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Agriculturally Important Microbes for Sustainable Agriculture

Volume I: Plant-soil-microbe nexus

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Part I

Role of Soil Microbe Interaction

Plant Beneficial Rhizospheric Microbes (PBRMs): Prospects for Increasing Productivity and Sustaining the Resilience of Soil Fertility

1

Abhijit Sarkar, Madhumonti Saha, and Vijay Singh Meena

Abstract

The efficient microorganisms in the vicinity of plant roots that exert positive effects on plant growth are known as plant beneficial rhizospheric microbes (PBRMs). One of the salient features for the effectiveness of PBRMs is their ability to proliferate at hosts' rhizosphere, rhizoplane or the root interior. They are directly or indirectly involved in plant growth promotion and development by releasing particular compounds, increasing the uptake of certain nutrients from the soil and lessening or preventing the plants from deleterious pathogens. Indirect plant growth promotion is achieved by the inhibition of the detrimental effects of phytopathogenic organisms, which can be obtained by the production of siderophores, i.e. metal-chelating agent. Several bacterial species also have been reported in biocontrol of soil-borne phytopathogens and the synthesis of antibiotics. Production of hydrogen cyanide (HCN) and/or fungal cell wall degrading enzymes (e.g. chitinase and β-1, 3-glucanase) help PBRMs to sup-

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press the effect of phytopathogens. Direct plant growth promotion involves symbiotic and non-symbiotic PBRMs which function through production of plant hormones such as auxins, gibberellins, ethylene, cytokinins and abscisic acid. Some of the PBRMs are functioning as a sink for 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene in higher plants, by hydrolyzing it into α-ketobutyrate and ammonia and in this way promoting root growth by lowering indigenous ethylene levels in the rhizospheric environment. PBRMs also help in solubilization of nutrient-bearing minerals (indigenous sources of phosphates, potash and other nutrients), enhance resistance to plant stress, stabilize soil aggregates and improve soil structure and organic matter content. PBRMs could able to retain more soil organic N and other nutrients in the plant-soil system, which can reduce the need for fertilizer N and P and help in nutrient acquisition. Evidently, PBRMs maintain enormous prospects in advanced and sustainable plant production, including, improved plant tolerance to stress, better uptake of plant nutrient from soils and reduced application of chemical inputs. Besides, PBRMs in the soil bear a peculiar relation to soil fertility. Various investigations have documented the increased health and productivity of different plant species by the application of plant beneficial rhizospheric microorganisms under both the normal and abiotic-stressed conditions. Attempts should be directed towards maximizing the identified benefits of PBRMs in all developing countries. If the benefits of PBRMs in crop production can be maximized, this will certainly help to fight against hunger. This chapter discusses the major functions of PBRMs in broad terms, but efforts were made to present specific usage of PBRMs to enhance plant nutrient uptake, for better plant response to environmental stress, and unexplored potentials in developing countries.

Keywords
Rhizosphere • PBRMs • Stress resistance • Nutrient acquisition • Sustainability

1.1 Introduction

Plants are the sources of food, oxygen, fuel, fibre, medicine and residence for every animal on this planet Earth. Whereas, these plants uptake their own requirements mainly from soil through its root system. Thus, root-soil interaction is running simultaneously from the beginning and evolution of life, where they assemble benefits from their symbiotic association with each other (Meena et al. 2013a, 2016a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Ahmad et al. 2016; Parewa et al. 2014; Kumar et al. 2015, 2016b). This root-soil-associated phase is known as rhizosphere (rhiza = root, sphere = area of influence).The rhizosphere is the narrow region of soil that is directly influenced by plant roots in association with root hairs, plant-produced materials and concerted soil microorganisms (Hartmann et al. 2009). It may expand up to 2–3 mm from the root surface, which can be

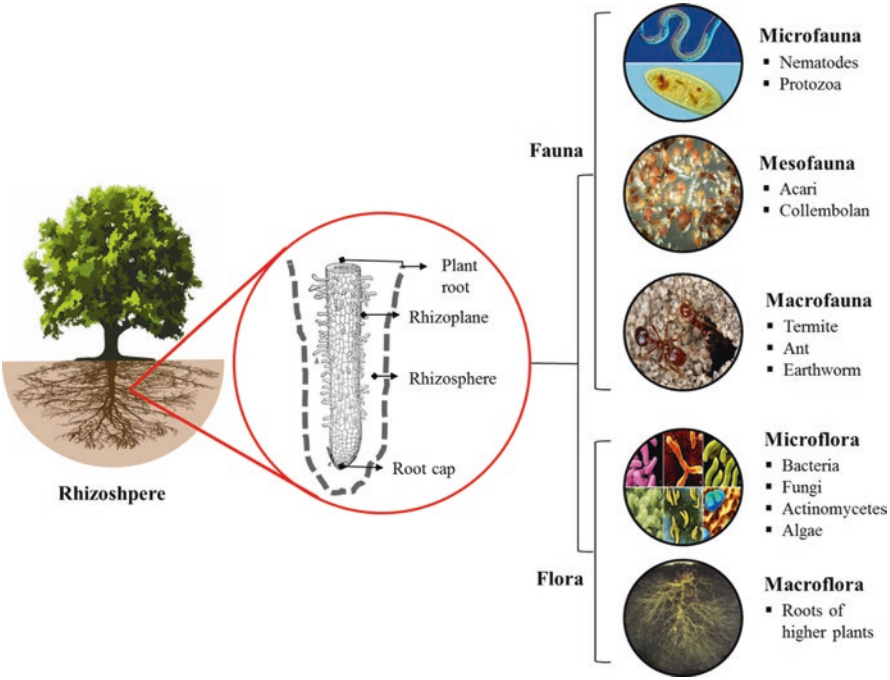

Fig. 1.1 Distribution of microbes in rhizospheric zoo (Coyne 1999; Mendes et al. 2013)

differentiated into two distinct classes, named inner rhizosphere (endorhizosphere) and outer rhizosphere (ectorhizosphere). Endorhizosphere is a multilayered micro-environment that is composed by root surface coated with mucoid layer, and the ectorhizosphere is none other than rhizosphere soil. Largely, three distinct but connected components are identified in the rhizosphere: the root itself, the rhizoplane and the rhizosphere (soil).

There are important groups of organisms which are often present in soil: microflora, macroflora, microfauna, mesofauna and macrofauna (Fig. 1.1). This marginal zone of soil surrounding plant roots can encompass up to ~10^{11} microbial cells per gramme of root and ~30,000 prokaryotic species which can increase plant productivity (Mendes et al. 2013). On the basis of distance from root surface and microbial activity, plant root's micro-ecosystem is divided as rhizosphere (near root surface and higher microbial activity) and non-rhizosphere (bulk soil and lower microbial activity).

In 1946 H. Katznelson suggested the concept of R:S ratio which is the ratio between microbial population in rhizosphere (R) and non-rhizosphere (S) soil. This ratio is situation specific, and it varies from species to species of plants and rhizospheric microbes. During seed germination and seedling emergence, the growing plant interacts with a scale of microorganisms present in the adjoining soil (Katznelson et al. 1948). This can impart a better idea of the relative stimulation of rhizospheric microorganisms on the plant species (Prakash and Verma 2016;

Priyadharsini and Muthukumar 2016; Meena et al. 2015f, 2016b; Jaiswal et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a).

As seeds germinate and roots grow throughout the soil, they secrete organic metabolites which supply the driving force for the activation of microbial populations in a zone which includes plant root and the adjacent soil in a few millimetre (mm) of thickness. This is referred as the rhizosphere effect (Morgan et al. 2011) and considered as the qualitative estimation of the degree or extent of plant growth that are affected by those microorganisms, while R:S ratio is used as quantitative measure. These plant beneficial microbes (PBMs) are very indispensable in biogeochemical cycles which are the determinants of plant health and soil fertility and have been used for crop production for decades. Generally, the microbe functions in different ways such as secreting regulatory chemical compounds for the plants, facilitating resource acquisition of certain nutrients (N, P, K, Fe, S, etc.) from the soil and reducing or impeding the plants from the inhibitory effects of various pathogens in the forms of a biocontrol agent (Kumar et al. 2017; Raghavendra et al. 2016; Zahedi 2016; Meena et al. 2015a, b; Das and Pradhan 2016; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016).

Evidently, these rhizospheric microbes hold infinite potential in advanced and sustainable plant production, including reinforced plant tolerance to stress, modulated plant hormone levels and limited use of chemical inputs. Regular use of enormous amounts of chemical inputs is causing unsuitable environment. Now, try to better understand the function of inoculants as biofertilizers in nutrient absorption, and plant response to environmental stress is more enthralling. The plant beneficial rhizobacteria may reduce the worldwide dependence on precarious agricultural chemicals which weaken the agroecosystems. This chapter emphasizes the comprehension of the rhizosphere and plant beneficial rhizospheric microorganisms under the present aspects (Rawat et al. 2016; Yasin et al. 2016; Meena et al. 2015e, 2016c, d; Saha et al. 2016b; Yadav and Sidhu 2016; Teotia et al. 2016; Bahadur et al. 2016b).

1.2 Rhizosphere Deposits and Priming Effect

The chemicals which are released by the roots within the soils are generally known as root exudates. Then the root products contributed to the surrounding soil are generally called as rhizodeposits. Root exudates, a fraction of rhizodeposition, are abundant in carbon and energy sources that govern the occurrence and growth of the microbes in the rhizosphere. Other fractions of rhizodeposition are lysates, mucilage, secretions and dead cell materials that may take part in plant development (Sommers et al. 2004; Dardanelli et al. 2010).

It is learned that both the qualitative and quantitative formulations of root exudates are influenced by different environmental factors such as pH, soil type, oxygen status, light intensity, soil temperature, nutrient accessibility and the presence

Table 1.1 Various compounds in root exudates (rhizodeposits) of different plant species

Amino acids	α-Alanine, β-alanine, asparagines, aspartate, cysteine, cystine, glutamate, glycine, isoleucine, leucine, lysine, methionine, serine, threonine, proline, valine, tryptophan, ornithine, histidine, arginine, homoserine, phenylalanine, aminobutyric acid, α-aminoadipic acid
Enzymes	Acid/alkaline-phosphatase, invertase, amylase, protease
Inorganic ions and gaseous molecules	HCO_3^-,OH^-, H^+, CO_2, H_2
Organic acids	Citric acid, oxalic acid, malic acid, fumaric acid, succinic acid, acetic acid, butyric acid, valeric acid, glycolic acid, piscidic acid, formic acid, aconitic acid, lactic acid, pyruvic acid, glutaric acid, malonic acid, tetronic acid, aldonic acid, erythronic acid
Purines/nucleosides	Adenine, guanine, cytidine, uridine
Sugars	Glucose, fructose, galactose, ribose, xylose, rhamnose, arabinose, desoxyribose, oligosaccharides, raffinose, maltose
Vitamins	Biotin, thiamin, pantothenate, riboflavin, niacin

Adapted from Dakora and Phillips 2002

of microorganisms. These factors may have a significant effect on root exudation than differences due to the plant species (Singh et al. 2004).

The exudation of a broad extent of chemical compounds (Table 1.1) which improve the chemical and physical characteristics of the soil thus modulates the structure of soil microbial circle in the adjacent region of root surface (Dakora and Phillips 2002). There are six major regions of rhizodeposition in the immediate vicinity of the root surface: (a) loss of cap and border cells, (b) loss of insoluble mucilage, (c) loss of soluble root exudates, (d) loss of volatile organic carbon, (e) loss of C to symbionts and (f) loss of C due to death and lysis of root epidermal and cortical cells. Then these rhizodeposits may alter the soil properties such as pH and carbon availability, influencing the diversity and activity of microbial populations (Haichar et al. 2008).

Generally, structure of the rhizobacterial community is decided by the plant species with their differences in the formulation and quantity of root exudates that possibly affects the microbial populations. Concerning how plant roots specify soil microbes to build the microbial community in the rhizosphere is an important empirical idea when considering the use of beneficial microbes as plant growth promoters (PGP); these vigorous communications of root exudates and activity of those microbes can conduct to a better root growth (Adesemoye et al. 2009; Drogue et al. 2014).

Change in soil organic matter (SOM) decomposition as a result of plant root and associated microbes activity is often analogous to rhizodeposition. It is also familiar as rhizosphere priming (Kuzyakov 2002), which plays a pivotal role in microbial activity, soil carbon (C) pools distribution and their reactions to global climate change. Rhizosphere priming may be altered by soil nutrient availability, but it itself can also influence nutrient supply to plants. These bilateral effects may be of specific importance in understanding the sustained increase in plant growth and nutrient supply in response to the advancement in atmospheric CO_2 level (Drake et al.

2013; Saha et al. 2016b; Verma et al. 2014, 2015c; Meena et al. 2014a, 2016e; Sharma et al. 2016).

1.3 Plant Beneficial Rhizospheric Microbes (PBRMs)

1.3.1 Rhizospheric Microbes and Nutrient Acquisition

Increasing crop losses may be the result of underutilization of essential nutrients by plants from soil. Presence and/or application of PBRMs in rhizosphere as biofertilizer enhances the nutrient recovery efficacy of plants, and increment in crop yield subsequently occurs. For each and different nutrient, PBRMs and plants have specific mechanisms. So, let us know what are the possible mechanisms (Fig. 1.2) involved in nutrient acquisition by PBRM plant interaction. In the following sections, it has been thoroughly discussed (Verma et al. 2015b; Meena et al. 2013b; Shrivastava et al. 2016; Masood and Bano 2016).

Nitrogen (N) is the most essential nutrient for development and productivity of crops. Minimizing the use of chemical fertilizers by using biological fertilizers based on microorganisms inoculum involved in nitrogen fixation is one of the

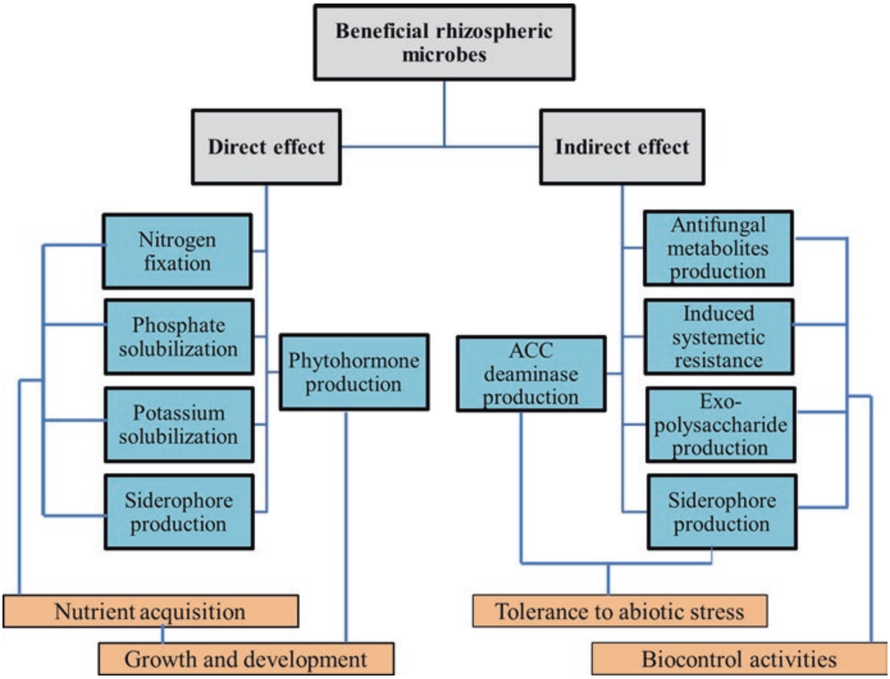

Fig. 1.2 Schematic diagram representing the direct and indirect effects of plant beneficial rhizospheric microbes (PBRMs)

worthwhile initiatives in sustainable agriculture. In the biological N_2 fixation (BNF), the atmospheric N_2 is converted into plant accessible forms by nitrogen-fixing microorganisms (NFM) utilizing a complex enzyme system known as nitrogenase (Boddey et al. 1991; Shridhar 2012).

Generally NFM are categorized as (a) symbiotic N_2-fixing bacteria (NFB) along with the members of the *Rhizobiaceae* family having symbiotic association with leguminous plants (e.g. *Rhizobia*) (Ahemad and Khan 2012; Zahran 2001) and (b) non-symbiotic (free-living, associative and endophytes) nitrogen-fixing microbes, such as cyanobacteria (*Anabaena*, *Nostoc*, *Tolypothrix*), *Azotobacter*, *Azospirillum*, *Gluconacetobacter diazotrophicus* and *Azoarcus*, etc. (Bhattacharyya and Jha 2012; Wani et al. 2013). Besides this, other NFB associated with non-legumes include the species of *Acetobacter*, *Achromobacter*, *Alcaligenes*, *Arthrobacter*, *Azomonas*, *Bacillus*, *Beijerinckia*, *Clostridium*, *Corynebacterium*, *Derxia*, *Desulfovibrio*, *Enterobacter*, *Erwinia*, *Herbaspirillum*, *Klebsiella*, *Lignobacter*, *Mycobacterium*, *Methylosinus*, *Rhodopseudomonas*, *Rhodospirillum* and *Xanthobacter* (Khan et al. 2009).

On a global scale, BNF provides the largest input of nitrogen to agricultural soils. Inoculation of these efficient PBRMs species usually increases plant's productivity. If *Rhizobium* is inoculated as biofertilizer in the crops such as groundnut, pigeon pea, soybean, etc., it can supply ~19–22 kg ha^{-1}which can raise the production by ~17–33%. Similarly, the use of non-symbiotic bacteria *Azotobacter* and *Azospirillum* in soybean (Alves et al. 2004), *Burkholderia vietnamiensis* in rice (Govindarajan et al. 2008) and *Pantoea*, *Bacillus and Klebsiella* in maize crops (Ikeda et al. 2013) can provide ~20–30 kg N ha^{-1} and simultaneously increased the crop yield by ~10–30%. The relative contribution of BGA as a percentage of total nitrogen fixed in paddy fields varies widely and is estimated to be ~15–35 kg N ha^{-1}in the South Asia.

Phosphorus (P) is the second most essential plant growth-limiting nutrient after nitrogen. Even though P has large reservoir, the amount of available forms is very low to the plants. To conquer the P deficiency in soils, routine application of phosphate fertilizers is not only expensive, but also it is environmentally unacceptable. In these circumstances, microorganisms accompanied with phosphate-solubilizing and phosphate-mobilizing activity are termed as phosphate-solubilizing microbes (PSMs) and phosphate-mobilizing microorganisms (PMMs), which may supply the accessible pool of P to the plants. Hence, it may be a replacement to the chemical phosphatic fertilizers (Khan et al. 2009).

Bacterial/rhizobacterial genera like *Azotobacter*, *Bacillus* (*B. megaterium*, *B. circulans*, *B. subtilis*, *B. polymyxa*) (Kim et al. 2003), *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas* (*P. striata*) and *Serratia* are described as the most significant PSB (Bhattacharyya and Jha 2012). However, commonly, the solubilization of inorganic phosphorus occurs as a result of the exertion of low-molecular-weight organic acids (gluconic and keto-gluconic acids) which are secreted by various soil bacteria (Zaidi et al. 2015). Conversely, the organic phosphorus is mineralized by the synthesis of a variety of different phosphatise enzymes, which catalyses the hydrolysis of phosphoric esters (Glick 2012). Besides this, vesicular arbuscular mycorrhizae (VAM) are also very much convenient in making unavailable form of soil nutrients into readily available form by exploring the large volumes of soil (Velazquez et al. 2016; Meena et al. 2014b, 2015c; Sindhu et al. 2016; Bahadur et al. 2016a).

Their hyphae developed superficially from the roots ranging from a few centimetres (cm) up to several meters in the soil. As a consequences, it increases the effective absorbing surface area of the host plant root by as much as ten times, resulting in increased absorption of static nutrients such as phosphorus, zinc, copper, etc. in the soil by ~60 times.

