 F_2 + 12H^+ = 6H_2PO_4^- + 10Ca^{2+} + 2F^-}$$

Related reactions include:

$$\begin{aligned}
&\mathrm{H_2PO_4^- + HO \quad soil \rightarrow H_2PO_4 \quad soil + OH^-}\\
&\mathrm{F^- + HO \quad soil \rightarrow F \quad soil + OH^-}\\
&\mathrm{2F^- + Ca^{2+} \rightarrow CaF_2}\ \text{(Sanyal and De Datta 1991; Hong Qing et al. 1997)}
\end{aligned}$$

As RP releases P through dissolution, it is largely held in insoluble forms dominated by Ca-P. Forms of Fe-P and Al-P represent considerably smaller fractions. Concentration of calcium in solution has been shown to be inversely related to dissolution of RP (Wilson and Ellis 1984). As per the findings of Mutuo et al. (1999) studied the release of P from TSP and RP and found that while TSP samples had considerably more extractable P at 1 week, the levels were close to equal at 7 months and were equal at 18 months. Extractable P levels increased slightly in the RP samples between 1 week and 7 months while dropping by more than half in the TSP samples in the same time period.

6.3 Solubilization of RP Through Composting Technology

6.3.1 Raw Materials

In India, it is estimated that ~500–550 Mt. of crop residues are produced per year (MNRE 2009; MoA 2012). There is a wide variability in the generation of crop residues and their use across different regions of the country depending on the crops grown, cropping intensity, and productivity of these crops. These crop residues are used as animal feed, for soil mulching, for thatching of rural homes, as well as a source of domestic and industrial fuel. At present three quarters of the crop residues are disposed by burning in the field, particularly in northern states of India primarily to clear the leftover straw and stubbles after the harvest (Biswas 2011). Nonavailability of labor, high cost of residue removal from the field, and increasing use of combines in harvesting the crops are main reasons behind burning of crop residues in the fields. As a result of burning, considerable amounts of both organic carbon and nutrients are lost. Burning of crop residues also causes environmental pollution which is hazardous to human health and produces greenhouse gases causing global warming due to emissions of toxic and greenhouse gases like CO, CO_2, and CH_4.

Recently, Pathak et al. (2010) have estimated that ~93 Mt. of crop residues are burnt on-farm in the country. Therefore, appropriate management of crop residues assumes a great significance. One of the alternative options of utilization of these large quantities of nutrient-rich crop residues is by converting them into value-added product like compost. The nutrient values of ordinary compost in terms of major nutrients (N, P and K) are very low because of low concentration. The demerits of these materials could be overcome by introducing some low-grade minerals like RP. The low-grade RPs are available in Jhabua (Jhabua RP) from Madhya Pradesh State Mining Corporation Ltd., Meghnagar, Madhya Pradesh; Mussoorie (Mussoorie RP) from Pyrites, Phosphate and Chemicals Ltd., Dehradun, Uttaranchal; Purulia (Purulia RP) from West Bengal Mineral Development and Trading Corporation Ltd., Purulia, West Bengal; and Udaipur (Udaipur RP) from Rajasthan State Mines and Minerals Ltd., Udaipur, Rajasthan. All the RPs are of sedimentary origin and categorized as low grade because of their low P content. The chemical constituents of the RPs (100-mesh size particle) were reported by Biswas and Narayanasamy (2006) and given in Table 6.2.

6.3.2 Phosphorus-Solubilizing Microorganisms (PSMs)

Naturally occurring rhizospheric PSMs date back to 1903 (Khan and Zaidi 2007). Bacteria/rhizobacteria are more effective in P solubilization than fungi. Among the whole microbial population in soil, phosphorus-solubilizing bacteria (PSB) constitute 1–50%, while phosphorus-solubilizing fungi (PSF) are only 0.1–0.5% in P-solubilization potential (Chen et al. 2006). These efficient microorganisms

Table 6.2 Properties of the RPs found in India

Properties	Jhabua RP	Mussoorie RP	Purulia RP	Udaipur RP
Total P (%)	7.25 ± 0.09	8.25 ± 0.05	9.87 ± 0.18	8.62 ± 0.08
WSP (%)	0.003 ± 0.01	0.001 ± 0.0	0.004 ± 0.001	0.002 ± 0.001
CSP (%)	1.10 ± 0.06	1.19 ± 0.04	1.25 ± 0.05	1.26 ± 0.06
CISP (%)	6.15 ± 0.09	7.06 ± 0.09	8.62 ± 0.10	7.36 ± 0.06
K (%)	0.13 ± 0.02	0.39 ± 0.01	0.36 ± 0.01	0.19 ± 0.02
Ca (%)	9.0 ± 1.20	12.0 ± 0.50	7.8 ± 0.20	6.4 ± 0.30
Mg (%)	3.48 ± 0.13	5.88 ± 0.23	5.64 ± 0.14	5.64 ± 0.14
S (%)	0.40 ± 0.05	0.52 ± 0.07	0.31 ± 0.06	0.39 ± 0.03
Fe (mg kg^{-1})	5870 ± 25	7020 ± 40	8720 ± 50	6850 ± 35
Mn (mg kg^{-1})	904 ± 5	1200 ± 25	3680 ± 21	2764 ± 16
Zn (mg kg^{-1})	213 ± 8	486 ± 11	631 ± 12	261 ± 5
Cu (mg kg^{-1})	40 ± 3	70 ± 4	120 ± 5	70 ± 4

Adapted from Biswas and Narayanasamy (2006)

Table 6.3 Biodiversity of phosphate-solubilizing microorganisms (PSMs)

Bacteria	*Alcaligenes* sp., *Aerobacter aerogenes*, *Achromobacter* sp., *Actinomadura oligospora*, *Agrobacterium sp.*, *Azospirillum brasilense*, *Bacillus* sp., *Bacillus circulans*, *B. cereus*, *B. fusiformis*, *B. pumilus*, *B. megaterium*, *B. mycoides*, *B. polymyxa*, *B. coagulans*, *B. chitinolyticus*, *B. subtilis*, *Bradyrhizobium* sp., *Brevibacterium* sp., *Citrobacter* sp., *Pseudomonas* sp., *P. putida*, *P. striata*, *P. fluorescens*, *P. calcis*, *Flavobacterium* sp., *Nitrosomonas* sp., *Erwinia* sp., *Micrococcus* sp., *Escherichia intermedia*, *Enterobacter asburiae*, *Serratia phosphoticum*, *Nitrobacter* sp., *Thiobacillus ferrooxidans*, *T. thiooxidans*, *Rhizobium meliloti*, *Xanthomonas* sp.
Fungi	*Aspergillus awamori*, *A. niger*, *A. tereus*, *A. flavus*, *A. nidulans*, *A. foetidus*, *A. wentii. Fusarium oxysporum*, *Alternaria tenuis*, *Achrothcium* sp., *Penicillium digitatum*, *P. lilacinium*, *P. balaji*, *P. funiculosum*, *Cephalosporium* sp., *Cladosporium* sp., *Curvularia lunata*, *Cunninghamella*, *Candida* sp., *Chaetomium globosum*, *Humicola insolens*, *Humicola lanuginosa*, *Helminthosporium* sp., *Paecilomyces fusisporous*, *Pythium* sp., *Phoma* sp., *Populospora mytilina*, *Myrothecium roridum*, *Mortierella* sp., *Micromonospora* sp., *Oidiodendron* sp., *Rhizoctonia solani*, *Rhizopus* sp., *Mucor* sp., *Trichoderma viride*, *Torula thermophila*, *Schwanniomyces occidentalis*, *Sclerotium rolfsii*
Actinomycetes	*Actinomyces*, *Streptomyces*
Cyanobacteria	*Anabaena* sp., *Calothrix braunii*, *Nostoc* sp., *Scytonema* sp.
VAM	*Glomus fasciculatum*

involved in P-acquisition include mycorrhizal fungi and PSMs. A nematofungus *Arthrobotrys oligospora* also has the ability to solubilize the phosphate rocks (Duponnois et al. 2006). Population of PSMs depends on different soil properties (physical and chemical properties, organic matter, and P content) and cultural activities. Larger populations of PSB are found in agricultural and rangeland soils. The biodiversity of PSMs is given in Table 6.3.

6.3.2.1 Bacteria

It has been known for a long time that significant variation in the ability to solubilize P in soil exists within the bacterial community. Those that are known to enhance P availability include species of the common soil bacteria *Pseudomonas*, *Azotobacter*, *Burkholderia*, *Bacillus*, and *Rhizobium*. Among the soil bacterial communities, ectorhizospheric strains from *Pseudomonas* and *Bacilli* and endosymbiotic rhizobia have been described as effective P solubilizers (Igual et al. 2001). Some effective rhizobacterial strains from bacterial genera *Pseudomonas*, *Bacillus*, *Rhizobium*, and *Enterobacter* along with *Penicillium* and *Aspergillus* fungi are the most powerful P solubilizers (Whitelaw 2000). *Bacillus megaterium*, *B. circulans*, *B. subtilis*, *B. polymyxa*, *B. sircalmous*, and *Pseudomonas striata* could be referred as the most important strains (Kucey et al. 1989). The recent isolation of a super solubilizer (*Serratia marcescens*) has also suggested that selected bacteria could be used to develop environmentally friendly processes for fertilizer production (Ben Farhat et al. 2009). Recent work on *P. fluorescens* strains isolated from a range of agricultural fields has suggested that significant variation also exists within a single bacterial species (Browne et al. 2009; Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b, 2015e, 2016e; Shrivastava et al. 2016; Teotia et al. 2016). A study by Hariprasad et al. (2009) has also indicated that the selection for one bacterial trait may not always be the best use of inoculation technology.

6.3.2.2 Fungi

A range of non-mycorrhizal soil fungi have been screened and selected for their P-solubilizing capacity. Of those identified, many are commonly found in agricultural soils such as *Penicillium* sp., *Mucor* sp., and *Aspergillus* sp., which has been shown to increase plant growth by 5–20% after inoculation (Dwivedi et al. 2004; Babana and Antoun 2006; Gunes et al. 2009). In addition, a range of *Trichoderma* sp. have also been identified and found to stimulate plant growth both in the laboratory and field (Rudresh et al. 2005; Meena and Biswas 2014). As with many ectomycorrhizal fungi, P-solubilizing non-mycorrhizal fungi (e.g., *Emericella rugulosa*, *Penicillium* sp.) appear to employ three strategies for mobilizing soil P, namely, acidification of the soil, the release of organic acid anions (e.g., citrate, oxalate, gluconate), and the release of acid and alkaline phosphatases and phytase (Yadav and Tarafdar 2007; Xiao et al. 2009).

6.3.2.3 Actinomycetes

The role of actinomycetes in P solubilization has attracted interest in recent years because these groups of soil organisms are not only capable of surviving in extreme environments (e.g., drought, fire, etc.) but also possess other potential benefits (e.g., production of antibiotics, phytohormone-like compounds, etc.) that could simultaneously benefit plant growth. Numerous P-solubilizing actinomycete species have been isolated from the rhizosphere (Barreto et al. 2008), and their presence in soil has been linked to enhanced efficiency of P use. Further, re-inoculation of soil with isolates selected for P solubilization has been shown to stimulate plant growth when supplied with phosphate rock (Hamdali et al. 2008).

Overall, however, the taxonomic groups and mechanisms of P solubilization within the actinomycetes remain poorly elucidated. A study by Hamdali et al. (2008) has indicted that ~20% of actinomycetes can solubilize P, including those in the common genera *Streptomyces* and *Micromonospora*. In contrast to most fungi, most of the P-solubilizing actinomycetes identified to date do not appear to acidify the external medium. However, they do release large quantities of organic acid anions (e.g., citrate, formiate, lactate, malate, succinate), which are implicated in the P dissolution process and possibly other P dissolution-promoting organic substances (Hoberg et al. 2005; Hamdali et al. 2010). After uptake, the P is stored in polyphosphate within the mycelium (Hamdali et al. 2010). It is suggested that actinomycetes may enhance P availability through the release of phosphatases; however, the significance of this in soil remains unknown (Sahu et al. 2007). The thermo-tolerant properties of actinomycetes enhance P availability during the composting of organic wastes (Chang and Yang 2009).

6.4 Methodology of Rock Phosphate (RP)-Enriched Composting

The RP-enriched compost can be prepared by trench or pit method as per the procedure outlined earlier by Biswas and Narayanasamy (2006). General steps of RP-enriched composting are shown in Fig. 6.2. Trench or pit is filled layer-wise (5–6 layers). Biodegradable organic material crop residues, farm wastes, animal feed wastes, and tree leaves are spread on the floor of the trench (~20 cm thick layer). Crop residues were soaked in water for 24 h, and RPs were mixed thoroughly with it. To enhance activity of the natural and added microflora, a uniform dose of urea solution @ 0.25 kg N per 100 kg of crop residues was sprayed. Fresh cow dung @ 5 kg per 100 kg of crop residues was made into slurry and sprinkled to each treatment as natural inoculums. A uniform dose of *Trichoderma viride* was inoculated @ 50 g per 100 kg of crop residues (on fresh mycelia weight basis) to hasten the composting.

The whole composting mass was then mixed thoroughly. The surface of the composting mass was plastered with slurry prepared from soil and fresh cow dung. The pots were covered with polyethylene sheets to avoid excessive wetting by rain. Turning was done at monthly intervals to provide adequate aeration. Moisture content (~50–60% of field capacity) was maintained throughout the composting period. *A. awamori* was introduced @ 50 g per 100 kg of crop residues (on fresh mycelia weight basis) 1 month after the starting of composting in order to avoid thermophilic condition (~55–65 °C temperature) prevailing during the first month. Composting was continued till the C/N ratio reached a level between 10:1 and 15:1 (after 130 days of composting).

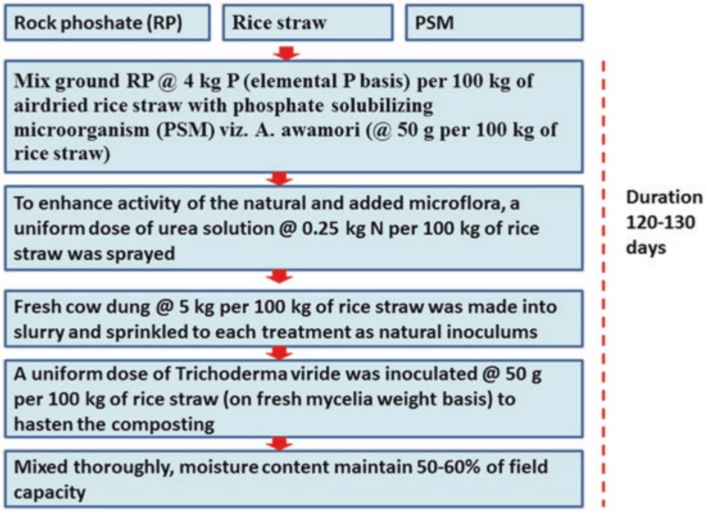

Fig. 6.2 Methodology of RP-enriched compost preparation. (Adapted from Biswas and Narayanasamy 2006)

6.5 Mechanism of Rock Phosphate (RP) Dissolution During Composting

6.5.1 Microbial Decomposition of Crop Residues

The organic substrate, bulking agents, and the amendments used in composting are mostly derived from plant material. Lignocellulose, the composite of the predominant polymers of vascular plant biomass, is composed of polysaccharides like cellulose and hemicellulose and the phenolic polymer lignin. Hence, the capacity of microorganisms to assimilate organic matter depends on their ability to produce the enzymes needed for degradation of the substrate components, i.e., cellulose, hemicelluloses, and lignin (Gaind et al. 2009). The more complex the substrate, the more extensive and comprehensive is the enzyme system required. Through the synergistic action of microorganisms, complex organic compounds are degraded to smaller molecules, which can then be utilized by microbial cells. Many efficient organisms, viz., fungi, bacteria, and invertebrates like earthworms, play an important role during composting. Hundreds of species of fungi are able to degrade lignocellulose. There are mainly three types of fungi living on dead wood that preferentially degrade one or more wood components, viz., soft rot fungi, brown rot fungi, and white rot fungi. Soft rot fungi (*Ascomycetes* and *Fungi imperfecti*) can efficiently decompose cellulose but are reported to degrade lignin slowly and incompletely. The brown rot fungi (*Basidiomycetes*) generally exhibit preference for the carbohydrate components of wood with activity toward lignin largely confined to demethylation. White rot fungi are capable of degrading both lignin and cellulose. The ~80%

of the fungal population belongs to the genera *Aspergillus* and *Penicillium.* However, the most extensively studied lignocellulolytic fungi are *Trichoderma* and *Phanerochaete.* Under appropriate conditions bacteria degrade cellulose, and hence many bacterial strains are known to solubilize and modify the lignocellulosic structures extensively. But their ability to mineralize lignin is limited.

Cytophaga and *Sporocytophaga* are dominant cellulolytic microorganisms in all types of composting processes. *Cellulomonas* and *Cytophaga* are the aerobic mesophilic bacteria able to degrade cellulose. More than one-half of the *Bacillus* sp. examined to date produces extracellular cellulases. Mesophilic aerobic and anaerobic forms of *Bacillus*, *B. subtilis*, *B. polymyxa*, *B. licheniformis*, *B. pumilus*, *B. brevis*, *B. firmus*, *B. circulans*, *B. megaterium*, and *B. cereus* are known to be cellulose and hemicellulose degraders. Actinomycetes isolated from soil and related substances show primary biodegradative activity, secreting a range of extracellular enzymes and exhibiting the capacity to metabolize recalcitrant molecules. Composting heavily relies on such prolific actinomycete activity. Actinomycetes follow a characteristic pattern of lignocellulose decomposition with the release of lignin-rich, water-soluble fragments that are slowly metabolized thereafter or can be recovered as value-added products (Saritha et al. 2013).

6.5.2 Phosphorus Mobilization by Microorganisms

These efficient microorganisms are an integral component of the P cycle and are important for the transfer of P between different pools of P. In particular, microorganisms are effective in releasing P from inorganic and organic pools of P through solubilization and mineralization (Ghani et al. 1994; Hilda and Fraga 2000). The process-mediated mechanisms include the following: (1) through stimulation of metabolic processes that are effective in directly solubilizing and mineralizing P from poorly available forms of inorganic and organic P and (2) by displacement of sorption equilibria that results in increased net transfer of phosphate ions into solution or an increase in the mobility of organic forms of P. These processes include the excretion of hydrogen ions, the release of organic anions, and the production of phosphatase enzymes that are able to hydrolyze inorganic and organic P. In composting, lignocellulosic materials do not give good yields of organic acids without some pretreatment because of the slow rate of hydrolysis and low level of available sugars (Velazquez et al. 2016; Meena et al. 2015c; Sindhu et al. 2016; Bahadur et al. 2016a; Masood and Bano 2016).

However, the microorganisms having lignocellulolytic activity and particularly *P. chrysosporium* are characterized by its high lignolytic enzyme activity. Therefore, crop residues were mineralized successfully in fermentation systems by *A. niger* and *P. chrysosporium*. It is important that composting with *A. niger*, a high value of acidity (mainly citric acid) was produced. Recently, *P. chrysosporium* was reported to produce low-molecular-weight organic acids thus lowering pH outside of the fungal hyphae (Makela et al. 2002). In addition, some metal-chelating compounds released by white rot fungi, including *P. chrysosporium*, have been reported to take part in wood mineralization (Milagres et al. 2002). The overall effect of the extracellular compounds with their properties of chelators is the most likely reason for some RP solubilization by *P. chrysosporium* although other mechanisms could be also involved bearing in mind that the abovementioned processes occur in the early stage of fungal development and the amount of the released compounds is low. However, this work demonstrated that, although *P. chrysosporium* is not a typical organic acid producer, it can be used efficiently in RP solubilization providing a percentage of soluble P at least comparable to that obtained by *A. niger*. Some bacterial species have mineralization and solubilization potential for organic and inorganic phosphorus, respectively (Hilda and Fraga 2000; Khiari and Parent 2005). Phosphorus-solubilizing activity is determined by the ability of microbes to release metabolites such as organic acids, which through their hydroxyl and carboxyl groups chelate the cation bound to phosphate, the latter being converted to soluble forms (Sagoe et al. 1998). General sketch of P solubilization by PSM in compost is shown in Fig. 6.3.

Phosphorus solubilization is carried out by a large number of saprophytic bacteria and fungi acting on sparingly soluble RPs, mainly by chelation-mediated mechanisms (Whitelaw 2000). Important PSM, their ecological niches and organic acids produced are given in Table 6.4. The PSB dissolve the RP-P through production of low-molecular-weight organic acids mainly gluconic and ketogluconic acids (Deubel et al. 2000), in addition to lowering the pH of compost. The pH of compost is lowered through biotical production of proton/bicarbonate release (anion/cation balance) and gaseous (O_2/CO_2) exchanges. Inorganic acids, e.g., hydrochloric acid, can also solubilize phosphate, but they are less effective compared to organic acids at the same pH (Kim et al. 1997; Singh and Amberger 1998).

6.5.3 Forms of P Present in Rock Phosphate (RP)-Enriched Compost

There has been little direct study on the composition of P that had been solubilized during composting. This is despite the potential importance that chemical form might have upon subsequent bioavailability and reactivity within soil. It could be postulated that a wide range of P forms might be produced, from simple orthophosphate ions to polyphosphates and a wide range of organic P-containing compounds (Table 6.5). Reddy (2007) who applied low-grade phosphate rock to the litter of soybean showed that ~71–92% of the total solubilized P was converted to organic P. While changes in C and N forms have been reported, evidence for changing forms of P during the compost period is more circumstantial. For example, Biswas et al. (2009) described some changes in P during decomposition.

An increase in total P content over time was proportional to the loss in organic matter during decomposition. Water-soluble P significantly increased when composting was done without RP, but decreased during composting with RP. Moharana and Biswas (2016) reported that the ordinary compost of different substrates con-

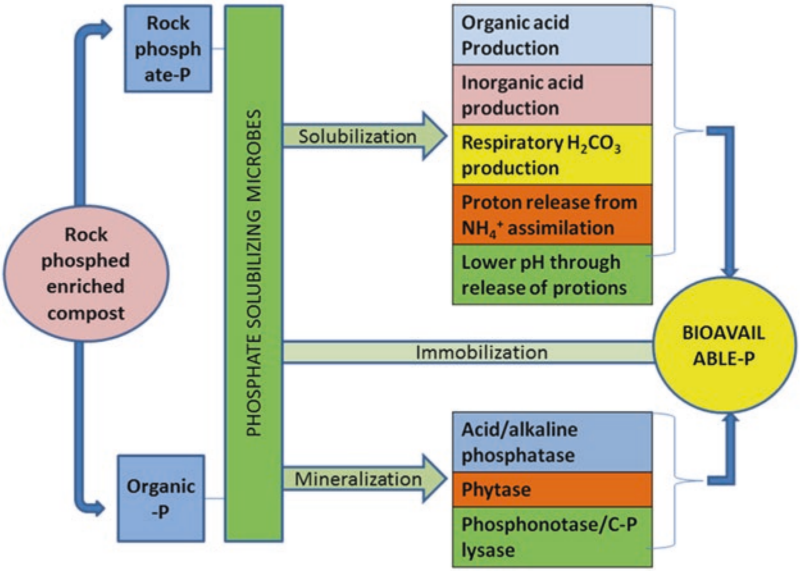

Fig. 6.3 Schematic representation of mechanism of compost-P solubilization/mineralization and immobilization by PSMs

Table 6.4 Important PSM, their ecological niches, and organic acids produced

Organism	Ecological niche	Predominant acids Produced	References
Aspergillus japonicus, A. foetidus	Indian RP	Oxalic, citric, gluconic, succinic, tartaric acid	Singal et al. (1994)
Aspergillus niger, *Penicillium* sp.	Soil	Citric, glycolic, succinic, gluconic, oxalic, lactic	Sperber (1958)
Aspergillus flavus, A. niger, Penicillium canescens	Stored wheat grains	Oxalic, citric, gluconic succinic	Maliha et al. (2004)
Aspergillus niger	Tropical and subtropical soil	Gluconic, oxalic	Chuang et al. (2007)
Aspergillus sp., *Penicillium* sp., *Chaetomium nigricolor*	Lateritic soil	Oxalic, succinic, citric, 2-ketogluconic	Banik and Dey (1983)
P. radicum	Rhizosphere of wheat roots	Gluconic	Whitelaw et al. (1999)
Bacillus megaterium, *Pseudomonas* sp., *Bacillus subtilis*	Rhizospheric soil	Lactic, malic	Taha et al. (1969)
Enterobacter agglomerans	Wheat rhizosphere	Oxalic, citric	Kim et al. (1997)
Penicillium rugulosum	Venezuelan phosphate rocks	Citric, gluconic acid	

Table 6.5 Summary of experiments involving the utilization of rocks phosphate by composting technology

RP	Compost substrate	Observation	References
Jhabua, Mussoorie, Purulia, Udaipur	Rice straw	RP along with *Aspergillus awamori* to crop residue during composting helped to enhance the mobilization of unavailable P in RP to available forms of P. Inoculation with *A. awamori* into the composting mass increased the content of total P (2.35%) as well as WSP (0.05% P) and CSP (0.85% P) significantly	Biswas and Narayanasamy (2006)
Udaipur	Rice straw, mustard stover and tree leaves	The Olsen-P content increased up to 90 days of composting and thereafter, decreased till the end of 120 days in all the composts, indicating that 90 days of composting is optimum for plant use as far as its availability of phosphate is concerned	Moharana et al. (2015)
Udaipur	Rice straw, wheat straw, chickpea stover, mustard stover and tree leaves	Highest CSP was found in the RP enriched compost of rice straw (1.53%), followed by wheat straw (1.35%), chickpea stover (1.27%), mustard stover (1.16%), and tree leaves (0.89%)	Moharana and Biswas (2016)
Jhabua, Hirapur	Soybean leaf litter	The decomposition of soybean leaf litter has the potential to solubilize P from insoluble low-grade RPs. It mobilized P to the extent of 20.2% of total P within a period of 2 months	Reddy (2007)
Lalitpur	Post-methanation bio-sludge	A laboratory study revealed that 1-month incubation was long enough to produce good quality organic P fertilizers having higher water-soluble P, lower C/P ratio, higher population of phosphate-solubilizing microorganisms, and higher phosphatase activity in comparison to biogas sludge	Shrivastava et al. (2011)
Togo	Poultry manure	Co-application of RP with manure could be a low cost means of improving the solubility of natural RP and improve their agronomic effectiveness	Agyin-Birikorang et al. (2007)

tained lower citrate-soluble P (CSP) values than RP-enriched composts. Mobilization of RP-P by different crop residues during composting is given in Fig. 6.4. This may be attributed due to contribution of more P from RP in enriched composts. During the decomposition of organic residues, the microbial population increases and hence there is more demand for P.

These microorganisms can assimilate the labile form of phosphates and release it when they die. Moreover, the organic acids released during decomposition can increase the H^+ activity and make the P in RP more soluble. It was also found that

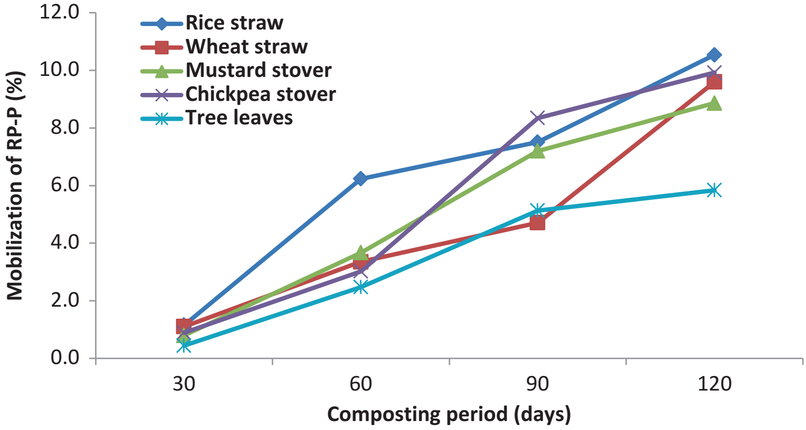

Fig. 6.4 Mobilization of RP-P by different crop residues during composting. (Adapted from Moharana and Biswas 2016)

RP-enriched compost had more of the total P and CSP compared to ordinary composts. The P soluble in citric acid increased significantly during initial composting with RP, but after 60 days citric acid-soluble P decreased. Various possible reasons might explain this observation which include some form of precipitation/sorption reaction of soluble P with RP components (Singh et al. 1980), while Mishra et al. (1984) observed that initially there was an increase in soluble P, which later converted to di- and tricalcium phosphates that were citric acid-soluble when *Aspergillus awamori* was grown in a medium with RP as the only source of P. Table 6.6 described the fractionation of phosphorus in various RP-charged compost prepared using rice straw inoculated with and without *Aspergillus awamori* which was reported by Biswas and Narayanasamy (2002).

In vitro studies with *A. awamori* also revealed that after a certain period of incubation citric acid-soluble P also decreased and was converted into a citric acid-insoluble apatite form (Biswas and Narayanasamy 2006). Goenadi and Siswanto (2000) also reported an increase in citric acid-soluble, but not water-soluble P, during an incubation of Moroccan phosphate rock with *A. niger*. Biswas et al. (2009) and Moharana and Biswas (2016) reported that Olsen-P content increased up to 90 days of composting and, thereafter, decreased up to 120 days in all the composts using various substrates. This indicates that 90 days of composting is optimum for plant use as far as its availability of phosphate is concerned. Rashad et al. (2010) also prepared compost containig rice straw and soybean residue enriched with RP and found similar result. They confirmed that high-quality products were obtained from inoculated piles supplemented with buffalo manure inoculation which enhanced P availability from RP and enhanced its agronomic effectiveness for long period and offers a cheaper source of P fertilizer which increase the feasibility of the produced compost.

Table 6.6 Fractionation of phosphorus in various RP-charged composts prepared using rice straw inoculated with and without *Aspergillus awamori*

	Fractions of total phosphorus (% P on material basis)			
Treatment	Water-soluble P	Citrate-soluble P	Citrate-insoluble P	Organic P
Control (straw alone)	0.059 (15.9)	0.100 (26.8)	0.193 (51.7)	0.023 (6.2)
RP				
Jhabua	0.050 (3.9)	0.537 (42.4)	1.023 (80.7)	0.061 (4.8)
Mussoorie	0.025 (1.2)	0.713 (34.9)	1.158 (56.6)	0.142 (6.9)
Purulia	0.051 (1.8)	0.888 (31.6)	1.714 (61.1)	0.153 (5.5)
Udaipur	0.060 (2.6)	0.755 (33.1)	1.360 (59.6)	0.106 (4.7)
Charged rate				
2% elemental P	0.044 (2.6)	0.610 (35.4)	0.957 (55.6)	0.105 (6.1)
4% elemental P	0.049 (1.8)	0.836 (31.2)	1.670 (62.2)	0.126 (4.7)
Aspergillus awamori				
Without	0.044 (2.1)	0.600 (29.2)	1.304 (63.6)	0.101 (4.9)
With	0.049 (2.1)	0.846 (36.0)	1.324 (56.3)	0.130 (5.5)
CD ($p = 0.05$)				
Control vs. rest	SIG	SIG	SIG	SIG
RP	0.006	0.096	0.151	0.022
Levels of P (LP)	0.004	0.068	0.107	0.015
Aspergillus (PSM)	0.004	0.068	0.107	0.015

Adapted from Biswas and Narayanasamy (2002)
Note: Figures in parentheses indicate percent of total P

6.6 Factors Affecting Phosphorus Availability in Compost

The RP-enriched composts are organomineral fertilizers, prepared with RP and a range of organic materials. These composts have been shown to be an effective way to incorporate RP with various organic sources while improving soil properties. The mineralization of insoluble forms of P present in RP by organic acids released during decomposition of organic matter is the major advantage of preparation of enriched compost. Organic acids released from the various organic materials used in the composting help in breaking down the RP faster during the composting period by pushing the dissolution reaction to the forward direction. The availability of P also increases due to inoculation with PSM, which are also known to produce organic acids, namely, citric, oxalic, tartaric, acetic, lactic, gluconic, α-ketogluconic, etc. (Biswas and Narayanasamy 2006; Biswas et al. 2009). These acids are the source of H^+ ions that are considered the primary mechanisms attributed to solubilization of RP and make it available for plant. By providing a favorable environment for the growth and activities of the desired PSM in the system, better availability of nutrients in compost can be achieved. The abiotic and biotic factors playing key role in availability of nutrients are described next.

6.6.1 Nature of the Substrate

All kinds of organic residues amenable to the enzymatic activities of the microorganisms can be converted into compost if suitable conditions for biodegradation are provided. As the substrate becomes the only source of food to the microorganisms in compost, the nature of the substrate is the most basic controlling factor in any composting process. Most of the substrates are largely made up of polymers, which are insoluble in water. The extracellular enzymes released by the microbes hydrolyze these polymers into monomers, which then dissolve into water and enter the microbial cell where further decomposition takes place. The maturity of the compost also depends upon the nature of the substrate (Moharana and Biswas 2016). If the substrate is of plant origin, then the main constituents are the carbonaceous compounds such as cellulose, hemicellulose, and lignin. Nitrogenous constituents (proteins) occur to a lesser extent. Protein constituents, cellulose, and hemicellulose decompose easily. Although cellulosic substrates form good raw material for composting, lignin, being a complex aromatic polymer, is resistant to microbial attack to a considerable extent. However, it is not entirely recalcitrant to microbial decomposition; it undergoes slow degradation. The elevated temperature found during the thermophilic phase is essential for rapid degradation of lignocellulose (Tuomela et al. 2000).

A number of fungi, particularly those belonging to the basidiomycetes group, are well known for their ability to decompose lignin (Muthukumar and Mahadevan 1983). Bharadwaj (1995) noted that some bacteria and actinomycetes also possess lignolytic characteristics. In the beginning of the composting process, simple carbohydrates are converted to carbon dioxide and water, and degradation of nitrogenous compounds results mainly in the production of ammonia. In the later stages of composting, cellulose and hemicellulose are utilized by the compost microflora, and finally lignin is also subjected to degradation. Besides mineralization, organic matter is converted to humic substances.

The nature of the substrate plays a major role in the composting process as well as nutrient mineralization. Moharana and Biswas (2016) studied the amounts of release of P during the composting process of different substrates enriched with RP. It is evident that at the end of 120 days of composting, the highest WSP (0.104%) was recorded in rice straw compost, followed by chickpea stover (0.096%), wheat straw (0.091%), mustard stover (0.085%), and the lowest in tree leaves compost (0.073%) (Fig. 6.5). The WSP fraction at 120 days of composting varied from 3.5 to 4.5% of the total P in all the composts. The amount of CISP varied from 0.80 to 1.13% during different composting period which comprised of 32.7–54.0% of total P with different raw materials, the highest content being found in tree leaves and lowest in rice straw. At the end of composting, the highest CSP was found in the RP-enriched compost of rice straw (1.53%), followed by wheat straw (1.35%), chickpea stover (1.27%), mustard stover (1.16%), and tree leaves (0.89%).

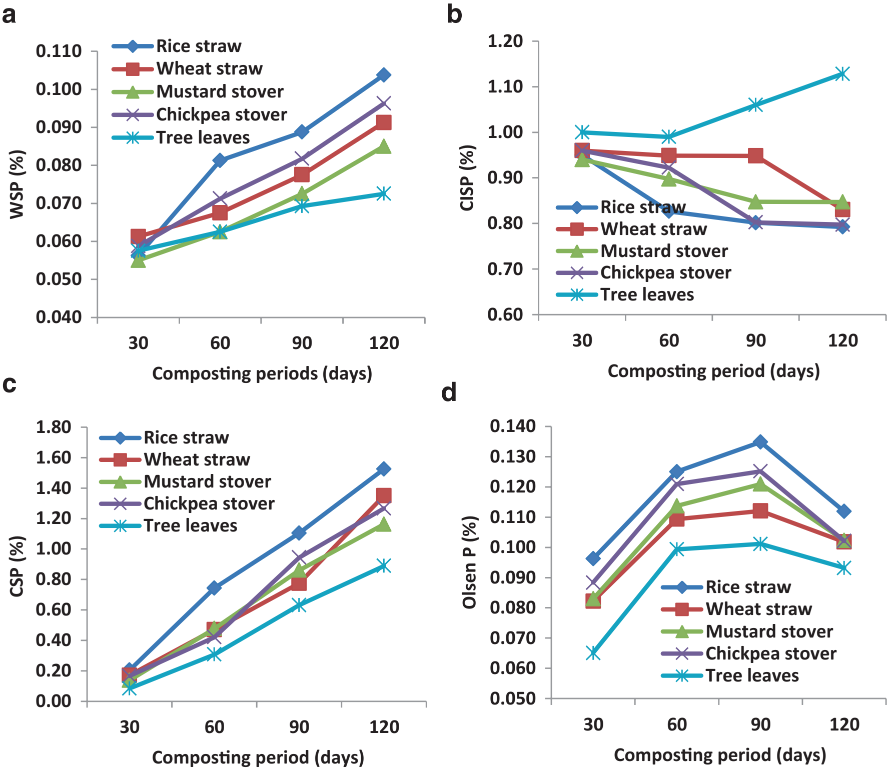

Fig. 6.5 Changes in P fractions as influenced by crop residues and RP during preparation of various composts. (Adapted from Moharana and Biswas 2016)

6.6.2 pH

The demonstration of pH changes acts as a potential P solubilization mechanism during composting. The drop in pH during the very early stages of composting is typically due to anaerobic conditions that are established in the waste materials prior to the commencement of the composting process, resulting in the formation of organic acids. As aerobic conditions are provided through forced aeration and turning of the composting mass, an increase in pH is observed as these organic acids are degraded. During the process, the mineralization of proteins, amino acids, and peptides leads to the release of ammonium or volatile ammonia which also contributes to the increase in pH. In studies conducted by Beck-Friis et al. (2001), it was observed that there was an initial decrease in pH and increase in concentrations of short-chain fatty acids, particularly lactic acid, during the start of the process.

These acids are produced as a result of degradation of the more easily degraded materials such as sugars, starch, and fats. The decrease in pH during the initial period of composting is expected because of the acids formed during the metabolism of readily available carbohydrates. After the initial stage, the pH is expected to rise, with evolution of free ammonia, and then stabilize or drop slightly again to near neutral pH as a result of humus formation with its pH buffering capacity at the termination of composting activity (Fogarty and Tuovinen 1991). The microbial P solubilization via acidification is well documented for several fungi and bacterial species (Gyaneshwar et al. 1999; Illmer and Schinner 1992; Ben Farhat et al. 2009) and is often found to be particularly successful when P is associated with Ca. The amount of protons released into the compost medium is often significantly influenced by N content. In general, a greater reduction in pH together with more solubilized P can be observed with NH_4^+ as the sole N source compared to NO_3^-, due to the extrusions of protons to nitrification for NH_4^+. In contrast, Reyes et al. (1999) found a decrease in P solubilization by *Penicillium rugulosum* from various P-bearing minerals (hydroxyapatite, $FePO_4$, $AlPO_4$) when higher concentrations of NH_4^+ were supplied. In light of this observation, decreasing pH during composting could be due to the production of organic acids and the incomplete oxidation of organic matter (Meena et al. 2013c, 2014b, 2015d; Singh et al. 2015, 2016).

These acids are able to dissolve the mineral phosphate and make it available for the plant. Organic acid anions can also solubilize RP through chelation reactions (Vassilev et al. 2006; Biswas et al. 2009; Meena and Biswas 2014) and by ligand exchange reactions through competition with phosphate anions that are adsorbed to crystalline $Fe(OH)_3$ and $Al(OH)_3$ surfaces (Trolove et al. 2003). Acid phosphatases and phytases secreted by the microorganisms also have an important role in P solubilization of RP to available form (Singh and Amberger 1998; Nishanth and Biswas 2008).

6.6.3 Electrical Conductivity

Generally, it is found that electrical conductivity (EC) increases during composting as volatile solids are degraded and the amount of water-soluble salts increases. The continuous decrease in the EC values from the starting of composting process might be attributed to the reduction of water-soluble substances and the volatilization of ammonia as well as precipitation of mineral salts during the process. The ultimate EC values of the matured composts had less than 1.5 dS m^{-1} which made the final product of composts acceptable as soil amendments (Rashad et al. 2010). The EC values increased with progress composting with RP, which might be due to an increase in salt concentration following degradation of organic matter and dissolution of RP (Hellal et al. 2012).

6.6.4 C/N and C/P Ratio

The C/N ratio represents very good index of maturity level for the organic substance, as it significantly affects the microbiological growth. The activities of the heterotrophic microorganisms involved in the process are dependent upon the N and C content. These microorganisms use C as the energy source, whereas the N is used for synthesis of proteins. During the oxidation reactions that involve the release of carbon dioxide (CO_2), the major portion of the C (approximately two-thirds) is used by the microorganisms as the energy source, while the remaining portion serves to form protoplasm of the cells, along with N, P, K, and other micronutrients.

Presence of excessive carbon slows the microbiological activities, whereas excessive N helps rapid decomposition, which, in turn, causes big N loss through volatilization. The C/N ratio narrows as the composting progresses because of the conversion of organic C to CO_2. Materials containing higher C/N ratios require more time for completion of the maturation phase. It can be noted that the C/N ratio of compost should not be too high, as an application of such composts can result in immobilization of available N, causing N deficiency in plants (Kostov et al. 1991). It had been documented that vinasse containing carbon and nitrogen in highly biodegradable forms helped in the proliferation of microbial population and would be the best compromise to optimize the composting process and obtain a high-quality product only when added in a moderate amount (Diaz et al. 2002). It has been stated that the C/N ratio of mature compost should ideally be ~10, but this is hardly ever achievable, due to the presence of recalcitrant organic compounds or materials that resist decomposition due to their physical or chemical properties (Jimenez and Garcia 1992). Some authors reported that a C/N ratio below 20 is indicative of an acceptable maturity (Poincelot 1974; Golueke 1981), with a ratio of 15 or even less being preferable. According to Sharma et al. (1997), good quality compost has a C/N ratio of the order of 15–20.

As per the findings of Gagnon and Simard (1999), it is indicated that materials with high P, humic substances, and low C/P ratio released more P. Moharana and Biswas (2016) reported that RP-enriched rice straw compost had high P content and relatively low C/P ratio. Due to its lower C/P ratio compared to other organic composts, it is also expected to decompose easily and contribute toward available pool of P. Garg and Bahl (2008) suggested that the increase in P may also be attributed to the release of appreciable quantities of CO_2 during organic matter decomposition and complexing of cations like Ca^{2+}, which is mainly responsible for fixation of P in alkaline, particularly calcareous soils. Badanur et al. (1990) reported that a significant increase in available P with crop residue and green manure incorporation may be due to the release of organic acids during decomposition which, in turn, helps in releasing P by solubilizing native P. Meena and Biswas (2014) ascribed it due to increased microbial biomass carbon by promoting microbial activities and enhanced activities of phosphatase and dehydrogenase responsible for P solubilization.

6.6.5 Enzyme Activities

Phosphatases describe a broad group of enzymes that catalyze the hydrolysis of both esters and anhydrides of H_3PO_4 (Tabatabai 1994). Its activities have been shown to be inhibited by increasing concentrations of orthophosphate (end-product) as well as other polyvalent anions (e.g., MoO_4^{2-}, AsO_4^{3-}) and high concentrations of several metals [Zn, Hg, Cu, Mn (II), Fe (II)]. Among the variety of phosphatase enzyme classes released by PSM, phosphomonoesterases are the most abundant and best studied. Depending on their pH optima, these enzymes are divided into acid and alkaline phosphomonoesterases, and both can be produced by PSM depending upon the external conditions (Kim et al. 1998; Jorquera et al. 2008). Typically, acid and alkaline phosphatases predominate in during composting. Enzyme assay showed much higher values in the first month, followed by a declining trend as the composting proceeded. Inoculated fungi and native flora degraded the resistant component of substrate when there was scarcity of available components (Gaind et al. 2009).

The decrease in dehydrogenase activity to low values toward end of composting indicates that there is no more active decomposition taking place and compost has reached maturity (Tiquia 2005). Godden et al. (1983) found that cellulase, invertase, and alkaline phosphatase activities increased during early stages of composting of cattle manure and remained constant during the thermophilic and curing period. On the contrary, Garcia et al. (1992) and Ayuso et al. (1996) observed that the activities of urease, protease, and phosphatase decrease during sewage sludge composting.

6.6.6 Moisture

Moisture is one of the composting variables that affect microbial activities, as it provides a medium for the dissolution of RP. Moisture content of ~60–70% is generally considered ideal for decomposition. Moisture management requires a balance between microbial activity and oxygen supply. Very low (<30%) or high moisture content (>75%) inhibits microbial activities due to early dehydration or anaerobiosis (Bertoldi et al. 1983; Tiquia et al. 2002). Excess moisture will fill many of the pores between particles with water, thereby limiting oxygen transport. This in turn would create anaerobic conditions and brings about putrefaction, resulting in disagreeable odor and undesirable products. On the other hand, if the composting substrate is supplied with insufficient water, the growth and proliferation of microorganisms as well as the rate of decomposition of the organic material would be slowed down or even stopped. It is important, therefore, to ensure adequate moisture in each layer of the compost heap.

6.6.7 Organic Acid Production

The mineralization of insoluble forms of P present in RP by organic acids released during decomposition of organic matter is the major advantage of preparation of RP-enriched compost. Organic acids released from the various organic materials used in the composting help in breaking down the RP faster during the composting period by pushing the dissolution reaction to the forward direction. Acidification

Table 6.7 Organic acid production during straw composting with RP

Treatment	Organic acids (μg g^{-1})						
	Glycolic	Oxaloacetic	Succinic	Fumaric	Malic	Tartaric	Citric
	At 30 days of composting						
Wheat straw	415	378	280	328	265	275	370
+N	429	397	298	435	289	398	405
+N + M	354	353	340	450	523	742	996
+N + M + MP	345	130	333	342	530	328	37
+N + M + HP	353	138	332	345	525	337	53
CD (5%)	11	13	9	12	9	15	8
	At 60 days of composting						
Wheat straw	268	67	362	248	232	34	21
+N	295	90	385	250	240	98	43
+N + M	243	202	400	258	295	178	62
+N + M + MP	245	175	385	250	285	85	0
+N + M + HP	240	173	392	253	288	81	0
CD (5%)	9	12	16	5	7	8	4

Adapted from Singh and Amberger (1998)
N nitrogen, *M* molasses, *MP* Mussoorie phos, *HP* Hyper phos

alone often does not fully explain the solubilization of mineral P (Asea et al. 1988; Whitelaw et al. 1999). Organic acid production during straw composting with RP was given in Table 6.7. Low-molecular-weight organic acid anions (carboxylates) released by microbes have been frequently found in inorganic P solubilization studies (Reyes et al. 1999; Patel et al. 2008). Reported organic acid anions secreted by PSMs include gluconic, 2-ketogluconic, citric, malic, malonic, oxalic, succinic, lactic, tartaric, and glycolic acids (Gyaneshwar et al. 2002).

Nevertheless, organic anion release is often found to be accompanied by medium acidification, but it is important to note that it is not the organic anions that cause acidification, because they are already in their dissociated forms when released into the compost. It is rather the secretion of protons compensating the loss of net negative charges that can cause a drop in pH. Gluconic and 2-ketogluconic acid frequently reported to be released by bacteria have been shown to partially lose their P mobilization ability (Rodriguez and Fraga 1999; Intorne et al. 2009). In contrast, gluconic, citric, and oxalic acid are often found to be released by fungi (Reyes et al. 1999; Whitelaw et al. 1999). In general, tri-carboxylic anions such as citrate show a higher potential in solubilizing inorganic P than do di-carboxylic acids (gluconate, oxalate, etc.).

6.6.8 Organic Matter

Organic matter can complex with released P from RP, making it more available than insoluble P complexes formed in the compost. It is thought that the P released from RP and taken up by microorganisms is available over a longer period of time as they decompose slowly. Organic matter may also form complex calcium (Ca^{2+}) ion in the compost solution, thereby increasing the dissolution of RP. It has been found that incorporation of RP with compost increases the amount of loosely bound P in soils and significantly decreases the fraction held as Ca-P compared to incorporation of RP alone (Singh and Amberger 1995). These microorganisms play an important role in recycling many of the organic phosphorus compounds in compost. For P from organic compounds to be available, it needs to be hydrolyzed and mineralized by the microbial biomass, which is a fundamental process for the release of orthophosphate ions (Hayes et al. 2000; Oehl et al. 2004).

Through a mineralization process, organic P compounds represent an important P source for microorganisms with low levels of bioavailable P (Makarov et al. 2005; Parfitt et al. 2005). Depending on the type of bond, organic P compounds are classified as orthophosphate monoester, orthophosphate diester, and phosphonates. Orthophosphate monoester presents only one covalent bonding where P is linked to the O–C molecule, forming species P–O–C. Some compounds that present this bond type include myo-inositol hexakisphosphate, glucose-6-phosphate, para-nitrophenyl phosphate, and nucleotides. Orthophosphate monoesters are also a product of the degradation of the macromolecules phospholipids and nucleic acid. These compounds have been found in several organic residues, mainly manure, compost, and sewage sludge, which are potential inositol phosphate sources in soil, when applied to agricultural land.