In India, inoculation with VAM fungi (*Glomus mosseae*, *G. fasciculatum*, *Acaulospora laevis* and *Gigaspora gilmorei*) resulted increased plant productivity (Kumar et al. 2009). These PSB and PSF (fungi) correspondingly represent ~1–50% and 0.1–0.5% of the total population of microorganisms present in the soil (Chabot et al. 1993; Khan et al. 2009).

The PSB solubilize inorganic soil phosphates, being $Ca_3(PO_4)_2$, $FePO_4$ and $AlPO_4$, through the production of organic acids, siderophores and hydroxyl and carboxyl groups that chelate the cation bound to phosphate and the latter being converted into soluble forms (Sharma et al. 2013). Bacterial isolates belonging to genera *Enterobacter*, *Pantoea* and *Klebsiella* solubilize $Ca_3(PO_4)_2$ to a greater extent than $FePO_4$ and $AlPO_4$ (Chung et al. 2005). Hence, microorganisms play an important role in the soil phosphorus cycle by mediating phosphorus availability to plants, increasing the capacity of plants to acquire phosphorus from the P-deficient soil directly by solubilizing inorganic phosphorus and facilitating their mobilization through the enlargement of root surface area (Richardson and Simpson 2011).

India is blessed with sufficient supply of potassium (K) in soil, though the K reserve is limited, which results to a huge foreign exchange to import K fertilizers. In this context utilization of native sources such as K-bearing minerals (K-feldspar, phlogopite, biotite, muscovite and green sands), waste mica as enriched compost (Nishanth and Biswas 2008) and bio-intervention of these K-bearing minerals could be a viable and alternative technology to solubilize insoluble K into plant available pool.

The usefulness of K-bearing minerals as K fertilizers in agriculture is less due to their limited accessibility. Some efficient microorganisms play significant induction in K solubilization and K release from K-bearing minerals (Reitemeir 1951); those microorganisms are commonly described as potassium-solubilizing bacteria (KSB), potassium-solubilizing rhizobacteria (KSR) and potassium-dissolving bacteria (KDB). A broad group of bacteria named *Pseudomonas* sp., *Acidithiobacillus ferrooxidans*, *Bacillus circulans*, *B. mucilaginosus*, *Burkholderia*, *B. edaphicus* and *Paenibacillus* sp. have been reported to release potassium in available form from potassium-bearing minerals in soils (Liu et al. 2012; Bagyalakshmi et al. 2012; Saiyad et al. 2015; Verma et al. 2015a).

As per the finding of Hutchens et al. (2003), they reported that some specific bacteria generate mucilage like exopolysaccharides which form a cover on all the sides of the bacterial cell and invade the silicate minerals chelating with silicon and hence facilitate K from those silicate structure. It was found that various organic ligands include exudates, extracellular enzymes, metabolic by-products and chelates, and both light and compound organic acids (oxalic, citric, gluconic acids) and

Table 1.2 Rhizospheric microorganisms and their produced siderophore

Microorganisms	Siderophores
Bacteria	
Bacillus, *Arthrobacter*, *Nocardia*	Ferrioxamines
Azotobacter, *Agrobacterium*	Catecholate
Bacillus	Schizokinen, Bacillibactin
Staphylococcus	Staphyloferrin
Escherichia coli	Enterobactin
Mycobacterium tuberculosis	Mycobactin
Erwinia chrysanthemi	Chrysobactin, achromobactin
Salmonella sp.	Salmochelin
Bordetella sp.	Alcaligin
Pseudomonas sp.	Pyoverdines
Fungi	
Basidiomycetes (*Ustilagosphaerogena*)	Desferriferrichrome
Ascomycetes (*Neurospora crassa*)	
Zygomycetes (*Rhizopus*)	Rhizopherin
Deuteromycetes	Fusarinines, malonichrome
Fusarium roseum	Fusarinines, triacetylfusarinines
Aspergillus fumigants	Pistillarin
Penicillium bilaii	
Vesicular arbuscular mycorrhizae	
Wilcoxinarehmii and *Cenococcum geophilum*	Fericrocin
Higher plants	
Graminaceous plants	Phytosiderophores
	Mugineic acid
	Deoxymugineic acid
	Epoxy-mugineic acid

Adopted from Hider and Kong 2010

siderophores improve the destruction of aluminosilicate mineral which could perform an essential role in the solubilization of elements such as K, Si and Fe from the minerals like muscovite and biotite (Hutchens et al. 2003).

Potassium-solubilizing microorganisms (KSMs) have capability to perform multiple roles in agriculture. Thus, KSB can be applied as bioinoculants to maintain the extraction of potassium and sustain its availability for the plant (Zhang and Kong 2014) and efficiently used as K-biofertilizer for sustaining crop production and maintaining soil K (Meena et al. 2013c, 2015d; Singh et al. 2015, 2016).

Iron is essential for the survival and proliferation of all forms of life. In aerobic (oxidized) conditions, iron occurs predominantly as Fe^{3+}, which may probably form insoluble hydroxides and oxy-hydroxides that results in unavailability of iron to both plants and microorganisms (Rajkumar et al. 2009). Bacteria, fungi and mycorrhizae usually obtain iron by the secretion of siderophores (Table 1.2), which have intensive specificity and affinity for chelating with the iron.

Siderophores are chemically low-molecular-weight (<1000 Da) non-proteinous amino acids, which are released from the rhizospheric microbes in response of iron deficiency, having high association constants for complexing with the Fe^{3+} (Krewulak and Vogel 2008; Lemanceau et al. 2009). Simultaneously, plants also release low-molecular-weight phenolic root exudates, which have great importance for the acquisition of the cationic micronutrients from the rhizosphere, known as phytosiderophore (Marschner et al. 1986; Zhang et al. 1991).

These phytosiderophores are non-hydroxylated (deoxymugineic acid) and hydroxylated (mugineic acid; epi-hydroxymugineic acid) in nature, which forms single negatively charged Fe(III) complexes. Degree of hydroxylation improves stability of phytosiderophore-Fe(III) complex (von Wiren et al. 2000). However, it is likely that phytosiderophore promoted nonsteady-state dissolution mechanisms that contribute to the high iron efficiency of graminaceous plants (Takagi et al. 1984). The reduction strategy (reduction of ferric chelates at the root surface by ferric-chelate reductase oxidase and iron-regulated transporter genes) of non-graminaceous plants and the chelation strategy of graminaceous plants (Kobayashi and Nishizawa 2012) are two distinct strategies developed by plants to acquire sparingly soluble iron from the rhizosphere (Reichard et al. 2005).

Similarly, Fe-siderophore complex around the bacterial membrane is reduced to Fe^{2+} and moreover is then liberated within the cell from the siderophore through a gating process adjoining with the inner and outer membranes both in gram-negative and gram-positive rhizobacteria. The bacterial genera *Burkholderia*, *Enterobacter* and *Grimontella* impended different strains having the capacity of high siderophore production. The secretion of siderophores by bacteria might encourage the plant growth, therefore enriching nutrition (direct effect) or suppressing the growth of phytopathogens (indirect effect) by the isolation of Fe from the surroundings (Dimkpa et al. 2009).

Besides, inoculation of plant beneficial microorganisms can raise the uptake of several other nutrients such as Ca, K, Cu, Mn and Zn by the plants. This uptake mostly occurs due to acidification of the soil rhizosphere through the organic acid production or through activation of proton pump ATPase. In this case, the soil pH is decreased which improves the solubilization of these essential nutrients (Mantelin and Touraine 2004).

1.3.2 Biocontrol Activities of Plant Beneficial Rhizospheric Microbes

Plant growth and development can be obtained indirectly via biocontrol activity in opposition to plant pathogens. Representatives of the bacterial genera *Bacillus*, *Pseudomonas*, *Serratia*, *Stenotrophomonas* and *Streptomyces* and the fungal genera *Ampelomyces*, *Coniothyrium* and *Trichoderma* are well-defined microorganisms which are responsible for resistant action and include hindrance of the pathogen by the production of antibiotics, toxins and surface-active compounds (biosurfactants); competition for nutrients, minerals and colonization sites (Table 1.3); and a

Table 1.3 Different biocontrol agents produced by PBRM that control disease, pathogen and insect at different crops

Disease/pathogen/insect	Crops	PBRM
Myzus persicae (Sulzer)	Bell pepper	*Bacillus amyloliquefaciens*
Fusarium avenaceum	Chickpea	*Enterobacter sp.*
Cotton aphids	Cucumber	*Bacillus sp.*
Root rot	Mung bean	*Pseudomonas aeruginosa*
Myzus persicae	Pepper	*Bacillus licheniformis*
Myzus persicae	Pepper	*Bacillus subtilis* G803
Rhizosphere fungi	*Prunus cerasifera* L.	*Azospirillum brasilense*
Myzus persicae	Red pepper	*Bacillus cereus* MJ-1
Fungal disease	Sesame	*Paenibacillus polymyxa* E681
Blue mould	Tobacco	*Bacillus pumilus* SE 34
Rhizoctonia bataticola	Tobacco	*Pseudomonas* sp.
Tobacco necrosis virus	Tobacco	*Pseudomonas fluorescens*
Tomato mottle virus	Tomato	*Bacillus amyloliquefaciens*
Acyrthosiphon kondoi	White clover *Medicago*	*Pseudomonas sp.*

Adopted from Bhattacharyya and Jha 2012

procedure that grows extracellular cell wall deteriorating enzymes such as chitinase and β-1,3-glucanase (Whipps 2001; Compant et al. 2005; Haas and Defago 2005).

Effective plant growth acceleration and biological control of plant maladies by rhizobacteria include one or more procedures (Fig. 1.3), which involve the generation of phytohormones, parasitism, antibiosis, competition for niches and nutrients and induced host defence (Lugtenberg and Kamilova 2004; Adesemoye et al. 2009).

In general, niche ejection, induced systemic resistance (ISR) and production of antifungal metabolites are the cardinal functions of biocontrol activity in PBRMs (Lugtenberg and Kamilova 2009). Many rhizobacteria have been described to grow antifungal metabolites such as HCN, phenazines, pyrrolnitrin, 2,4-diacetylphloroglucinol, pyoluteorin, viscosinamide and tensin (Bhattacharyya and Jha 2012). The ISR is the circumstance in which the mutual cooperation of some rhizobacteria with the host root protects the plants from some pathogenic bacteria, viruses and fungi (Lugtenberg and Kamilova 2009). Several strains from *Pseudomonas*, *Bacillus* and *Azospirillum* genera are the dominant group of that have been characterized for generating the ISR response.

Furthermore, ISR comprises jasmonate and ethylene signalling inside the plants, and these hormones activate resistance capacity of the host plant against a range of plant pathogens (Glick 2012). Many discrete bacterial ingredients induce ISR, such as lipopolysaccharides (LPS), siderophores, flagella, cyclic lipopeptides, 2, 4-diacetylphloroglucinol, homoserine lactones and volatiles like acetoin and 2,3-butanediol (Lugtenberg and Kamilova 2009). With the development of materialistic PGPR in India, the sheath blight of rice due to *Rhizoctonia solani* was alleviated over the control ~38%, and grain yields were significantly increased (~3901 and 1938 kg ha^{-1}) over control (~2690 and 1550 kg ha^{-1}) (Kumar et al. 2009). The

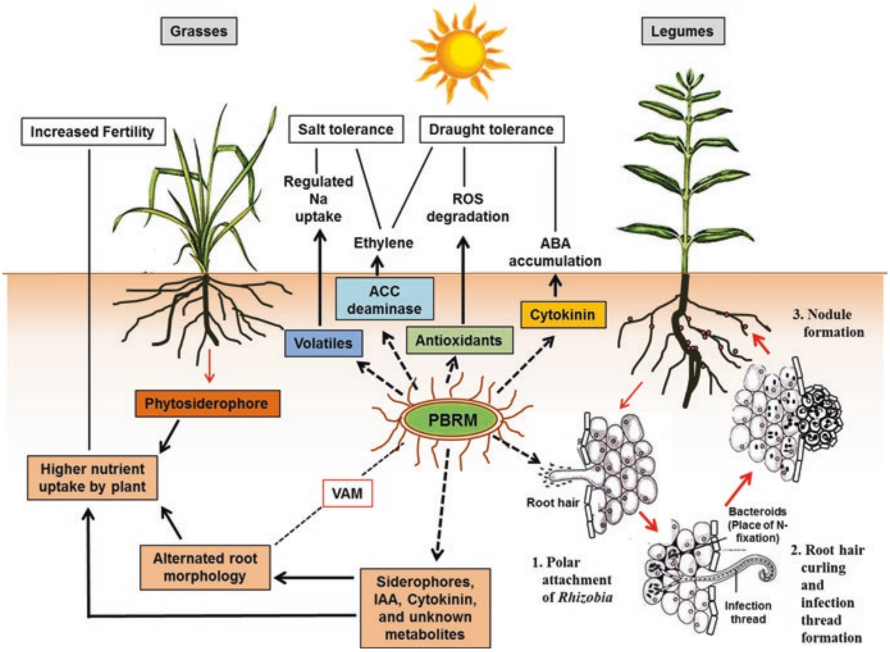

Fig. 1.3 Nutrient acquisition and induced systemic resistance (ISR) against draught, salt and fertility stress by different efficient PBRMs (Coyne 1999; Yang et al. 2009). The *dashed arrows* represent PBRMs secreted compounds; *solid arrows* indicate the components affected by PBRMs secreted compounds (*VAM* vesicular arbuscular mycorrhiza, *ABA* abscisic acid, *ROS* reactive oxygen species, *ACC* 1-aminocyclopropane-1-carboxylate, *PBRM* plant beneficial rhizospheric microbes, *IAA* indole acetic acid)

practice of using microorganisms as bioinoculants for suppressing of the plant diseases is a method of biological control, which is an eco-friendly approach (Lugtenberg and Kamilova 2009).

1.3.3 Rhizospheric Microbes in Plant Stress Resistance

'Stress' in plants can be defined as any external factor that negatively influences plant growth, productivity, reproductive capacity or survival. This includes a wide range of factors which can be broadly divided into two main categories: abiotic or environmental stress factors and biotic or biological stress factors. Biotic stress can be defined as the stress which is induced by living organisms, such as other plants, weeds, fungi, bacteria, different faunal groups, etc., whereas abiotic stress is the result of nonliving stressors, such as high winds, extreme temperature and rainfall, drought and unwanted and devastated natural calamities, like cyclone, tornado, flash flood, etc.

Under these abiotic and biotic stresses, endogenous ethylene production is significantly increased which adversely affects the growth of the roots and as a whole the growth of the plant. In this concern, some distinct soil microorganisms produce some growth factors and metabolic products that positively influence plant metabolism which is not directly associated with pest or pathogen resistance (biotic stress). A number of mechanisms have been investigated aiming to reduce the levels of ethylene in plants. One of these mechanisms involves the activity of the enzyme 1-aminocyclopropane-1-carboxylase (ACC) produced by soil bacteria and degrades an ethylene precursor that, in turn, depresses the plant's stress response to a variety of biotic and abiotic stress factors (Farajzadeh et al. 2012). Soil bacteria also produce the auxin, indole acetic acid (IAA) which influences plant physiology, often resulting in enhanced root growth which stimulates plant growth. Naturally, microbial metabolites that positively influence plant vigour also impact plant resistance to pests and pathogens (Kim et al. 2011).

The AA's rhizosphere is the immediate adjacent zone of plant root and a nutrient-rich environment due to adequate supply of sugars, amino acids, organic acids, flavonoids, iso-flavonoids, phytohormones and enzymes; it is also the most vulnerable environment during activity of stressors and stress conditions. Thus, controlling and sustaining rhizosphere in its healthy manner are a major challenge for agricultural science societies. The applications of beneficial microbes in agricultural production systems were introduced long time ago, and there was enhancing manifestation that beneficial microbes can increase plants' tolerance to unfavourable environmental difficulties, which comprises salt stress (Egamberdiyeva and Islam 2008), drought stress (Zahir et al. 2008), weed infestation (Babalola 2010), nutrient deficiency and heavy metal contaminations (Sheng 2005).

The term 'induced systemic tolerance' (Fig. 1.3) has been applied to define the potentiality of PGPR to induce tolerance to salt and drought conditions (Yang et al. 2009). In this concern *Rhizobium trifolii* inoculated with *Trifolium alexandrinum* (berseem) has shown excessive biomass and large number of nodulation under salinity stress condition (Hussain et al. 2002; Antoun and Prevost 2005). Marulanda et al. (2009) rightly observed that the combination of *Pseudomonas putida* or *Bacillus megaterium* and AM fungi had been efficiently mitigating the drought stress. Photosynthetic ability and the anti-oxidative activity of rice plants liable to drought stress had shown to increase after inoculation with the arbuscular mycorrhiza (Ruiz-Sanchez et al. 2010).

The auspicious effects of mycorrhizae have also been described under both the saline and drought stress conditions (Aroca et al. 2013). Not only mycorrhizae but also identification of diverse salt-tolerant rhizobacteria has displayed favourable interactions with plants under stressed conditions. These PGPR (*Rhizobium*, *Azospirillum*, *Pseudomonas*, *Flavobacterium*, *Arthrobacter* and *Bacillus*) exert osmoregulation, resistance to starvation, oligotrophic and endogenous metabolism and useful metabolic methods to acclimatize under arid and brackish environments (Lugtenberg et al. 2001; Egamberdiyeva and Islam 2008). When plants are illuminated to the stress situations, they may increase ethylene inside the cell and cause plant damage (Argueso et al. 2009).

Higher accumulation of ethylene can be hazardous because it persuades defoliation and other cellular mechanisms that exert influence on crop development (Desbrosses et al. 2004). Many growth-promoting microorganisms damage 1-amin ocyclopropane-1-carboxylate (ACC) (a precursor of the ethylene) through the production of the enzyme ACC deaminase, which consequently accelerates plant growth and development by lowering ethylene levels in plants. Production of calcisol by PGPRs, viz. *Pseudomonas alcaligenes* PsA15, *Bacillus polymyxa* BcP26 and *Mycobacterium phlei* MbP18, may involve in stress tolerance against salinity and high temperature (Egamberdiyeva 2007).

The PBRMs that produce 1-aminocyclopropane 1-carboxylate (ACC) deaminase alleviate various types of stresses, because these antagonistically affect the phytopathogenic bacteria, and other stresses due to polyaromatic hydrocarbons, salt and draught (Glick et al. 2007). It is argued that ACC deaminase producing PBRMs are responsible for lower plant ethylene levels, often a result of various stresses. The optimal functioning of these bacteria includes the synergistic interaction between ACC deaminase and both plant and bacterial auxin, indole-3-acetic acid (IAA).

These bacteria not only directly promote plant growth, they also protect plants against flooding, drought, salt, flower wilting, metals, organic contaminants and both bacterial and fungal pathogens. With their physiological adjustment and genetic potential for increasing tolerance to drought, salinity and high temperatures, the PBRMs could advance plant growth in deteriorated soil system (Maheshwari et al. 2012; Yang et al. 2009). Corresponding production of siderophore and phytosiderophore from PGPR and plant root in the response of Fe deficiency may colonize in the rhizosphere and acts as an aid to eliminate the stress imposed by high levels of heavy metals, such as Al, Cd, Cu, Ga, In, Pb and Zn. The performance of the microbial population in the rhizosphere to decompose the pollutants allows plants to grow as natural vegetation under the polluted condition.

1.3.4 Rhizospheric Microbes and Crop Growth

The modes of action of growth-promoting microbes involve intricate mechanisms to promote plant growth, development and protection against plant diseases. These are accomplished by the two main processes: biofertilization (enhancing the accessibility of nutrients to plant) and phytostimulation (regulation of plant growth, usually by the production of phytohormones). In the phytostimulation processes of plant growth, phytohormones play an important role in a direct way. The phytohormones which are produced by them include indole acetic acid (IAA), auxin, cytokinins, gibberellins and inhibitors of ethylene (Table 1.4). These hormones can be secreted by the plant themselves and with their associated microorganisms such as *Azospirillum* sp., which is also having nitrogen-fixing potentiality (Steenhoudt and Vanderleyden 2000).