Orthophosphate diester is a compound where orthophosphate is bound to O–C by two ester linkages forming the C–O–P–O–C molecule. Major diester-P sources in organic waste include nucleic acid and are derived from phosphoprotein and phospholipids. Makarov et al. (2005) investigated the organic P composition in plants, bacteria, and fungus by means of P-31 NMR, demonstrating that the proportion of P species in bacteria and plants are very similar in base to ratios of monoester and diester orthophosphate in alkaline extract, while fungi differ considerably and present high proportions of monoesters (phospholipid prevalence) and polyphosphate. Phosphonates correspond to anions of phosphonic acid and are similar to phosphates except that they have a carbon-phosphorus (C–P) bond instead of the carbon-oxygen-phosphorus (C–O–P) linkage. Phosphonates are highly water-soluble, poorly soluble in organic solvents, and are not volatile (Nowack 2003). Several investigators have demonstrated a strong correlation between organic carbon and P (Borie et al. 1989; Escudey et al. 2001). They also determined that P associated with humic acid ranged from 51% to 68% of organic P and P associated with fulvic acid varied from 32% to 49% of organic P. This illustrates the role of organic matter in P retention through the formation of stable complex P-humus and confirms that the ultimate sink for P is not readily available to plants (Bangar et al. 1985; Borie et al. 1989).

6.7 Economic Aspects and Feasibility

In general, it must be recognized that a fair cost analysis is difficult because of the difficulty in obtaining published data regarding RP solubilization based on composting. However, in aiming to use the potential of microbial techniques for RP solubilization, particularly which based on organic wastes, some important considerations must be mentioned. Organic wastes are the cheapest source of composting substrate. However, these prices are not valid in the case of direct application of organic wastes as the biotransformation, organic acid production, and RP solubilization processes occur simultaneously. Therefore, the critical cost of the overall economic balance should include mainly the process operation costs. Composting and RP can be carried out non-septically, but these processes include difficulties related to operation control and scaling-up constraints. According to Biswas (2008), the cost of retail price of 1 kg P_2O_5 and K_2O from diammonium phosphate (DAP) and muriate of potash (KCl) is Rs 16.22 and Rs 7.43, respectively. And cost of preparation of enriched compost using RP and waste mica is only Rs 7. A new technology has been developed to prepare RP-enriched organomineral fertilizer (RP-enriched compost). This would reduce dependence on costly inorganic P fertilizers and save precious foreign exchange, besides providing an environmentally sound and economically feasible solution to problems of waste management.

6.8 Conclusions and Future Research Directions

Replenishing the soil with necessary macronutrients, including phosphorus, is imperative in intensive agriculture to avoid nutrient mining and soil degradation. The decision to promulgate the use of RP as an alternative P source is a complex one that involves consideration of various factors and their interactions. Furthermore, many of the world surveys of RP deposits should be reassessed in more detail due to considerable changes in the technology and economics of mining and processing. In developing countries where farmers are poor, such as in India, indigenous alternative sources of plant nutrients, which may be cheaper, are sought over imported fertilizers. The use of indigenous sources of RP would help minimize the energy use during its conversion into chemical phosphatic fertilizers. The product would help the farmers in reducing their expenditures to purchase chemical fertilizers and would also reduce the import budget on national level. The co-composting of RP with various organic materials offers a cheap, low technology, and therefore widely applicable method of improving P solubility and bioavailability of P. The addition of low-grade RP along with PSM to crop residue during composting improves the quality of compost in terms of its total P content as well as helps to enhance the mobilization of unavailable P in RP into their available forms. The composting of organic wastes with RP has been demonstrated to be an effective method for producing end-products which are ensuring their maximum benefit for agriculture.

However, the compost should be of high quality in order to guarantee its marketability.

There is an unlimited market for good quality compost; the organic matter is simply recycled back to soil where it came from. However, good marketing programs, and optimizing the use of compost, need to be the basis of a successful compost project. The issue of compost marketing so far is not finding much a use for the finished compost but rather finding cost-effective applications. This requires knowledge of the products, their potential uses, limitations, and estimating the value of the product to the end user. It is also important to adapt the marketing strategy to meet the local requirements by considering soil characteristics, agricultural practices, social customs, climate, transportation costs, seasonal variations, etc. In addition to ensuring a safe product, compost standards provide a valuable marketing tool.

The consumer can be satisfied with the knowledge that the product quality is consistent and suitable for the desired application. Considering the lower economic status of Indian farming community, high capital investment on the other hand often leads to lower quantity application. Studies on synchronization of nutrients mineralization and crop demand will provide information on the efficient use of RP-enriched compost in a more integrated manner with inorganic fertilizers for achieving sustainable higher crop productivity. It will offer an effective utilization of crop residues and low-grade RP as source of plant nutrients and reduce the dependency of costly chemical fertilizers.

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Chapter 7
Zinc Solubilizing Bacteria for Zinc Biofortification in Cereals: A Step Toward Sustainable Nutritional Security

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Abstract Food production and security for the ever-increasing population are becoming a key challenge for the scientists. The food security demands not only enhanced agricultural productivity but also improvement in produce quality while reducing adverse impact of agricultural practices on natural resources and the environment. Inadequate nutrition is popular among poor community. Malnutrition of micronutrients is also common due to less concentration present in food. The concentration of micronutrients is very low in cereals due to dependence on cereals; we are taking micronutrients far below the required ones in daily nutrition and are suffering the deficiency of these micronutrients. Among these, Zn is a part of enzymes that regulates the rate of metabolic reactions involved in the development and growth of crop plants and human beings. Zinc deficiency is a common issue not only in plants but in human being and animals as well. Approximately one third of total population of poor world is at high risk of Zn deficiency because they rely on cereals for their daily caloric intake. Its deficiency is a global problem for plants and can be found in every part of the world. More than 70% of Pakistani soils are zinc deficient. So, the cereal crops grown on these soils are zinc deficient. Zn deficiency is the largest cause of death and diseases in humans. This situation demands some effective strategies to overcome Zn deficiency in edible crops, to enhance the grain Zn content and to minimize adverse effects of Zn deficiency on humans thus reducing malnutrition. Many strategies are available to overcome the zinc deficiency in plants and human beings as well. Most important and sustainable strategy is the use of zinc solubilizing bacteria. Zinc solubilizing bacteria alone or with organic materials may also increase the bioavailability of native and applied zinc to the plants

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through different mechanisms of actions. In this chapter, importance of zinc with a special reference to zinc solubilizing bacteria and their mechanisms of action for improving the yield and quality of cereals to achieve the nutritional food security has been discussed in detail.

Keywords Biofortification · Biofertilizers · Nutritional security · Zinc solubilizing bacteria · Organic acids · *Bacillus* sp. · Plant growth promoting bacteria · Malnutrition

7.1 Introduction

Human population is estimated to reach ~7.5–10.5 billion in 2050 with a larger contribution of poor countries such as Asia and Africa (Wood 2001). Due to the shortage of irrigation water and environmental concerns, there is a great challenge to fulfill the food requirement of world's population (Singh et al. 2011). Unluckily, agriculture system of the whole world has always been planned to give maximum benefit to the farmers with no interest in human's health. Quickly occurring micronutrient deficiency in the developing world is a hidden outcome of the agricultural revolution that was adopted to prevent starvation. New agriculture policies now need to meet the energy and nutritional requirements (Welch and Graham 2004).

Food security is the state achieved when food systems operate in such a way that "all people, at all times, have physical and economic access to sufficient, safe, and nutritious food to meet their dietary needs and food preferences for an active and healthy life" (Alexandratos 1995). In recent times, efforts have been made to evaluate the increase in agriculture production which is the most important to attain food security for increasing world population for the next half century (Crosson and Anderson 1995). These observations have concluded that nutritional security is the only thing which increases sustainability over the next quarter to half century to feed the continuously increasing world population (Crosson and Anderson 1995; Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015, 2016b; Ahmad et al. 2016).

Malnutrition and poverty are the most important factors which threaten the millions of peoples in developing countries. Zinc as an essential micronutrient for plants was recognized for the first time by Sommer and Lipman (1926). In developed countries, the use of essential micronutrients in soil is considered as pillar of agriculture. Plant nutrition is an important factor for enhancing over all plant growth and the plant quality products (Mousavi 2011).

A global study to evaluate nutrient status of 30 different countries was conducted by Sillanpaa (1982). They collected a total of ~3538 soil and plant samples for nutrient analysis. Pakistan, Turkey, Iraq, Syria, India, and Lebanon were the countries where soil Zn status was the lowest. Rafique et al. (2006) showed a nutrient indexing of farmer-grown rain-fed wheat in 1.82 M ha of Potohar plateau. In more than

80% of the sampled fields, the crop was zinc deficient with good relationship between surface soil ammonium bicarbonate-diethylenetriaminepentaacetic acid extractable Zn content and plant Zn concentration. Keeping in view the different reasons of low zinc bioavailability, there is need to review the methods which could be helpful for improving zinc bioavailability to plants (Meena et al. 2016a, b; Parewa et al. 2014; Prakash and Verma 2016; Kumar et al. 2016a).

In India, more than 50% of the agricultural soils are Zn deficient. Any approach to improve the zinc uptake and its transport to grains has important practical consequence (Kabata-Pendias and Pendias 2000). Zinc is a nutrient which is required by the plants in small quantity because plants absorb Zn from soil solution (Reed and Martens 1996).

Zinc is a crucial nutrient which is required not only by plants but by humans and microorganisms as well. Humans require Zn throughout their lives in a very minute quantity to complete the growth, development, and physiological functions (Hambidge and Krebs 2007). Zinc deficiency ranked as the fourth main micronutrient deficiency in humans; it affects approximately 66% of the world's population (Zhang et al. 2011). In Pakistan, ~37% of children are highly suffering from zinc malnutrition (Harvest Plus 2012). Inadequate nutritional intake of Zn is the major reason behind Zn deficiency (Cakmak et al. 2010). To solve the issue of Zn shortage, enhancement of bioavailable contents in soil can improve the Zn contents in cereals in developing world (Gurmani et al. 2012; Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Meena et al. 2015a; Jaiswal et al. 2016; Jha and Subramanian 2016).

The developed world has made remarkable success in improving micronutrient malnutrition through dietary diversification, fortification by processing food, supplementation, and improved public health care, but in developing countries, these strategies are often too expensive and difficult to sustain (Mayer et al. 2008). Plant scientists are looking for various approaches to solve the problem of Zn deficiency among human populations by using fertilizer applications and breeding techniques to increase bioavailable Zn contents in cereal grains (Frossarad et al. 2000). On the other hand, biofortification through microbes is an effective technique to overcome micronutrient malnutrition by growing staple food crops (cereals) with the maximum levels of bioavailable micronutrients and minerals that may have impact on improving the micronutrient concentration (Qasim et al. 2007; Nagesh et al. 2012; Raghavendra et al. 2016; Zahedi 2016; Meena et al. 2015b, f; Dotaniya et al. 2016).

Biofortification is the most resent technique to enhance the bioavailability of micronutrients, for example, Fe and Zn in cereals that are staple food in most of the developing world (Stein 2010). Similarly, the use of plant growth-promoting rhizobacteria (PGPR) having good potential of improving micronutrients availability including Zn has been acknowledged as the most recent technology to eliminate Zn deficiency among peoples which might be due to their environmental friendly and economical nature (Saravanan et al. 2011). In this review, the combined results are mentioned which shows the significance of Zn with respect to a variety of approaches to overcome its concentration in staple food crops.

7.2 Zinc as an Essential Nutrient for Plant, Human, and Animals

Zinc is a vital nutrient for normal growth and development of plants, animals, and human as well. In plants, it is required for optimum fruit size, crop production, and yield. Zinc is also used in the carbonic anhydrase activity which is a part of all photosynthetic tissues and important for biosynthesis of chlorophyll (Xi-wen et al. 2013). Generally, Zn has key role in the activation of enzymes, synthesis of protein, and oxidation and metabolism of carbohydrates. It has been reported that use of micronutrients and zinc-containing fertilizers improves crop quality, while the deficiency of these elements causes a decline in photosynthesis process, RNA, carbohydrates, and protein synthesis leading to reduced quality of crops and limited crop performance (Efe and Yarpuz 2013).

It is well documented that zinc has a major role in plant physiology, for example, photosynthesis, chlorophyll synthesis, nitrogen metabolism, protein synthesis, resistance to stresses, and protection from oxidative stress (Cakmak 2008). Maize has been recognized by farmers for a long time as a crop of high response to zinc supply. In arid and semiarid areas, zinc application to crops is very important because maize growth is considered to be highly sensitive to many external and internal stresses, which in turn induce grain yield reduction (Subedi and Ma 2009; Rawat et al. 2016; Yasin et al. 2016; Meena et al. 2016c, d; Saha et al. 2016a; Yadav and Sidhu 2016; Bahadur et al. 2016b; Das and Pradhan 2016; Dominguez-Nunez et al. 2016). The foliar application of zinc is a simple way for making quick correction of plant nutritional status, as reported for wheat (Erenoglu et al. 2002) and maize (Grzebisz et al. 2008). It is clear that the proper application of zinc to maize is necessary to boost up the growth and yield of maize.

Zinc is directly involved in auxin synthesis in plants (Skoog 1940); so its deficiency leads to leaf distortion and restriction of internodes (Irshad et al. 2004). Auxins are known to play a basic role in cell division and elongation (Teale et al. 2006). The most distinct Zn deficiency indications are stunted growth and small leaves (Irshad et al. 2004), which are probably due to variations in auxin metabolism, particularly of IAA (Alloway 2003). Brown et al. (1993) reported that addition of zinc in calcareous field of plants significantly increased tryptophan concentration which is a precursor for the biosynthesis of IAA in rice grains (Saha et al. 2016b; Verma et al. 2014, 2015b; Meena et al. 2014a, e; Teotia et al. 2016).

Zinc is also involved in sustaining the structural and functional integrity of biological membranes (Sadeghzadeh and Rengel 2011). As Zn is an integral part of Cu/Zn superoxide dismutase (SOD), it is involved in detoxifying reactive oxygen species (Cakmak and Marschner 1988) and avoiding damage to membrane lipids and sulfhydryl groups in Zn-scarce plants (Cakmak 2000b). It is important to observe the impairment of membranes caused by Zn deficiency which cannot be inverted contrasting that caused by calcium (Ca) deficiency (Welch et al. 1982; Cakmak 2000a).

Moreover, the Zn-deficient plants had reduced pollen production, leading to an increased fraction of empty grain positions (Marschner 1995). Zinc is also a central part of transcription factors which are important for cell proliferation and differentiation (Vallee and Falchuk 1993). It can be recognized to reduced enzyme activities (antioxidants) and high oxidative stress which damage the chloroplasts due to obstruction of energy spillover from PS-II to photosystem-I (PS-I) (Chen et al. 2009). Such destruction of photosynthetic centers decreases leaf photosynthetic capacity due to a decreased number of PS-II units per unit leaf area, making them susceptible to photo destruction (Chen et al. 2008). A decrease in CO^2 assimilation is mainly due to reacting oxygen species (ROS)-induced damage to the photosynthetic apparatus and a decline in Rubisco activity (Sasaki et al. 1998) in Zn-deficient plants. Nevertheless, accumulation of saccharides in leaves (Cakmak 2000b) due to a decline in CO^2 concentration and stomatal conductance may be a credible reason for decreased photosynthetic rate under Zn scarcity (Marschner 1995).

The contact of Zn with membrane proteins of sulfhydryl groups and phospholipids further adds for the protection of membranes. Being a prosthetic component of enzymes within cells, i.e., isomerases, dehydrogenases, transphosphorylases, aldolases, and RNA and DNA polymerases (Lo pez-Millán et al. 2005), Zn is involved in the production of energy and synthesis of protein (Hänsch and Mendel 2009). It also takes part in synthesis of nucleic acid, lipid, and carbohydrate metabolisms (Marschner 1995), and it forms RNA and DNA complexes, convincing their stability (Coleman 1992).

Zinc deficiency is common in humans, animals, and plants. More than 30% of world's population undergoes severe Zn deficiency (Welch 2002). Zinc plays a basic role in cellular functions of all living organisms and is also improving the immune system of human. The optimal dietary consumption for human adults is 15 mg Zn/day. Zinc has catalytic and also structural component of several body enzymes. Deficiency of Zn may cause by unsatisfactory consumption and inappropriate absorption of Zn in the body. The human body suffers from hair and memory loss, skin complications, and weakness in body muscles due to Zn deficiency. During pregnancy, insufficient Zn intake also causes stunted brain development of the fetus. Infertility has also been perceived in Zn-deficient men. Zinc deficiency causes congenital diseases like acrodermatitis enteropathica (Zimmermann 2001; Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b, e; Shrivastava et al. 2016).

Zinc has no store house in human body (Johnson 1993). As it is a basic component of hundreds of proteins or proteins which are zinc binding and nucleic acid, zinc is located almost uniformly throughout the human body, but it is not measurable; therefore, nowadays, it is a big challenge in the detection and diagnosis of zinc deficiency in human body by estimating zinc concentration in serum and other tissues (Hambidge and Krebs 2007). It is a common recommendation that an average male needs 11 mg Zn per day, while an average female needs 9 mg of Zn daily. During pregnancy and lactation, the female needs 13–14 mg of Zn on daily basis. Newborns from 7 months to 3 years of age need 3 mg, 4–8 years of age need 5 mg, and children from 9 to 13 years age need 8 mg of Zn/day (Hotz and Brown 2004). Zn is stored in the rice husks and grains, and with the intake of this cereal, zinc deficiency in human can be diminished. Zn-rich foods are beef, pork, chicken, and breakfast cereals; nuts like roasted peanuts, almonds, walnuts, and oats; and dairy products like yogurt, cheese, and milk (Cakmak 2002; Velazquez et al. 2016; Meena et al. 2013c, 2015c; Bahadur et al. 2016a; Masood and Bano 2016).

In animal production, the significance of trace minerals has a great concern for producers, veterinarians, feed manufactures, and food scientists. Sufficient Zn absorption and uptake are required for many metabolic functions such as immunity response to pathogen, reproduction, and growth. In immune system, functions of Zn are protein synthesis, energy production, antibody production, antioxidant enzyme production, stabilization of membranes against bacterial endotoxins, and maintenance of lymphocyte replication (Kidd et al. 1996). Inadequate intake of Zn results in lowered cellular immunity and decreased antibody response (Fletcher et al. 1988).

The Zn mineral supplementation for cattle boosts recovery rate in infectious bovine rhinotracheitis; it is usually in virus-stressed cattle (Chirase et al. 1991). It is founded that zinc methionine increases antibody titer against bovine herpesvirus 1 (Spears et al. 1991). During lactation, Zn supplementation to dairy cows results in fewer mammary gland infections (Spain et al. 1993). Cattle reproductive system may be cooperated if copper, manganese, or zinc rank is in the marginal to deficient. In cattle, the common deficiency symptoms are infertility, decreased conception, embryo death, and delayed or suppressed estrus (Corah and Ives 1991). Insufficient Zn concentration has been related with abnormal estrus, reduced fertility, and altered myometrial contractibility with prolonged labor and abortion (Maas 1987). In view of the role of all minerals (micronutrients) in growth, zinc functions as components in several enzyme systems related with protein and carbohydrate metabolism (Sindhu et al. 2016; Meena et al. 2014b, 2015d; Singh et al. 2015, 2016).

7.3 Fate of Zinc and Factor Effecting Zinc Bioavailability in Soil

The zinc applied to the soil is either used by the microorganisms and plants or gets fixed/adsorbed on the soil colloids (Alloway 2008). Calcareousness of the soil, pH, soil texture, soil water, and microbial community in soil and organic matter are the factors which affect the zinc availability in soil (Imran et al. 2014). When the amount of Zn available to the plant is not sufficient, quality of production and crop yields are badly affected. Therefore, certain minimum level of Zn supply is necessary for proper function of crop plants (Meena et al. 2017).

The availability of Zn in soil is mostly measured by the process of adsorption/desorption and its partitioning between the solid and solution phase (Gaudalix ME Pardo 1995; Catlett et al. 2002). Sorption of zinc is low in acidic soil (Zhao and Selim 2010) compared to neutral soil. Zn is retained more in clayey soils compared to sandy soils. Usually, flooding reduces the Zn bioavailability in soil (Neue et al. 1994) that is why water contents in soil is an important factor to determine the zinc bioavailability (Patnaik et al. 2008). Higher concentration of iron reduced the zinc bioavailability in soil under anaerobic conditions (Mandal and Hazra (1997).

Adsorption isotherms can be used to determine the equilibrium relationship between the amounts of dissolved and adsorbed species at a given temperature. These measure the factors of quantity, intensity, and capacity which are important for calculating the amount of soil nutrient essential for maximum plant growth. Soil texture, clay minerals, organic matter, CEC, $CaCO_3$, and the properties which need not to be measured in order to determine soil requirements using sorption technique affect the amount of nutrients required by soil (Solis and Torrent 1989).

Zinc deficiency, a frequent problem of plants (Hotz and Brown 2004), can be found anywhere in the world and almost all crops respond positively to Zn application (Welch 2002). Standard soils inherit their trace elements, for example, Zn, primarily from the rocks through geochemical and pedochemical weathering processes. In addition to mineralogical composition of the parent material, Zn level in the soil during soil formation is also dependent on the climate, type, and intensity of weathering and various other predominating factors (Saeed and Fox 1997).

Soil organic matter increases the Zn solubility and reduces its fixation that results in its more uptakes by plant roots (Cakmak 2009a, b). So, Zn availability in soil could be increased with the use of organic matter (Yoo and James 2002). The decrease in available Zn observed under flooded and submerged conditions is attributed to the changes in pH value and the formation of insoluble Zn compounds. Temporarily, the insoluble Zn compounds formed with Mn and Fe hydroxides from the adsorption on carbonates and breakdown of oxides, specifically magnesium carbonate.

7.4 Zinc Biofortification

Malnutrition has affected more than half of the world's population. It is the most serious problem of developing countries where population is living below the poverty line. Micronutrients are vital for most of the living organisms, including humans who need a supply of 16 mineral microelements, which can be supplied through a balanced diet (Borg et al. 2009). In the early 1960s, Zn deficiency in the human body was first speculated with considerable supportive evidence (Prasad 2008). At present, nearly two billion people in the developing world are suffering from Zn deficiency. Soil Zn deficiency is among the major global micronutrient deficiencies and has recently received more attention.

The industrialists and pharmacists are trying to improve the quality of good crops through fortification and supplementation, respectively, which are laborious and costly. Poor people in the villages don't have access to industrially fortified food because of their high cost and unavailability in the village area (Tanumihardjo 2008). Biofortification is the process of increasing bioavailable concentration of essential elements in edible portions of crop plants through agronomic intervention or genetic selection (White and Broadley 2009).

Past efforts on agriculture production have primarily been focused on increasing crop yields; however, the accompanying decrease of mineral concentrations in grains was found as a new problem threatening the development of crop yields and even the food security. The ultimate goal of modern agriculture has been modified to produce nutritious foods sufficiently and sustainably (Zhao and Mcgrath 2009). The contents of nutrients in the edible parts of staple food crops, e.g., maize, rice, wheat, and barley, contribute to the main mineral intake of people in the developing countries. Therefore, increasing concentrations of mineral elements, like Zn and Fe, is the most effective approach for public health to control in staple food crops malnutrition in Zn-deficient areas.

In this context, biofortification by microorganisms as bio-inoculants to enhance the native zinc availability to crop plants for accumulation to achieve the objective of low input and sustainable agriculture to overcome zinc deficiency in humans could be a viable option (Mader et al. 2010). Microbes having zinc solubilizing activity include both bacteria and fungi. It is considered that strains belonging to the genera *Bacillus*, *Gluconacetobacter*, *Azotobacter*, *Azospirillum*, and *Pseudomonas* have been reported as zinc solubilizers (Saravanan et al. 2007). Fungal strains like are arbuscular mycorrhizae and *Trichoderma* have also been reported to possess zinc solubilizing activity (Paul and Clark 1989).

7.5 Strategies to Enhance Zinc Biofortification in Cereals

Fortification is considered the best approach to enhance Zn contents in edible portion of the crops (Harvest Plus 2012). Biofortification of micronutrients in cereal crops is now popular in poor countries to solve Zn deficiency problems (Cakmak 2008; Zhao and Mcgrath 2009; Bouis and Welch 2010). Various approaches are included in cereal fortification to enhance micronutrients (Zn) in grains (Pfeiffer and Mcclafferty 2007). Increasing concentration of Zn in grains is the only possible way to overcome the Zn deficiency in poor countries because they use cereals as staple food (Pahlvan and Pressaraki 2009; White and Broadley 2011). Scientists especially plant scientists are looking for some methodologies to increase Zn in grains (Cakmak 2008). Different diet factors, e.g., amino acids (Methionine and histidine), organic acids, and EDTA (chelating agent), are supportive for the bioavailability of Zn, while phytate fibers and some other elements as Fe^{+2}, Cu^{+2}, and Ca^{+2} decrease its bioavailability (Lonnerdal 2000). It is reported in the previous studies that increased Zn bioavailability to grains reduces the phytate concentration (Cakmak et al. 2010). Zinc absorption can be enhanced by different organic acids such as citric acid, ascorbic acid, malic acid, and lactic acid. EDTA solubilizes Zn-phytate and converts it into Zn-EDTA. In Pakistani conditions, fortification is the best approach to increase Zn contents in wheat grains (Harvest Plus 2012). There are different strategies for improving zinc biofortification which are given below. In different approaches of fortification, genetic biofortification and agronomic biofortification are most prominent.

7.5.1 Plant Breeding Strategies for Zinc Biofortification

The major objective of genetic biofortification is to develop new varieties with potential to uptake and accumulate more Zn contents in edible portion. This aim can be achieved by conventional breeding and genetic engineering techniques.

To produce desired characteristics in crop, altering of genetics is required and known as plant breeding. Plant breeding and genetics are main approaches in plant biofortification. Genetic approaches are considered very powerful to accumulate the micronutrients in food crops. Agronomists are paying attention on crop yields only without taking care of nutritional status in crops (Khoshgoftarmanesh et al. 2009). It is concluded from the previous literature that the increase in crop yield is ultimately associated with reduction in micronutrient concentration in grains. It has been documented that low-yielding varieties have more potential to accumulate micronutrients as compared to high-yielding varieties (Monasterio and Graham 2000; White and Broadley 2005).

It is important to mention that the enrichment of zinc contents in plant tissues is just the result of less growth and poor yields (Zhao and Mcgrath 2009; White and Broadley 2011). The success achieved in the development of high Zn accumulative varieties is admirable (Pfeiffer and Mcclafferty 2007; Bouis and Welch 2010). Many problems are associated with this approach like Cd can be translocated to plants through same mechanism (Intawongse and Dean 2006), and its mobility is comparatively high with respect to the other heavy metals (Reeves and Chaney 2008).

Furthermore, the proteins belonging to ZIP family (metal transporter in plants) transport Cd to plants (Yang et al. 2009; Assunc et al. 2010), which is the main problem and difficulty in breeding programs. The other serious issue with this strategy is instability of newly incorporated Zn character in the genotypes (Welch and Graham 2004). Zinc translocation in wheat grains is affected by many factors such as climate and genotype interaction (Gomez et al. 2010; Zhang et al. 2010). On the other hand, it takes many years to develop a new variety (Monasterio et al. 2007). Plant breeding approaches are time-consuming that's why it is not possible for developing countries.

7.5.2 Biotechnology

We cannot ignore the transgenic approaches in the development of bio-fortified varieties. Many transgenic crops have been produced up till now having better concentration of Zn in grains. The expression of ZIP family such as bZIP19 and bZIP23 (transcription factors) is used to increase the Zn contents in cereals grains (Assunc et al. 2010). Various transport proteins present in cell membrane are the targets for zinc contents in the different parts of plants. These transport proteins are responsible for uptake and accumulation of zinc in the vacuole together with enzymes concerned in the synthesis of substances that bind Zn^{2+} in the rhizosphere. Gene overexpression encoding a transport protein of root can particularly enhance the Zn^{2+} uptake in the rhizosphere (Gustin et al. 2009), for example, wheat grain zinc contents can be enhanced by the overexpression of NAC transcription factor (NAM-B1) (Uauy et al. 2006).

7.5.3 Agronomic Strategies

Agronomic approaches in the perspectives of either health or in sustainable agriculture are appreciable, and the Zn contents can easily be enhanced in cereal grains by using these approaches. In the previous studies, the benefits of agronomic biofortification are described with respect to economics and health benefits (White and Broadley 2011). Zn fertilization is considered as short term and easy remedy of Zn deficiency (Cakmak 2008).

Various varieties have different capacity to accumulate Zn in plants. Different fertilizers, e.g., zinc sulfate ($ZnSO_4$) have the potential to increase growth and yield of crops that also increases Zn concentration in grains (White and Broadley 2005). Zn application either by soil or foliarly applied to crops significantly increases crop vigor (Cakmak 2008; Zhao and Mcgrath 2009). Zn application to soils also reduces the concentration of anti-nutrient, e.g., phytic acid in case of Zn (Cakmak et al. 2010). In most of the soils, soluble Zn is very low (Knight et al. 1997), so the solution is the use of chelating agents (synthetic), e.g., ethylenediaminetetraacetate (EDTA) (Sahi et al. 2002).

In less fertile soils, the application of NPK is necessary to obtain proper growth and yield of the crops; with the application of these macronutrients, the root length is also enhanced that supports to uptake the micronutrients. Zinc availability of applied fertilizer in soil also depends on soil pH, e.g., NH^{4+} application to soil results in acidification of soil (rhizosphere) which enhances the transfer of Zn from the soil to the plants, whereas NO_3 application causes more alkalinity to the soil and reduces Zn transfer rate (Hartikainen 2005). Application of Zn-containing fertilizers seems to be a possible and efficient solution of Zn-deficient soils, due to lack of resources especially in poor countries. On the other hand, it is well documented that various synthetic chelating agents are costly (Kos and Lestan 2003). Due to heavy metal, plant growth becomes restricted. But the continuous use of synthetic fertilizers in agriculture has escalated the expenses of production and damaged the soil, water, and air environment. There is need of the hour to develop Zn application methods for effective results.

7.5.4 Zinc Solubilizing Bacteria (ZSB)

One of the new concepts and novel approaches for biofortification of crops is the use of microbial strains. These microorganisms have the ability to improve the quality of crops through enhanced uptake of micronutrients due to their growth-promoting traits, viz., nutrient solubilization, siderophores production, and exopolysaccharides production, in addition to some other growth-promoting attributes (Ahmed et al. 2011). Inoculation of crops with such microbial strains for biofortification may not only help us to deal with the problem of malnutrition through increased nutrient concentration in grains but also improve crop yield and soil fertility. Cereals (wheat, rice, maize) are the main staple food in most parts of the world including nutrient-deficient countries. Healthy foods can be produced for undernourished people globally through specific microbial strains.

Rhizosphere is the zone of soil around roots that is an ideal habitat for microbial population as compared to bulk soil. The rhizosphere microflora may be helpful to the plants through different mechanisms, e.g., production of organic acids and phytohormones, mobilization of nutrients, fixation of atmospheric nitrogen, altering native level of phytohormones, and improving plant stress tolerance to salinity, toxicity, drought, metal, and pesticide load. Microflora also acts as a biocontrol agent for the plants (Khalid et al. 2009).

Though every mechanism has its own importance, mobilization of nutrients by microflora is considered to play pivotal role to enhance nutrient content in plant tissues. There are sufficient reports demonstrating substantial potential of plant growth-promoting bacteria and fungi in improving zinc bioavailability in the rhizosphere of plants and zinc content in plant tissues (Subramanian et al. 2009).

Since these bacteria play an important role in improving the quality of food, thus, they would be given key importance in future while devising approaches to alleviate Zn malnutrition in humans through food, especially where diverse food is not available to common people and they can also not afford food supplements. Among microorganisms, both fungi and bacteria are reported to improve plant Zn availability in the rhizosphere and also enhance zinc in edible portion of the cereals (Subramanian et al. 2009). Effectiveness of zinc solubilizing bacteria for enhancing plant growth and biofortification of cereals is presented in Table. 7.1.

7.6 Mechanisms of Action of Zinc Solubilizing Bacteria

Some organisms use single mechanism, while others use multiple mechanisms to improve zinc availability in soil and finally enhance zinc uptake in plant tissues. Soil pH influences the availability of micronutrients. A slight change in soil pH may improve the availability of micronutrient in soil. It has been reported that availability of Zn increased 100 times by decrease of one unit in pH (Havlin et al. 2005). Thus, bioavailable fraction of Zn can be enhanced decreasing the pH of alkaline soil.

It has been reported that the plant growth-promoting bacteria release organic acids and extrude protons which lower down the pH of rhizosphere (Wu et al. 2006; Fasim et al. 2002). For example, during solubilization of Zn phosphate in the culture, *Pseudomonas fluorescens* secreted 2-ketogluconic acid and gluconic acid. Similarly, Fasim et al. (2002) reported proton extrusion and 2-ketogluconic acid by

Table 7.1 Effectiveness of zinc solubilizing bacteria for enhancing plant growth and biofortification of cereals

Name of bacterial strain	Crop	Experimental condition	Response/results	References
Azotobacter; *Azospirillum*	Corn	Greenhouse	Caused significant increase in Zn contents of grain	Biari et al. (2008)
Bacillus sp. AZ6	Maize	Growth room	Improved growth and physiology of plants	Hussain et al. (2015)
Pseudomonas; *Bacillus* sp.	Maize	Pot	Significantly enhanced total dry mass (12.96 g) and uptake of N (2.268%), K (2.0%), Mn (60 ppm), and Zn (278.8 ppm)	Goteti et al. (2013)
Consortia *A. lipoferum* (JCM-1270, ER-20), *Pseudomonas* sp. (K-1, 96-51); *Agrobacterium* sp. (Ca-18)	Rice	Field	Inoculation has positive impact on growth, physiology, yield, and zinc biofortification of rice	Hafeez et al. (2002) and Tariq et al. (2007)
Burkholderia; *Acinetobacter*	Rice	Greenhouse	Bacterial inoculations significantly enhanced the total Zn uptake/pot (52.5%) as compared to control. A reduction of nearly 38.4% in phytate	Vaid et al. (2014)
Endophytic strains, *Sphingomonas* sp. SaMR12; *Enterobacter* sp., SaCS20	Rice	Greenhouse	Increased Zn bioavailability in rhizosphere soils and elevated grain yields and Zn densities in grains	Wang et al. (2014)
Bacillus aryabhattai strains MDSR7, MDSR11, and MDSR14	Soybean and wheat	Microcosm	Strains MDSR7 and MDSR14 substantially influenced mobilization of zinc and its concentration in edible portion, yield of soybean and wheat	Ramesh et al. (2014)
Providencia sp. PW5, *Anabaena* sp. CW1, *Calothrix* sp. CW2, and *Anabaena* sp. CW3	Wheat	Field	Improved the nutritional quality of wheat grains, in terms of protein content and important micronutrients (Fe, Cu, Zn, and Mn)	Rana et al. (2012)

bacteria which solubilized zinc oxide and phosphate. When *Pseudomonas* and *Bacillus* spp. were inoculated in broth culture, a change in pH was observed which solubilized ZnS, ZnO, and $ZnCO_3$ (Saravanan et al. 2004).

Martino et al. (2003) found that mycorrhizal fungi secreted organic acid to solubilize Zn from insoluble Zn_3 $(PO_4)_2$ and ZnO. Subramanian et al. (2009) also reported that inoculation of arbuscular mycorrhizae lowered the rhizospheric soil pH and contributed to release of zinc from mineral fraction. However, degrees of

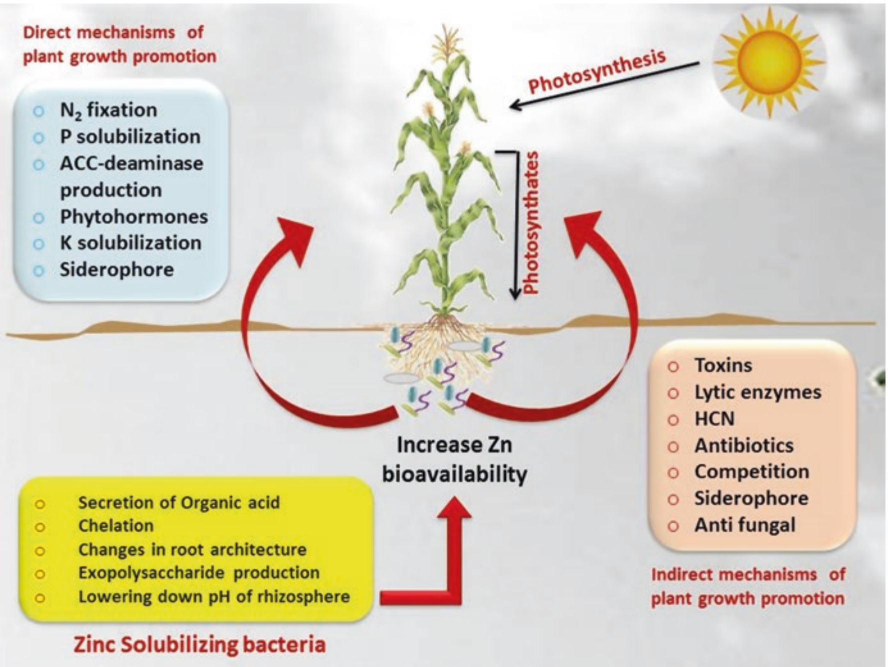

Fig. 7.1 Mechanism of zinc solubilizing bacteria for improving zinc bioavailability through direct and indirect mechanism of action

reduction in rhizosphere pH varied among microorganisms (Giri et al. 2005). Wu et al. (2006) observed a decrease in pH up to 0.47 units with bacterial inoculation. Thus, pH goes down due to the release of organic acids and H^+, which ultimately improves Zn solubilization and uptake by plants. Zinc solubilizing bacteria increase the availability of zinc through different mechanisms of action in the rhizosphere which ultimately improve its uptake by the plant. Different mechanisms used by zinc solubilizing bacteria to improve zinc bioavailability are summarized in Fig. 7.1, and some important ones are discussed below.

7.6.1 Zinc Chelation

Due to low persistency and high reactivity of Zn in soil solution, plant-available Zn fraction in the soil is low. Bioavailability of Zn in root zone could be increased by Zn-chelating compounds (Obrador et al. 2003). These compounds are either synthetic or released by the plant roots and potential rhizosphere microflora into the rhizosphere to chelate the Zn and increase its availability in root zone of the plants. Bacterial metabolites form complexes with Zn^{2+} (Tarkalson et al. 1998) and reduce their reaction with the soil. These Zn chelates consequently move toward the roots and release chelating ligand (Zn^{2+}) at the root surface, making them free to chelate another Zn ion from the soil solution.

Chelation is the dominant phenomena to improve Zn bioavailability and uptake by plant roots through microorganisms. This is the possible mechanism used by bacteria, e.g., *Pseudomonas monteilii*, *Microbacterium saperdae*, and *Enterobacter* cancerogenesis the manufacture of Zn-chelating metallophores for enhancing water soluble Zn which is bioavailable in soil for plant uptake (Whiting et al. 2001).

In another study, Tariq et al. (2007) reported that biofertilizer containing *Pseudomonas* sp. (96-51), *Azospirillum lipoferum* (JCM-1270, ER-20), and *Agrobacterium* sp. (Ca-18) released fixed zinc and made it bioavailable for longer period of time to rice by producing chelating agent ethylenediaminetetraacetic acid. Inoculation of *Penicillium bilaji* enhanced Zn bioavailability to plants through chelating mechanism (Kucey 1987)

7.6.2 Organic Acids Production

It is well documented that bacteria usually *Bacillus* sp. and *Pseudomonas* sp. have the ability to produce organic acids which decrease pH, and in this way micronutrients, e.g., Zn, become available to plants (Saravanan et al. 2004). It is also found that PGPR (plant growth-promoting rhizobacteria) possibly produce gluconate (Saravanan et al. 2011) or the derivatives of gluconic acids, e.g., 2- ketogluconic acid (Fasim et al. 2002), 5-ketogluconic acid (Saravanan et al. 2007), and various other organic acids (Tariq et al. 2007) for the solubilization of zinc. *Bacillus* sp. AZ6 has the ability to solubilize insoluble source by releasing organic acids like cinnamic acid, ferulic acid, caffeic acid, chlorogenic acid, syringic acid, and gallic acid in a liquid medium (Hussain et al. 2004). Solubilization of insoluble zinc was accompanied by enhancement in the H^+ concentration in the medium, due to the production of 2-ketogluconic acid and other organic acids (Fasim et al. 2002). All these mechanisms help to enhance zinc availability, uptake, and its concentration in the crops.

7.6.3 Changes in Root Architecture

Zinc is immobile nutrient in soil and is taken up by plants specifically by diffusion (Havlin et al. 2005). Due to low exogenous application and poor native bioavailability, depletion zones are formed in rhizosphere. For maximum uptake of Zn to the plants, it should be bioavailable. Zinc bioavailability can be increased either by more Zn application or improving root growth and surface area so that roots can take nutrients from long distance. Effect of mycorrhizal fungus on root architecture is well known.

Mycorrhizal fungus increase the surface area of the roots which helps to uptake plants more zinc from long distances. Burkert and Robson (1994) reported that arbuscular mycorrhizae can obtain Zn from the distance of 40 mm from the root surface. Subramanian et al. (2009) found that mycorrhizal fungus increased the Zn concentration up to 4% in the grain and increased in root length as compared to the plants with no fungal inoculation. Similarly, Tariq et al. (2007) reported extensive increase in root weight, length and volume, and zinc (Zn) biofortification of rice with the inoculation of zinc solubilizing bacteria.

7.7 Role of ZSB with Combination of Zinc and Other Amendments

Different organic amendments also enhance Zn bioavailability of complex Zn by decreasing the soil pH by releasing chelating agent's release. Organic matter also increased microbial biomass carbon which increases the rate of decomposition of organic matter. Organic amendments which are generally ignored by the farmers can ensure the availability of macro- and micronutrients. Improvement in carbon and activities of microflora in soil with the addition of organic amendments ensures better soil quality and also has a beneficial impact on soil fertility by mineralization process. It is very important to increase bioavailability of zinc to plants by solubilizing fixed Zn and by reducing fixation of the applied Zn-containing fertilizers (Imran et al. 2014). This can be achieved either by using different organic amendments or potential zinc solubilizing bioinoculants alone or in consortium.

Soil organic matter increases availability of zinc in rhizosphere and reduces fixation, which results in its more uptake by plant roots (Marschner 1993; Obrador et al. 2003; Cakmak 2009a, b). Organic matter increases zinc bioavailability due to the production of polysaccharides (Hodgson 1963). Similarly, with the addition of soil organic carbon, an increase in DTPA extractable zinc was observed (Sidhu and Sharma 2010). In a recent study conducted by Hussain et al. (2004), significant increase in Zn contents in maize plant through combined use of organic amendment and zinc solubilizing bacteria was observed. They reported that the bioaugmented zinc significantly increased the zinc contents while caused a decrease in phytate contents in maize grains.

7.8 Bacterial Inoculants

Bacterial inoculants are also helpful in increasing availability of zinc in soil and its further uptake by plants to improve plant zinc content in edible portion of the cereals (wheat, rice, and maize). Several bacterial species have the ability to solubilize insoluble zinc compounds (ZnO, $ZnCO_3$, ZnS) in liquid medium (Saravanan et al. 2007) and in soil (Tariq et al. 2007).

The *Bacillus* and *Pseudomonas* species can solubilize various insoluble zinc compounds like zinc sulfide (ZnS), zinc oxide (ZnO), and zinc carbonate ($ZnCO_3$) to a greater extent in liquid medium (Saravanan et al. 2004). Similarly, inoculation with bacterial strain *G. diazotrophicus* PA15 solubilized insoluble sources of zinc compounds like ZnO, $ZnCO_3$, and $Zn_3(PO_4)_2$ after 48 h of incubation in a broth media (Saravanan et al. 2007). *P. aeruginosa* have the potential to solubilize insoluble zinc compound, e.g., ZnO, in liquid medium (Fasim et al. 2002). It has also been widely reported that bacterial inoculation increases plant Zn content (Tariq et al. 2007; Biari et al. 2008; Hussain et al. 2004). Whiting et al. 2001 reported that with bacterial inoculants bioavailable zinc in rhizosphere soil increases about 0.45 fold.

Inoculation of *Azospirillum* and *Azotobacter* was useful in controlling zinc deficiency in wheat crop, and up to 18% increase in zinc uptake was recorded as compared to un-inoculated control under no Zn application (Eleiwa et al. 2012). Likewise, bacterial inoculants like *Azotobacter* and *Azospirillum* showed significant increase in grain zinc in corn (Biari et al. 2008) and also observed increase in Zn content in seed with *Azotobacter chrooccoccum* DSM2286, *Azospirillum brasilense* DSM2286, *Azospirillum sp.* strain 21, and *Azotobacter sp.* strain 5, as compared to un-inoculated control. Consortium of *Rhizobium leguminosarum*-pr-1 and *Pseudomonas* sp. increased the zinc content in shoots was observed by Mishra et al. (2012), while Tariq et al. (2007) found 133% more zinc in grain of rice as compared to un-inoculated control.

The bacterial inoculation also relieved the deficiency symptoms of zinc in plant. *P. aeruginosa* 7NSK2, and *Bacillus* M-13 increased Zn acquisition in barley and wheat (Sadaghiani et al. 2008). Therefore, use of such bacterial inoculants could be valuable to approach to increase zinc availability in soil and its subsequent availability to plants.

7.9 Conclusion and Future Outlook

Nutrients mobilization from zinc solubilizing bacteria is considered the most critical function to improve zinc bioavailability in soil for the plants. There is a good deal of research to solubilize the insoluble zinc in soil. In this chapter, we have critically discussed the efficiency of zinc solubilizing bacteria to promote Zn availability in soil and uptake by plants. The use of Zn solubilizing bacteria is very effective, economic, and environmental friendly approach to increase Zn contents in the edible portion of crops to fulfill human requirements.

There are number of mechanisms due to which zinc solubilizing bacteria improve the overall growth and yield of cereals because plant-microbe interactions are very complex. Zn solubilizing bacteria can be used as biofertilizers; they can enhance survival and growth of plant, improve soil fertility, and increase yield and zinc contents in cereal grains. It can reduce the dependence on chemical/synthetic fertilizers. Likewise biofertilizers are environmental friendly and can improve crop production. It is a possible and economical method to increase Zn concentration in foods to overcome Zn malnutrition in developing world.

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Chapter 8
Towards the Mechanisms of Nutrient Solubilization and Fixation in Soil System

Jyoti Rawat, Pankaj Sanwal, and Jyoti Saxena

Abstract Growth and development of plants depend on the nutrients present in the soil; thus it becomes necessary to provide the essential nutrients to plants. Soil is a major reservoir through which plants obtain nutrients for their growth. However, most of the nutrients in the soil occur in insoluble forms making the availability of nutrients restricted for the plants. Although chemical fertilization is a quick and efficient method, it is currently not recommended due to detrimental effects on soil and environment. On the other hand, the biological fertilization has proved to be an efficient method to supply necessary nutrients to the plants and maintain sustainability. Biofertilizers consist of a group of beneficial microorganisms that are capable of hydrolyzing essential nutrients from insoluble compounds, thus making them available for plants. A large number of microorganisms including bacteria, fungi and actinomycetes have properties which enhance the solubility of metal ions by various mechanisms such as change of soil pH or direct chelation of metal cations. The present review focuses on the mechanisms and processes associated with microbial solubilization and fixation of nutrients in soil.

Keywords Nitogen (N) · Phosphorous (P) · Potassium (K) · Zinc (Zn) · Iron (Fe) · Solubilization mechanisms

8.1 Introduction

Soil is the major source of nutrients required by plants, which directly influence growth, yield and quality of crops. The primary nutrients are nitrogen (N), phosphorus (P) and potassium (K) as they are required in larger quantities (Daliparthy et al. 1994), whereas all other essential macronutrient elements are secondary nutrients

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because they are not limiting thus rarely added to soils as fertilizers. N is required for the formation of amino acids (building blocks of protein) and is a necessary component of vitamins such as biotin, thiamine, niacin, riboflavin and nucleic acids (Kalra and Sharma 2015). It is essential for plant cell division, directly involves in photosynthesis, aids in production and use of carbohydrates and affects energy reactions in the plant (Schaetzl and Anderson 2005). On the other hand, P is mainly involved in photosynthesis, respiration, energy storage and transfer and cell division and enlargement (Shukla et al. 2014). It promotes early root formation and growth, improves quality of fruits, vegetables and grains and is vital for seed formation (Kadiri et al. 2013). It helps plants to survive in harsh winter conditions, increases water-use efficiency and hastens maturity (Zimdahl 2015). Another important macronutrient is K which helps in protein synthesis, carbohydrate metabolism and break down and translocation of starch (Read et al. 2006; Meena et al. 2013a; Bahadur et al. 2014; Kumar et al. 2016b). It also activates enzymes and controls their reaction rates and improves quality of seeds and fruits and winter hardiness in plants. Besides, it increases photosynthesis, water-use efficiency and disease resistance (Rehm and Schmitt 2002). K is also vital for animal and human nutrition, and thus healthy fruits, vegetables and grains must have adequate levels of K (Brian 2007). Besides, plants also require carbon, hydrogen and oxygen in bulk, which are taken from air and water to make up the mass and weight of plants (Hafeez et al. 2013).

Secondary nutrients include calcium (Ca), magnesium (Mg) and sulphur (S). Ca is utilized for continuous cell division and translocation of photosynthetic products from leaves to fruiting organs. It participates in enzymatic and hormonal processes, strengthens the cell wall structure and helps in protecting the plant against heat stress and diseases. Besides, it participates in metabolic processes of other nutrients uptake and regulation of the stomata. S is involved in formation of chlorophyll; synthesis of oil, enzymes and vitamins; production of proteins; and promotion of quality and yield of crops. Mg is the key element for chlorophyll production and P utilization and mobility. It also acts as an activator and component of many plant enzymes and enhances iron utilization in plants (Maathuis 2009).