Different strains of *Pseudomonas* and *Bacillus* can produce well-characterized phytohormones or growth stimulator that leads crops to have higher amounts of fine plant roots which have the enlarged surface area for the absorption of water and

Table 1.4 Plant beneficial rhizospheric microorganisms (PBRMs) as an efficient phytohormone producer in various plants

Phytohormones	Crops	PBRMs
Gibberellin	Alder	*Bacillus sp.*
	Soybean	
	Soybean	
Cytokinin	Soybean	*Pseudomonas fluorescens*
	Lettuce and rapeseed	*Rhizobium leguminosarum*
	Wheat	*Paenibacillus polymyxa*
Indole acetic acid (IAA)	Soybean	*Bradyrhizobium japonicum*
	Soybean	*Bradyrhizobium amyloliquefaciens*
	Wheat	*Azospirillum brasilense*
	Radish	*Bradyrhizobium* sp.
	Rice	*Enterobacter cloacae*
	Rice	*Aeromonas veronii*
	Lettuce	*Agrobacterium* sp.
	Lettuce	*Alcaligenes piechaudii*
	Lettuce	*Comamonas acidovorans*
Jasmonic acid (JA)	Soybean	*Bradyrhizobium japonicum*
	Soybean	*Bradyrhizobium amyloliquefaciens*
Salicylic acid (SA)	Soybean	*Bradyrhizobium japonicum*
	Soybean	*Bradyrhizobium amyloliquefaciens*

Adopted from Bhattacharyya and Jha 2012; Masciarelli et al. 2014

nutrients from the surrounding soils. Indole-3-acetic acid (IAA) is a commonly produced phytohormone by growth-promoting rhizospheric microorganisms and which is believed to be associated with cell division, cell enlargement and root initiation (Salisbury 1996). Auxin is a group of plant hormones significant in the advancement of lateral root formation. Enhanced lateral root leads to an increased ability to absorb the essential nutrients for the plant.

Auxins are mostly secreted by *Azospirillum*, and it is commonly described that their formation, rather than the nitrogen fixation, is the main feature responsible for the stimulation of lateral root growth and, hence, advanced plant development (Bloemberg and Lugtenberg 2001). Other groups of plant hormones include gibberellins and cytokinins, both of which regulate shoot development; howsoever their effects on root enlargement are not well researched (Fig. 1.3). They meet important functions for plant growth and health by several processes. Immediate plant growth promotion occurs either from enhanced nutrient availability or from hormonal incitement. Variant methods are engaged in the inhibition of plant pathogens, which is mostly indirectly related with plant growth.

Plant growth and productivity are greatly affected by the mutual associations between plant roots and the surrounding soil, including the microbial communities. These microbes are either autochthonous or applied as crop inoculation such as *Azospirillum* (Cassan and Garcia de Salamone 2008), *Bacillus* (Jacobsen et al. 2004), *Pseudomonas* (Loper 1988), *Rhizobium* (Long 2001), *Serratia* (De

Vleesschauwer et al. 2007), *Stenotrophomonas* (Ryan et al. 2009) and *Streptomyces* (Schrey and Tarkka 2008). Besides, some fungal genera like *Ampelomyces*, *Coniothyrium* and *Trichoderma* have been stated also to be advantageous for the host plant (Harman et al. 2004).

1.3.5 Role of Rhizospheric Microbes in Soil Fertility and Sustainability

'Zero Hunger Challenge' is the major goal of human efforts. This goal can be achieved by sustainable increment in the arena of agricultural productivity to satisfy the demands of abruptly spreading human population. Growing more and more foods from less and less farm holdings is a demand feature of our economy. Not only we have touched the limits of land ready for cultivation, but agricultural margin is also narrowing at the proportion of a million acres per annum due to enlargement of our cities, industrial areas and highways construction. Then we should consider our soil with great concern. Microorganisms in the soil show a unique relation to soil fertility. The presence of rhizosperic microbial communities in association with PBRMs has pivotal role to prolong soil function, in both natural and maintained agricultural soils (Bharti et al. 2016) (Table 1.5).

Soil organisms exceed soil fertility by doing a number of functions that are advantageous for plants. This chapter assesses five of these functions of PBRMs:

1. PBRMs can accelerate the nutrient release from native source of nutrient in soil and applied organic residues. Phosphate-solubilizing PBRMs and potassium-solubilizing PBRMs accelerate the weathering reactions of P- and K-bearing minerals, especially when in direct contact with mineral surfaces either by production of organic acids or formation of biofilms or may take part in nutrient mobilization by proliferation of root length as mycorrhizal fungi (Basak and Biswas 2009; Saha et al. 2016a; Hodge 2017).
2. In the symbiotic association, *Rhizobia* or *Bradyrhizobia* fix atmospheric nitrogen gas and make it available to the leguminous plants. Free-living (*Enterobacter*, *Azotobacter*) and associative (*Azospirillum*) nitrogen-fixing rhizobacteria, nevertheless, absorb this gas and transform it into cell protein. When the cells waste away, other microbes invade the protein and convert the nitrogenous components to ammonium, so which becomes readily available for the plants.
3. The process of 'the priming effect' has described as early as 1926 but still poorly understood. Positive priming (extra decomposition of SOM) or negative priming (reduction of SOM decomposition) is depending on the metabolic activity of PBRMs (van der Wal and de Boer 2017). In terrestrial ecosystems, large quantities of carbon are held in SOM 'the key to soil fertility' and altered by soil microbes that supply SOC and organically bounded nutrients to plants.
4. Bioremediation of agricultural toxic chemical inputs (pesticides) in soil is mostly acted by microorganisms (Zhuang et al. 2007). Some PBRMs having enzymatic activity in soil, which can disintegrate agricultural pesticides or other toxic

Table 1.5 Different PBRMs of vegetable and food grains and their activities

Host plants		PBRM inoculants	PBRM abilities
Vegetables	Brinjal	*Azotobacter* spp., *Azospirillum* spp.	Biofertilizer
		Pseudomonas fluorescens	Biocontrol against bacterial wilt
	Tomato	*Bacillus subtilis*, *B. cereus*, *Arthrobacter* spp., *Trichoderma viride*, *Pseudomonas fluorescens*, *P. putida*, *P. marginalis*, *P. syringae*	Induced systemic resistance and biocontrol against late blight
	Potato	*Bacillus subtilis*, *B. cereus*, *Azotobacter* spp.	Biofertilizer, induced systemic resistance against late blight
	Broccoli	*Bacillus cereus*, *Brevibacillus reuszeri*, *Rhizobium rubi*	Biofertilizer
	Cabbage	*Bacillus subtilis*, *B. megaterium*, *Pantoea agglomerans*	Improved nutrient uptake, induced systemic resistance
	Okra	*Bacillus firmus*, *B. subtilis*	Induced systemic resistance against root knot nematode
	Radish	*Pseudomonas fluorescens*, *Bacillus subtilis*	Induced systemic resistance
	Chilli	*Bacillus* spp., *Arthrobacter* and *Serratia* spp.	Induced systemic resistance against anthracnose disease of chilli (*Colletotrichum gloeosporioides*) and endophytic bacteria
	Spinach	*Bacillus megaterium*	Induced systemic resistance against *Rhizoctonia*, *Pythium*, *Fusarium* and *Phytopthora*
		B. subtilis	
		B. licheniformis	
		B. cereus	
		B. subtilis	
		Paenibacillus polymyxa	
		Pseudomonas putida	
	Cucumber	*Bacillus pumilus*	Biocontrol against angular leaf spot (*Pseudomonas syringae*)
		Bacillus spp.	Biocontrol against root rot (*Pythium* sp.)
Food grains	Rice	*Pseudomonas fluorescence* Aur6,	Biocontrol against *Magnaporthe grisea*
		Chryseobacterium balustinum, BGA	Salinity
			N fixation
	Wheat	*Bacillus circulans, Glomas* spp., *Cladosporium herbarum*, *Calothrix* sp., *Anabaena* sp.	Biofertilization
		Arthrobacter sp., *Bacillus subtilis*	Salinity controller

(continued)

Table 1.5 (continued)

Host plants		PBRM inoculants	PBRM abilities
	Maize	*Serratia liquefaciens*, *Bacillus* sp.	Biofertilization
			Biocontrol to root pathogens
		Pseudomonas spp.	Phytostimulation
		Azospirillum brasilense, *Bradyrhizobium japonicum*	
	Soybean	*Bradyrhizobium japonicum*, *Bacillus subtilis*, *Bacillus thuringiencis*	Biofertilization enhancer
			Phytostimulation
		Pseudomonas flaviporus, *Bradyrhizobium japonicum*	
	Bean	*Rhizobium tropici*, *Azotobacter brasilence*, *Glomus sinuosum*, *Glomus intraradices*, *Gigaspora albida*, *Pseudomonas fluorescens*	Biofertilization enhancer (N and P)
			Biocontrol against *Rhizoctonia solani*

Adopted from Choudhary and Johri 2009; Zaidi et al. 2015; Montano et al. 2014

materials added to soil; either by bioremediation of contaminated soils through seizing poisonous heavy metal species and/or destroying xenobiotic compounds (Kuppusamy et al. 2016).

5. Biological functions in soil can ameliorate soil structure. Some bacteria and fungi produce brown-coloured substances during organic matter decomposition, which can bind soil particles both physically and chemically into micro-aggregates. The hyphal networks of fungi can cross-link with the soil particles that help in the genesis and maintenance of soil aggregates (Lehmann et al. 2017).

Being an inherent part of soil and as most of the soil function is microbial imparted, soil organisms play an essential role in conserving soil health and sustainable crop production even after decades. The main target in the upcoming decades would be on secured and eco-friendly approaches by accomplishing the beneficial microorganisms in sustainable crop production. Commonly, there are divergent in naturally occurring microorganisms, whose inoculation to the soil ecological environment improves soil physicochemical properties, soil microbial proliferation, soil quality, plant growth and crop productivity (Morris and Blackwood 2015).

1.4 Future Prospects

Attempt should be directed towards enhancement of biological diversity and be a beneficiary from identified soil microbes. Due to population growth and growing food demand, accelerated, sustainable and eco-friendly agriculture is growing with the use of biofertilizers and biopesticides, which have turned into the ideal model for the Asian continent as well as Indian subcontinent. If the aids of these microorganisms in crop production can be widen, this will certainly take an action against hunger. The production performance of a specific rhizospheric microorganism may be further enlarged with the development and adaptation according to the prevalent soil conditions. Subsequently, they are supposed to partly substitute the chemical fertilizers, pesticides and synthetic growth regulators which have numerous side effects to sustainable agriculture (Verma et al. 2015c). Notwithstanding the fact that a lot of associative and endophytic bacteria have indicated plant growth-promoting properties at the point of laboratory and greenhouse level, but these bacteria have dimed to show their consistency under natural conditions. Accordingly, a challenge is affixed for standard optimization of the applied efficient PGPR (PBRMs) strains and the amount of fertilizers to be added to get the maximum output. One of the major challenges encompasses the specification of plant genotype, age and suitable associative bacteria. Considering this suitability, it would help to increase productivity by adopting the specific strain for inoculation.

1.5 Conclusions

The current chapter is an attempt to illuminate the concept of beneficial rhizobacteria in the present scenario. The latest criterions of a wide range of utilizations of these beneficial microorganisms have been presented absolutely to extract large prospects regarding their activity and applicability for sustainable agriculture. Thus, these PBRMs manifested as biofertilizers are essential for conserving good soil fertility, preferable soil conditions and prolonged agricultural productivity. The diverse groups of soil microorganisms do not live unaided but form an interconnected system, more or less in balanced condition with the environment. All have played an enormous role in the advancement of soil fertility by weathering and solubilization of the immobile nutrient sources. Soil organic matter decomposition, humification, aggregate formation, bio-catalytic activity, biocontrol against plant pathogens and parasites along with improving soil health with proper aeration cause better soil fertility in sustainable manner. Their actions are concerned with the formation of structural systems of soils which help in increasing agricultural productivity. Such plant growth-stimulating mechanisms might assist in higher production of crop grains in a more feasible way, still on marginal farm, and thus assign to avoid the alterations between food and balanced energy production. PBRMs (mycorrhizae and rhizospheric bacteria) improved the soil health in different ecosystems and provide a sustainable alternative to enhanced crop production.

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2

Rhizosphere Microorganisms Towards Soil Sustainability and Nutrient Acquisition

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Abstract

The importance of soils and its function is conclusive; the soil is a living entity that needs to be improved under sustainable approach. It is apparent that soil biota contributes substantially to effective soil functioning and maintenance of soil sustainability. The increase of food production to meet out the food security demand of an ever-increasing population has been highly dependent on integrated nutrient management input but ignores the potential of bioagents. The significance of rhizosphere microorganism can be enormous as they are able in managing nutrient transformation, nutrient acquisition and use, and thus crop sustainability. The soil sustainability and nutrient use efficiency (NUE) can be enhanced by modification of rhizosphere through the best management approaches such as agronomic practices, nutrient management, use of organic and biofertilizers, and regulation of rhizosphere processes.

Keywords

Rhizosphere • Soil sustainability • Nutrient availability • PGPR • Bioremediation

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2.1 Introduction

Agriculture in the twenty-first century faces more challenges, like decline in productivity and degradation in soil quality. As per the United Nations estimates, the global human population is projected to reach ~9 billion by 2050 (Wood 2001). The feeding of our ever-increasing population is one of the largest challenges for maintaining the worldwide agricultural sustainability. The soil being a critical component on the earth is not only for sufficient food production but also for maintaining worldwide environmental sustainability for the next generation (Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Kumar et al. 2015, 2017a; Ahmad et al. 2016; Zahedi 2016). These existing technologies have reached to its plateau and are hitherto extremely difficult to further increase the food production. Therefore, exploring nonconventional resources is an urgent need not only to increase the demand of ever-increasing population but also to sustain our ecosystem from the further degradation. Sustainability in the agriculture production cannot be attained without microbiological population in soil under the present circumstances (Vaxevanidou et al. 2015; Patil et al. 2014).

These efficient microorganisms are key factor of the living biomass of the soil system (Whitman et al. 1998). Soil microorganisms play significant roles in agriculture mainly by improving plant nutrition and soil health, as well as soil quality (Barea 2004; Barea et al. 2013; Lugtenberg 2015) and degrading organic pollutants. The function of agriculture ecosystem depends largely on soil microbial dynamics (Barea 2004). These efficient soil microorganisms maintain the organic matter (OM) mineralization and thus regulate nutrient cycling. The beneficial saprophytic rhizosphere microbes improve plant performance work as a decomposer of OM substances, plant growth-promoting bacteria/rhizobacteria (PGPB/PGPR), and other plant growth-promoting (PGP) activities. The efficient PGPR must have the ability to survive and multiply in rhizosphere microbes with indigenous microbes, at least for the time needed to express their beneficial PGP (Martinez-Viveros et al. 2010). The rhizosphere microorganisms improve nutrient cycling processes that include N fixation, P mobilization, and the release of other nutrients to soil solution for plant nutrition (Richardson et al. 2009; Barea and Richardson 2015).

The rhizosphere soils contain efficient microbes, and researcher differentiates them into beneficial and harmful categories based on their beneficial effect on soil sustainability, crop growth, and yield (Welbaum et al. 2004; Bais et al. 2006; Brimecombe et al. 2007; Jat et al. 2015). Microbes play vital roles in soil sustainability and nutrient acquisition. Without soil microbes life on the planet would not be possible. An increased knowledge of rhizospheric chemistry-based symbioses in plants could provide potential ways of developing sustainable agriculture with minimal risk to the environment. Therefore, rhizosphere microorganisms have a key role to improve NUE and crop sustainability simultaneously (Bahadur et al. 2016a, b; Das and Pradhan 2016; Dominguez-Nunez et al. 2016; Verma et al. 2014, 2015b; Yadav and Sidhu 2016; Yasin et al. 2016).

2.2 Why Soil Sustainability Is So Important?

Providing as well as feeding rapidly growing human population is one of the greatest challenges worldwide. The requirement of food will be ~29 Mt, while their availability will be only ~22 Mt by 2020. Best management practices (BMPs) and recommended management practices (RMPs) of soil system ensure that mineral nutrients do not become deficient or toxic to plants as well as humans and that appropriate crop/mineral nutrients enter the food chain. Soil management is important, both directly and indirectly, to crop productivity, environmental sustainability, and human health. Because of the projected increase in worldwide population and the consequent necessity for the nutritional security, the management of soils will become increasingly important in the coming years because the traditional agriculture will not be able to meet the needs of the next generation (Altieri 2004).

2.3 The Rhizosphere: A Hot Spot for Microbial Activities

The rhizosphere is the narrow region of soil system that is immediately near to the root surface and that is more affected by rhizospheric phenomena. The term “rhizosphere” was first time used by Lorenz Hiltner in 1904. The root exudates include carbohydrates, sugar, organic acids, vitamins, flavonoids, nucleotides, enzymes, hormones, and volatile compounds, inorganic ions, and gaseous molecules. The exudates act as messengers that stimulate interactions between roots and soil organisms. Therefore, rhizosphere is the most dynamic environment in the soil with a high microbial diversity. It is well established that microorganism’s population is higher in rhizosphere (Table 2.1) than bulk soil (Brimecombe et al. 2001; Bahadur et al. 2017; Verma et al. 2017b; Kumar et al. 2017a).

In the rhizosphere, the populations of microorganisms may fluctuate from few thousands to millions (Nihorimbere et al. 2011). This plant-microbe interaction has shown many beneficial effects on plant growth and developments (Singh et al. 2004), PGP increased availability and uptakes of nutrients, and disease suppression (Morrissey et al. 2004; Haas and Defago 2005; Mendes et al. 2011). However, increased resistance to abiotic and biotic stresses (Zolla et al. 2013; Badri et al. 2013), all these leads to increases in crop productivity and soil sustainability as well as nutrient availability (Bardgett et al. 2014; Nath et al. 2017; Sarkar et al. 2017; Verma et al. 2017a).

Table 2.1 Presence of microbes in the rhizosphere and non-rhizosphere soil system

	Rhizosphere	Non-rhizosphere	
Microorganisms	Microbes g^{-1} dry soil		R:S ratio
Bacteria	1200×10^6	53×10^6	23.0
Fungi	12×10^5	1×10^5	12.0
Actinomycetes	46×10^6	7×10^6	7.0
Algae	5×10^3	27×10^3	0.2

Table 2.2 Microbial-mediated soil nutrient availability

Nutrient	Microbial transformation
Sulfur	Mineralization, immobilization, oxidation, reduction
Nitrogen	Immobilization, nitrification, denitrification, urea hydrolysis, N_2 fixation
Phosphorus	Mineralization, immobilization, extracellular P activity, facilitated uptake by VAM
Potassium	K solubilization, mobilization, and mineralization
Zinc	Facilitated uptake by mycorrhizal fungi, Zn solubilization
Copper	Facilitated uptake by exudates and mycorrhizal fungi
Iron	Change in oxidation state, production of siderophores, chelation
Manganese	Change in oxidation state in soil system

2.4 Role of Rhizosphere Microorganisms in Soil Sustainability and Nutrient Acquisition

Rhizosphere microorganisms play important roles in agriculture mainly by improving soil-plant nutrition and health, as well as soil quality of the ecosystem (Barea et al. 2013; Lugtenberg 2015). The rhizosphere is a multifaceted, complex "melting pot" of components and processes affecting plant growth and development and thus ecosystem functioning (Table 2.2). The plant-microbe interactions may be classified into beneficial, neutral, or harmful to the plant, depending on the beneficial and harmful effect on specific microorganisms and plants (Bais et al. 2006). Exploring this multicomponent complex of rhizosphere and its possible relationship to soil sustainability will become crucial in order to maintain food production with reduced fertilizers and pesticide inputs (Bakker et al. 2012; Dotaniya et al. 2016; Jaiswal et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a, b; Singh et al. 2015; Teotia et al. 2016; Velazquez et al. 2016; Verma et al. 2015a).

2.4.1 Organic Matter (OM) Decomposition

The OM has been considered as one of the most important components in improving soil health and agricultural sustainability. The rhizosphere microorganisms play an important role in regulating soil organic matter (SOM) decomposition and nutrient cycling due to the direct influences by roots that are often referred as rhizosphere processes. These rhizosphere processes may include exudates, water uptake, nutrient mobilization by roots and microorganisms, and SOM decomposition. These efficient rhizosphere processes are major paths for nutrient and water availability. Therefore, rhizosphere effect on the SOM decomposition is significant in mediating plant-soil interactions.