Plants also need small quantities of iron (Fe), chlorine (Cl), manganese (Mn), zinc (Zn), copper (Cu), boron (B) and molybdenum (Mo), known as trace elements or micronutrients because these elements are needed in a minute amount (Hochmuth and Hanlon 2010). As far as micronutrients are concerned, the role of only iron and zinc is described in the current chapter. Fe plays a very important role in reactions involving cell division and growth, boosting formation of chlorophyll and acting as an oxygen carrier (Sinha 2014; Rout and Sahoo 2015). Whereas, Zn promotes plant growth hormones and enzyme system, necessary for chlorophyll production and carbohydrate and starch formation (Broadly et al. 2007; Yadav 2010). It also helps in seed production. In addition to these above described nutrients, B, Mo, Cu, Mn and chlorine are also essential for the germination of pollen grains and formation of seed and cell wall (Hansch and Mendel 2009; Shukla et al. 2014). Besides, these micronutrients increase sugar content, intensify colour and improve flavour of fruits and vegetables. The deficiency of any of the macro- or micronutrient in soil affects the growth of the entire plant (White and Brown 2010).

The major nutrients are usually present in relatively large amount in the soil, but the plant-available fraction and the concentration in the soil solution may be insufficient to satisfy plant requirements (Rengel 2001). The excessive use of chemical fertilizers has generated several environmental problems including the greenhouse effect, ozone layer depletion and acidification of water. In soil most of the nutrients are in unavailable form and must be converted into available forms to be utilized by all plants. Natural nitrogen fixation is done under the influence of lightning (electric discharge in the clouds) and thunder; N_2 and O_2 of the air react to form nitric oxide (NO) but that is not sufficient. These problems can be solved by the use of beneficial microorganisms (biofertilizers) found in rhizosphere (Saadatnia and Riahi 2009). Microbes are potential alternate that could satisfy plant nutrient requirement mostly by solubilizing the complex forms of nutrients in soil. Soil microbes are of great importance in cycling of nutrients, not only by controlling the forms of these elements but also by regulating the quantities of nutrients available to plants. Within the rooting zone, plants take up mineral nutrients, which are recycled back into the soil when plants get decomposed. Weathering reactions also contribute to nutrient cycling (Huntington et al. 2000; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015, 2016a; Ahmad et al. 2016; Meena et al. 2015f, 2016a; Dotaniya et al. 2016; Jaiswal et al. 2016; Jha and Subramanian 2016).

These efficient microorganisms can dissolve minerals by direct or indirect action under aerobic and anaerobic conditions (Kurek 2002). These modes of action include fixation of N_2 and solubilization of P, Zn and K. Different microorganisms are used to provide different kind of nutrients in the soil. Species of cyanobacteria, *Azotobacter chroococcum*, *Azospirillum spp.*, *Acetobacter nitrogenifigens*, *A. peroxydans*, *Gluconacetobacter kombuchae*, *G. johannae*, *G. azotocaptans* and *G. diazotrophicus* (Kumar and Rao 2012; Shridhar 2012; Saravanan et al. 2007) can supply nitrogen to the plants by fixing the nitrogen from atmosphere, whereas *Bacillus megaterium*, *B. circulans*, *B. subtilis*, *B. polymyxa*, *B. sircalmous*, *Pseudomonas striata*, *P. fluorescens*, *Burkholderia* and *Enterobacter* species (Minaxi and Saxena 2010; Anand et al. 2016) are the phosphate-solubilizing bacteria that are used as biofertilizers to solubilize phosphorus in soil (Oteino et al. 2013). Several genera of rhizobacteria belonging to *Pseudomonas* and *Bacillus* (Jha et al. 2013; Saxena et al. 2013a, b), and fungi belonging to *Aspergillus* and *Penicillium* sp. (Saravanan et al. 2003; Jain et al. 2010; Saxena et al. 2013a, b), *Phomopsis* sp. (Sutjaritvorakul et al. 2013) and ericoid mycorrhizae, *Oidiodendron maius* Cd8 (Martino et al. 2003) were reported to solubilize zinc.

The metal solubilizing mechanisms include protons, chelated ligands and oxido-reductive systems present on the cell surface and membranes (Goteti et al. 2013). In addition, excretion of metabolites such as organic acids, proton extrusion, or production of chelating agent production of inorganic acids such as sulphuric acid, nitric acid and carbonic acid could also facilitate the solubilization. Muentz (1890) showed the first evidence of microbial involvement in solubilization of rock potassium. Prior studies have shown that the application of K-solubilizing bacteria (KSB) and K-bearing minerals increased the amount of available K in the soil and promoted plant uptake of K (Sheng et al. 2002; Sheng 2005; Basak and Biswas 2009; Abou-el-Seoud and Abdel-Megeed 2012).

Increasing the availability of nutrients in the rhizosphere, positively influence root growth and morphology, and promote other beneficial plant-microbe symbioses. Increases in plant growth parameters (plant biomass, nutrient uptake, tissue N content, plant height, leaf size and root length) were observed in different crops inoculated with *Pseudomonas*, *Azospirillum* and *Azotobacter* strains (Siddiqui and Shaukat 2002; Shaukat et al. 2006).

All essential nutrients required for plant growth with limited mobility in soils are transported to roots by diffusion, which is a very slow process. As a result, the management of these nutrients is very important. There are various basic physical, chemical and biological processes that control mobility of nutrients in soil. Plant community development depends to a great extent on the availability of soil nutrients, but recent studies underline the role of symbiotic, herbivorous and pathogenic soil biota (Deyn et al. 2004). A number of possible mechanisms of plant adaptation to soils with low nutrient availability have been suggested (Rengel 2001). The release of organic substances from roots is another key process which influences nutrient availability in the rhizosphere, production of chelating metabolites and redox activity. Rhizodeposition including root exudation can influence plant growth directly by making cations available for uptake through processes such as chelation or indirectly by influencing soil microbial activity (Parewa et al. 2014; Prakash and Verma 2016; Meena et al. 2016b; Priyadharsini and Muthukumar 2016; Das and Pradhan 2016; Dominguez-Nunez et al. 2016).

Simultaneous application of *Rhizobium* with phosphate-solubilizing microorganisms (PSMs) (Perveen et al. 2002, Demissie et al. 2013) or arbuscular mycorrhizal (AM) fungi (Zaidi et al. 2003; Bagyaraj et al. 2015) has shown to stimulate the plant growth more than with their sole inoculation in certain situations when the soil is P deficient. Phytohormones such as the indole acetic acid and the gibberellins are produced in great concentration in the soil through the endophytic fungi (*Phoma glomerata* LWL2 and *Penicillium* sp. LWL3) and earthworms which can also favour the leaching of the elements (Bertrand et al. 2015). The abscisic acid (ABA) triggered an increase of cytosolic Ca^{2+} in guard cells and initiated a signalling cascade that resulted in stomatal closure (Ache et al. 2000).

Sustainability
In recent decades, there has been remarkable concern about sustainability in agriculture to balance human needs while conserving natural resources and maintaining the quality of environment. Trend for sustainability in agricultural systems incorporates both improvements in food productivity and positive effects on environmental goods and services. Nutrient management has been an indispensable part of sustainable agriculture (Alley and Vanlauwe 2009). There are 20 nutrients which are recognized as essential for good crop growth. In order to ensure food security in developing countries, the strengthening of agricultural production systems towards supporting productivity of grains and income generation has utmost importance (Kumar et al. 2017; Meena et al. 2015a, b; Raghavendra et al. 2016; Zahedi 2016; Rawat et al. 2016; Yasin et al. 2016; Bahadur et al. 2016b). Thus soil nutrient management involves not only the physical properties and mineral structure of the soil

but also the balance between soil pathogens and beneficial microbes. Low and unbalanced fertilization leads to reduction of soil nutrients and crop yields and indirectly reduces soil structure which in turn promotes soil erosion (Singh and Ryan 2015).

On the other hand, beneficial microbes/biofertilizers inhabiting rhizosphere are likely to provide benefits to the crops in a sustainable manner. Integration of beneficial microbes to the soil increases nutrient availability, reduces disease and nutrient loss and helps in degradation of toxic compounds (Nyamangara et al. 2011). Also, these microbes facilitate nutrient uptake leading to plants' better quality, more production and lesser harm to environment. Reduction in use of chemical fertilizers, improved crop production and the development of commercial bioinoculants for the promotion of growth and yield of agronomically important plants would be the focus of the sustainable agriculture which can easily be accepted by farmers and help in managing a sustainable environmental system (Meena et al. 2015e, 2016c, d; Saha et al. 2016a; Yadav and Sidhu 2016; Teotia et al. 2016).

8.2 Macronutrients

8.2.1 Nitrogen

Among all the major plant nutrients, nitrogen (N) is often the most important for plant growth and crop yield. Although atmosphere contains ~78% nitrogen gas (N_2), but due to the stability of the gas, organisms cannot use it directly. N is present in all living organisms in proteins, nucleic acids and other biomolecules. It typically makes up around 4% of the dry weight of plant matter. Deficiency of N in soil results in stunted growth and yellowish leaves of plants. It has been studied that inadequate supply of available N frequently results in plants that have slow growth, depressed protein levels, poor yield of low-quality produce and inefficient water use (Mikkelsen and Hartz 2008; Hayat et al. 2010). There are two forms of N, which are classified as organic and inorganic. Organic form of N is found in compounds such as amino acids, nucleic acids, enzymes and proteins in cells of all living beings and humus. Inorganic forms include ammonia (NH_3), ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-) and nitrogen gas (N_2). Plants and microorganisms can use inorganic (available) forms. However, maximum N in the soil is present in the unavailable or organic form. Plants normally use nitrogen in only ammonium and nitrate forms (Saha et al. 2016b; Verma et al. 2014, 2015b; Meena et al. 2014a, 2016e; Sharma et al. 2016).

These forms are readily taken up by plants and are beneficial for plant growth. On the other hand, nitrite is considered as toxic to plants. N in the soil interacts with the atmosphere, soil particles, soil solution (the water that surrounds or moves through the soil), microorganisms and plants. All organisms use the ammonia (NH_3) form of nitrogen to manufacture all nitrogen-containing components necessary for life (Lindemann and Glover 2008; Mikkelsen and Hartz 2008).

There are several avenues for the conversion of N into their available forms. N fixation is the process in which atmospheric N_2 gas is converted to ammonium (NH_4^+). Microorganisms oxidize available NH_4^+ to NO_3^- in order to get energy, and the process is called biological nitrogen fixation (BNF). The microbial conversion of ammonium to nitrate (nitrification) is rapid and thus is the preferred form to be taken up by crops. Rhizobia (species of *Rhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Allorhizobium* and *Sinorhizobium*) and *Frankia* are two important N-fixing groups of bacteria, which have been studied extensively. *Frankia* forms root nodules on woody plants (Tilak et al. 2005), whereas rhizobia on legumes. There are multiple advantages of this kind of symbiosis. Plants can derive N for themselves, thus considerably increasing their protein content, it may provide nitrogen to associated crops of different plant species and it may leave N in the soil which in turn gets available for other crops (Chen 2006).

Biological Nitrogen Fixation

Biological N fixation can be represented by the given equation, and this reaction is performed exclusively by prokaryotes (the bacteria and related organisms):

$$N_2 + 8H^+ + 8e^- + 16\ \text{ATP} \xrightarrow{(\text{Nitrogenase})} 2NH_3 + H_2 + 16\text{ADP} + 16\ \text{Pi}$$

Symbiotic Nitrogen Fixation

Symbiotic N fixation in plants is the association between legumes and bacteria in the genus *Rhizobium*. N-fixing bacteria are very choosy in selection of roots of particular legume crops to infect, invade and form root nodules (Chandrasekar et al. 2005). Rhizobia form symbiotic relationships with legumes (bean family) such as clover, alfalfa, beans and peas by responding chemotactically to flavonoid molecules released by the legume host as signals (Viviene and Felix 2004). *Anabaena* and *Nostoc* species are good examples of symbiotic N-fixing cyanobacteria and are common symbionts in lichens, bryophytes (*Anthoceros*), aquatic fern (*Azolla*) and cycad roots. *Azolla* is frequently added to rice fields for N fixation.

Mechanism of Nitrogen Fixation

Rhizobia infect their hosts and induce root nodules by root hair penetration and infection thread formation by entering via wounds or sites of lateral root surfacing. Region of active N_2 fixation often appears red or pink in colour due to the presence of leghaemoglobin. The interaction between a particular strain of rhizobia and the legume is mediated by a "Nod factor" secreted by the rhizobia. Different strains of rhizobia produce different Nod factors and different legumes produce different specific receptors (Verma et al. 2015a; Meena et al. 2013b; Shrivastava et al. 2016; Velazquez et al. 2016; Bahadur et al. 2016a; Masood and Bano 2016). The process of root hair penetrations and infections thread formation was explained in great detail by Hirsch (1992) and Lhuissier et al. (2001). Infection starts with rhizobial attachment to emerging root hair of host. Afterwards, deformation and curling of the root hair occur with the root hair surface. Subsequently, the point of infection gets hydrolyzed to permit penetration of the rhizobia. Rhizobial strains then move down the root hair towards the root cortex, and they remain enclosed within a

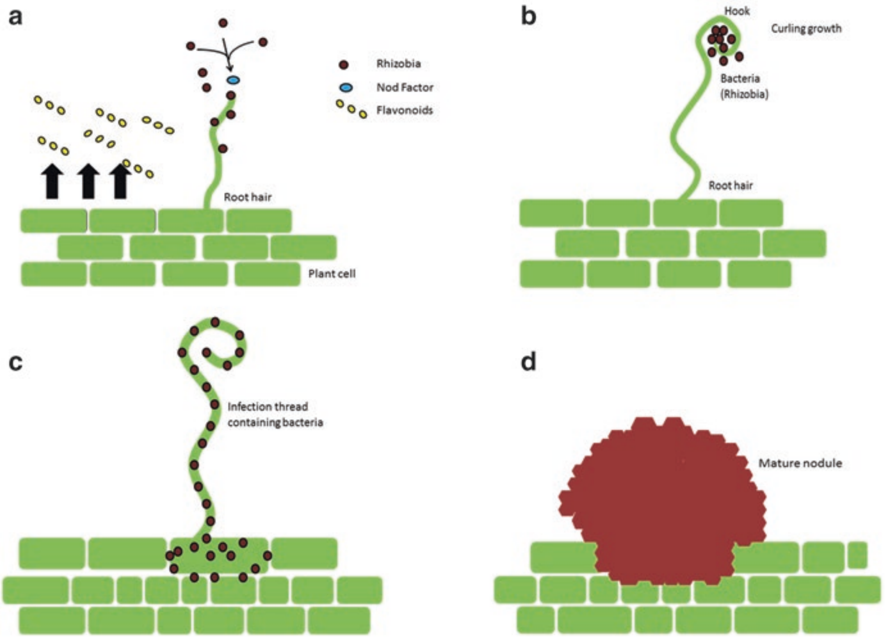

Fig. 8.1 (**a**–**d**) Nodule formation for nitrogen fixation. (**a**) Bacteria contact a susceptible root hair. (**b**) Bacteria infect root hair and cause curl. (**c**) Inner cortex and pericycle cells under division; infection thread carrying bacteria. (**d**) Mature nodule

plant-derived material. When the infection thread reaches a cell deep in the cortex, it bursts and the rhizobia are engulfed by endocytosis into membrane-enclosed symbiosomes.

The cortex cells then begin to divide rapidly forming a nodule and rhizobia multiply within the nodule cells (Fig. 8.1a–d). Thus, the development of nodules, while dependent on rhizobia, is well-coordinated. In addition, the legume host supplies the enzyme complex nitrogenase which consists of two proteins, an iron and a molybdenum-iron protein. The bacteroids need oxygen for its cellular respiration. However, nitrogenase is highly sensitive to oxygen. Thus the complex process is made easier by the oxygen carrier protein, i.e. leghaemoglobin which facilitates oxygen diffusion. In this way, the microsymbiont takes sufficient oxygen to generate energy within a low oxygen concentration. In contrast to *Rhizobium*, *Frankia* can form specialized vesicles in which nitrogenase is protected from oxygen (Meena et al. 2013c, 2014b, 2015c, 2015d; Sindhu et al. 2016; Singh et al. 2015, 2016).

Nitrification

In nitrification process *Nitrosomonas* and *Nitrococcus* convert NH_3 to NO_2^-, and then another soil bacterium, *Nitrobacter*, oxidizes NO_2^- to NO_3^- as shown:

$$NH_3 + 1.5\ O_2 \rightarrow NO_2^- + H^+ + H_2O$$

$NO_2^- + 0.5O_2 \rightarrow NO_3^-$ Assimilation

Assimilation is the process by which plants and animals incorporate the NO_3^- and ammonia formed through N fixation and nitrification because nitrates are easily assimilated by the plants.

Ammonification

Assimilation of N compounds generates large quantities of organic N, proteins, amino acids and nucleic acids. In ammonification or mineralization process, conversion of organic N into ammonia takes place. During ammonification a group of decomposing microorganisms (bacteria and fungi) break down nitrogenous wastes and organic matter found in animal waste and dead plants and animals and convert it to inorganic ammonia (NH_3) for absorption by plants as ammonium ions. The ammonia produced by this process is excreted into the environment and becomes available for either nitrification or assimilation.

Denitrification

At last NO_3^- is reduced to N gases (N_2 or N_2O) and lost to the atmosphere. This process is called denitrification which occurs through facultative anaerobes in anaerobic environments.

Non-symbiotic Nitrogen Fixation

Though the maximum biological nitrogen fixation is attributed to the microorganisms living symbiotically with higher plants, however certain free-living soil microorganisms (non-symbiotic and associated nitrogen fixers) are also responsible for the conversion of N to ammonium biologically. Non-symbiotic N fixation is known to be of great agronomic significance. Some important non-symbiotic nitrogen-fixing bacteria included the genera *Achromobacter*, *Acetobacter*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Azomonas*, *Bacillus*, *Beijerinckia*, *Clostridium*, *Corynebacterium*, *Derxia*, *Enterobacter*, *Herbaspirillum*, *Klebsiella*, *Pseudomonas*, *Rhodospirillum*, *Rhodopseudomonas* and *Xanthobacter* (Tilak et al. 2005).

Aerobic bacteria belonging to the genus *Azotobacter* represent a diverse group of free-living diazotrophic (with the ability to use N_2 as the sole nitrogen source) microorganisms commonly occurring in soil. The genus *Azotobacter* included six species, with *A. chroococcum* most commonly inhabiting various soils all over the world (Mahato et al. 2009). In free-living diazotrophs, the nitrogenase-generated ammonium is assimilated into glutamate through the glutamine synthetase/glutamate synthase pathway. Many free-living N-fixing cyanobacteria also carry out N fixation, e.g. *Anabaena*, *Nostoc*, *Aulosira*, *Cylindrospermum* and *Trichodesmium*. These are also important ecologically as they live in water-logged sods where denitrifying bacteria can be active. *Aulosira fertilissima* is the most active N fixer in rice fields, while *Cylindrospermum* is found to be active in sugarcane and maize fields.

8.2.2 Phosphorus

P is the second important key element and major growth-limiting nutrient after N. Though it is highly abundant in soils in both organic and inorganic forms, its availability is limited due to its insoluble occurrence. The P content in average soil is about 0.05% (w/w), but only 0.1% of the total P is available to plants because of its poor solubility and quick fixation in soil (Illmer and Schinner 1995). Phosphorus accounts for about 0.2–0.8% of the plant dry weight. The insoluble forms of P such as tricalcium phosphate $(Ca_3PO_4)_2$, aluminium phosphate (Al_3PO_4), iron phosphate (Fe_3PO_4), etc. may be converted into soluble P by P-solubilizing organisms inhabiting different soil ecosystems (Gupta et al. 2007; Song et al. 2008; Khan et al. 2013; Sharma et al. 2013).

Solubilization

Some microorganisms are known to be involved in the solubilization of insoluble phosphate (Hong et al. 2006). It has been studied that microbial biomass assimilated soluble P and prevented it from adsorption or fixation (Khan and Joergensen 2009). Release of P by phosphate-solubilizing microorganisms from insoluble and fixed/adsorbed forms is considered as an important aspect regarding P availability in soils. Though P is present in immobilized form (Henry and Smith 2006), it can be made available either by absorption, chemical precipitation or both processes (Tilak et al. 2005). Release of root exudates such as organic ligands can also alter the concentration of P in the soil solution (Hinsinger 2001). Some bacterial species have mineralization and solubilization potential for organic and inorganic P, respectively (Hilda and Fraga 2000; Khiari and Parent 2005). The production of organic acids by microorganisms seems to be the main cause for solubilization of inorganic phosphatic compounds into the forms available to plants, but the other factors such as CO_2, H_2S and alkalinity production have also been implicated. Phosphate solubilization takes place through various microbial processes/mechanisms including proton extrusion, release of organic anions and production of siderophores and acid phosphatase (Yadav and Tarafdar 2001) or alkaline phosphatase (Tarafdar and Claassen 1988) enzymes. *Enterobacter agglomerans* was found to have capacity to solubilize hydroxyapatite and hydrolyze the organic P (Kim et al. 1998).

Of the various strategies adopted by microbes, the involvement of organic acids (OA) secreted by microorganisms has been a well-recognized and widely accepted theory as a principal means of P solubilization. Inorganic forms of P are solubilized by a group of heterotrophic microorganisms, which excrete low molecular mass organic acids in which hydroxyl and carboxyl groups of acids chelate cations (Al, Fe and Ca) and decrease the pH of soil to release P in soil (He et al. 2002; Stevenson 2005). Various studies have identified and quantified organic acids and defined their role in the solubilization process (Maliha et al. 2004; Khan et al. 2010; Marra et al. 2012). The organic acids reported in P solubilization are 2α-ketogluconic acid, lactic acid, succinic acid, formic acid, malic acid, citric acid, oxalic acid, fumaric acid, tartaric acid, propionic acid, acetic acid, isobutyric acid, isovaleric acid, valeric acid and A-isocaproic acid (Chen et al. 2006; Yi et al. 2008; Khan et al. 2013).

However, according to Deubel et al. (2000), gluconic and keto gluconic acids were the major acids which played key role in P solubilization. The OA produced by many P solubilizers, for example, bacterial cultures (species of *Pseudomonas*, *Enterobacter*, *Arthrobacter*, *Bacillus*, *Azotobacter*, *Rhodococcus*, etc.) or fungi (species of *Aspergillus*, *Penicillium*, *Fusarium*, *Trichoderma*, etc.), in the natural environment or under in vitro conditions chelate mineral ions or decrease the pH (Pradhan and Shukla 2005; Rawat et al. 2015; Saxena et al. 2016). Consequently, the acidification of microbial cells and their surrounding led to the release of P ions from the P mineral by H^+ substitution for Ca^{2+} (Goldstein 1994; Mullen 2005; Trivedi and Sa 2008).

Inorganic acids such as hydrochloric acid can also solubilize phosphate but are less effective as compared to organic acids at the same pH (Kim et al. 1997). P desorption potential of different carboxylic anions lowers with decrease in stability constants of Fe or Al organic acid complexes (KAl or KFe) in the following order: Citrate > Oxalate > Malonate/Malate > Tartrate > Lactate > Gluconate > Acetate > Formiate (Ryan et al. 2001).

P solubilization is also carried out by a large number of saprophytic bacteria and fungi acting on sparingly soluble soil phosphates, mainly by chelation-mediated mechanisms (Whitelaw 2000). Many aerobic PSMs excrete 2-ketogluconic acid which acts as powerful chelator of calcium and thus solubilize various forms of hydroxyapatites, fluorapatites and aluminium phosphate. Humic and fulvic acids also release during microbial degradation of plant remains and chelate Ca, Fe and aluminium present in insoluble phosphates.

Organic anions and associated protons are effective in solubilizing precipitated forms of soil P (e.g. Fe-P and Al-P in acid soils, Ca-P in alkaline soils), chelating metal ions associated with complexed forms of P and facilitating the release of adsorbed P through ligand exchange reactions (Jones 1998). According to Deubel et al. (2000) the solubilization of Ca-P resulted from the combined effect of pH decrease and carboxylic acid synthesis. Carboxylic acids were mainly responsible for Al-P and Fe-P solubilization (Khan et al. 2007; Henri et al. 2008). Carboxylic anions replaced phosphate from sorption complexes by ligand exchange thus chelated both Fe and Al ions associated with phosphate (Whitelaw 2000).