SOM decomposition is mediated by rhizosphere processes (Sallih and Bottner 1988; Cheng and Coleman 1990). This OM in the soil system is more or less continuously transformed by different chemical and biochemical mechanisms into various ranges of compounds (Marschner and Rengel 2007). The SOM contains various compounds which are the main energy source for the soil biota. Soil organisms have appropriate biochemistries and life processes to embezzle such energy for their growth; in doing so, the compounds are further transformed and cycled between compartments (Masood and Bano 2016; Meena et al. 2016a; Shrivastava et al. 2016; Sindhu et al. 2016; Singh et al. 2016; Kumar et al. 2017b).

2.4.2 Nutrient Transformation and Availability

Plant-microbe-soil interactions strongly modulate nutrient availability in soil system. In rhizosphere soil, the activity of microbes and plant roots is clearly distinct from the bulk soil (Marschner et al. 2003). The plant/crop roots must compete with the root system of neighboring plant species for space, water, and mineral nutrients. Next to water and temperature, nutrients are the most crucial environmental factors required for growth and development of crops (Akhtar and Siddiqui 2010). Soil-plant-microbe interactions have various effects such as positive, negative, and neutral; these efficient systems help to remediate the polluted soil system (Morgan et al. 2005; Kuzyakov and Xu 2013).

These various efficient rhizosphere microorganisms like free-living and symbiotic nitrogen-fixing rhizobacteria contribute a lot to meet nutrient demand. Moreover, the phosphate and potassium solubilizing bacteria (PSB and KSB) have the capability to convert inorganic unavailable P and K form to soluble forms available to plants. The soil biota are also involved in the cycling of other nutrient elements of pertinence to agricultural production systems including various macro- and micronutrients (Tebo et al. 2004; Weber et al. 2006; Meyer et al. 2007; Eriksen 2009). The mycorrhizae (VAM) can also influence the uptake of a range of elements by plants, including macro- and microelements, its work mainly phytoremediation or uptakes of heavy metals (Clark and Zeto 2000; Meena et al. 2015a, b, 2016b; Saha et al. 2016b; Sharma et al. 2016).

Other than rhizobacteria, fungi are fundamental for soil ecosystem functioning especially in agricultural soils. It was estimated that the 1.5 million fungal species are present in the natural ecosystems but only few (5–10%) have been described formally (Hawksworth 2001; Bianciotto and Bonfante 2002). The arbuscular mycorrhizal fungi (AMF) increase the plant growth (Akhtar and Siddiqui 2008; Akhtar and Panwar 2011). The AMF have a high affinity toward enhanced P nutrition in plants (Verma et al. 2017a). These efficient AMF could also scavenge the available P, Fe, and Zn through their extra radical hyphae (Akhtar and Siddiqui 2008). Additional to their contribution in plant nutrition, AMF are able to improve soil structure and mitigate plant stress (Gianinazzi et al. 2010; Meena et al. 2013b, 2014a, 2016c, d; Priyadharsini and Muthukumar 2016; Raghavendra et al. 2016; Rawat et al. 2016; Saha et al. 2016a).

These efficient rhizosphere microbes have shown their influence toward the uptake of various macro- and micronutrients (Table 2.3) (Wu et al. 2005; Adesemoye et al. 2008). In another field study, inoculation of chickpea and barley with strains of *M. mediterraneum* significantly enhanced the K, Ca, and Mg along with P and N in both crop plants (Peix et al. 2001).

Table 2.3 Microbiological properties in bulk and rhizosphere soils of different plantations

		MBC	MBN	MBP	
Tree species		mg kg^{-1}			Microbial C/N
Siberian elm	Bulk soil	36.8(4.9)	7.0(0.6)	1.8(0.1)	5.2(0.8)
	Rhizosphere soil	52.7(5.2)	9.4(1.0)	2.1(0.2)	5.6(1.0)
	T-test	**	*	NS	NS
Simon poplar	Bulk soil	73.6(7.2)	6.7(0.2)	2.6(0.1)	10.9(1.2)
	Rhizosphere soil	90.7(6.4)	8.2(0.6)	2.8(0.2)	11.1(1.1)
	T-test	*	*	NS	NS
Mongolian pine	Bulk soil	45.6(3.2)	4.9(0.5)	1.6(0.1)	9.4(1.0)
	Rhizosphere soil	48.4(4.2)	8.0(0.9)	1.8(0.2)	6.1(0.7)
	T-test	NS	**	NS	*

Adopted from Zhao et al. (2010)

Data are means with standard errors given in parentheses (n = 5). NS denotes no significant difference (by paired samples T-test)

* Significant differences between bulk and rhizosphere soils at $P < 0.05$

** Significant differences between bulk and rhizosphere soils at $P < 0.01$

2.4.3 Plant Growth-Promoting (PGP) Activities

The bacteria present in the rhizosphere act as PGPR; they have the ability to enhance PGP atmospheric N fixation, hormone production, specific enzymatic activity, and plant and insect protection by producing antibiotic and other pathogen-depressing substances (Kamnev and Lelie 2000). However, the N_2-fixing, PSB, and KSB are important for crop plants as they increase N, P, and K uptake and play a crucial role as PGPR in the biofertilization (Zhang et al. 2013). In general, huge bulk inorganic/chemical fertilization is applied to replenish soil N and P demand with the resultant in high cost and environmental risk. Most of the P-fixed in the form of insoluble compounds is unavailable to plants. Thus, the application of such efficient microbes as eco-friendly biological agents may contribute to minimize the use of expensive P and K fertilizers.

2.4.4 Biocontrol Agents

A broad range of efficient microorganisms carry out biocontrol activities in the rhizosphere soils. These microbes play a major role to control diseases, which is a form of biological control and is an environment-friendly approach. Many rhizosphere bacteria have been reported to produce antifungal compounds like HCN, phenazines, pyrrolnitrin, 2,4-diacetylphloroglucinol, and pyoluteorin (Bhattacharyya and Jha 2012). The biocontrol ability of the PGPR depends on a wide variety of traits, such as the production of various antibiotic compounds, iron chelators, and exoenzymes (Meena et al. 2014b, 2015c, d; Prakash and Verma 2016).

Table 2.4 Effect of PGPR on various PGP activities under sustainable agriculture

PGPRs	Responses	Crop	References
Pseudomonas and *Azotobacter*	Stimulates growth and yield	Chickpea	Rokhzadi et al. (2008)
P. putida strain R-168	Enhance seed germination, growth parameters	Maize	Gholami et al. (2009)
P. fluorescens strain R-93, *P. fluorescens* DSM 50090, *P. putida* DSM291, and *A. lipoferum* DSM 1691	Increase growth, leaf nutrient contents and yield	Banana	Kavino et al. (2010)
P. putida strains R-168 and DSM-291	Improves seed germination, seedling growth and yield	Maize	Nezarat and Gholami (2009)
R. leguminosarum and *Pseudomonas* sp.	Enhance yield and P uptake	Wheat	Afzal and Asghari (2008)
P. putida strain	Growth stimulation	Tomato	Gravel et al. (2007)
Azospirillum brasilense	Improve growth attributes	Wheat and maize	Dobbelaere et al. (2002)
P. fluorescens strain	Growth and yield	Pearl millet	Niranjan et al. (2003)
Azotobacter and *Azospirillum* strains	Growth and productivity	Canola	Yasari and Patwardhan (2007)
P. alcaligenes PsA15 and *B. polymyxa*	Enhance nutrient uptake	Maize	Egamberdiyeva (2007)
Rhizobium leguminosarum	Direct growth promotion	Canola and lettuce	Noel et al. (1996)

2.4.5 Soil Bioremediations

The soil is an important habitat for thousands of microbes (Table 2.4); these efficient microbes are habitats between soil particles and soil organic matter in rhizosphere (Akhtar et al. 2013). Many soil microbes are capable of degrading toxic compounds including herbicides, pesticides, solvents, and other organic compounds and might provide a reasonable and effective measure of disposing toxic compounds (Murali and Mehar 2014).

Due to the degrading and sequestration capability of the microbial communities toward the toxic compounds and heavy metals (HMs), microbes have been used for bioremediation of soil contaminated with HMs (Table 2.5) (Dell'Amico et al. 2005; Kao et al. 2006; Umrania 2006).

The organic pollutants can be degraded by plants/crops/microbes through biochemical reactions taking place within the rhizosphere. The phytodegradation of organic pollutants may also be enhanced by rhizospheric activity (Mirsal 2004). The AMF were also demonstrated to PGP and degradation of toxic pollutants in soils with increased pollutant concentrations especially ectomycorrhizal fungi (Table 2.6). They promote the establishment of plants at HM-contaminated soil by immobilizing heavy metals in the soil, thereby reducing the availability of metals to plants (Jentschke and Godbold 2000; Meharg and Cairney 2000; Fomina et al. 2005).

Table 2.5 PGPR as biocontrol agents against various plant diseases

PGPR	Experimental conditions	Disease	References
Bacillus strain	Greenhouse	Blight of squash	Zhang et al. (2010)
B. pumilus strain SE34	Laboratory	Blue mold disease in tobacco	Zang et al. (2002)
B. pumilus strain INR7	Field	Bacterial wilt in cucumber	Zehnder et al. (2001)
B. pumilus strain SE34 and *B. subtilis* strain IN937b	Greenhouse	Cucumber mosaic cucumovirus (CMV) in tomato	Zehnder et al. (2000)
B. cereus strains B101R, B212R, and A068R	Greenhouse	Foliar diseases in tomato	Silva et al. (2004)
Pseudomonas spp.	Rice	Rice sheath rot	Saravanakumar et al. (2009)
P. fluorescens	Saline field	Saline resistance in groundnut	Saravanakumar and Samiyappan (2007)
P. fluorescens	Rice	Sheath blight disease	Radjacommare et al. (2002)
B. subtilis strain GBO3 and *B. pumilus* strain INR7	Greenhouse/ field	Downy mildew in pearl millet	Niranjan et al. (2003)
Bacillus sp. and *Azospirillum* strains SPS2	Greenhouse	Rice blast	Naureen Zakira et al. (2009)
B. amyloliquefaciens 937a and *B. subtilis* 937b	Field	Tomato mottle virus	Murphy et al. (2000)
P. fluorescens strain CHA0 + chitin bio-formulations	Greenhouse/ field	Banana bunchy top virus (BBTV)	Kavino et al. (2008)
B. strains BB11 and FH17	Greenhouse	Blight of bell pepper	Jiang et al. (2006)
Burkholderia strains MBf21 and MBf15	In vitro/in vivo	Maize rot	Rodriguez et al. (2008)

2.4.6 Drought and Nutrient Stress/Deficiency

Diverse environmental stresses like drought, salinity, and nutrient deficiencies are connected to soil-derived limitations. These stresses are inducing a series of morphological, physiological, biochemical, and molecular changes in the plant root system to adapt to the stress conditions and/or to modify the environment from which the stress is originated. Variation in the soil nutrient composition is a common condition in agricultural systems. Indeed, only ~30 to 50% of applied N fertilizers and ~10 to 20% of P fertilizers are used in crops (Adesemoye and Kloepper 2009). Furthermore, there is a general trend worldwide in reducing the use of chemical inputs in agriculture due to environmental concerns (Meena et al. 2013c, 2016e; Parewa et al. 2014). Water and nutrient acquisition from soils is governed by plant roots and their interaction with the abiotic and biotic components of soil (Hartmann

Table 2.6 Soil bioremediation of pollutants using plant-microbe interaction

Plant/crops	Pollutants	Microorganisms	References
Populus deltoides niger	1,4-Dioxane	Actinomycetes	Schnoor et al. (1998)
Senecio glaucus	Oil	*Arthrobacter*	Radvan et al. (1995)
Barley	2, 4-D	*Burkholderia cepacia*	Jacobsen (1997)
Populus deltoides	PAH	*Kurthia* sp.	Bisht et al. (2014)
		Micrococcus sp.	
Alfalfa	Pyrene, anthracene, and phenanthrene	Not identified	Schwab et al. (1995)
Oat, lupine, and rape	Pyrene	Not identified	Liste (2000)
Prairie grasses	PAHs	Not identified	Qiu et al. (1994)
Grasses	Naphthalene	*Pseudomonas putida*	Kuiper et al. (2001)
Wheat	2,4-D	*Pseudomonas putida*	Kingsley et al. (1994)
Sugar beet	PCBs	*Pseudomonas fluorescens*	Brazil et al. (1995)

PAHs polyaromatic hydrocarbons, *PCBs* polychlorinated biphenyls, *2,4-D* 2,*4*-dichlorophenoxyacetic acid

et al. 2008). The soil biotic component includes microorganisms that are living symbiotically or in association with plant roots. These microorganisms might enhance acquisition of nutrients in low-nutrient soils and alleviate the effects of low water availability. But there are only few studies that provided information regarding rhizosphere soil microorganisms to plants in mitigating with stresses derived from nutrient and water availability (Saleem et al. 2007; Hayat et al. 2010; Kang et al. 2010; Smith et al. 2010; Meena et al. 2015e).

2.5 Management of Rhizosphere System for Soil Sustainability and Productivity

It is well known that nutrient has unsounded effects on many aspects of root development, thus accompanying rhizosphere process (Zhang et al. 2010; Meena et al. 2015f). Most of the mineral nutrients were taken up by plants through the rhizosphere where root exudates play a dominant role in driving interactions among soil-plant-microbe system. However, the plant root exudates consist of a complex mixture of various acids, sugars, and enzymes, which have major direct or indirect effects on the acquisition of mineral nutrients required for PGP activities (Dakora and Phillips 2002). The rhizospheric chemistry/phenomena can enhance P mobilization and acquisition from soil by plants (Zhang et al. 2010). It is suggested that optimizing crop combination and BMPs, RMPs, and INM in intercropping systems through better understanding of rhizosphere interactions provides an effective approach to improve sustainable crop production with high yield, significantly higher NUE (Zhang et al. 2012).

2.5.1 The Cultural Management/Practices

Rhizospheric modification and root distribution along with the cropping system play a significant role toward the sustainable rhizosphere management. The subsurface irrigation systems can be adopted to improve soil characteristics and root distribution/modification, in relation to the physical properties of the soil and fertilization practices (Clothier and Green 1994; Yang et al. 2004).

2.5.2 Efficient Fertilization

The injudicious fertilization can result in considerable decreases of rhizosphere microorganisms population and eco-friendly insects, crop susceptibility or aggravation of soil physical properties, and pollution (HMs) of water resources through leaching causing irreparable damage to the overall system. One of the more promising practices is the innovative BMPs and RMPs, which reduces fertilization rate (Hakim et al. 2013). Other practices for managing the fertility of soil-plant system include supplying nutrients through drip irrigation (Postel et al. 2003; Palada and Wu 2005), applying organic manures (FYM, VC) to increase soil-buffering capacity (Glaser et al. 2002), and localized amendment as strategies for problematic soils.

2.5.3 Use of Organic and Biofertilizers

The organic farming (OF) system has become popular due to consumer concern with human health and the environment safety. Organic fertilization for the nutrient supply is more balanced, which helps to maintain soil sustainability and crop productivity. Among the beneficial effects of organic manures include (1) enhancement of soil biological activity, (2) enhancement of colonization of mycorrhizae, (3) improved root growth due to better soil structure, and (4) slow release of nutrients which contribute to the residual pool of organic N and P in the soil, reducing N leaching loss and P fixation (Singh and Mandal 2000).

2.6 Concluding Remarks

The rhizosphere microbial activity in the rhizosphere contributes significantly to sustainable agriculture. Efficient rhizosphere microorganisms, like AMF/rhizobacteria, contribute essentially to enhance NUE and crop sustainability. Application of these efficient microbes in the soil-plant system has the capacity to improve the plant fitness in unfavorable conditions of soils and increase the nutrient uptake efficiency (NUE) as well as water use efficiency (WUE). The rhizosphere management involves manipulating root growth, rhizosphere modification, RMPs and BMPs in intercropping, and the use of efficient crop genotypes with an aim to exploit the biological potential for efficient nutrient acquisition by plant roots rather than overuse of chemical/inorganic fertilization. The nutrient inputs in intensive farming systems should be optimized to achieve both high crop productivity and high NUE through maximizing rhizosphere efficiency in nutrient mobilization and acquisition. So all these activities make the rhizosphere the most dynamic environment in the soil.

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PGPR: Heart of Soil and Their Role in Soil Fertility

3

Ishwar Prakash Sharma, Satish Chandra, Narendra Kumar, and Dinesh Chandra

Abstract

Soil is an excellent niche for the growth of microorganisms which includes plant growth-promoting rhizobacteria (PGPRs). PGPRs have great potential for plant growth promotion as they control pest and disease and have been considered important in sustainable agriculture. PGPRs induce and/or synthesize various growth-promoting and biocontrolling chemicals which are useful for sustainable agriculture and environment. These chemicals are phytohormones, antibiotics, enzymes, etc., which react with the soil and provide better health to the plants. PGPRs directly or indirectly circulate their products to soil for better soil health which further enhance the soil immunity followed by influencing plant growth, productivity, and yield. Soil immune system works strongly by the activities of soil microbes which are considered as a heart of soil. These soil microbes are responsible for increasing soil fertility and productivity which are considered important for sustainable agriculture.

Keywords

PGPR • Immunity • Sustainable agriculture • Soil fertility • Biomolecules

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3.1 Introduction

Soil is an excellent niche for the growth of microorganisms including bacteria. Out of these some bacteria are able to colonize soil surrounding plant roots, rhizosphere (Hiltner 1904; Kennedy 2005); these bacteria are rhizobacteria. These bacteria have the ability to induce plant growth and biocontrol activities (Meena et al. 2016e). In the coming years, food security and feed will be a major global challenge for increasing human population; now, we need to increase the sustainability of agricultural productivity to meet the increasing demand for food. More than half of the population still relies on agriculture as its principal source of income, and it is a source of raw material for a large number of industries (Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Zahedi 2016; Kumar et al. 2017). Therefore, these bacteria are an important biological tool for the abovementioned challenges.

Agricultural crops are mostly affected by diseases and/or pests which can be biologically prevented by these PGPRs and other symbiotic rhizospheric microorganisms which are mostly found in the rhizosphere of all plants (Trudgill and Blok 2001; Sharma and Sharma 2016). For the managing of pest and disease, a large number of synthetic chemicals are being used, which pose environmental hazards, besides being costly and uneconomical (Joshi et al. 2006; Maheshwari et al. 2012; Youssef and Eissa 2014; Gupta et al. 2015). The quantity and quality of agricultural production are affected by the use of chemicals in agriculture practices; recently, these interactions are an important discussion subject under the agriculture-environment relationships (Ladha et al. 1997; Eser and Geçit 2010; Gupta et al. 2015; Meena et al. 2016f; Mahmood et al. 2016a, b; Ahmad et al. 2016a, b; Sharma and Sharma 2016). PGPRs are used to replace these chemicals by a variety of mechanisms, viz., formation of soil structure, decomposition of organic matter, recycling of elements, mineral nutrient solubilization, production of plant growth regulators, degradation of organic pollutants, root growth stimulation, soil fertility enhancement, biocontrol of plant pathogens, etc. (Ahemad and Khan 2009; Akhtar et al. 2012; Sivasakhti et al. 2014; Gupta et al. 2015).

Many studies show that the use of microbial-based products is a common practice for controlling plant pest population and preventing diseases of crops (Lacey et al. 2001; Goettel et al. 2010; Dogan et al. 2016; Meena et al. 2013c, 2015e). The major influences that the rhizosphere microorganisms have on plants today become an important biological tool to govern the health of plants in eco-friendly manner. They are involved in various biotic activities of the soil ecosystem to make it dynamic for nutrient turnover and sustainable for crop production (Ahemad and Khan 2009; Akhtar et al. 2012; Gupta et al. 2015). Hence, PGPRs are economic and secure alternative strategy for enhancing plant growth and development as they are able to increase the soil health and immunity toward soil pests and diseases.

3.2 Role of PGPR in Soil Fertility

Soil is the natural niche for soil microorganisms which play an important role in soil processes and determine plant productivity (Meena et al. 2014b, 2015c, d). PGPRs are involved in all beneficial activities within the soil like decomposition of crop residues, synthesis of soil organic matter (SOM), mineralization of SOM, immobilization of mineral nutrients, phosphate solubilization, nitrification, nitrogen fixation, phytohormone synthesis, and disease suppression which help in soil fertility improvement and ultimately enhancing the productivity (Prasad et al. 2015). Soil moisture is a necessary condition for PGPR colonization in the rhizosphere (Shrivastava et al. 2014). Rhizobacteria associated with roots are responsible for the synthesis of large number of biomolecules which get mixed with the soil and further improve soil health. They also act on the plant residues, where various organic compounds undergo decomposition and mineralization (Kumar et al. 2015; Ahmad et al. 2016a, b; Bahadur et al. 2016a; Verma et al. 2014, 2015b; Yadav and Sidhu 2016; Yasin et al. 2016). These mineralized chemicals enter the soil body where they agitate and add value to the soil. Apart from this mechanism, they also synthesize many growth-responsible chemicals which ultimately affect plant root morphology (Fig. 3.1).

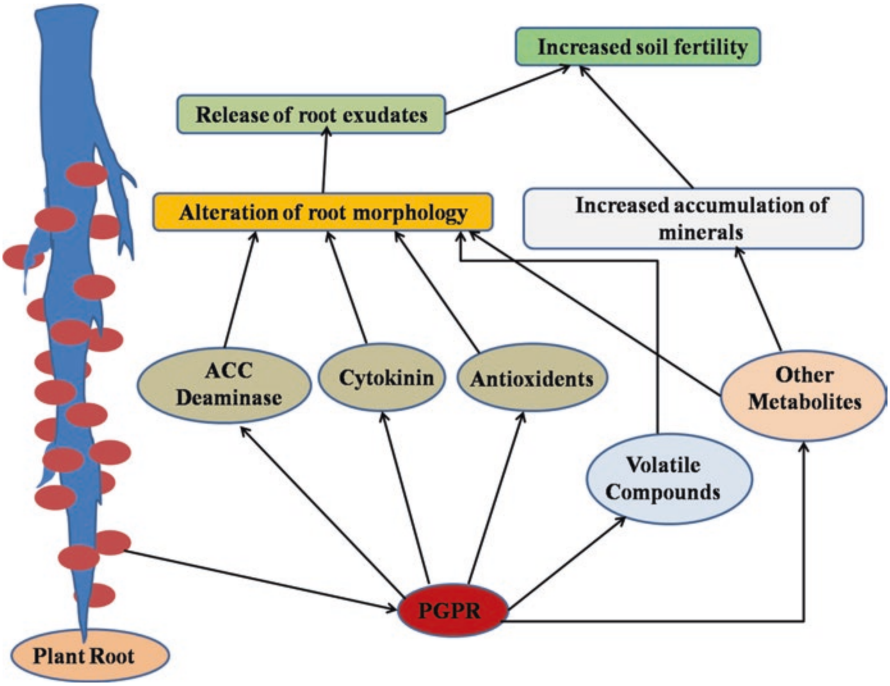


Fig. 3.1 An overview of soil fertility enhancement mechanism through PGPRs

Rhizobacteria have great potential to increase nutrient availability in the soil (Choudhary et al. 2011; Meena et al. 2013b, 2014a, 2015f). Nitrogen is essential for amino acid and protein synthesis which is the most limiting nutrient to plants and accumulated from atmospheric nitrogen through biological nitrogen-fixing mechanism in the soil as well as in plant roots (Lloret and Martinez-Romero 2005; Raymond et al. 2004). Some PGPRs have the ability to solubilize phosphate in the soil body, resulting in an increased availability of phosphate ions in the soil which are easily available to plants (Wani et al. 2007; Bahadur et al. 2016b; Das and Pradhan 2016; Dominguez-Nunez et al. 2016; Teotia et al. 2016; Velazquez et al. 2016; Verma et al. 2015a). Various volatile compounds and other metabolites (enzymes, proteins, antibiotics, etc.) also produced by PGPRs are highly involved in improving soil health and plant growth. Many bacterial species from different genera including *Bacillus*, *Pseudomonas*, *Serratia*, *Arthrobacter*, and *Stenotrophomonas* have been reported as volatile compound producers. Various enzymes (chitinase, beta-glucanases, etc.) are release in the soil body by these bacteria which suppress the growth of many pathogens in the soil and contribute to the biocontrol activity (Vejan et al. 2016). Overall, the soil body is healthy through all these mechanisms, and such healthy soil becomes potential for good yield and productivity, thus making the soil highly fertile (Meena et al. 2016c, d; Parewa et al. 2014).

3.3 Plant Growth-Promoting Rhizobacteria (PGPR)

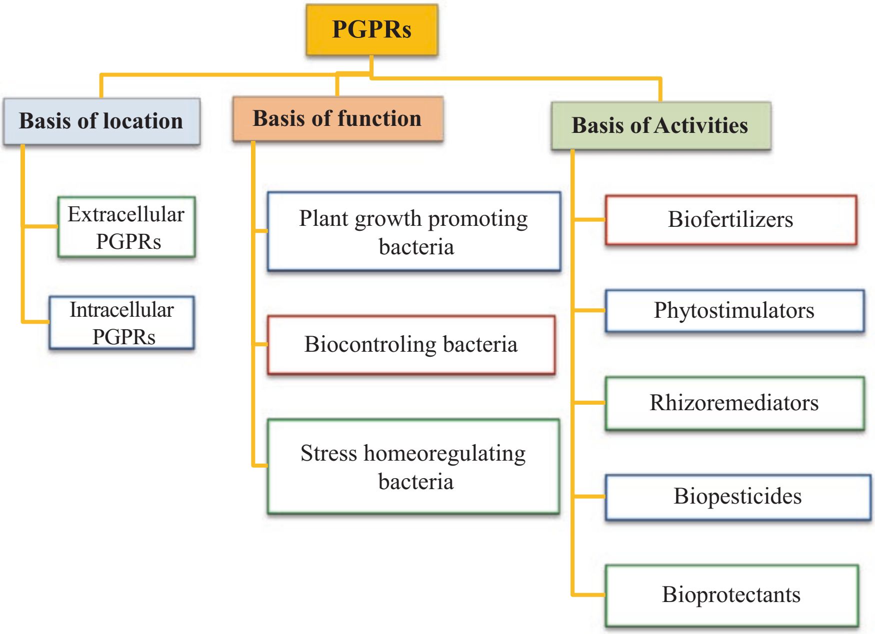
In vitro promotion of plant growth and root pathogen biocontrol through *Pseudomonas* strains was the first evidence of the rhizospheric bacteria which could be a good source for sustainable agriculture (Burr et al. 1978; Kloepper et al. 1980). The term plant growth-promoting rhizobacteria (PGPR) was first suggested by Kloepper et al. (1989). Previously, Theophrastus (372–287 BC) already suggested and recommended the remedying defects of different soil samples because of the presence of soil biota in the soil heart (Tisdale and Nelson 1975). The study of Hellriegel and Wilfarth (1888) suggested that rhizospheric bacteria have the ability to convert atmospheric N_2 in the roots of legumes. Still there are several groups of rhizobacteria that have been reported and have the ability to promote plant growth and induce resistance against various stresses (Meena et al. 2015b; Prakash and Verma 2016; Priyadharsini and Muthukumar 2016). In the rhizosphere, very important and intensive interactions take place between the plant, soil, microorganisms, and soil microfauna as they share the same niche. Many biochemical interactions as well as exchanges of signal molecules between plants and soil microorganisms have been studied which significantly influence plant growth and crop yields (Pinton et al. 2001; Werner 2004).

PGPRs may colonize in the rhizosphere, root surface, or intercellular spaces of the host plant (Lugtenberg and Bloemberg 2004). They are free-living bacteria (Kloepper et al. 1989), while some PGPRs invade living plant tissue and cause unapparent and asymptomatic infections (Sturz and Nowak 2000) and are referred to as endophytes. However, in accordance with their degree of association with the plant root cells, PGPRs can be classified into extracellular plant growth-promoting rhizobacteria (ePGPR) and intracellular plant growth-promoting rhizobacteria (iPGPR) (Gray and Smith 2005; Meena et al. 2015a, 2016b; Raghavendra et al. 2016; Rawat et al. 2016; Saha et al. 2016a). iPGPRs can enter plant cells and are able to produce specialized structures, so-called nodules. On the other hand, ePGPRs are found in the rhizosphere, or within the apoplast of the root cortex, but not inside the cells. According to their close proximity to the plant root, ePGPRs can be divided into three classes, i.e., living near the roots but not in contact, colonizing on the root surface, and living in the intercellular spaces of the root cortex (Gray and Smith 2005; Dotaniya et al. 2016; Jaiswal et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a, b; Masood and Bano 2016; Singh et al. 2015, 2016).

PGPRs act against phytopathogens by secretion of many biochemicals like toxin, enzymes, proteins, antibiotics, etc. Plant-associated microorganisms have been extensively examined for their role in natural and induced suppressiveness of soil-borne diseases. Applications of PGPRs have been reported to increase the production of antibiotics and inhibit root penetration of phytopathogens (Handelsman et al. 1990; Sikora 1992; Sikora and Hergarten 1992; Liu and Sinclair 1992; Yu et al. 2002).

3.3.1 Classification of PGPRs

PGPRs are classified on the basis of their locations, functions, and activities.



3.3.1.1 On the Basis of Location

According to their location in the rhizosphere, they are divided into two categories (Gray and Smith 2005; Martinez-Viveros et al. 2010).

Extracellular PGPRs (ePGPRs)

These PGPRs are found in the rhizosphere, in the rhizoplane, or in the spaces between cells of the root cortex, but they are never present inside the cells. Examples are species of *Pseudomonas*, *Bacillus*, etc., which are present in the soil as well as in the intercellular space of cortical cells as endophytes.

Intracellular PGPRs (iPGPRs)

These generally exist inside the cells specially in specialized nodular structure. Examples are *Rhizobia* and *Frankia*, both of which are associated with higher plants and present inside the cells where they fix atmospheric nitrogen.

3.3.1.2 On the Basis of Functionality

On this basis, PGPRs are divided into three groups, viz., plant growth-promoting, biocontrol, and stress homeoregulating bacteria.

Plant Growth-Promoting Bacteria

Some rhizobacteria directly induce plant promotion via nitrogen fixing (Glick et al. 1999; Rubio and Ludden 2008; Ahemad and Khan 2012; Glick 2012; Kuan et al. 2016), phytohormone production like IAA (Spaepen and Vanderleyden 2011; Glick 2012; Ahemad and Kibret 2014; Wang et al. 2015), cytokinin (Cassán et al. 2009; Hussain and Hasnain 2009; Vacheron et al. 2013), GA3 (Richardson et al. 2009; Dodd et al. 2010; Goswami et al. 2016), siderophore production (Glick et al. 1999; Sharma et al. 2003; Khan et al. 2009; Rajkumar et al. 2010; Ahemad and Kibret 2014), and phosphate solubilization (Bashan and de Bashan 2010; Bhattacharyya and Jha 2012; Glick 2012; Ahemad and Kibret 2014; Gupta et al. 2014, 2015; Meena et al. 2016) (Table 3.1).

Biocontrolling Bacteria

Bashan et al. (1993) for the first time suggested these bacteria. They indirectly promote plant growth by releasing phytotoxic substances such as hydrogen cyanide, chitinase, pectinase, cellulase, ethylene, antibiotics, etc., which are responsible for controlling plant pathogens (Ramamoorthy and Samiyappan 2001; Yu et al. 2002; Bashan and de-Bashan 2010; Bhattacharyya and Jha 2012; Gupta et al. 2015; Sharma and Sharma 2016; Meena et al. 2016) (Table 3.2).

Stress Homeoregulating Bacteria

These bacteria suggested by Sgroy et al. (2009) can facilitate plant growth directly or indirectly in biotic and abiotic stresses. Direct facilitation by these bacteria includes releasing stress-related phytohormones, such as abscisic acid (Cohen et al. 2009, 2015), salicylic acid (Zhang et al. 2002; Beneduzi et al. 2012), and jasmonic acid (Vejan et al. 2016; George et al. 2016); plant growth regulators, like cadaverine (Sgroy et al. 2009; Kaushal and Wani 2016); and stress signaling molecules such as

Table 3.1 Some PGPR strains involve in phytohormone production in different plants (Bhattacharyya and Jha 2012)

Phytohormones	PGPR strain	Host plant
IAA	*Aeromonas veronii*	Rice
	Agrobacterium sp.	Lettuce
	Alcaligenes piechaudii	Lettuce
	Azospirillum brasilense	Wheat
	Bradyrhizobium sp.	Radish
	Comamonas acidovorans	Lettuce
	Enterobacter cloacae	Rice
	Rhizobium leguminosarum	Radish
Cytokinin	*Paenibacillus polymyxa*	Wheat
	Pseudomonas fluorescens	Soybean
	Rhizobium leguminosarum	Rape and lettuce
Gibberellin	*Bacillus* sp.	Alder

Table 3.2 Some PGPRs and their antibiotic production and target pathogen (Bhattacharyya and Jha 2012)

Antibiotics	PGPRs	Target organisms
Bacillomycin	*Bacillus*	*Aspergillus flavus*
Kanosamine	*B. cereus*	*Phytophthora medicaginis*
Zwittermycin A	*B. cereus*, *B. thuringiensis*, *B. subtilis*	*Phytophthora*, *Sclerotinia sclerotiorum*
Iturin	*B. subtilis*	*Pythium ultimum*, *Rhizoctonia solani*, *Fusarium oxysporum*
Iturin A, surfactin	*B. subtilis*	*Rhizoctonia solani*
Pyrrolnitrin	*Burkholderia cepacia*, *Pseudomonas fluorescens*, *Enterobacter agglomerans*	*Rhizoctonia solani*, *Gaeumannomyces graminis var. tritici*, *Agrobacterium tumefaciens*, *Clavibacter michiganensis*, *Xanthomonas campestris*, *Pseudomonas syringae*
2,4-DAPG, pyoluteorin, phenazines	*Pseudomonas fluorescens*	*Xanthomonas oryzae*, *Pythium ultimum*, *Gaeumannomyces graminis var. tritici*
Phenazine-1-carboxylate	*Pseudomonas fluorescens*, *P. aureofaciens*	*Gaeumannomyces graminis var. tritici*, *Sclerotinia homeocarpa*
Phenazine-1-carboxamide	*P. chlororaphis*	*Fusarium oxysporum f. sp. radicis-lycopersici*
Viscosinamide	*Pseudomonas fluorescens*	*R. solani*, *Pythium ultimum*
Amphisin	*Pseudomonas fluorescens*	*Pythium ultimum*, *R. solani*
Geldanamycin A	*Streptomyces hygroscopicus*	*R. solani*
Oligomycin A	*Streptomyces libani*	*Botrytis cinerea*
Polyoxin D	*Streptomyces cacaoi*	*R. solani*

1-aminocyclopropane-1-carboxylate (ACC) deaminase (Glick et al. 1999; Vejan et al. 2016; Mahmood et al. 2016a, b).

3.3.1.3 On the Basis of Activities

On this basis, Somers et al. (2004) divide PGPRs into following categories:

(A) *Biofertilizers* – Many of the PGPRs enhance soil fertility and productivity by involving in nutrient cycling. Different types of biofertilizers are being used such as:
  1. Nitrogen-fixing biofertilizers like *Rhizobium*, *Bradyrhizobium*, *Nitrosomonas*, *Azospirillum*, *Azotobacter*, etc.
  2. Phosphorus-solubilizing and phosphorus-mobilizing biofertilizers like *Bacillus*, *Pseudomonas*, *Mycorrhiza*, etc.
  3. Plant growth-promoting biofertilizers like *Pseudomonas*, *Bacillus*, etc.

(B) *Phytostimulators* – Certain bacteria stimulate the plant growth by producing different phytohormones like *Pseudomonas*, *Azospirillum*, *Bradyrhizobium*, etc.

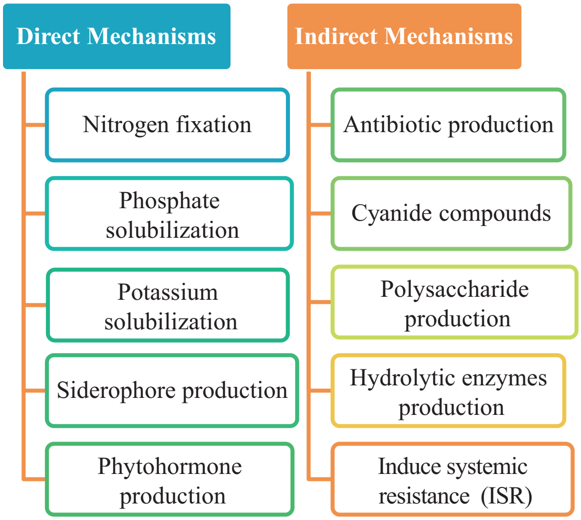
(C) *Rhizoremediators* – Many of the bacteria are used in degradation of herbicides, pesticides, and other hazardous organic compounds and/or pollutants in the soil which could be helpful in plant growth by increasing soil fertility.

(D) *Biopesticides* – Many of the bacteria produce antibiotics and other toxic compounds which are helpful in the reduction of pathogens, e.g., *Pseudomonas* and *Bacillus* spp.

(E) *Bioprotectants* – *Large* numbers of bacteria are helpful in the disease suppression which directly and indirectly enhance plant growth.

3.4 PGPR Mechanism

PGPRs promote plant growth directly as well as indirectly (Castro et al. 2009) as follows:



3.4.1 Direct Mechanism

Directly, PGPRs promote plant growth by providing essential nutrients (N, P, Fe, etc.) and enhancing phytohormone level. Generally these bacteria are involved in different nutrient cycles like N_2 and P cycle; directly the nutrients are provided to plants by these bacteria through nutrient mineralization and solubilization processes. On the other hand, these bacteria are also involved in many phytohormone (IAA, gibberellic acid, cytokinins) pathways (Kloepper et al. 2007). Among all the phytohormones, IAA is the most common which is produced by PGPR (Barazani and Friedman 1999).

3.4.2 Indirect Mechanism

PGPRs are the well source for biocontrol which inhibit the phytopathogen, so they are indirectly helpful to plant growth (Glick 2012). PGPRs are powerful resource of disease suppression which are economically as well as environmentally safe. PGPRs have a variety of mechanisms which make them a biocontrol agent. They produce antibiotics (Mazurier et al. 2009), cell wall-degrading enzymes like cellulose and β-1,3-glucanase, and cyanide compounds like HCN (Duffy et al. 2003; Ramatte et al. 2003) which are helpful in reducing phytopathogens and enhancing plant growth. Some molecules such as 2, 4-diacetylphloroglucinol (2, 4-DAPG) and pyoluteorin are also produced by some PGPRs (de Souza et al. 2003; Beneduzi et al. 2012) which are responsible for disease suppression.

By using the above mechanisms, PGPRs defense against phytopathogens and pests results in resistance to the plant. This resistance is either systemic acquired resistance (SAR) or induced systemic resistance (ISR). SAR is activated in plant tissues after pathogen attacks, immediately plant signals are produced, and defense responses occur in distal tissues through the vascular system (Pieterse et al. 2009). As the resistance induced, the plant is protected from pathogenic fungi, bacteria, viruses and nematodes. A large number of defense enzymes like phenylalanine ammonia lyase (PAL), chitinase, β-1,3-glucanase, peroxidase (PO), polyphenol oxidase (PPO), lipoxygenase (LOX), superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) are involved in the resistance and activate ISR (Meena et al. 2016a; Saha et al. 2016b; Sharma et al. 2016; Shrivastava et al. 2016; Sindhu et al. 2016).