The term mycorrhiza (phosphate absorbers) denotes “fungus roots”. It is a symbiotic association between host plants and certain group of fungi at the root system, in which both are benefited by obtaining the needed nutrients, with the help of the fine absorbing hyphae of the fungus. There are six genera of fungi that contain species, which are known to produce Arbuscular mycorrhizal fungi (AMF) with plants. Two of these genera, *Glomus* and *Sclerocytis*, produce chlamydospores only, whereas four genera form spores that are similar to azygospores: *Gigaspora*, *Scutellospora*, *Acaulospora* and *Entrophospora.*

Several reports have examined the ability of different bacterial and fungal species to solubilize insoluble inorganic phosphate compounds, such as tricalcium phosphate, dicalcium phosphate, hydroxyapatite and rock phosphate. Strains from the bacterial genera *Pseudomonas*, *Bacillus*, *Rhizobium*, *Burkholderia*, *Achromobacter*, *Agrobacterium*, *Micrococcus*, *Aereobacter*, *Flavobacterium* and

Erwinia were found to be the most powerful P solubilizers (Whitelaw 2000). *Bacillus megaterium*, *B. circulans*, *B. subtilis*, *B. polymyxa*, *B. sircalmous*, *Pseudomonas striata* and *Enterobacter* could be referred to as the most cited strains in literature (Subbarao 1988; Kucey et al. 1989). It has been well studied that mixed cultures of PSMs (*Bacillus*, *Streptomyces*, *Pseudomonas*, etc.) were more effective in mineralizing organic phosphate than single strains (Molla et al. 1984). On the other hand, the most efficient phosphate-solubilizing fungal genera were *Aspergillus*, *Penicillium*, *Trichoderma*, *Eupenicillium*, *Talaromyces*, yeast etc. (Mittal et al. 2008; Oliveira et al. 2009; Ogbo 2010). A nemato-fungus *Arthrobotrys oligospora* has also been demonstrated by Duponnois et al. (2006) to solubilize the phosphate rocks.

Mineralization (Enzymatic Degradation of Complex Organic P Compounds)
Conversion of organic forms of phosphatic compounds to utilizable forms with different microbes by mineralization process is well studied. Numerous soil microbes and rhizosphere microflora possess the ability to transform organic P into soluble forms of P (Rodriguez et al. 2006). The mineralization process is mediated by the enzymes especially phosphatases (Yadav and Tarafdar 2003; Aseri et al. 2009) and phytases (Maougal et al. 2014), released by the soil microbes. *Bacillus* and *Streptomyces* spp. are able to mineralize very complex organic phosphates by production of extracellular enzymes like phosphoesterase, phosphodiesterase, phytase and phospholipase. The enzyme phosphatases (e.g. acid and alkaline phosphatases) released exterior to the cell (exoenzymes) is non-specific in nature and uses organic P as a substrate to convert it into inorganic form (Beech et al. 2001). Acid phosphatases (To-O et al. 2000) on the other hand are enzymes which are commonly found in fungi (Abd-Alla and Omar 2001), e.g. *Colletotrichum graminicola* (Schadeck et al. 1998), and degradation of organic P mediated by phosphatases varies greatly among different fungi (Guimaraes et al. 2006). Almost half of the microorganisms in soil and plant roots possess P mineralization potential under the action of phosphatases (Tarafdar et al. 1988). Production of acid phosphatases was considered as principal mechanism for mineralization of soil organic P by Hilda and Fraga (2000). The largest portion of extracellular soil phosphatases is derived from the microbial population (Dodor and Tabatabai 2003). Another well-known P-dissolving enzyme is phytase, which degrades phytate, and further causes release of P from phytic acid (Gaind and Nain 2015) as shown:

$$\text{Phytic acid} + 6H_2O \rightarrow \text{Inositol} + 6H_3PO_4$$

Plants and microorganisms increase exudation of P-hydrolyzing enzymes (phosphatases and phytase) under P deficiency. These enzymes break down organic P, thus making P available for uptake. Phosphatases are not effective in mineralizing phytate (inositol hexaphosphate), the major form of organic P in many soils. However, phytase specifically catalyses the breakdown of phytate.

Immobilization

Assimilation of P by microorganisms is also known as P immobilization. In this process inorganic ions are incorporated into microbial cell material. There are sizeable populations of PSMs in soil and plant rhizosphere which compete with other bacteria and even with plants for the assimilation of available phosphate and accumulate more phosphorus than plant. This stored phosphate is then released into the environment under different stress conditions or after mortality of PSMs, and released P is taken up by the plants or microbes to fulfil their phosphorus requirement.

Carbon Dioxide

Carbon dioxide (CO_2) produced by microorganisms is also considered as an effective mechanism for promoting the availability of phosphorus and its uptake by plants. It was believed by the early researchers in this field that CO_2 produced by plant roots and microflora was responsible for solubilization of inorganic phosphates in soils (Stoklasa and Ernest 1908). Later, it was found that CO_2 increased the availability and absorption of phosphates in calcareous soils (Truog 1912). Solubilization of inorganic P by bacteria and fungi is due to water charged with CO_2 reacts with $Ca_3\ (PO_4)_2$ to release soluble P (Moreau 1959). PSMs are well known to produce acidity by CO_2 evolution (carbonic acid); this type of acidification takes place generally in solubilization of calcium phosphates. The reactions may be summarized as follows:

$$Ca_3\left(PO_4\right)_2 + CO_2 + H_2O \rightarrow 2CaHPO_4 + CaCO_3$$
$$Ca_3\left(PO_4\right)_2 + 2CO_2 + 2H_2O \rightarrow Ca\left(H_2PO_4\right)_2 + 2CaCO_3$$

Inorganic Acids

Nitric or sulphuric acids may be produced due to oxidation of nitrogenous compounds or inorganic compounds of sulphur by nitrifying bacteria and *Thiobacillus* spp., respectively. These acids react with chemical phosphates and convert them into soluble forms. The possible reactions may be summarized as

$$Ca_3\left(PO_4\right)_2 + 2HNO_3 \rightarrow 2CaHPO_4 + Ca\left(NO_3\right)_2$$
$$Ca_3\left(PO_4\right)_2 + 4HNO_3 \rightarrow Ca\left(H_2PO_4\right)_2 + 2Ca\left(NO_3\right)_2$$
$$Ca_3\left(PO_4\right)_2 + H_2SO_4 \rightarrow 2CaHPO_4 + CaSO_4$$
$$Ca_3\left(PO_4\right)_2 + 2H_2SO_4 \rightarrow Ca\left(H_2PO_4\right)_2 + 2CaSO_4$$

Hydrogen Sulphide

An additional mechanism involved for ferric phosphate solubilization is hydrogen sulphide (H_2S) production. Few PSMs under anaerobic conditions liberate H_2S which reacts with insoluble ferric P to release solubilized ferrous sulphate. H_2S thus formed reduces ferric phosphate to black ferrous sulphide with the release of available phosphate as shown in the reaction:

$$FePO_4 + H_2S \rightarrow FeS + H_2PO_4^-$$

Under anaerobic conditions H_2S may be formed by the reduction of sulphur-containing amino acids by several heterotrophic microorganisms or from sulphate by sulphur-reducing bacteria of the genus *Desulfovibrio*.

8.2.3 Potassium

The potassium (K) is the third major essential macronutrient for plant nutrition, growth and development. Its demand for agricultural use is growing steadily at 3–3.5% per annum (Manning 2010). Ninety-eight percent of total K in soil is in the unavailable mineral forms (Sparks 1987). Some aluminosilicate minerals such as feldspars and micas constitute the biggest K pool in soils; however K contained in this pool is mostly not available to plants (Barre et al. 2007; McAfee 2008). Due to its high solubility in water, it leaches out from rocky or sandy soils, which results in K deficiency. Further, K deficiency may result in higher risk of pathogens, wilting, necrosis, chlorosis, brown spotting and higher chances of damage from frost and heat (Jagessar and Allen 2012). Consequently, K deficiencies become a problem because K decreases easily in soils due to crop uptake, runoff, leaching and soil erosion (Sheng and Huang 2002). It has been studied by Oborn et al. (2005) that the fixation process of K is relatively fast, whereas the release of fixed K is very slow due to the strong binding force between K and clay minerals. Plants can absorb K only in soluble form and the availability of K to crop plants in soil is generally low. There are several mechanisms for K solubilization that have been well studied. These pathways include acid hydrolysis, secretion of soluble small molecules and insoluble macromolecules, chelation of mineral elements via the secretion of polymers bound in the cell membrane and direct biophysical forces which can fracture mineral grains to decrease particle sizes and generate fresh and more reactive surfaces.

Microbial Mineral Weathering

Microorganisms play a key role in the weathering of major types of rocks releasing various elements they need as nutrients (Calvaruso et al. 2006). Microbial weathering is a known and potential mechanism that includes redox reactions through the production of organic acids which ultimately lead to weakening of chemical bonds in minerals for promoting mineral dissolution (Harley and Gilkes 2000) and chelating molecules for mineral degradation (Lian et al. 2008). Bacteria can produce a wide range of low molecular weight organic exudates such as oxalates and citrates (Neaman et al. 2005). Some soil microorganisms such as *Pseudomonas* spp., *Burkholderia* spp., *Acidithiobacillus ferrooxidans*, *Bacillus mucilaginosus*, *B. edaphicus* and *B. megaterium* were able to release K from K-bearing minerals by excreting organic acids (Sheng et al. 2002). These organic acids either directly dissolve rock K (K-containing primary minerals) or chelate the primary mineral's silicon ions to bring the K into solution (Bennett et al. 1998; Basak and Biswas 2009).

The organic acids are known to facilitate the weathering of soil minerals through the formation of metal-organic complexes and by enhancing the exchange of H^+ for K^+ (Hinsinger and Jaillard 1993; Wang et al. 2007, 2011). Major organic acids released are citric and oxalic acids by maize (Kraffczyk et al. 1984), tartaric acid by pak choi and radish (Chen et al. 2000) and malic acid by oil seed rape (Zhang et al. 1997).

In addition to organic acids, the H^+ concentration in soil solution (soil pH) also plays a key role in K release from clay minerals. Similarly, amino acids detected in root exudates of wheat and sugar beet were found to enhance the release of K from clay minerals (Rengel and Damon 2008). Also, microorganisms (such as bacteria, algae, fungi and protozoa) used carbonic acid formed from CO_2 to attack the mineral surface, promoting the chemical weathering of rocks and minerals (Gadd 2007; Park et al. 2009). Some exopolymers exuded by bacteria, including slimes, sheaths or biofilms and even dormant spores, have property to secrete one or more metabolic products which further react with ions or compounds in the environment, resulting in the deposition of mineral particles. The depletion of K in rhizosphere soil solution below a threshold level (10–20 M) has been reported to be a key signal to activate the root exudation mechanism (Hosseinpur et al. 2012; Schneider et al. 2013).

The rhizosphere microorganisms play a pivotal role in the enhancement of crop production by the solubilization of unavailable form of metal into available form. Zhang et al. (2011) and Sangeeth et al. (2012) found KSB isolate K03 and *Paenibacillus glucanolyticus* IISRK2 in the tobacco and black pepper rhizosphere, respectively. Earlier, *Bacillus laterosporus* K77 could also solubilize K very efficiently (Luo et al. 2011). Isolation of K-solubilizing microorganisms (KSMs) from different rhizosphere soil such as sugarcane, tobacco and maize was evaluated by Zhang and Kong (2014), Setiawati and Mutmainnah (2016) and Parmar et al. (2016). Concurrently, diversity of KSMs and their interactions with plants were well described by Velazquez et al. (2016). Besides, certain microbes, viz. *Thiobacillus ferrooxidans*, *T. thiooxidans* and *L. ferrooxidans*, were found to use bioleaching mechanism for the release of K. The enhancement of K availability by rhizosphere microorganism was adequately reviewed by Meena et al. (2014) recently.

The solubilization of K from aluminosilicate minerals was also observed by some fungi (Glowa et al. 2003). Many rock-inhabiting fungi are melanised; melanin pigmentation conferred extra-mechanical strength to the hyphae to penetrate the rock surface and crevices (Dornieden et al. 1997; Sterflinger and Krumbein 1997) and also offered protection from metal toxicity (Gadd 1993). It was demonstrated by Yuan et al. (2000) that ectomycorrhiza could mobilize K from clay minerals and thus enhanced K uptake by plants. There are reports showing the promotion of overall plant growth by KSB (Egamberdiyeva and Hoflich 2003; Basak and Biswas 2009). It has been suggested that rhizosphere microorganisms contribute in solubilization of fixed forms of soil minerals K in the soil and inoculation of such KSMs in soil has shown to improve solubilization of insoluble mineral K and enhancement in crop productivity. Influence of potassium-solubilizing bacteria on crop productivity and quality of tea (*Camellia sinensis*) was studied by Bagyalakshmi et al. (2012). A related study on KSMs in evergreen agriculture done by Meena et al. (2016a, b, c, d, e) revealed the rhizosphere microorganisms as crucial components of sustainable agricultural ecosystems which were found to be involved in sustaining soil as well as crop productivity under organic matter decomposition, nutrient transformations and biological nutrient cycling.

K fixation and release are greatly influenced by the relative amounts of these fractions and the kind of clay minerals present in the soil. Mineral dissolution studies with cultures of bacteria and fungi showed a dramatic increase in the dissolution rates of feldspar, biotite, quartz, apatite and other minerals due to acidic microbial byproducts (Callot et al. 1987; Paris et al. 1996). Microorganisms like *Aspergillus niger*, *Bacillus extroquens* and *Clostridium pasteurianum* were found to grow on muscovite, biotite, orthoclase microclase and mica in vitro (Archana et al. 2013). Lian et al. (2008) reported K release from a K-bearing mineral (K-feldspar and illite) by thermophilic strain of *Aspergillus fumigatus*, and Glowa et al. (2003) evaluated the ability of fungus *Piloderma* sp. in extracting K from biotite, microcline and chlorite and found that the species was able to acquire K from three minerals out of which biotite was more biodegradable. Biofilm (a thin but strong layer of mucilage adhering to a solid surface and containing a community of bacteria and other microorganisms) helped to accelerate weathering of minerals like biotite and anorthite (Rawat et al. 2016).

Biofilms and biocrusts are normally supposed to cause higher weathering rates due to biodegradation (Warscheid and Braams 2000). KSMs, namely, *Bacillus edaphicus*, *B. circulans*, *Paenibacillus* sp., *Acidithiobacillus ferrooxidans*, *Pseudomonas* spp. and *Burkholderia* spp., have been reported to release K from K-bearing minerals in soil (Sheng et al. 2008; Lian et al. 2002; Rajawat et al. 2012; Liu et al. 2012; Basak and Biswas 2012; Singh et al. 2010). Recently, a high temperature resistant potassium solubilizing bacterial strain was isolated from earthworm's gut which was further demonstrated as *Streptomyces* sp. (Liu et al. 2016).

8.3 Micronutrients

8.3.1 Zinc

Zn is one of the vital micronutrient required relatively in small concentrations (5–100 mg kg^{-1}) for optimum plant growth and plays an important role in metabolism (Hughes and Poole 1991). Natural level of Zn in the soil ranges from 10 to 300 mg kg^{-1} with an average of 50 mg kg^{-1} (Mulligan et al. 2001). Soils are naturally rich in total Zn but poor in available forms. It is estimated that 30% of the world‘s cultivated soils are deficient in Zn (Suzuki et al. 2006).

Several genera of rhizobacteria belonging to species of *Pseudomonas*, *Bacillus*, *Burkholderia* and *Acinetobacter* were reported to solubilize Zn (Vaid et al. 2014). Recently, novel zinc-solubilizing bacteria were isolated from agricultural land and identified as *Stenotrophomonas maltophilia* (ZSB-1), *Mycobacterium brisbanense* (ZSB-10), *Enterobacter aerogenes* (ZSB-13), *Pseudomonas aeruginosa* (ZSB- 22) and *Xanthomonas retroflexus* (ZSB-23) (Kumari et al. 2016). A Zn-solubilizing bacterium, *Bacillus* sp., was used as biofertilizer for Zn in soils where native Zn was higher or in conjunction with insoluble cheaper Zn compounds like zinc oxide (ZnO), zinc carbonate ($ZnCO_3$) and zinc sulphide (ZnS) instead of costly zinc sulphate (Mahdi et al. 2010). Raj (2007) found that Zn can also be solubilized by *B. subtilis*, *Thiobacillus thiooxidans* and *Saccharomyces* sp. and can be used as biofertilizers for solubilization of fixed Zn.

Plants take up Zn as divalent cation (Zn^{2++}). The solubility of Zn in soils is affected by pH, amount of metal, cation exchange capacity (CEC), organic matter content and soil mineralogy (Martinez and Motto 2000). Microorganisms solubilize the metal forms by protons, chelated ligands and oxidoreductive systems present on the cell surface and membranes. There are two main mechanisms of Zn fixation: one operates in acidic soils and is closely related to cation exchange, and the other operates in alkaline conditions where fixation takes place by means of chemisorptions (chemisorptions of Zn on calcium carbonate formed a solid solution of $ZnCaCO_3$) and by complexation by organic ligands (Alloway 2008).

The Zn solubilization could also be due to production of organic acids, viz. gluconic acids (especially 2-ketogluconic acids). A number of organic acids such as acetic, citric, lactic, propionic, glycolic, oxalic, gluconic acid, etc. have been considered due to their effect in pH lowering by microorganisms (Cunningham and Kuiack 1992). Organic acids secreted by microflora increase soil Zn availability in two ways; they are probably exuded both with protons and as counterions and, consequently, reduce rhizosphere pH. The release of organic acids that acidify the microenvironment near rhizosphere is thought to be a major mechanism for Zn solubilization.

8.3.2 Iron

Fe is an essential plant nutrient and is required for a variety of metabolic processes in almost all living organisms. It is a metal ion found in proteins (Shi et al. 2005) and plays important roles for fundamental biological processes like respiration, photosynthesis, N_2 fixation, methanogenesis and DNA synthesis (Andrews et al. 2003). Despite being one of the most abundant elements in the earth's crust, the bioavailability of iron in soil is limited because of very low solubility of the Fe^{3+} ions. Fe deficiency in most soils was not triggered by low total Fe concentrations where soils contain between 1 and 6% total Fe, but by low Fe availability (Kraemer 2004). A limiting factor of Fe availability was found to be the low solubility and slow dissolution kinetics of Fe-bearing minerals (Kraemer 2004). Fe can exist in two different readily interconvertible oxidation states (reduced ferrous and oxidized ferric) under physiological conditions.

Siderophore Production

The availability of Fe for microbial assimilation in various microenvironments, such as the rhizosphere, is extremely limiting. Therefore, to survive in such environments, organisms secrete iron-binding ligands (siderophores), which can bind the ferric iron and make it available to the host microorganisms. The role of such Fe-chelating siderophores in plant growth promotion is well established (Katiyar and Goel 2004). Siderophores (iron-bearers) are low molecular weight (500–1000 daltons) metabolites with a high affinity for Fe^{+3} and low affinity for Fe^{+2}. In the aerobic environment, Fe accumulates in common mineral phases such as iron oxides and hydroxides and hence becomes inaccessible to organisms. Siderophores act as solubilizing agents for iron from minerals or organic compounds under conditions of iron starvation (Miethke and Marahiel 2007; Indiragandhi et al. 2008). Siderophores are highly electronegative and bind Fe (III), preferentially forming a hexacoordinated complex. The Fe ligation groups have been tentatively classified into three main chemical types; hydroxamate (aerobactin and ferrichrome), catecholates/phenolates (enterobactin) and hydroxyl acids/carboxylates (pyochelin). Some siderophores contain more than one of the three Fe-chelating groups.

However, siderophores are usually classified by the ligands used to chelate the ferric iron. Citric acid can also act as a siderophore. However, siderophores bind Fe (III) more effectively than organic acids such as oxalic and citric acids (Kalinowski et al. 2000).There are more than 500 different siderophores which are produced by bacteria, fungi and graminaceous plants. Microorganisms produce a great number and variety of siderophores, whereas few phytosiderophores are produced by Fe-efficient grasses. Nearly all aerobic and facultative anaerobic bacteria produce siderophores with a few exceptions (Kraemer 2004). There is a well-identified group of bacteria, widely known as magnetotactic bacteria, which accumulate large amounts of extracellular iron for the synthesis of intracellular magnetite or greigite crystals. The intracellular iron content of *Magnetospirillum gryphiswaldense* may account for up to 4% of the dry weight (Faivre and Schuler 2008), which is around 150 times higher than the iron content of non-magnetic bacteria such as *Escherichia coli* (0.027% iron per dry weight) (Abdul-Tehrani et al. 1999).

Out of all siderophore compounds isolated, the majority have been either hydroxamates or phenolates-catecholates (Kraemer 2004). Fungi generally produce siderophores with hydroxamate Fe (III)-binding groups and bacteria produce siderophores with catecholate Fe (III)-binding groups (Neubauer et al. 2002). Pathogenic bacteria, *Bacillus anthrax*, released two siderophores, bacillibactin and petrobactin, to scavenge ferric iron from Fe protein. Mugineic acid is a phytosiderophore with carboxylate-, hydroxyl- and amine-binding groups (Kraemer 2004).

8.4 Conclusions

The available amount of nutrients in soil is generally not enough for plant growth. As a result, the nutrients which are utilized in the large amounts by crops are commonly added in the form of chemical fertilizers nowadays. The use of living microorganisms (biofertilizer) on the other hand accelerates mineralization of organic residues in soil, therefore makes the nutrients more available. The nutrient management strategies to improve nutrient solubilization, operation at depressed pH and/or the operating conditions are effective towards enhanced availability of nutrients in soil. Use of efficient microorganisms not only helps in solubilizing nutrients successfully but also improves the growth and yield of plants. Thus microbial inoculants are utmost approach and a viable alternative to overcome limitations of synthetic fertilizers and restoration of the fertility of soil. Moreover, application of beneficial microorganisms/biofertilizers in consortium along with soil amendments could be a better choice for farmers for sustainable crop production.

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Chapter 9
Role of PGPR in Sustainable Agriculture: Molecular Approach Toward Disease Suppression and Growth Promotion

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Abstract Plant concomitant bacteria play a substantial part in plant growth promotion and disease suppression. However, to deliver the best up to their capacity, efficient colonization of the plant roots is of utmost importance. The microbes introduced to the soil, either as a single inoculant or as a consortium, interact with host plant and initiate cascade of reactions which result in plant growth and defense responses. PGPR produce extensive variety of secondary metabolites, allelochemicals, which may work as starting signals or enhancing the necessary reactions. Their action methodology and molecular machineries offer a great cognizance for their application in control of crop diseases. These genes are either upregulated or downregulated, and their expression decides the fate of plant growth and mechanism by which plant resists the disease. Number of genes which will be expressed, encode several metabolites responsible for better growth and synthesis of antimicrobial compounds. Recent developments in expression profiling methods and availability of extensive genome sequence data have permitted important advancements in understanding of responses toward disease resistance in plants. In the later part, we discussed how DNA microarray fits with the current part of PGPR in plant growth promotion and disease resistance. Overall, this chapter will help to better understand the molecular mechanisms behind plant and rhizobacteria interactions.

Keywords PGPR · Microarray · Microbial consortium · Allelochemicals

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9.1 Introduction

To improve crop production and accomplish food security, synthetic fertilizers have largely been used highly in agricultural practices to balance nutrient deficiencies of soils and greater food production. Due to repeated use, such chemical fertilizers have lethal impact on soil fertility and crop productivity. The situation is alarming now; thus, scientists want to find low-cost, environmentally caring, and easy-to-operate choices to overcome fertilizer toxicity problems. For sustainable agriculture, the use of biofertilizer is among the important components for improving soil fertility (Zaidi et al. 2015). It is important to exploit renewable input which can maximize the ecological benefits and minimize the environmental hazards (Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2016b). Plant growth-promoting rhizobacteria (PGPR) attracted most of the attention due to their low cost, easy access, and simple mode of application. PGPR can be used either alone or in consortia and always resulted in incredible positive impact on agricultural production (Dinesh et al. 2015).

PGPR have been characterized in their potential to associate with several microbes including arbuscular mycorrhizal fungi (AMF) and develop a multilateral interaction to enhance growth as well as yield. In association with the soil microorganism irrespective of AMF, PGPR are capable of altering plant growth by means of several mechanisms as well as increasing soil nutrient availability (Ghignone et al. 2012; Pii et al. 2015). However few studies have been conducted to study the metabolic pathways of plant when inoculated with either AMF or additional PGPR strains, and most of the studies have been performed in controlled sterilized environment and carried out under greenhouse (Lekberg and Koide 2014; Glaeser et al. 2015) and to examine the active compounds (Walker et al. 2011; Salvioli et al. 2015).

Biotic and abiotic stresses are one of the major limitations on agricultural efficiency globally, and these problems are increasing day by day. Several extenuation strategies are needed to cope with these stresses. PGPR could play a substantial role in mitigation of various stresses in plants (Kumar et al. 2015, 2016a Ahmad et al. 2016; Meena et al. 2016a, b; Parewa et al. 2014; Prakash and Verma 2016; Jha and Subramanian 2016). These advantageous microorganisms colonize the rhizosphere of plants and introduce tolerance by producing exopolysaccharides, plant hormones, and volatile compounds and encouraging buildup of osmolytes, antioxidants, and enzymes, production of siderophore, synthesis of antibiotics and/or fungicidal compounds, upregulation or downregulation of respective genes, and modification in root morphology in response to biotic and abiotic stresses (Verma et al. 2013; Vurukonda et al. 2015).

9.1.1 Plant Growth-Promoting Rhizobacteria (PGPR)

A zone surrounding plant roots having multifaceted relations amid the soil microbes and the plant is known as rhizosphere. For the very first time, the term “rhizosphere” was coined by Hiltner (1904) as a region of supreme microbial actions. This zone has improved physical, chemical, and biological properties which have sufficient influence to alter the number of microbes, their diversity, and bustles in rhizospheric environment (Dutta and Podile 2010). Species of plant and their adjoining fundamental environmental conditions have a vital part in determination of the root microbiome (Zachow et al. 2014; Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Meena et al. 2015a, f; Dotaniya et al. 2016; Jaiswal et al. 2016).

This zone may contain both advantageous and detrimental contents released from microbes beneath, and they have the capacity to alter plant growth, morphology, and crop yield. The rhizospheric bacteria are termed as rhizobacteria which are free-living root-associated bacteria that either inhabit on the root surface or inside the plant roots (Kloepper and Beauchamp 1992), and many of them are advantageous for plant growth and health (Parray et al. 2016). These particular beneficial rhizobacterial species are classified as plant growth-promoting rhizobacteria (PGPR) which are helpful in upsurging plant developments without creating any environmental contamination (Calvo et al. 2014). However, other advantageous rhizobacteria include species of symbiotic rhizobia, mycorrhizal fungi, and some actinomycetes. They release certain plant growth substances and increase accessibility of nutrients for the plants (Persello-Cartieaux et al. 2003; Raghavendra et al. 2016; Zahedi 2016; Meena et al. 2015b, 2016c; Rawat et al. 2016; Yasin et al. 2016; Das and Pradhan 2016; Dominguez-Nunez et al. 2016).

Different genera of bacteria *Pseudomonas*, *Enterobacter*, *Bacillus*, *Variovorax*, *Klebsiella*, *Burkholderia*, *Azospirillum*, *Serratia*, and *Azotobacter* were recognized as PGPR, among them *Bacillus* and *Pseudomonas* sp. were mostly reported (Nadeem et al. 2010; Verma et al. 2014; Zaidi et al. 2015; Huang et al. 2016; Kejela et al. 2016). The term PGPR can be subdivided in two groups, extracellular PGPR (ePGPR) and intracellular PGPR (iPGPR) based on their location. PGPR present in the rhizospheric soil or present in rhizoplane are termed as ePGPR, whereas PGPR which are found in the inner side of roots or nodule-like structures are termed as iPGPR (Figueiredo et al. 2011). Mostly known ePGPR are *Flavobacterium*, *Agrobacterium*, *Serratia*, *Azospirillum*, *Caulobacter*, *Burkholderia*, *Pseudomonas*, *Arthrobacter*, *Bacillus*, *Erwinia*, *Micrococcus*, *Chromobacterium*, *Azotobacter*, etc. Best known iPGPR are *Bradyrhizobium*, *Allorhizobium*, *Rhizobium*, *Azorhizobium*, and *Mesorhizobium* (Bhattacharyya and Jha 2012; Gopalakrishnan et al. 2015; Saha et al. 2016a, b; Yadav and Sidhu 2016; Meena et al. 2014a, 2015e, 2016d; Verma et al. 2014, 2015b; Sharma et al. 2016; Teotia et al. 2016; Bahadur et al. 2016b).

PGPR advance growth of plant by any of the two mechanisms, direct or indirect, even though the differences between these two are not clear (Ashraf et al. 2013). Direct mechanisms have activities like (1) nitrogen fixation, (2) nutrient solubilization (P, K, and Zn), (3) production of plant growth regulators, and (4) production of organic acids (Hayat et al. 2010; Verma et al. 2014).

Indirect mechanisms include (a) improvement of symbiotic relationships with rhizobia and mycorrhizal fungi, (b) inhibition of pathogenic microorganisms, (c) deactivation of detrimental release by plant pathogenic microbes, (d) synthesis of hydrolyzing enzymes which can be used against fungal cell wall, (e) synthesis of HCN, and (f) insect pest control (Saraf et al. 2014; Babu et al. 2015).

Production of PGPR-induced chemicals, allelochemicals, like siderophores, antibiotics, biocidal volatiles, lytic enzymes, and detoxification enzymes like ACC deaminase, chitinase, and glucanase also helps in the process. These allelochemicals are natural pesticides and remove problems like pest infestation and soil and environmental pollution (Barazani and Friedman 2001; Farooq et al. 2011; Saraf et al. 2014). Among all categories, exudates from plant roots play an important role for increasing microbial density, their flourishment, and survival in the root zone (Glick et al. 1998). These PGPR, the most popular group of advantageous bacteria, are known for their multivariate abilities like plant growth (Vacheron et al. 2013), disease control (Lugtenberg and Kamilova 2009), induced tolerance against abiotic stresses (Jing et al. 2007), and bioremediation.

9.1.2 PGPR and Plant Growth

An enormous number of bacterial species came under PGPR category in the last few years due to knowledge of new habitats, availability of better facilities for laboratory tests, and molecular identification. The presence of efficient PGPR in the rhizosphere is known to heighten shoot and root, root hair growth, root colonization, plant biomass, increase in the number of tillers, weight of panicles, grain production, and the suppression of pathogens (Khalid et al. 2004; Artursson et al. 2006; Smith and Read 2008; Ashrafuzzaman et al. 2009; Lucas et al. 2009; Richardson et al. 2009; Gopalakrishnan et al. 2010; Piromyou et al. 2011).

The affirmative properties of PGPR on different crops and vegetables like chickpea, wheat, barley, maize, pearl millet, sorghum, cotton, sunflower, tomato, potato, etc. have been reported (Babu et al. 2015). The use of PGPR to stimulate the plant growth for best agriculture practices has increased nowadays. The utilization of beneficial bacteria for agricultural enhancements and increasing crop yield requires the assortment of proficient root-colonizing bacteria which have proven plant growth abilities. In this way, we can minimize the application and dependency on chemical fertilizers. Such practices have unfriendly effects on the environment in a long run (Verma et al. 2015a; Meena et al. 2013b, 2016e; Shrivastava et al. 2016; Velazquez et al. 2016; Bahadur et al. 2016a; Masood and Bano 2016).

Legumes provide the essential proteins in vegan diet all over the world, mainly in India; thus, it is needed to improve their yields and sustain soil fertility using eco-friendly microbial inoculants. Several reports are available on the useful effects of *Rhizobium* and *Bradyrhizobium* on legumes in terms of biological nitrogen fixation (Werner 1992; Smith 1992). This helps in saving nitrogen fertilizer, and it also makes soil nitrogen available for subsequent crops (Jensen and Hauggaard-Nielsen 2003). Chickpea is a main leguminous crop. It is among the most important pulse crops grown in India, which has been well familiar as a valued source of protein, where mainstream population is vegan. India is on the world map for the largest production of chickpea, ~ 64% of the global production (Ahlawat 2000). Seed treatment of chickpea (*C. arietinum* L.) with *R. leguminosarum* BHURC04 caused noteworthy increase in numbers of nodules, straw production, crop yield, and uptake of nitrogen and phosphorus in grains over uninoculated trial (Yadav and Verma 2014).

Rice has the highest requirement of nitrogen for growth as it consumes one-third of the nitrogen applied as chemical fertilizer in soil (Buresh et al. 2008). It becomes important to find substitutes to reduce the usage of nitrogen fertilizers for rice crops. There are several studies defining the usage of diazotrophic bacteria because of their capability to fix atmospheric N_2 and solubilize inorganic P and phytohormone production (Divan-Baldani et al. 2000; Garcia de Salamone et al. 1996; Meena et al. 2013c, 2014b; 2015c; Sindhu et al. 2016; Singh et al. 2016). Bacteria from the genera *Pseudomonas*, *Azospirillum*, *Burkholderia*, *Herbaspirillum*, *Bacillus*, *Paenibacillus*, *Brevundimonas*, *Serratia*, and *Xanthomonas* are frequently used as biofertilizers. Most of them synthesize phytohormones and show other PGPR traits like nitrogen fixation, phosphate solubilization, and siderophore production (Pérez-Montano et al. 2013). Inoculation of wheat crop with *P. fluorescens* strain which has been characterized as an efficient ACC deaminase producer reduces the use of nitrogen, phosphorus, potassium, and other chemical fertilizers (Shaharoona et al. 2008).

At the same time, treated crops with lower fertilizer doses offered higher grain production, harvest index, and protein contents. Mavrodi et al. (2012) isolated 11 new strains of *Pseudomonas*. These strains viz. 15D11R, 48B8R, 48G9R, Wood3R, and Wayne1R significantly augmented shoot length with root weight of the wheat saplings. Maize inoculated with *Burkholderia cepacia*, *A. brasilense*, and *H. seropedicae* in individual experiments showed a strong increases in total plant and grain dry weight (Riggs et al. 2001). Usage of *P. fluorescens* DR54 on maize increased plant growth and soil phosphorus pools in field trial (Krey et al. 2013). Several authors suggested positive role of the genera *Azospirillum*, *Achromobacter*, *Burkholderia*, and *Arthrobacter* as phytostimulators (Cassán et al. 2009). These strains showed good shoot growth, root weight, and nutrient uptake in maize plants. Five formulations of *Bacillus*, viz., LS254, LS255, LS256, LS257, and LS213, were used to treat pearl millet. Such treated plants presented early occurrence of seedlings and noteworthy improvement in growth. Few more attributes are plant height, fresh and dry weight of plants, area of leaf, number of tillers and ear heads, their length and girth, and yield of pearl millet (Raj et al. 2003; Meena et al. 2015d; Singh et al. 2015).

Tomato is known for its nutritional values, having abundant vitamins and minerals, and it is among the world's largest vegetable crops grown. There are several studies showing the effect of PGPR on tomato. A study of six isolates of PGPR, *P. putida*, *P. fluorescens*, *S. marcescens*, *B. amyloliquefaciens*, *B. subtilis*, and *B. cereus*, has been done for their effects by Almaghrabi et al. (2013) on the growth of tomato plants. Best results with shoot dry weight, plant height, and fruit yield were given by plants treated with *S. marcescens*. Another study by Anupama et al. (2014) used five different PGPR strains, *P. aeruginosa* AN Rai-27, *P. putida* MA Rah-43, *B. subtilis* TN Vel-35, *B. cereus* KA Mys-39, and *A. chroococcum* KR Tri-17. These strains are found positive for phosphate solubilization, IAA production, macronutrient uptake, and enhanced chlorophyll contents thus resulted in better plant development and fruit production. Miao et al. (2015) isolated *Burkholderia* sp. 7016 from soybean rhizosphere which significantly enhanced the height of shoot and root and weight of root and shoot with increased stem diameter in tomato plant. Dinesh et al. (2015) studied four PGPR varieties, *Burkholderia cepacia*, *Bacillus amyloliquefaciens*, *Serratia marcescens*, and *Pseudomonas aeruginosa*, for growth promotion of ginger. This study showed higher sprouting and greater rhizome yield with *B. amyloliquefaciens* and *S. marcescens* (Meena et al. 2017) (Table 9.1).

9.1.3 PGPR and Disease Suppression

Extreme utilization of fertilizers, produced chemically, might be harmful for soil microbes which ultimately lead toward degraded soil fertility and may be responsible to pollute the environment. Diseases due to pathogenic microbes can be restricted by the use of chemicals effectively, and this step looked suitable too for general agricultural practitioners, but today disproportionate uses of chemicals are causing serious environmental complications. This is today's need to search and use alternative approaches to substitute the chemicals and to better practice with bioformulations of fertilizers and pesticides. Moreover, the world of agriculture is fronting possible risk for development of chemical resistance (Verma et al. 2015c).

There are three main rice pathogens *Xanthomonas oryzae*, *Rhizoctonia solani*, and *Magnaporthe oryzae* responsible for bacterial leaf blight, sheath blight, and blast on rice plants, respectively. Maximum studies on the use of PGPR as biocontrol in rice are focused on management of these diseases (Chithrashree et al. 2011). From the field of rice, certain fluorescent pseudomonads are found active against *Verticillium* sp., *R. solani*, *Fusarium* sp., *R. solanacearum*, and *B. subtilis*. According to the study, pseudomonads isolated from rice fields produced three times more antagonistic metabolites in comparison to isolates from maize fields (Lawongsa et al. 2008). *B. subtilis* CEN3 and *B. cereus* CEN5 can inhibit growth of several *Fusarium* rice pathogens like *F. proliferum*, *F. verticillioides*, *F. fujikuroi*, *Magnaporthe salvinii*, and *M. grisea* under lab conditions (Etesami and Alikhani 2015). *S. fredii* KCC5 and *P. fluorescens* LPK2 are found suitable for suppression of *Fusarium* wilt in *C. cajan* (Kumar et al. 2010).

The chickpea crop can be prevented from wilting and root rot diseases caused by fungi *F. oxysporum* and *R. solani* if treated with *P. aeruginosa* (Mehmood et al. 1999). *Bacillus* formulations LS256, LS257, and LS254 significantly reduced downy mildew in pearl millet. In experiments, LS256, LS257, and LS254 demonstrated effective in plummeting downy mildew. Once seeds were treated by LS256 and LS257 along with mixing in soil, they resulted in 65% protection against the disease (Raj et al. 2003). Mavrodi et al. (2012) have isolated new strains of *Pseudomonas*, namely, 14B2R, 15G2R, 29G9R, 39A2R, 48G9R, and Wood 3R from agricultural soils and river silt that expressed the ability to reduce disease symptoms of two wheat-infecting fungal pathogens, *R. solani* and *Pythium ultimum*, and the latter four also suppressed *Rhizoctonia oryzae* and *Pythium irregulare*. The toxigenic fungus

Table 9.1 PGPR strains/consortia showing plant growth promotion

Plant	PGPR strain/ consortium	Plant growth promotion	References
Alyssum serpyllifolium	*Pseudomonas* sp.	Plant growth promotion due to secretion of IAA and siderophores	Ma et al. (2011)
Cynara scolymus	*P. putida*	Production of IAA, siderophores, HCN, and ammonia	Ahemad and Kibret (2014)
Phaseolus vulgaris	*R. tropici*	An increase in nodule number, nodule weight, root weight, and shoot weight	Pérez-Montano et al. (2013)
	A. brasilense		
	Rhizobium	Increased nodulation, plant growth, nutrient uptake, and seed yield	Elkoca et al. (2010)
	B. subtilis		
	B. megaterium		
Brassica oleracea	*Pantoea* sp.	Enhancement of growth, nutrient, and hormone	Turan et al. (2014)
Vigna radiata	*Bradyrhizobium MRM6*	Plant growth promotion due to secretion of IAA, siderophores, HCN, and ammonia	Ahemad and Kibret (2014)
Lactuca sativa	*P. mendocina*	Enhanced plant biomass	Nadeem et al. (2014)
	G. mosseae		
Zea mays	*A. brasilense*	Better seed germination and nodule formation	Pérez-Montano et al. (2013)
	B.japonicum		
	P. aeruginosa	Siderophores, HCN, and ammonia	Ahemad and Kibret (2014)
Pisum sativum	*Rhizobium* sp.	Plant growth promotion due to secretion of IAA, siderophores, HCN, and ammonia	Ahemad and Kibret (2014)
Glycine max	*M. oryzae*	Improved nodulation	Parthiban et al. (2012)
	B. japonicum	Enhanced seed germination, nodule formation, and early development of soybean seedlings	Cassan et al. (2009)
	A. brasiliense		
	P. rhizosphaerae		
Fragaria ananassa	*P. agglomerans*	Increased yield, growth, and nutrition	Ipek et al. (2014)
	Pseudomonas sp. and *Bacillus* sp.	Increased fruit yield, plant growth and leaf P and Zn contents	Esitken et al. (2010)
Trifolium subterraneum	*P. putida*	A noteworthy increase in shoot and root dry weight	Nadeem et al. (2014)
	G. fasciculatum		
Lycopersicon esculentum	*P. putida,*	Significant effect on lycopene, antioxidant activity, and potassium content	
	A. chroococcum		
	A.lipoferum		
	M. oryzae	Better shelf life and stress management	Joe et al. (2014)

(continued)

Table 9.1 (continued)

Plant	PGPR strain/ consortium	Plant growth promotion	References
Triticum aestivum	*A. brasilense*	Better root length, root surface area, average root diameter, and root numbers	Combes-Meynet et al. (2011)
	P. jessenii	Increased grain yield, nutrient concentration, and soil enzyme activities	Mader et al. (2011)
	P. synxantha		
	Klebsiella sp.	Production of IAA, siderophores, HCN, and ammonia	Ahemad and Kibret (2014)

Fusarium is one of the major genera which is very much harmful for maize. Some PGPR such as *Bacillus amyloliquefaciens* and *Microbacterium oleovorans* were able to protect maize against *Fusarium verticillioides* (Pereira et al. 2011).

Tomato is most commonly and devastatingly affected by the early blight disease caused by *Alternaria solani*. This disease mostly causes harm to foliage, stem, and fruits which result in high defoliation, reduced production, and low fruit quality. Four strains (*B. subtilis* TN Vel-35, *A. chroococcum* KR Tri-17, *B. cereus* KA Mys-39, and *P. aeruginosa* AN Rai-27) allowed active fortification to tomato plants in response to early blight disease. This might be due to the higher production and activity of siderophores, HCN, chitinase, and glucanase in combination with improved activity of antioxidant peroxidase (POX) and polyphenol oxidase (PPO) enzymes in the vicinity (Anupama et al. 2014; Youssef et al. (2016).

The fungal pathogens cause diseases in potato during storage, transport, and marketing practices (Youssef et al. 2016). Such events bring substantial economic losses in the quality and quantity of the potato all over the world. Recep et al. (2009) treated potato with 17 PGPR strains, consisting of different species of *Bacillus*, *Burkholderia*, *Pseudomonas*, and *Flavobacterium*, and tested them for antifungal activity in lab and field conditions against *F. sambucinum*, *F. oxysporum*, and *F. culmorum*. They found the best antagonism in *B. cepacia* strain OSU-7 followed by BA-140 and OSU-142.

Curtobacterium flaccumfaciens causes bacterial wilt disease in common bean (*Phaseolus vulgaris*), which transmits through seeds. Disease is controlled by treatment of two different strains of *Bacillus subtilis* UFLA285 and ALB629, ranging from ~ 42 to 76%, respectively (Martins et al. 2013). Dinesh et al. (2015) found that *B. amyloliquefaciens* and *S. marcescens* among other tested PGPR strains resisted *Pythium myriotylum* (~ 48%) causing soft rot in ginger. Treatment of *Arabidopsis* roots by *P. fluorescens* WCS417r protects plants from *P. syringae*, *X. campestris*, *F. oxysporum*, *A. brassicicola*, and *P. parasitica*. This strain can also trigger ISR effectively in plants like radish, tomato, bean, carnation, etc. (Verhagen et al. 2004). Table 9.2 shows antagonistic activities against different pathogens by PGPR strains/consortia.

Table 9.2 PGPR strains/consortia effective against different plant pathogens

Plant	PGPR strain/consortium	Antagonistic activity against pathogens	References
Capsicum annum	*B. amyloliquefaciens* + *B. pumilus*	*S. rolfsii*, *R. solanacearum*, *C. gloeosporioides*	Sarma et al. (2015)
Solanum lycopersicum			
Capsicum annum	*P. fluorescens*	*P. aphanidermatum*	Muthukumar et al. (2010)
Cicer arietinum	*P. aeruginosa* + *T. harzianum* + *Mesorhizobium* sp.	*S. rolfsii*	Singh et al. (2014)
Cucumis sativus	*T. harzianum* + *Pseudomonas* sp.	*F. oxysporum*	Alizadeh et al. (2013)
	P. macerans + *Paenibacillus* sp.	*R. solanacearum*	Li et al. (2010)
Glycine max	*P. fluorescens*, *S. maltophilia*, *C. balustinum*	*X. axonopodis*	Algar et al. (2014)
Gossypium hirsutum	*Azospirillum* sp. + *P. fluorescens*	*R. bataticola*	Marimuthu et al. (2013)
Lycopersicon esculentum	*Methylobacterium* sp.	Ethylene production, protein synthesis	Yim et al. (2013)
Oryza sativa	*Pseudomonas* sp.	*M. oryzae*	Spence et al. (2014)
	P. fluorescens, *C. balustinum*	*M. grisea*	Pérez-Montano et al. (2013)
	X. oryzae	*B. subtilis*	Chithrashree et al. (2011)
	P. fluorescens, *C. balustinum*	*P. oryzae*	Lucas et al. (2009)
Pisum sativum	*P. aeruginosa* + *T. harzianum* + *B. subtilis*	*S. sclerotiorum*	Jain et al. (2014)
Solanum lycopersicum	*B. subtilis*	*A. solani*	Babu et al. (2015)
	Pseudomonas + *T. harzianum* + *G. intraradices*	*F. oxysporum*	Sarma et al. (2015)

9.1.4 Microbial Consortium in Plant Growth and Disease Suppression

Once any PGPR strain mixed with any non-PGPR strain or with PGPR strain of different species, in various combinations in rhizospheric soil, that mixture is better known as microbial consortium (Vacheron et al. 2013). It is reported that the use of PGPR strains in combination or consortium may well improve the effectiveness, consistency, and uniformity of the PGPR strains under varied soil and environmental circumstances. If microbes have compatibility and have no suppressive effect on each other, their application in consortium with efficient strains may be a better way to deal with disease suppression and plant growth promotion (Stockwell et al. 2011; Jain et al. 2012). Studies reported that microbes like *Bacillus*, *Pseudomonas*, *Trichoderma*, *Rhizobium*, etc. were used to advance microbial consortia (Jetiyanon 2007; Muthukumar et al. 2010; Srivastava et al. 2010; Alizadeh et al. 2013).

In numerous reports, it was investigated that inoculation of chickpea with *Rhizobium* sp. has increased nodule numbers and root and shoot properties with increased production (Babu et al. 2015). Combined application of *R. leguminosarum* (Cicer sp.) and *P. aeruginosa* has been found more noteworthy as *R. leguminosarum* strain is excellent in nitrogen fixation and *P. aeruginosa* well complement its actions comparatively others (Yadav and Verma 2014). The PGPR strains *S. fredii* KCC5 and *P. fluorescens* LPK2 showed improved shoot development, root development, and root colonization and enhanced nodulation (Kumar et al. 2010). Meanwhile co-inoculation of *Mesorhizobium* BHURC03 and *P. aeruginosa* BHUPSB02 followed by *Mesorhizobium* sp. and *B. megaterium* BHUPSB14 was reported very beneficial for noteworthy improvement in growth, nutrient content, and production of chickpea (Verma et al. 2013, 2014).

Combined application of *R. leguminosarum* (*Cicer* sp.) and *P. aeruginosa* has been found more noteworthy as *R. leguminosarum* strain is excellent in nitrogen fixation and *P. aeruginosa* well complement its actions comparatively others (Yadav and Verma 2014). Microbial consortia made up of triple inoculation of *B. megaterium*, *A. chlorophenolicus*, and *Enterobacter* gave higher wheat grain and straw yield response compared to dual or single inoculation of any strain under pot and field experiments (Kumar et al. 2014).

Several studies reported the advantages of microbial consortium over single PGPR in enhancing plant growth when inoculated with plants (Walker et al. 2011; Jha and Saraf 2012; Sudharani et al. 2014). This might be due to colonization of hair and cortical cells which enhance root surface area, consequently results in better acquisition of nutrients as well as plant hormones (Shishido et al. 1999). Significantly enhanced yields of wheat have been obtained when consortia of PGPR and AMF were applied (Rosas et al. 2009). Furthermore, Amalraj et al. (2015) conducted the growth promotion study of sunflower using consortia of *Azospirillum brasilense* (ASP20), *Azotobacter chroococcum* (AZB 29), *Bacillus megaterium* var. phosphaticum (PSB037), and *Trichoderma viride* (CRITV01), and a significant growth enhancement was observed.

Different direct or indirect plant-microbe-soil interactions occur in the rhizosphere which can be beneficial, non-beneficial, and pathogenic. Accordingly they select their mechanism like arresting growth of pathogens (de Leon and Montesan 2013). Once plants come into contact with harmful microbes, they trigger the defense mechanism. These defense responses will be much more effective once plants are primed with PGPR consortium. It is reported that consortia made up of *T. harzianum*, *B. subtilis*, and *P. aeruginosa* are very effective against *S. sclerotiorum* in pea (Jain et al. 2012); *P. aeruginosa*, *T. harzianum*, and *Mesorhizobium* sp. against *S. rolfsii* in chickpea plants (Singh et al. 2013); and *B. licheniformis*, *P. aeruginosa*, and *Streptomyces fradiae* against sunflower necrosis disease (Srinivasan and Mathivanan 2009). Bioformulations developed by species of *Pseudomonas* and *Beauveria bassiana* proved to be effective against leaf folder pest and sheath blight disease in rice. Recently, Figueroa-López et al. (2016) studied the antagonistic activity of *Bacillus megaterium* (B5), *Bacillus cereus* (B25), and *Bacillus* sp. (B35) and proved to be effective against several diseases in maize.