3.5 Conclusions

Several microbes from soil have been studied and are responsible for the improvement of soil fertility and productivity, crop production and protection, and compost preparation and decomposition. The products from these soil bacteria have been exploited to control many diseases. Recent development of molecular biology made it possible to develop transgenic plants by improving genetics. Similarly, the environmental exploitation is also well documented in the literature. Due to lack of information on microbial diversity of various microorganisms, it is a novel approach in exploring the uninformed microbial diversity in agriculture, environment, and human health. The antagonistic effect of these bacteria toward pathogens is one of the most important traits when they are present in quorum in the soil where they interact with plant roots and other microorganisms also. The diversity of metabolites with antagonistic activity produced by several bacteria some of these might produce more than one compound simultaneously which act through several mechanism like two compounds (CHAO and Pf-5) are synthesize by *P. fluorescens* strains they act simultaneously, first one acts as an antibiosis and other one acts on nutrients competition (Bouizgarne 2013). These bacteria induce systemic resistance by synthesizing several chemicals (DAPG, HCN, pyoverdine, etc.) which defends against phytopathogens. All these biochemicals in soil regulate the soil immune system where they circulate throughout the soil body; hence, they defense against the pathogens and result in better health of soil for better productivity.

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Strength of Microbes in Nutrient Cycling: A Key to Soil Health

4

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Abstract

Nowadays, due to continuous degradation in soil quality, a healthy soil system is the result of a complex network of physical, chemical, and biological soil quality indicators. Healthy soils provide a balance between the needs of both farmers and community. Soil organic matter (SOM) helps to sustain the soil health as well as its quality, inactivate toxic compounds, suppress pathogens, and protect environmental sustainability. It implies interactions among the soil's internal and external components for the sustainable food production system. The efficient soil microbes play an important role, since they are responsible to drive various biological transformations and different pools of carbon (C) and macro- and micronutrients, which facilitate the subsequent establishment of soil-plant-microbe interaction. The diversity of microbes in soil system is enormous. This article emphasizes the role of microbes for soil health through the decomposition of SOM present in soil system. Toward the global knowledge of soil microbial dynamics, its function is increasing rapidly, but the knowledge of rhizospheric complex is limited, despite of their importance in regulating soil-plant systems.

Keywords

Soil health • Microorganisms • Nutrient transformations • Sustainable

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4.1 Introduction

The importance of soil is increasing at an alarming rate due to the rapidly growing worldwide population as healthy soils will be less to meet the future food supply due to growing pressure on land for urban expansion, biofuel production, and natural resource extraction (Meena et al. 2013a; Bahadur et al. 2014; Jha and Subramanian 2016; Kumar et al. 2016a, b). The soil develops by degeneration of rocks as well as minerals, through biotic actions of microbes sustained by them (Bahadur et al. 2017; Verma et al. 2017b; Kumar et al. 2017a; Nath et al. 2017). It represents dynamic ecosystems, making it appropriate to think about them in terms such as health, vitality, and soil sustainability. Soils are the resources that provide humans with ~90% of all the food we consume. Our one major challenge is to manage soils in a sustainable fashion so that they will meet the needs of the next generation (Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015; Ahmad et al. 2016; Meena et al. 2015f, 2016a; Parewa et al. 2014; Dotaniya et al. 2016; Jaiswal et al. 2016). Meanwhile, measurement of soil processes and its properties linked to these also depends on the use and location of the soil. Previously, not only the physical and chemical properties were given importance, but nowadays also the role of soil biodiversity in maintaining soil fertility and crop productivity (Singh 2015).

Soils are establishment of all terrestrial ecosystems and are considered home to a vast diversity of rhizospheric macro- and microorganisms. They provide food or nutrients to the macro-/microorganisms that live above and below the ground and play significant role in buffering and filtering of soil system. Therefore, soils are very important to existing societies (mainly human) as we depend on our day-to-day work (Dominati et al. 2010; Prakash and Verma 2016; Meena et al. 2016b; Priyadharsini and Muthukumar 2016; Kumar et al. 2017a; Bahadur et al. 2016b; Das and Pradhan 2016; Dominguez-Nunez et al. 2016).

Soils support a diversity of life and conception is similar to human health; it is not difficult to understand or recognize when the system is viewed as a whole. The strength of soil comes from the life that exists within it – soil microorganisms, ranging from genes and species to communities. It is an excellent indicator of soil health (Nielsen and Winding 2002; Takoutsing et al. 2016). Variation in microbial population and activities is considered as early signs of soil degradation and amelioration. These efficient rhizospheric microorganisms are a vitally important component of the soil habitat where they play significant roles in soil-plant systems functioning through controlling nutrient cycling reactions essential for sustaining soil quality and also contributing to the genesis and maintenance of soil structure (Meena et al. 2015a, b, e; Raghavendra et al. 2016; Zahedi 2016; Rawat et al. 2016; Yasin et al. 2016; Teotia et al. 2016).

There is an infinite abundance of microbes that exist within the soil system. However, very little is known about the tiny creature which is responsible for numerous processes occurring in soil and maintaining productivity in natural and managed agroecosystems (Meena et al. 2016c, e; Saha et al. 2016a; Yadav and Sidhu 2016). Investigation on rhizospheric chemistry in relation to mainly nutrients and microbes is difficult as we cannot see them, so they are out of sight and out of mind;

most methods for studying these critters are rife with difficulties, and though we can identify thousands of different species, we only really know what a small percentage of them are doing in the soil. Only ~1% of the microbes' species have been identified or cultured. In short, we have a lot left to learn by understanding what microbes are doing, under what conditions they dominate, and how to sustain nutrient cycling (Meena et al. 2014a, 2016d; Saha et al. 2016b; Verma et al. 2014, 2015b; Bahadur et al. 2016a; Masood and Bano 2016).

Soil microbes have an enormous influence on soil-plant-microbe interactions and play a significant role for maintaining soil quality. The most important of these interactions is nutrient cycling. Under the healthy soil-plant system, soil biota regulates the flow, root growth, and storage of nutrients. Even fertilization may pass through efficient rhizospheric microbes before being utilized by the crop/plant (Dubey et al. 2016; Verma et al. 2017a).

4.2 Soil Health

In the long-term soil fertility, the more we are supporting the next generation. A healthy, fertile soil laid the groundwork for a strong and resilient food production system. Nowadays, one of the major tasks is to manage and maintain soil in a sustainable fashion. In the mid-1990s, the term soil health was introduced; several scientists gave various definitions of soil health, and one of the most commonly proposed definition is by Doran and Safley 1997 "The continued capacity of soil to function as a vital living system, within ecosystem and land-use boundaries, to sustain biological productivity, promote the quality of air and water environments, and maintain plant, animal and human health." This definition encompasses a time component, reflecting the importance of continuous function over time and the dynamic nature of soil-plant system (Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013c).

Soil is a finite and nonrenewable resource because regeneration of soil through various weathering processes (physical, chemical, and biological) of underlying rock requires geological time (Huber et al. 2001). The soil quality focuses on the continued capacity or buffering capacity of soil to sustain plant growth promoting (PGP) and is essential for the integrity of ecosystems to remain intact or to recover from disturbances (Pankhurst et al. 1997). However, the deterioration of soil quality is a major concern for human-animal-plant health (Singer and Ewing 2000).

Healthy soils are able to balance a range of functions to meet the needs of both farmers and community. It functions to sustain soil biota and plant life, store and cycle wastewater and nutrients, decompose SOM, inactivate toxic compounds, suppress pathogens, and protect soil and water quality. Meanwhile, healthy soil system had a concept that implies that the soil functions as a balance of each other, and it enhances the sustainability of production system (Meena et al. 2013b, 2015c; Shrivastava et al. 2016; Velazquez et al. 2016; Singh et al. 2015). The degradation in soil-water quality is a symptom of poor soil health (Takoutsing et al. 2016). Healthy soils function to sustain biological productivity, store and cycle water and nutrients, decompose organic matter, inactivate toxic compounds, suppress pathogens, protect water quality, and enhance catchment health. Hierarchy and emergence are properties of all systems including soils and the composition of soil (Dubey 2016). The soil health is the net result of undergoing conservation and degradation processes, depending highly on the biological component of the soil ecosystem, and influences plant health, environmental health, and food safety and quality (Parr et al. 1992; Halvorson et al. 1997; Singh 2015; Takoutsing et al. 2016). A healthy soil functions to buffer nutrients as well as contaminants and other solutes via sorption or incorporation with clay particles and SOM. The soil serves as an environmental filter for removing undesirable solid and gaseous constituents from air and water (Parr et al. 1992; Singer and Ewing 2000).

4.3 Soil as a Microbial Habitat

The biological activity in soil is largely concentrated in the topsoil, where the depth may vary from a few to ~120 cm. In the topsoil, the biological components (soil microorganisms) occupy a tiny fraction (<0.5%) of the total soil volume and make up <10% of SOM. They play a significant role in the cycling of nutrients and the decomposition of organic residues (Pankhurst et al. 1997). The organic residues are, in this way, converted to biomass or mineralized to CO_2, H_2O, and nutrients (Bloem et al. 1997). These efficient microbes are further associated with the transformation and degradation of waste materials and synthetic organic compounds (Meena et al. 2014b, 2015d; Singh et al. 2016; Sindhu et al. 2016).

The roles of these efficient rhizospheric microbes possess the ability to give an integrated measure of soil sustainability, an aspect that cannot be obtained with physical/chemical measures and/or analyses of diversity of higher organisms. Microbes respond quickly to changes; hence, they rapidly adapt to environmental conditions. This adaptation potentially allows microbial analyses to be discriminating in soil health assessment, and changes in microbial populations and activities may therefore function as an excellent indicator of change in soil health (Kennedy and Papendick 1995; Pankhurst and Hawke 1995; Singh 2015). Soil is a dynamic habitat for a variety of life-forms and provides a mechanical support to plants from which they extract nutrients. Soil organisms are constantly interacting with one another; sometimes these interactions are mutually beneficial, symbiotic, and competitive. It improves soil health because the “good” bacteria, fungi, nematodes, and insects are able to outcompete the “bad” ones and also contribute greatly by breaking down organic materials to make nutrients available to plants. Microorganisms act as an important link in the process of nutrient recycling. Thus, the same fundamental soil structure in different locations is found to support different biological communities. The microflora and microfauna present in the soil are depicted in Fig. 4.1. Soils are combinations of sand, silt, and clay particles and provide a diversity of microhabitats which supports a wide range of organisms. These organisms interact to modify the atmosphere between soil particles. The atmosphere within the soil differs from the above ground due to the use of the available oxygen present in

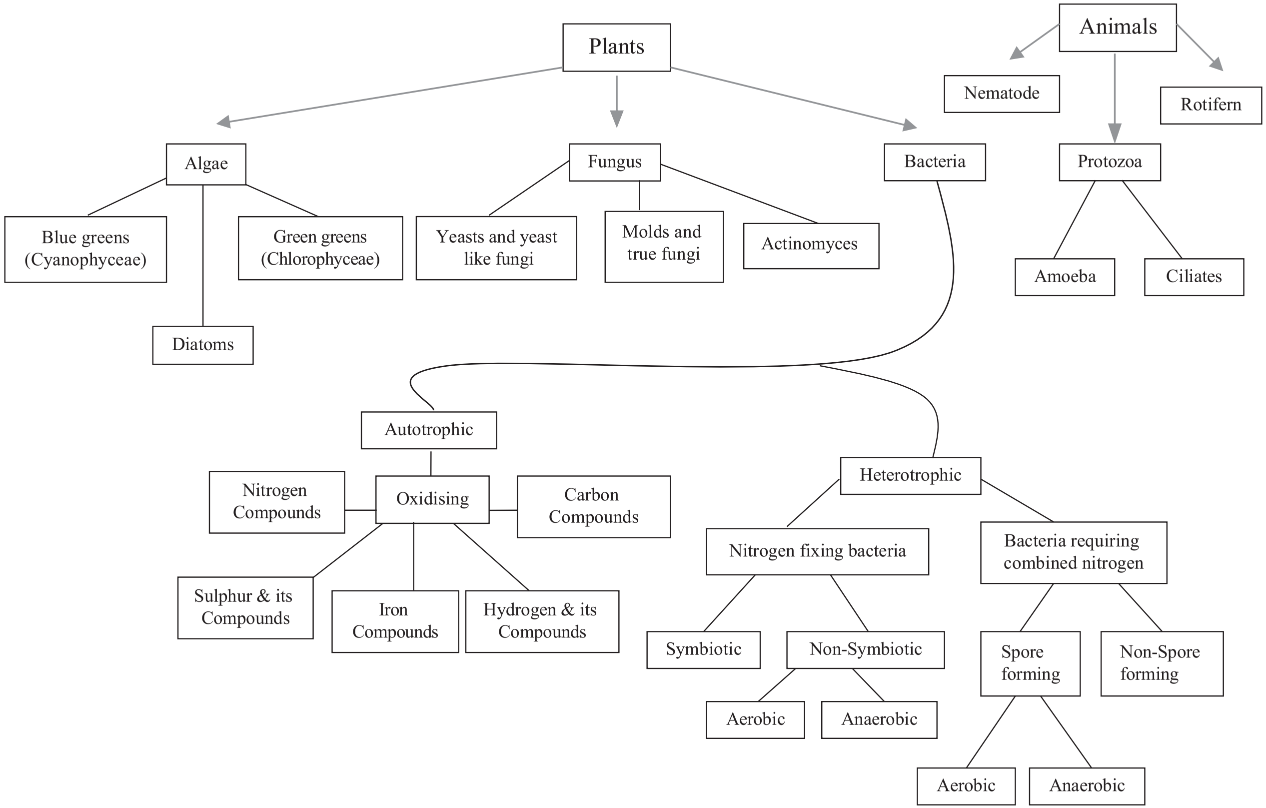


Fig. 4.1 The microflora and microfauna of the soil system

Table 4.1 Distribution of soil microorganisms

Depth	Organisms per gram of soil			
(cm)	Aerobic bacteria	Anaerobic bacteria	*Actinomyces*	Fungi
3–8	7,800,000	1,950,000	2,080,000	119,000
20–25	1,800,000	379,000	245,000	50,000
35–40	472,000	98,000	49,000	14,000
65–75	10,000	1000	5000	3000
135	100	400		3000

the soil by microbial and other metabolisms, and finally there is less oxygen beneath the ground. Similarly, carbon dioxide is generated as a by-product of microbial metabolism, and there is a higher concentration of carbon dioxide within soil than above ground (Sarkar et al. 2017; Verma et al. 2017a; Kumar et al. 2017b).

Soils contain many aerobic and facultative organisms, and because of the microbial manipulation of microenvironments, soils may harbor a large number of obligate anaerobes. The distribution of soil microorganisms is presented in Table 4.1. These rhizobacteria are the largest group of soil microbes, both in total number and in diversity. Nowadays, the great advances of molecular biological techniques like sensitive isotope studies which are yielding information on the metabolism of soil microbes are being used for taxonomic studies (Singh 2015; Dubey 2016). The cycling of nutrients is very important as without which, the continuation of life on earth would be impossible, as essential nutrients would rapidly be taken up by organisms and locked in a form that cannot be used by others. Soil is one part of the ecosystem and supports all terrestrial life-forms; therefore, protection of soil is of high priority, and a thorough understanding of soil enzyme activities is a critical factor in assuring that soil remains healthy. A better understanding of soil enzymes in maintaining the soil health will provide an opportunity for an integrated biological assessment of soils. The response of microbes to environmental stress is rapid compared to higher organisms, due to their high surface to volume ratio (Pankhurst and Hawke 1995).

These efficient microbial communities can be considered as architects of soils (Rajendhran and Gunasekaran 2008), and many ecosystem services that are linked to ecosystems, including plant production, safeguarding of drinking water, or C sequestration, are closely linked to microbial activities and their functional traits (Torsvik and Ovreas 2002; Lombard et al. 2011). Studies on the development of abiotic and biotic interactions are very complex (Ollivier et al. 2011). Microbes act on a scale of μm^3 and form biogeochemical interfaces with the soil matrix, shaping their own environment (Totsche et al. 2010; Monier et al. 2011) Finally, most functional traits, for example, the degradation of plant litter or the development of food web structures and closed nutrient cycles, are not a result of a single organism but of microbial communities which closely interact which each other (Aneja et al. 2006; Simon and Daniel 2011; Sharma et al. 2012).

4.4 Microbial Decomposition of Organic Matter and Nutrient Availability

Soil organic matter acts as a storehouse for nitrogen, phosphorus, and sulfur. There is very little inorganic nitrogen in soils and much of it is derived from organic forms. The organic matter decomposition is largely an enzymatic process and facilitated by extracellular hydrolytic enzymes produced by soil microorganisms. Soil enzymes are involved in the biochemical processes during organic matter decomposition. The important soil enzymes are amylase, arylsulfatase, cellulase, chitinase, dehydrogenase, phosphatase, and urease which are released from plants, animals, organic compounds, and microorganisms and soils (Gupta et al. 1993; Ganeshamurthy et al. 1995). The rate of SOM decomposition is influenced by environmental factors such as temperature, moisture content, and microbial diversity (Debnath and Hajra 1972). In principle, the breakdown of organic matter involves four stages, viz., (a) breakdown of compounds that are easy to decompose – like sugars, starches, and proteins; (b) breakdown of compounds that take several years to decompose like cellulose (an insoluble carbohydrate found in plants) and lignins (a very complicated structure that is part of wood); (c) breakdown of compounds that can take up to ~10 years to decompose – like some waxes and the phenols; and (d) breakdown of compounds that take thousands of years to decompose which include humus-like substances which are the result of integration of compounds from breakdown products of plants and those generated by microorganisms (Chakroborty and Sen 1967). Mineralization of organic matter is the biological process where organic compounds in organic matter are chemically converted by the microorganisms in soil to simpler organic compounds, other organic compounds, or mineralized nutrients (Fig. 4.2). Therefore, incorporating organic matter into soils can change the amount of nitrogen (and other nutrients) available to plants, and those having a high C/N ratio will probably cause some nitrogen deficiency in the crops/plants, at least in the short term (Katherine et al. 2004; Ellert et al. 1997).

4.5 Mineralization and Humification

One of the most important functions of soil microorganism is the decomposition of various forms of organic matter present in the soil. It chiefly consists of residues of dead plant and animals and the excretory products of the living beings. These organic constituents need to be converted into simple inorganic forms (minerals) to make them available to the autotrophic organisms. This conversion of organic matter into simple inorganic forms is called mineralization which is rendered mainly through decomposition of organic matter by soil microorganism, mainly fungi and bacteria (Gupta and Germina 1988; Xu et al. 2015). The organic residues added to the soil are categorized into three groups: the easily degradable, moderately degradable, and difficultly degradable which are distinctly attached by different types of microbes.

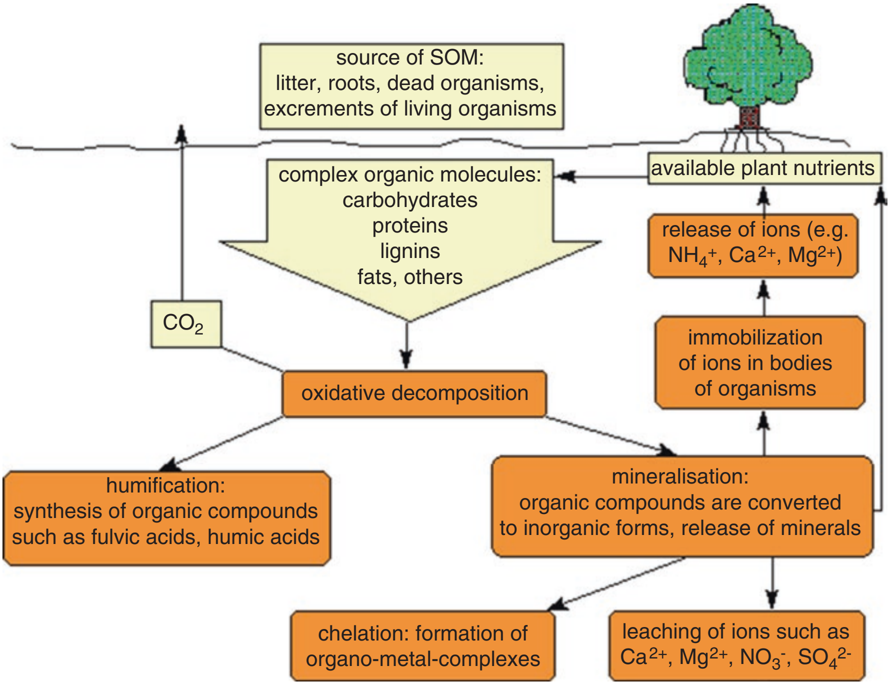


Fig. 4.2 An overview of SOM mineralization in the soil-plant system

The result of microbial mineralization is the release of energy, water, gases, etc. on the one hand and formation of complex amorphous substance humus, called humification, on the other hand. The rate of oxidation of biologically important elements such as nitrogen, carbon, sulfur, phosphorus, etc. during mineralization of organic matter is of paramount importance to plants. Microorganisms play a vital role to convert elements to usable forms to the plants for their use. Thus, the processes of mineralization and humification run in nature hand in hand (Billings and Ziegler 2005).