It is seen that antioxidant level increases few fold upon application of microbial consortium. Improvement in antioxidant level helps in stress tolerance. Plants control the echelons of reactive oxygen species (ROS) in a manner that H_2O_2 should suffer pathogen but not to the plant cells. H_2O_2 also helps in the process of lignification and cross-linking of cell wall polymers, thus strengthening the cell wall from invaders (Cessna et al. 2000; van Loon et al. 2006). Antioxidant level increases ~ 1.8–3.3-fold in treated chickpea with *P. aeruginosa* PHU094, *T. harzianum* THU0816, and *Mesorhizobium* sp. RL091 under *S. rolfsii* challenge. It shows better response in comparison with single microbial treatment (Singh et al. 2013). Higher activities of phenylalanine ammonia lyase and peroxidases were seen in palm treated with *P. fluorescens* and *T. viride* (Karthikeyan et al. 2006). Some enzymes like chitinases and β-1,3-glucanases produced by some microbes have antifungal activities. Jain et al. (2012) reported that these enzymes are produced by microbial consortium of *T. harzianum*, *B. subtilis*, and *P. aeruginosa* once infected by *S. sclerotiorum*.

9.1.5 Role of Allelochemicals/Metabolites Produced by PGPR in Plant Growth and Disease Suppression

Rhizobacteria present in root zone have significant role in altering the plant properties. First, plants release some exudates from roots which help in aggregation of rhizobacteria. Further, these rhizobacteria produce allelochemicals which improve plant growth by N-fixation, increasing availability of nutrients and inducing plant disease resistance. These established relations stimulate plant growth and crop yield.

The indirect mechanism of plant growth promotion involved the inhibition of plant pathogens by secreting some allelochemicals which restricts the growth of phytopathogens. Examples of these types of allelochemicals include siderophores, quorum-sensing molecules, antibiotics, lytic enzymes (e.g., chitinase), and biocidal volatiles such as HCN (Saraf et al. 2014). Siderophores are low molecular weight compounds, commonly produced by PGPR in iron-restrictive conditions, which function as cofactor for number of enzymes and an important constituent of several proteins (Neilands 1989; Whipps 2001). Inside the cell, the ferric ion ($Fe^{3+)}$ is transformed into ferrous ion (Fe^{2+}), which is further utilized by microbes for their growth. This ability reduces the race of nutrient utilization among the microbes in the rhizosphere and further enhances the existence of PGPR.

At the same time, this is the basic concept behind the practices of biocontrol (Barness et al. 1992). Siderophore production has been reported in many PGPR strains like *Alcaligenes* sp., *Serratia* sp., and *Acinetobacter* sp. (Ovadis et al. 2004; Sayyed and Patel 2011). The siderophore biosynthesis is strongly controlled by iron-sensitive *Fur* proteins, although the abilities of sequestering iron differ with every bacterial siderophore (Saraf et al. 2014). There are several antibiotics produced by PGPR strains that help in plant growth and suppress disease through antibiosis. *Bacillus* and *Pseudomonas*, the two most important genera among all PGPR strains, are best considered for antibiosis in the disease management (Jayaprakashvel and Mathivanan 2011).

Phloroglucinols are identified to induce systemic resistance in plants (Dwivedi and Johri 2003). Few strains of *P. fluorescens* are reported for the production of 2,4-diacetylphloroglucinol (DAPG) which actively participate in defense of plant roots against pathogenic microbes which are found in the soil, root colonization, and phytostimulation (Battu and Reddy 2009; Meynet et al. 2011). Biosynthetic loci for antibiotic production are highly conserved among all identified DAPG-producing fluorescent *Pseudomonas* sp. isolated over the globe including the United States, Europe, Asia, and Africa (Frapolli et al. 2007; Weller et al. 2007).

Cyclic lipopeptides (CLPs) are produced by gram-positive and gram-negative rhizobacteria. They are produced by fluorescent *Pseudomonas* sp. They are involved in bacterial swarming and possess antimicrobial as well as bio-surfactant properties. *P. fluorescens* DR54 and DSS7 produce three different CLPs known as amphisin, tensin, and viscosinamide (Saraf et al. 2014). Lipopeptides, another type of allelochemicals, are categorized into three different classes which include iturin, fengycin, and surfactin, classified on the basis of their sequences of amino acid and fatty acid branching (Stein 2005). Iturin family includes bacillomycin, mycosubtilin, and iturin A which are heptapeptides and possess high antifungal activity (Magnet-Dana and Peypoux 1994; Stein 2005). It was reported that the PGPR strain *B. amyloliquefaciens* FZB42 is characterized for the production bacillomycin D and also proved to be effective against *Fusarium oxysporum* (Koumotsi et al. 2007). The most studied lipopeptide is surfactin which is synthesized by three NRPSs, SrfA-C, and acyltransferase (Peypoux et al. 1999 and Stelller et al. 2004). A study by Chen et al. in 2009 reported that surfactin produced by *B. amyloliquefaciens* FZB42 protects the species against other bacterial species as well as facilitates the formation of biofilms, thus providing the bacterium a strong antagonistic potential during surface colonization.

Phenazines are heterocyclic secondary metabolites secreted by different Eubacteria and some Archaea (Mavrodi et al. 2010) and have been studied extensively for their antibiotic potential (Pierson and Pierson 2010). Several phenazine-1-carboxylic acid (PCA) compounds have been produced by different species of fluorescent pseudomonads such as *P. chlororaphis* (Pierson and Thomashow 1992), *P. aeruginosa* (Anjaiah et al. 1998), and *P. fluorescens* (Gurusiddaiah et al. 1986). PCA has been proved to be extremely effective against several fungal and bacterial pathogenic microbes, and a similar result has been recorded with the use of PCN (phenazine-1-carboxamide) against some phytopathogens of rice including *R. solani* and *X. oryzae* (Shanmugaiah et al. 2010).

Pyrrolnitrin is another class of antifungal metabolite which was first described by Arima et al. (1964) derived from the amino acid L-tryptophan. It was reported previously that it was produced by few species of fluorescent pseudomonads, for example, *P. fluorescens* (Kirner et al. 1998), *P. aureofaciens* (Elander et al. 1968), and *P. cepacia* (Cartwright et al. 1995). The antifungal activity of pyrrolnitrin was tested in several pathogenic fungus, and it was proved to be effective against a broad class of fungi including ascomycete, deuteromycete, and basidiomycete and functions as an effective biocontrol agent (Saraf et al. 2014).

Phytohormone like auxin indole acetic acid (IAA) is produced by maximum microbes present in rhizosphere (Patten and Glick 1996). This IAA plays a very substantial part in plant-microbe interaction (Spaepen and Vanderleyden 2011). IAA is reportedly involved in each facet of plant growth promotion (PGP) besides defense responses (Santner et al. 2009). Rhizobacteria produce IAA which has the capability to alter various physiological progressions by altering the plant auxin pool. This IAA, finally, increases root surface area and length so that plant gets better contact with nutrients present in soil (Santner et al. 2009). Similarly, this IAA released from rhizobacteria slackens wall of plant cells and enables larger volume of root exudates that offers extra sustenance for the advancement of root zone microbes (Glick 2012). This is why IAA is very important for plant growth promotion and disease suppression. Ethylene, a plant hormone, found in majority of higher plants, plays an important role in plant growth and development; in addition it also acts as an important indicator to plant's response toward various environmental stresses (Abeles et al. 1992).

During the presence of stressed environment, plants respond with enhanced ethylene concentration which is produced in the presence of high temperature, heavy metals, drought, salinity, organic pollutants, water logging, phytopathogens, and damage due to insect or nematode (Abeles et al. 1992). In the presence of high ethylene level, defoliation of plant occurs, and cellular process also gets affected which results in reduction of different crop parameters including root and shoot growth, crop yields, etc. (Saleem et al. 2007; Bhattacharyya and Jha 2012). PGPR possess an enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which stimulates plant growth and reduces ethylene levels in plants (Nadeem et al. 2007; Zahir et al. 2008). Examples of PGPR strains which have ACC deaminase activity include *Acinetobacter*, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Serratia*, *Rhizobium*, etc. (Nadeem et al. 2007; Zahir et al. 2008, 2009; Kang et al. 2010).

Rhizobacteria which produce ACC deaminase show major visible changes like root elongation, improvement in shoot growth, and nodulation as well as improved nitrogen, phosphorus, and potassium uptake in various crops (Nadeem et al. 2007, 2009; Glick 2012). Alkaloids are characterized as a strong fungi inhibitor, produced by several strains of microorganisms. Species of *Trichoderma* are reported for the production of different alkaloids such as elymoclavine and festuklavine, whereas

Penicillium produces alkaloids like agroclavine and ergometrine (Bekemakhanova and Shemshura 2001).

9.1.6 Effect of PGPR in Modification/Accumulation of Metabolites

Reports about PGPR showed that it can provoke alterations in root exudate activities to alter actions of enzyme, particularly flavonoids which have the tendency to change root exudation (Lavania et al. 2006; Shaw et al. 2006). *Chryseobacterium balustinum* Aur9 influences flavonoid exudation in soybean roots (Dardanelli et al. 2010), and *Azospirillum* may affect flavonoid secretion in Fabaceae roots (Burdman et al. 1996). This flavonoid secretion, with rhizobia, will react to plant flavonoids. PGPR also tend to modify secondary metabolites qualitatively and quantitatively as reported in maize by three different *Azospirillum* strains (Walker et al. 2011).

Azospirillum is also reported for modification of hydroxycinnamic derivatives and flavonoids in rice cultivars (Chamam et al. 2013). Strains of *Pseudomonas*, *Azospirillum*, or *Rhizophagus/Glomus* singly or in the form of consortium modify benzoxazinoids and diethyl phthalate in maize cultivar in field trials (Walker et al. 2012). PGPR also stimulate the accumulation of secondary metabolites and several compounds. *Bacillus subtilis* GB03 induces accumulation of glycine betaine and choline in *Arabidopsis* (Zhang et al. 2010). Accumulation of same compound is reported by Bharti et al. (2013) in *Bacopa monnieri* by *Pseudomonas pseudoalcaligenes.* Accumulation of proline, malondialdehyde, aldehydes, hydrogen peroxide, total soluble sugars, and starch is reported by numerous authors (Theocharis et al. 2012; Fernandez et al. 2012). These modifications and accumulations of various compounds by PGPR help plants in growth and withstand during different types of environmental stresses.

9.1.7 Impressions of PGPR at Molecular Level in Growth Promotion and Disease Suppression

PGPR strains have the tendency to alter the gene expressions in plants once exposed to pathogens or stress. There are studies which give insight how PGPR trigger signal to initiate plant responses. Promising genes which are reported in plant growth promotion are auxin-induced genes (At4g36110, At2g33830), NAM-like genes (At2g17040, At5g39610, At1g69490, At3g04070), and genes involved in C-compound and carbohydrate metabolism (e.g., β-galactosidase (At5g56870), xyloglucan endotransglycosylase-related protein (At4g14130), putative endoxyloglucan glycosyltransferase (At2g06850), xyloglucan endo-1,4-β-glucanase

(At4g30270), and UDP-glucose glucosyl transferase (At1g78270)) (Catala et al. 1997; Taguchi et al. 2001).

Application of *Azospirillum brasilense* Sp245 on rice gives higher expression of ethylene receptors (Vargas et al. 2012). These receptors are helpful in establishing relationship between plants and microbes. For instance, *Herbaspirillum seropedicae* stimulated the expression of genes accountable for the production of growth hormones like auxin and ethylene (Brusamarello-Santos et al. 2012). It is quite evident from a study that *Pseudomonas fluorescens* WCS417r is capable of altering the expression of 97 genes in roots and around 8000 genes in leaves (Verhagen et al. 2004). Likewise, *Pseudomonas fluorescens* Q8r1-96 is responsible for accumulation of defense-related compounds in wheat (Okubara et al. 2010; Maketon et al. 2012). *Arabidopsis* also showed increased expressions of defense-related genes in a compromised plant (Cartieaux et al. 2003; Wang et al. 2005). Such advantageous associations require mutual recognition, significant harmonization, and microbial responses to modify the plant resistance.

Most authors have reported their studies with gram-negative bacteria, mainly *Azospirillum* and *Pseudomonas* sp. to show the impact of root exudates on PGPR. Reports showing the effect of root exudates on gram-positive PGPR are comparatively less (Steenhoudt and Vanderleyden 2000). For example, *Bacillus amyloliquefaciens* FZB42 is a gram-positive PGPR. Fan et al. (2012) conducted a series of study elucidating the molecular aspects of this rhizobacterium with respect to its plant growth-promoting activity. A total of 302 genes were shown to be considerably regulated by root exudates. Among them, 261 genes were found to be upregulated, while 41 genes were downregulated.

The upregulated genes responsible for maltose metabolism, viz., *glvA*, *glvC*, and *glvR*, have showed the highest fold change (2.5–5.2-fold). The genes that are responsible for mobility and chemotaxis (*fliM*, *flip*, *cheC*, *cheD*, *hag*, *flgM*) and antibiotic production (*baeE*, *baeI*, *baeL*, *baeN*, *baeR*, *dfnJ*, *dfnI*, *dfnG*, *dfnF*, *mlnH*) were found to be induced in this study. *B. diazoefficiens* USDA110 and *B. japonicum* THA6 are commercially used as rhizobial inoculants for the production of soybean. The expression levels of *Glyma17g07330* (responsible for nodule formation), *dctA* (transports carbon from plant to bacteroids to help in their metabolism), *phbC* (influences PHB metabolism), *nifH* (helps in nitrogen fixation), and *otsA* (regulates trehalose synthesis) genes were enhanced in the presence of PGPR (Prakamhang et al. 2014). The same sets of genes were also seen to be affected in the study carried out by Libault et al. (2009). The role of dicarboxylate transport protein DctA encoded by *dctA* gene (Batista et al. 2009) and PHB polymerase encoded by phbC gene (Resendis-Antonio et al. 2011) in nodule development was also studied.

The molecular mechanisms behind plant-bacteria symbiosis were examined by infecting maize roots by *Bacillus amyloliquefaciens* subsp. *plantarum* FZB42. This study discovered that a total of 361 genes were influenced in the presence of maize root exudates. Out of these, many genes were found to be upregulated. For example, *tatCY* (encodes components of Tat pathway) and *secY* (encodes components of Sec pathway) have been stimulated in transcription. Only two genes were shown to be downregulated, i.e., *spoIIB* (encodes endospore development protein) and *ywcI* (unknown function). Besides the above listed genes, 63 genes were found to be helpful in plant-bacteria interactions (Fan et al. 2015). An exhaustive study by Mwita et al. (2016) demonstrated that PGPR *Bacillus atrophaeus* UCMB-5137 along with maize root exudate was used to imitate communications between bacteria and plants.

Interestingly, gene regulation in *B. atrophaeus* UCMB-5137 varied from the stated gene regulation in alike conditions in *B. amyloliquefaciens* FZB42, which is also known as a paradigm PGPR. Around 54 upregulated genes were responsible for cell surface protein biosynthesis, DNA replication, cell division processes, and posttranslational processing, and 152 downregulated genes were shown to be responsible for amino acid, nucleotide, carbohydrate, and fatty acid biosynthetic pathways, anaerobic respiration pathway, carbon and nitrogen utilization, mobility and chemotaxis, and inositol and lipid metabolism.

A. thaliana is a widely used model plant since it offers a noble investigational system for genetic studies. Timmusk and Wagner (1999) showed that *A. thaliana* upregulated *ERD1* and *RAB18* genes on application of drought stress with the support of ABA as a main mediator. He also showed that genes *ATVSP* (JA-responsive), *HEL* (ET-responsive), and *PR-1* (SA-responsive) were upregulated in response to the biotic stress induced by *P. polymyxa*. In another study by Cartieaux et al. (2003), the expression of different genes was observed in *A. thaliana* root colonized by *P. thivervalensis* MLG45 challenged by *P. syringae* pv. tomato DC 3000.

A total of 63 transcripts were modified in shoots. Among them 21 genes were downregulated (related with translation-initiation factor IF-1, ubiquitin-conjugating enzyme 4, chloroplast function, etc.), and 42 genes (related with stress tolerance, oxidation burst, wounding and disease resistance, etc.) were upregulated in the roots. Wang et al. (2005) used *P. fluorescens FPT9601-T5* in *Arabidopsis* as PGPR and challenged it with *P. syringae* pv. tomato DC3000 and found disease-resistant PR proteins (At2g43570, At3g04720, At3g57240, At3g57260), glutathione S-transferase (At5g17220), drought-induced protein (At4g15910), peroxidase (At2g37130), and stress-responding small protein (At4g02380). Srivastava et al. (2012) found *Pseudomonas putida* MTCC5279 stimulated upregulation of 520 genes and downregulation of 364 genes in *Arabidopsis.* Data showed that genes involved in biological process (15.58%), cellular component (13.62%), and molecular process (13.88%) were upregulated, while the downregulated genes in terms of biological function, molecular function, and cellular component were 21.30%, 13.62%, and 18.20% respectively. Genes which were upregulated allied with carbohydrate metabolism (At1g05030), nucleoside transferase (At1g63730), kinases (At1g06730, At1g53730), transcription factor (At1g12890, At1g01260), hormone synthesis (At3g23890), ABA signaling, ethylene suppression (At2g29090), etc. Genes which were found downregulated included butanoate metabolism (At5g06580), galactose metabolism (At5g17310), pentose phosphate pathway (At1g09420), purine and pyrimidine metabolism (At1g08260), histidine metabolism (At3g46100), etc. Figure 9.1 shows how these overexpressed genes are helpful in plant growth.

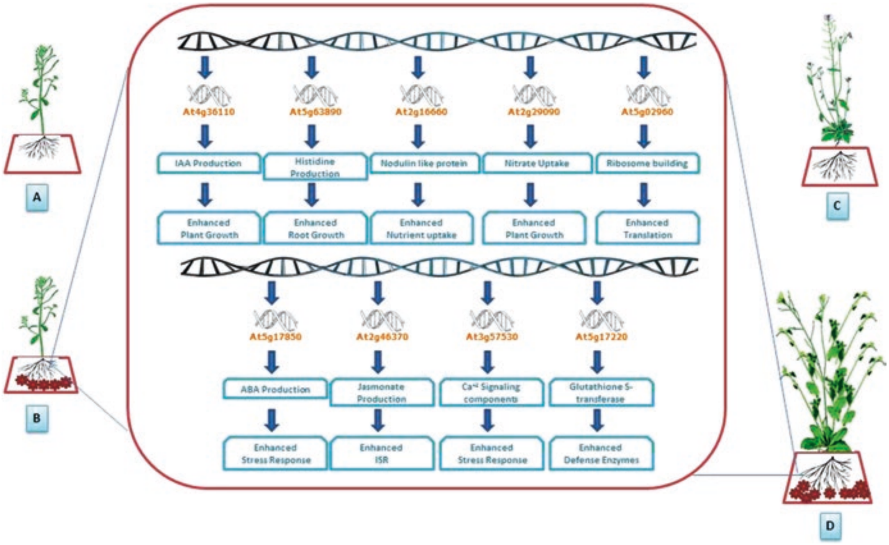

Fig. 9.1 Overexpression of genes responsible for better plant growth and disease resistance in *Arabidopsis* plant on induction of PGPR. (**a**) Plant without PGPR treatment. (**b**) Plant with PGPR treatment. (**c**, **d**) Aftereffects on plant

9.1.8 Identification of Altered Gene Expressions in PGPR-Primed Plants

There are numbers of techniques available which can help in understanding plant-pathogen interactions and signaling procedures. The numbers of responses are further initiated by interaction between plant and pathogens. Several studies reported the dramatic changes in the expression of housekeeping genes for pathogen defense in *Arabidopsis* (Wang et al. 2005; Srivastava et al. 2012). It becomes difficult to monitor these interactions and changes through traditional approaches. With the advancement of genome sequencing, it is possible now to study and discover various other related aspects. There are numbers of techniques on expression profiling that can identify several genes playing important role in plant defense like DNA microarray, EST (expressed sequence tag), SAGE (serial analysis of gene expression), cDNA-AFLP (cDNA-amplified fragment length polymorphism), etc. (Yin et al. 2014).

Among all, DNA microarray is an outstanding tool for identifying any upregulated and downregulated genes. This technique is very suitable for users because of its easy handling, widespread sampling ability, and high throughput (Kazan et al. 2001). This technique can be further divided into two groups: cDNA microarray and oligonucleotide-based array. Several authors reported their work by using these two techniques. Baldwin et al. (1999) recognized 117 defense-related genes in maize upon infection of *Cochliobolus carbonum*. Nadimpalli et al. (2000) identified 70 defense-related genes due to a lesion in maize, Chen et al. (2002) identified 74 transcription factors in *Arabidopsis*, and Cheong et al. (2002) identified multiple genes in *Arabidopsis* expressed on abiotic stress by using oligonucleotide-based array. Maleck et al. (2000) identified 300 genes responsible for defense in *Arabidopsis*; Sasaki et al. (2001) recognized 41 JA-responsive genes in *Arabidopsis*; Schenk et al. (2000) reported 705 genes which play a role toward fungal pathogen *Alternaria brassicicola* in *Arabidopsis*; Desikan et al. (2001) identified 175 H_2O_2-responsive genes in *Arabidopsis* by using cDNA microarray. Maleck et al. (2000) reported 413 ESTs that were linked with SAR. This work utilized cDNA microarray having 10,000 ESTs representing around 7000 genes or 25–30% of all *Arabidopsis* genes. Scheideler et al. (2002) observed changes in *Arabidopsis* transcripts after challenging it with *Pseudomonas syringae* by using custom cDNA microarray. Affymetrix ready to analysis chips made the microarray work more feasible.

Thus, many workers utilized the Affymetrix *Arabidopsis* GeneChip oligonucleotide array having around 8200 *Arabidopsis* genes (Zhu and Wang 2000). Chen et al. (2002) observed mRNA levels of 402 discrete *Arabidopsis* transcription factors under different environmental stresses. They observed that bacterial pathogen infection altered the expression of 74 transcription factors. The aforementioned examples reveal that DNA microarray is a precise tool for recognizing functions of genes and their change in expressions involved in complex processes, such as plant defense signaling.

9.2 Future Prospects

We should focus toward new techniques which can separate active biomolecules and set more intense interactions between microbes and plant. Future success could be more easy and fast if we can search more insights about rhizosphere biology and able to achieve any management technique for the population of soil microorganisms. Microbial formulations can play an important role in growth of plants in adverse conditions. To attain all these benefits, we need much more detailed mechanisms at biochemical and molecular level for making more effective consortium. We are also lacking in microbial consortia-regulated expression of transcription factors which are related with host defense responses in biotic and abiotic challenges.

Further, future marketing of such dried microbial inoculants with or without help of carrier could be also another food for thought. Such type of step can significantly lessen the usage of chemical fertilizers and give a boost for new eco-agri practices. But formulation development needs to consider the shelf life, stability, quality, and efficacy of the product. Since this eco-friendly approach will be governed under strict biosafety rules and regulations, hurdles in commercialization of PGPR formulations must be overcome. Instead of these factors, some other field practices are advised to be taken care of by farmers such as routinely systematic soil analysis, the use of organic manure, proper availability of moisture, and regular sterilization practices to maximize the biofertilizer efficacy. The government could arrange technical training programs in collaboration with research institutes on the production strategies and advise farmers on how to maintain the quality of PGPR formulations in a long run. Overall, the use of PGPR at a large level in sustainable agricultural practices could be very effective and useful.

9.3 Conclusions

There is a need to increase the production of crops, vegetables, and fruits manyfold to feed the burst of population in the coming years. At the same time, this target should be completed without harming the nature. The best way to achieve this need could be possible by increasing the soil fertility in an eco-friendly manner, and PGPR offer to play its best role. PGPR, once applied properly and sensibly, supply adequate quantities of both major and minor nutrients to plants and other growth-regulating constituents that help in growth, yield, and nutritive quality of crop. Applications of microbial consortia are more beneficial for plant growth as well as disease suppression in comparison to single PGPR strain. These multi-microbial consortia also work in withstanding adverse effects of several other abiotic stresses, too. Since microbial consortia are more reliable to face the challenges of different soil and environmental conditions hence to improve stability of released microbes in different agricultural fields, the use of microbial consortia is advocated.

Several techniques have emerged as powerful tools that are being used for genome-wide investigations of plant growth and defense responses after a challenge with different pathogens. They are actually used to recognize possible growth-related genes, defense-related genes, and probable regulatory elements, to illustrate and distinguish different pathways activated during various plant pathogen couplings, and to find cross-connection between different pathways. In the future, more advanced studies will be importantly required to examine specific genes or regulatory elements responsible for plant growth and disease suppression.

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