4.6 Role of Soil Enzymes in Organic Matter Decomposition

Soil enzymes are a group of enzymes whose usual inhabitants are the soil and are continuously playing an important role in maintaining soil ecology, physical and chemical properties, fertility, and soil health and responsible for overall process of organic matter decomposition in the soil system (Dick et al. 1996). They are important in catalyzing several vital reactions necessary for the life processes of microorganisms in soils and the stabilization of soil structure, the decomposition of organic wastes, organic matter formation, and nutrient cycling, hence playing an important role in agriculture (Fig. 4.3). The enzyme levels in soil systems vary in amounts primarily due to the fact that each soil type has different amounts of organic matter

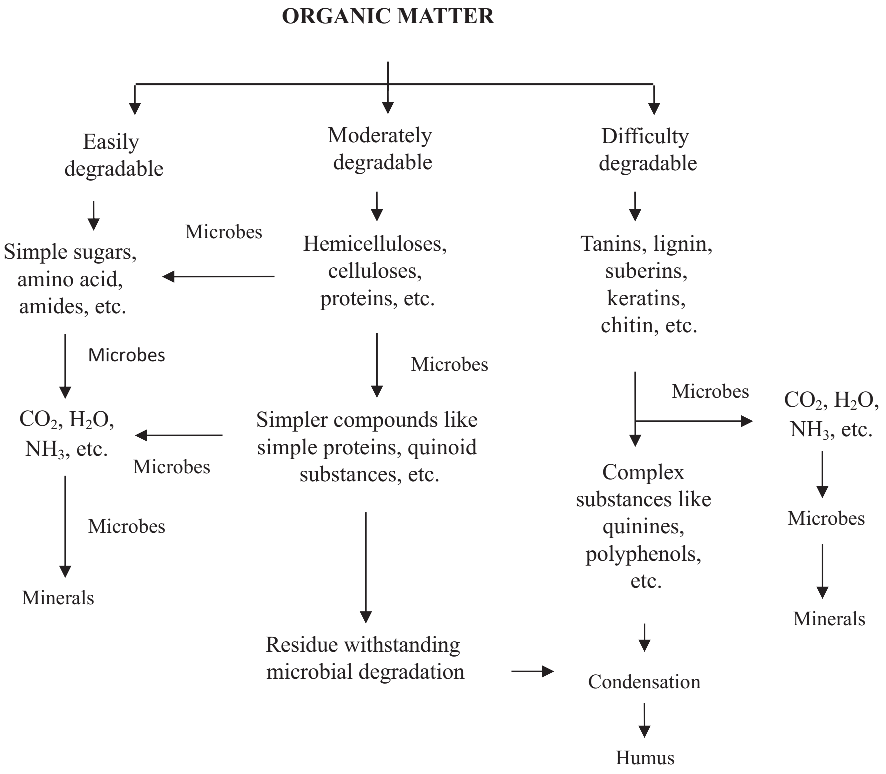


Fig. 4.3 Overview of microbial decomposition of organic matter

content, composition, and activity of its living organisms and intensity of biological processes. In practice, the biochemical reactions are brought about largely through the catalytic contribution of enzymes and variable substrates that serve as energy sources for various microorganisms (Mandels and Reese 1999; Kertesz and Mirleau 2004; Liebich et al. 2007). The enzymes are the direct mediators for biological catabolism of SOM and mineral components. Soil enzyme activities are closely related to SOM and soil quality; the changes are much sooner than other parameters, thus providing early indications of changes in soil sustainability (Dick et al. 1996).

These enzymes may include amylase, arylsulfatase, β-glucosidase, cellulase, chitinase, dehydrogenase, phosphatase, protease, and urease released from plants, animals, organic compounds, and microorganisms and soils (Ganeshamurthy et al. 1995; Xu et al. 2015). Factors affecting enzyme activity in soil are free enzymes adsorbed or otherwise bound to soil organic and inorganic fraction, released into the soil from lysed microbes through the action of bacteria, and accessible in dead non-lysed cells and any metabolic activity of living cells as roots present in soil system.

4.7 Amylase

The starch hydrolyzing enzyme amylase is known to be constituted by α-amylase and β-amylase. The α-amylases are synthesized by plants, animals, and microbes, whereas β-amylase is synthesized mainly by plants. It plays a significant role in the breakdown of starch, which converts starch-like substrates to glucose and β-amylase, which converts starch to maltose (Srinivasulu and Rangaswamy 2006). Plants may however influence the amylase enzyme activities of soil by directly supplying enzymes from their residues or excreted compounds or indirectly providing substrates for the synthetic activities of soil-pant-microbe system.

4.8 Arylsulfatase

Arylsulfatases are typically widespread in nature as well as in soils and are responsible for the hydrolysis of sulfate esters (Kertesz and Mirleau 2004). They are secreted by rhizobacteria into the external environment as a response to sulfur limitation, and its occurrence is often correlated with microbial biomass and rate of S immobilization. This enzyme has a role in the hydrolysis of aromatic sulfate esters ($R–O–SO_3$) to phenols (R–OH) and sulfate or sulfate sulfur (SO_4^{2-} or SO_4–S). So far, very little is known about specific microbial genera or species that play an important role in the soil organosulfur circle in which arylsulfatases are the key enzymes (Gupta et al. 1993; Ganeshamurthy et al. 1995).

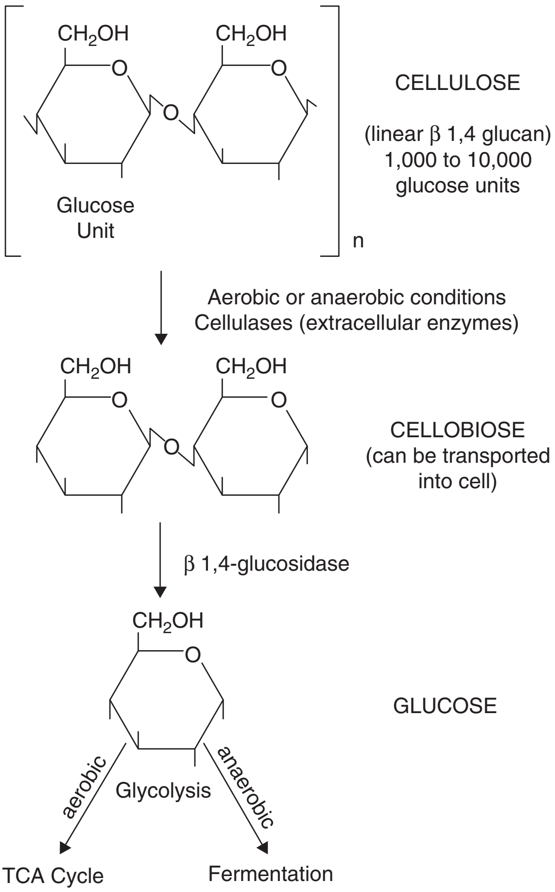
4.9 β-Glucosidase

Glucosidase is a common, predominant enzyme in soils and named according to the type of bond that it hydrolyses. It plays an important role in catalyzing the hydrolysis and biodegradation of various β-glucosidases present in plant debris decomposing in soil-plant system (Xu et al. 2015). Its final product is glucose, an important C energy source of life to microbes in the soil. It is characteristically useful as a soil quality indicator and may give a reflection of past biological activity, the capacity of soil to stabilize the soil organic matter, and can be used to detect management effect on soils.

4.10 Cellulases

The cellulose is the most abundant organic compound in the biosphere, comprising ~50% of the biomass synthesized by photosynthetic fixation of CO_2. Growth and survival of microbes are important in most agricultural soils which depend on the carbon source contained in the cellulose occurring in the soil (Srinivasulu and Rangaswamy 2006). Cellulases are a group of enzymes that catalyze the degradation of cellulose; polysaccharides are built up of β-1,4-linked glucose units (Fig. 4.4).

Fig. 4.4 The decomposition of cellulose to glucose



Many researchers reported that cellulases in soils are derived mainly from plant debris incorporated into the soil, and a limited amount may also originate from fungi and bacteria in soils. Since, cellulase enzymes play an important role in global recycling of the most abundant polymer, cellulose, in nature, it would be of critical importance to understand this enzyme better so that it may be used more regularly as a predictive tool in our soil fertility programs (Saha et al. 2003; Muter et al. 2008).

4.11 Chitinase

Chitinase or chitinolytic enzymes are key enzymes responsible for the degradation and hydrolysis of chitin (poly-β-1-4-(2-acetamido-2-deoxy)-D-glucoside). They are also considered as the major structural component for many fungal cell walls that use the hyperparasitism mechanisms against pest/pathogen attack. These biological agents also reduce disease-producing agents by using other mechanisms such as antibiosis or competition mechanisms and are produced or released by various organisms including plants and microorganisms.

4.12 Dehydrogenase

The dehydrogenase enzyme activity is commonly used as an indicator of biological activity in soils. This enzyme is considered to exist as an integral part of intact cells but does not accumulate extracellularly in the soil (Vasilchenko et al. 2004). It is also known to oxidize soil organic matter by transferring protons and electrons from substrates to acceptors.

Soil water content and temperature influence dehydrogenase activity indirectly by affecting the soil redox status (Debnath and Hajra 1972; Xu et al. 2015).

4.13 Phosphatases

In soil ecosystems, these enzymes are believed to play critical roles in P cycles as they are correlated to P stress and plant growth and are also good indicators of soil fertility. For example, when there is a signal indicating P deficiency in the soil, acid phosphatase secretion from plant roots is increased to enhance the solubilization and remobilization of phosphate, thus influencing the ability of the plant to cope with P-stressed conditions (Saha et al. 2003).

4.14 Proteases

Proteases in the soil play a significant role in N mineralization, regulating the amount of plant available N and plant growth. They are associated with inorganic and organic colloids (Chakroborty and Sen 1967). Extracellular enzyme activities are not only indicative of biological capacity of soil for the enzymatic conversion of the substrate but also have an important role in the ecology of microorganisms. Hence, there is a need to study the properties and factors affecting naturally occurring enzyme complexes as they reveal some unknown role(s) in maintaining soil health and fertility.

4.15 Concluding Remarks and Future Prospectives

Soil organisms (macro and micro) play a significant role in soil processes, including nutrient cycling. These efficient processes are essential to agriculture and forestry and for protecting the quality of water, air, and habitat. Soil enzymes act as a catalyst to sustain soil health and its fertility. Enzymes have significant effects on soil biology, environmental management, growth, and nutrient uptake in plants growing in ecosystems. However, their activities may be influenced by unknown cultural management practices either in a major or minor amount. Therefore, it is necessary to consider the effects on the soil health. Despite of significant importance of soil biological processes, the development of monitoring and management guidelines is limited. In the future, researches focusing more on the discovery of new microbial diversity in the soil might be significant practices that may positively influence the microbial activities for improved plant growth as well as rendering friendly biological environments in order to sustain other living beings.

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Quorum Sensing in Plant Microbe Interaction

5

Raghavendra M.P.

Abstract

The coordinated behaviors, at the population level, occur in bacteria due to communication between the cells, which is defined as quorum sensing (QS). These communications help the bacteria to respond in terms of extracellular factors which are involved in scavenging for nutrients; biosynthesis of exopolysaccharides, extracellular hydrolytic enzymes, siderophores, antibiotics, pigments, hypersensitive reaction; aiding motility; and providing scaffolding for biofilms to grow as well as those involved in conjugation and epiphytic fitness. Even in parasitic species, these signals help in regulation of bacterial growth, virulence, and damage caused to hosts. QS signal molecules are regulated by autoinduction and positive feedback mechanism at high cell densities. A detailed mechanism involved in QS is discussed in this chapter with special reference to rhizosphere microflora. The rhizosphere is a digestive system of the plants wherein several microorganisms influenced by root exudates in turn favor its growth. In the future, understanding QS related to plant growth-promoting bacteria and its interspecific bacterial communication may offer good opportunities to manipulate bacterial community structure in the rhizosphere for the benefit of agriculture.

Keywords

Quorum sensing • Rhizosphere microflora • Plant growth

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5.1 Introduction

Revitalization of the native soil systems for improved crop yield was emphasized in many literatures and even the study conducted by United Nations' Economic and Social Commission for Asia and the Pacific on "Sustainable agriculture and food security in Asia and the Pacific" emphasizes the same. There is a need of carrying out these processes using various eco-friendly biological amendments especially microorganisms. These organisms colonized in the rhizosphere share symbiotic and asymbiotic relationship with plants benefiting its growth directly or indirectly (Meena et al. 2013a; Bahadur et al. 2014; Kumar et al. 2016b).

Rhizosphere microflora along with other eukaryotic cell types is known to produce specific small signaling molecules through which they are able to sense their concentration in the environment. This behavior of accumulating signal molecules in response to increase in population density of the specific organism is named as quorum sensing (Fuqua and Greenberg 2002). The coordinated expression of the specific target genes of the entire population occurs when these signals reach the threshold. These interactions help these organisms to occupy particular habitat adapting to environmental conditions and resource levels and even to generate a coordinated protective response against several adverse conditions. These coordinated responses are generally induced by a group of chemical signaling and are referred to as quorum sensing (QS). QS signals produced by rhizosphere microflora are significantly higher compared to other organisms isolated from bulk soil. It is also evident from the work carried out on the QS signals with distinct chemical structures produced by Gram-negative rhizosphere bacteria and their potential to regulate a wide array of genes in the population (Hartmann et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015, 2016a; Jha and Subramanian 2016).

5.2 Biocommunication in Rhizosphere

The rhizosphere is defined as the soil around the roots which is under the influence of root exudates, whereas rhizoplane comprises of the microorganisms adhered onto the root surface. Roots are reported to secrete exudates with a wide array of chemicals involved in regulation of both beneficial and pathogenic microorganisms in the rhizosphere. The variation in these chemicals helps in stabilizing the equilibrium of beneficial microbes in terms of its number and by which evading the continuous attack by soilborne pathogenic bacteria (Walker et al. 2003; Bais et al. 2003). The cross talk between the plant roots and beneficial microbes is playing a vital role in growth and development of the entire plant kingdom in general and agricultural crops in particular (Manefield and Turner 2002; Kent and Triplett 2002; Sharma et al. 2003). The release of chemicals involved in trans-specific communication from roots can occur passively upon decay and may export signals actively to the extracellular environment.

Ten to 40% of the photosynthetic carbon assimilation is released by the plants as root exudates, and it is a mixture of sugars, amino acids, organic acids, sugar alcohols, and secondary metabolites (Bais et al. 2006). Due to its regular addition to soil than the senescent plant debris, their role in regulating the microbial activity through nutrient bioavailability and regulating phytotoxic elements is vital (Singh and Mukerji 2006; Neumann 2007). Thus, microbial activity including cell division, sporulation, and synthesis of secondary metabolites and even its number is very high in the vicinity of growing roots than the non-rhizosphere soil. It is observed that there is 12- to 25-fold difference in bacterial and fungal population between these soils (Kennedy 2005; Parewa et al. 2014; Ahmad et al. 2016; Jaiswal et al. 2016; Meena et al. 2016a).

The rhizosphere is a hotspot of several communications involving a wide range of microorganisms with diverse physiological importance (Bahadur et al. 2017; Verma et al. 2017b; Kumar et al. 2017a; Nath et al. 2017). Among these communications, quorum sensing and quorum quenching are attracting scientific community for its beneficial exploitation in plant growth regulations ultimately leading to yield enhancement. Gram-negative bacteria use homoserine lactones (LuxR/LuxI) as communication signals (Swift et al. 1999; Schauder and Bassler 2001), whereas Gram-positive bacteria use oligopeptides in quorum sensing. The mechanisms of quorum sensing are discussed in detail later in this chapter.

During quorum sensing, it is important for the organisms to differentiate between species-specific signaling and signaling associated with interspecies behavior modulations (Bassler 1999; Federle and Bassler 2003; Waters and Bassler 2006). Hence, they need to have competence in communication, which enables them to coordinate behaviors related to species specifically and also to coordinate with other diverse group of species (Hughes and Sperandio 2008). Mycorrhizal fungi stand as a best example for this; these fungi support the growth of bacteria by releasing few nutrients, and in turn soil bacteria with its wide array of enzymes degrade the complex soil organic nutrients and make it easily available for the fungi (Bonfante 2003; Bonfante and Anca 2009). It also supports the plant growth by extending its hyphae to the areas where plant roots are not able to reach; due to this extension, the plant gets sufficient nutrients supplied by both roots and fungi compared to uninfected roots. Volumes of information are available in these interactions, and it is also documented that if mycorrhizal associations were not available, several plants would have become extinct by this time (Meena et al. 2015f, 2016b; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016; Prakash and Verma 2016).

Smaller groups of the similar bacteria on the other hand use quorum sensing to develop dialects required to occupy specific niche in the ecosystem. It also helps in identifying the nonself species through species-specific and group-specific quorum sensing. While facing the competition for specific niche, the complex coordination among the species avoids the confusion and enables them to colonize the specific habitat with specialized characteristics acquired through such interactions (Taga and Bassler 2003). The law of limiting factor supported by adaptive radiation of the species is favored by coexistence of bacterial life with suitable interactions to scavenge the limiting factor required to colonize the specific habitat and suitably favored in competition with other groups of organisms (Sarkar et al. 2017; Verma et al. 2017a).

Of late, understanding of QS revealed that it is common in all bacteria including proteobacteria which exhibit QS mediated by N-acyl-homoserine lactone (AHL) (Fray 2002). These bacteria need special mention because they are reported to be common in the rhizosphere than in the bulk soil (Cha et al. 1998) and constitute an estimated two-thirds of temperate plant rhizospheres (Hawkes et al. 2007). After accepting the fact that quorum sensing plays an important role in rhizosphere colonization and soil fertility, several novel techniques such as extracting DNA from rhizosphere soil (Williamson et al. 2005), inoculating the specific bacteria to sterile soil to understand the interaction in controlled condition (Steidle et al. 2001), and understanding QS in natural habitat (DeAngelis et al. 2007) and compost (Burmolle et al. 2005) have taken place, but the role of QS in soil processes associated with biologically intact soils needs to be investigated thoroughly using sophisticated methods to understand the difficult interactions and signals associated with it.

It is interesting to note that even higher plants are also reported to secrete molecular compounds similar to bacterial AHL through root exudation (Bauer and Teplitski 2001). Few plants such as legumes, pea, and alfalfa are known to secrete mimic of the bacterial QS regulators required to regulate functions of plant-specific PGPR, which helps them to colonize specific plant and release antifungal compounds to inhibit the soilborne phytopathogens (Teplitski et al. 2000). Another interesting report is that the chemicals released in the root exudates are known to modify the AHL signaling in microbial populations by promoting or inhibiting AHL-mediated QS. To support this, Bauer and Teplitski (2001) reported the ability of *D. pulcra* an alga to produce over 30 halogenated furanone compounds having the ability to inhibit Gram-negative AHL signals. These compounds are similar to bacterial AHL in structure but prevent the Gram-negative bacteria to colonize algal surface, and by doing so, it favors the colonization by Gram-positive bacteria. This gives an idea that QS plays a vital role in selective colonization of root surface either regulated by chemicals released by plants or bacterial signaling system. Understanding this delicate communication in soil is the need of the hour to develop strategies for the next green revolution.

5.3 Mechanism of Quorum Sensing

QS in bacteria is explained related to the field of economics and is considered similar to the systems that control the production of public goods. Biologically, it is the production of costly product individually when accumulated in concentration benefits personally and also the population. For example, the exoenzyme, an enzyme released by the bacteria into the environment to break down complex food/carbon sources into simpler molecules, has to facilitate the easy uptake into the cells for further degradation to derive the energy. This special physiological ability of one organism keeps other organisms without this ability out of competition in a particular habitat. It is also true with pathogenic organisms having the ability to secrete/excrete molecules which are often toxic to other animals including human beings.

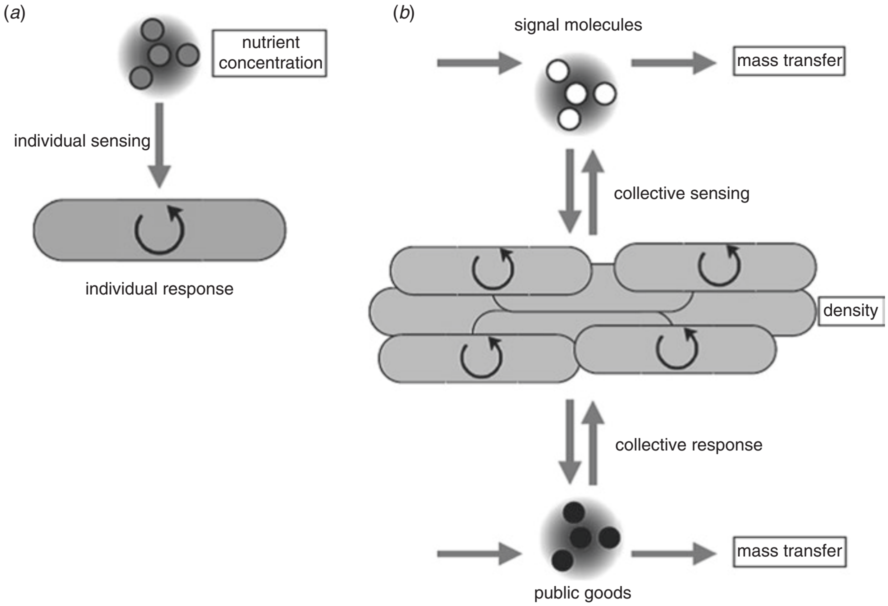

Fig. 5.1 Individual sensing versus collective sensing and responses; (**a**) individual sensing, (**b**) collective sensing (Popat et al. 2015)

Even antibiotics, which plays an important role in amensalism behavior, requires quorum sensing specially regulated by cell density (Fig. 5.1).

5.3.1 General Mechanism

Generally, quorum sensing in bacteria falls into three classes: the first is, as mentioned earlier, AHL-dependent LuxI/LuxR-type QS observed in Gram-negative bacteria, the second is the small peptide-mediated QS observed in Gram-positive bacteria, and the third observed in both these bacteria is luxS-encoded autoinducer 2 (AI-2) QS. These signal molecules are operating with precise sensing and regulatory network (Dunny and Leonard 1997; Miller and Bassler 2001; Schauder and Bassler 2001; Federle and Bassler 2003; Waters and Bassler 2005; Papenfort and Bassler 2016).

The detailed QS mechanism associated with Gram-negative bacteria mediated by AHL is available. AHL is freely diffusible and its concentration varies accordingly in proportion to cell density. The specific target genes are activated when LuxR-like protein recognizes AHL and binds to specific promoters on DNA, which in turn positively regulates the genes leading to the production of proteins. LuxI-like enzymes are reported to be responsible for production of specific AHL in association with acyl-ACP of the fatty acid metabolism (Miller and Bassler 2001; Fuqua and Greenberg 2002; Taga and Bassler 2003; Waters and Bassler 2005).

Two types of quorum sensing systems are reported in Gram-positive bacteria in contrast to Gram-negative bacteria (Dunny and Leonard 1997; Novick 2003; Fontaine et al. 2010; Fleuchot et al. 2011). The first comprises of a three-component signaling peptide referred to as autoinducing peptide (AIP) and the other is a two-component signal transduction system which specifically responds to an AIP (Miller and Bassler 2001; Dunny and Leonard 1997; Schauder and Bassler 2001). The difference observed between AHL signals and AIP is that the latter is not permeable through the cell membrane and hence requires an ATP-binding cassette transporter to transport AIP into extracellular environment (Dunny and Leonard 1997; Novick 2003). A signal peptide precursor is generally produced by Gram-positive bacteria which later cleaved at the double-glycine consensus sequence and obtained active AIP. Usually 5–25 amino acids with unusual side chains serve a signal peptide (Novick 2003). Further, the two-component signal transduction system comprising of membrane-bound histidine kinase and cytoplasmic regulator protein to regulate specific gene in response to the specific AIP leads to QS (Dunny and Leonard 1997; Schauder and Bassler 2001; Novick 2003).

Autoinducer 2 (AI-2) is the third type of QS observed both in Gram-positive and Gram-negative bacteria (Miller and Bassler 2001; Federle and Bassler 2003; Waters and Bassler 2005). Compared to other two QS systems which are generally for intraspecies interaction, AI-2 helps in interspecies communication and hence generally considered as "universal language" (Federle and Bassler 2003; Schauder and Bassler 2001). AI-2 which is a furanosyl borate first characterized in a marine bacterium *Vibrio harveyi* is reported to regulate bioluminescence which is cell density dependent (Chen et al. 2002; Vendeville et al. 2005). Further, its synthesis using luxS-encoded synthase, signal transduction, and regulation of the gene expression in cell density-dependent manner is well documented (Miller and Bassler 2001; Schauder and Bassler 2001; Federle and Bassler 2003; Waters and Bassler 2005; Vendeville et al. 2005).

5.3.2 QS Mechanism in Rhizosphere

Proteobacteria are reported as major colonizers of the rhizosphere, and hence the QS signals N-acyl-homoserine lactones (AHLs) produced by them are significantly high in the rhizosphere. More than 200 species of proteobacteria are known to produce about 40 different acyl-HSL signals with different specificities and are produced by the LuxI family of signal synthases which binds to highly specific receptors in the LuxR family that act as transcription factors. Most of the rhizosphere microflora is reported to exploit this coevolved signal and receptor circuit for its effective communication in the soil.

The major group observed in the rhizosphere is actinobacteria; in this group, QS is dependent on the production of autoregulatory factors of different chemical classes, mainly the butyrolactone class and the nucleotide-like B-factor class. The first class includes the A-factor of *Streptomyces griseus* (Yamada and Nihira 1998) and similar compounds found in other actinobacteria (Yamada et al. 1987; Kawabuchi et al. 1997). The nucleotide-like B-factor class has been isolated from *Amycolatopsis* (*Nocardia*) *mediterranei* (Kawaguchi et al. 1988). In actinobacteria, research efforts on QS have mostly focused on morphological differentiation and secondary metabolism. The role of QS during the interaction between actinobacteria and plants has not been examined in detail (Simao-Beaunoir et al. 2009).

5.4 Role of Biosurfactant in Rhizosphere Activity

It is observed that the production of biosurfactant is an important component of QS along with motility, signaling, differentiation, and biofilm formation (Kearns and Losick 2003; Van Hamme et al. 2006; Berti et al. 2007; Ron and Rosenberg 2011). It is well documented in *Pseudomonas* spp. wherein QS regulates rhamnolipid (biosurfactant) production (Dusane et al. 2010). These green surfactants are reported to enhance the plant microbe interaction leading to increased plant growth by enhancing the bioavailability of hydrophobic molecules, by increasing the wettability of the soil, and by distributing the chemical fertilizers applied to the soil properly. Hence, benefits of biosurfactants need to be exploited for sustainable agriculture.

There are also reports on biosurfactants playing a vital role in interaction between rhizosphere microflora. Ingham and Jacob (2008) have isolated a Gram-positive bacterium *Paenibacillus vortex*, a versatile swarmer with complicated colonial patterns, from the rhizosphere soil and were found highly sensitive to environmental conditions. These scientists provided greater insight into the transport of nonmotile fungus *Aspergillus fumigatus* with the help of swarming ability of the isolated bacteria. Both these organisms are reported to be inhabitants of the rhizosphere enjoying the mutual interaction; another interesting observation with this interaction is that the smaller bacterium is cooperatively transporting a larger one. The interaction between the swarming bacteria and fungus is reported to have more environmental impact and benefits in fungi in several ways (Ingham et al. 2011; Priyadharsini and Muthukumar 2016; Kumar et al. 2017b; Meena et al. 2015a, e; Raghavendra et al. 2016; Bahadur et al. 2016b; Das and Pradhan 2016).

In a similar finding, Lindum et al. (1998) reported the synthesis of serrawettin W2, a cyclic lipodepsipentapeptide required for swarming motility of *Serratia liquefaciens*, which is regulated in a cell density-dependent manner by an acyl-homoserine lactone-based quorum sensing system. Even swarming of *Bacillus subtilis* was reported to rely on the production of surfactin (Mendelson and Salhi 1996), a cyclic lipopeptide biosurfactant whose synthesis is also controlled by quorum sensing via two pheromone signal peptides, ComX and CSF (Solomon et al. 1996; Lazazzera et al. 1997). Kohler et al. (2000) reported that *Ps. aeruginosa* rhlA mutant was not able to swarm due to its inability to synthesize rhamnolipid.

5.5 Quorum Sensing for Biosurfactant Production

Cell-to-cell signaling regulates the expression of the rhlAB operon responsible for production of biosurfactants (Ochsner et al. 1994; Ochsner and Reiser 1995; Pearson et al. 1997; Pesci et al. 1997). RhlI, N-butyrylhomoserine lactone autoinducer synthase gene, and transcriptional activator encoding rhlR that are the major QS system and rhamnosyltransferase encoded by rhlC which is coordinately regulated along with rhlAB are responsible for biosurfactant production in microorganisms (Rahim et al. 2001). These systems are under the influence of nutritional factor and QS signals (Guerra-Santos et al. 1986). They also came out with interesting observation that the nutritional conditions supersede cell-to-cell communication and hence correlate more positively with upregulation of quorum sensing-controlled genes such as rhlAB. A similar conclusion was also expressed by Bollinger et al. (2001) related to sodA encoding manganese-cofactored superoxide dismutase. These reports highlight the need of understanding the role of nutritional factors and the QS signals in cell density-based gene regulation in microorganisms.

Through social traits bacteria get several benefits such as coordinated population behavior (*Vibrio fischeri*, *Ps. aeruginosa*, and *Staph. aureus*), biofilm formation to get protection from adverse environmental conditions, nutrient and niche protection in nocules (*Rhizobium* sp.), enhanced colonization and growth in specialized niches (siderophores production for iron acquisition in bacteria), autolysis to provide nutrients and DNA for biofilm development (*Ps. aeruginosa*), coordinated movement toward nutrient source (*Yersinia* sp., *Myxococcus xanthus*, *Ps. aeruginosa*), antibiotic resistance through production of extracellular enzymes to break down antimicrobials (*E. coli* and *Klebsiella* spp.), and also immune modulation to facilitate survival within the host (*Ps. aeruginosa*, *Porphyromonas gingivalis*, *Helicobacter pylori*) (Diggle et al. 2007).

5.6 Biofilm Formation on the Root Surface

Plant growth-promoting microorganisms are observed in optimal ecological niches having greater rhizodeposition. These organisms are concentrated on the root surface where the microcolonies or biofilms form (Munch et al. 2016). The biofilm formation has a wider impact on the microbial interaction and its associated plant growth-promoting ability. The biofilm forming beneficial and pathogenic bacteria which are associated with plant roots is tabulated in Table 5.1.

5.7 Beneficial Aspects of Quorum Sensing

Microorganisms being small are suitable models to understand the basic questions related to ecology and evolution of social interactions (Zahavi and Ralt 1984; Crespi 2001; Velicer 2003). In recent times, the beneficial traits acquired by these organisms in high-density population are developing a new insight into their community

Table 5.1 Biofilm formation by beneficial and pathogenic bacteria associated with plant roots

Bacteria	Nature of association	Plant name	References
Acinetobacter calcoaceticus P23	PGPR	Duckweed	Yamaga et al. (2010)
Azospirillum brasilense	PGPR	Wheat	Kim et al. (2005) and Sheludko et al. (2010)
Azorhizobium caulinodans	PGPR	Rice	Van Nieuwenhove et al. (2004)
Azotobacter chroococcum	PGPR	Cotton, wheat	Kumar et al. (2007)
Bacillus amyloliquefaciens S499	PGPR, biocontrol	*Arabidopsis thaliana*	Fan et al. (2011) Nihorimbere et al. (2012)
Bacillus cereus	Under conditions of stress by salt, heat, or desiccation	Wild barley	Trivedi et al. (2011)
Bacillus pumilus	Under conditions of stress by salt, heat, or desiccation	Wild barley	Trivedi et al. (2011)
Bacillus polymyxa	PGPR	Cucumber	Yang et al. 2004 Nihorimbere et al. (2012)
Bacillus subtilis	Biocontrol	*Arabidopsis thaliana*	Ellis and Cooper (2010) and Beauregard et al. (2013)
Bacillus megaterium C4	Nitrogen fixation, PGPR	Maize, rice	Liu et al. (2006)
Burkholderia cepacia Lu 10-1	Biocontrol	Mulberry	Ji et al. (2010)
Enterobacter agglomerans	Biocontrol	Cotton	Chernin et al. (1995)
Enterobacter cloacae	PGPR	Rice	Shankar et al. (2011)
Klebsiella pneumoniae	Beneficial	Wheat	Dong et al. (2004) and Liu et al. (2011)
Microsphaeropsis sp.	Biocontrol	Onion	Carisse et al. (2001)
Micrococcus sp. NII-0909	PGPR	Cowpea	Dastager et al. (2010)
Paenibacillus lentimorbus	Heavy metal tolerance	Chickpea	Khan et al. (2012)
Paenibacillus polymyxa	Biocontrol	Peanut	Haggag and Timmusk (2008)
Pantoea agglomerans	PGPR	Chickpea, wheat	Chauhan and Nautiyal (2010)
Pseudomonas aureofaciens	Biocontrol	Wheat	Sigler et al. 2001
Pseudomonas brassicacearum	Biocontrol	*Arabidopsis thaliana*	Lalaouna et al. (2012)
Pseudomonas chlororaphis	Biocontrol	Wheat	Chin-A-Woeng et al. (2000) and Shen et al. (2012)

(continued)

Table 5.1 (continued)

Bacteria	Nature of association	Plant name	References
Pseudomonas fluorescens	Biocontrol	Crop plant	Silby and Levy (2004) and Barahona et al. (2010)
Pseudomonas putida	Drought tolerance, bioremediation	Maize, sunflower, *A. thaliana*	Sandhya et al. (2009), Matilla et al. (2011), and Jakovleva et al. (2012)
Pseudomonas aurantiaca SR1	PGPR	Maize, wheat	Rosas et al. (2009)
Rhizobium alamii	Heavy metal tolerance	*Arabidopsis thaliana*, rapeseed	Schue et al. (2011)
Rhizobium leguminosarum pv. *viciae* 3841	Nitrogen fixation, PGPR, drought tolerance	Various legumes	Fujishige et al. (2006), Williams et al. (2008), and Janczarek and Skorupska (2011)
Rhizobium leguminosarum	Beneficial	Rice	Janczarek and Skorupska (2011)
Rhizobium sp. NGR234	Nitrogen fixation, PGPR	Legumes (cowpea)	Kysciak et al. (2011)
Rhizobium	Symbiosis	Legumes	Fujishige et al. (2006) and Robledo et al. (2012)
Sinorhizobium	Symbiosis	Legumes	Fujishige et al. (2006), Khan et al. (2012), and Amaya-Gomez et al. (2015)
Stenotrophomonas maltophilia	Biocontrol, PGPR	Crop plant	Ryan et al. (2008)
Shewanella putrefaciens CN-32	Microbial mediated geochemistry	Huang et al. (2011)	
Cyanobacteria sp.	PGPR, biocontrol	Prasanna et al. (2011)	

acquired behavior. Usually, microorganisms develop protective adaptations easily at high density than at low density to adverse environmental conditions such as acidic condition, alkalinity, pressure, etc. (Foster and Hall 1991; Foster 1995; Cui et al. 2001; Li et al. 2001). Even pathogenic bacteria such as *Staphylococcus aureus* require minimum cell density that is required to establish infections with upregulation of genes associated with virulence factor (Ji et al. 1995; Zahedi 2016; Meena et al. 2015b, 2016e; Rawat et al. 2016; Yasin et al. 2016; Masood and Bano 2016; Teotia et al. 2016). Even eukaryotic slime molds and prokaryotic myxobacteria respond to nutrient stress through aggregation of high-density groups (Rosenbluh et al. 1989; Rietdorf et al. 1996; vanOss et al. 1996).

The importance of rhizobacteria in the rhizosphere and the role of QS in regulating its activity related to plant root colonization and nutrient uptake through effective signaling pathways are well documented and described (Loh et al. 2002; Newton and Fray 2004; Nihorimbere et al. 2011; Podile et al. 2014).

The link between soil signaling and nitrogen cycling is also investigated by DeAngelis et al. (2008). They reported that many alpha-proteobacteria were newly found with QS-controlled extracellular enzyme activity, and even cell division, symbiotic plasmid transfer, gene expression in the rhizosphere, symbiosome development and nitrogen fixation, and nodule number in *Rhizobium* bacteria are regulated by QS. On the contrary, QS is also reported to play an important role in expression of genes associated with virulence factors (Meena et al. 2013c, 2016c; Saha et al. 2016a; Yadav and Sidhu 2016; Singh et al. 2015; Bahadur et al. 2016a). This supports an idea that developing QS mutants may be the next line of therapeutic target for disease management.

There is a positive relationship between population growth rate and population density in some species, which is first introduced by Allee et al. (1949) and hence known as the Allee effect. He suggested that there exist threshold densities for some species under some conditions, below which populations decline and thereby increase the likelihood of extinction and above which population growth rate increases as a function of density (Courchamp et al. 1999; Stephens and Sutherland 1999). This effect nowadays received renewed interest in conservation of plant and animal diversity, and it also suits very well into the concepts of QS in microorganisms (Darch et al. 2012; Meena et al. 2014b, 2015d, 2016d; Saha et al. 2016b; Verma et al. 2015b; Singh et al. 2016).

5.8 Quorum Sensing in Soil Microorganisms

Soil is the central organizer of the terrestrial ecosystem, and its physical, chemical, and biological processes have enormous impacts on ecosystem productivity, services, integrity, and human welfare. It is considered as a natural media for growth of several microorganisms associated with plant growth. The overall contribution of soil to the growth of plants is defined as the soil fertility. Several microorganisms inhabit the soil plant interface and create microenvironment which is physiologically dynamic supporting the biogeochemical cycle. These microorganisms in turn develop interactions which is an additional benefit for the plant growth (Verma et al. 2014; Meena et al. 2013b, 2014a, 2015c; Sharma et al. 2016; Verma et al. 2015a; Shrivastava et al. 2016; Velazquez et al. 2016; Sindhu et al. 2016). To sense environmental conditions and to change patterns of gene regulation accordingly, soil bacteria have evolved sophisticated signal transduction mechanisms. Soil microorganisms in general and rhizosphere microflora in particular are considered as treasure houses of the soil defining its fertility and plant growth promotion. Table 5.2 represents QS signals and its regulated functions.

Table 5.2 Activities of soilborne bacterial functions regulated by QS signals

Taxonomic class	Representative genus or species	QS signals produced	Known regulated functions	References
Actinobacteria	*Streptomyces* sp.	Gamma-butyrolactones	Antibiotic compound synthesis, differentiation	Chater (1993) and Shaaban et al. (2016)
Alpha-proteobacteria	*Agrobacterium tumefaciens*	OOHL	Ti plasmid transfer, virulence	White and Winans (2007)
	Bradyrhizobium sp.	AHLs	Not determined	Pongsilp et al. (2005)
		Bradyoxetin	Expression of nod genes	Loh et al. (2002)
		pCHL	Not determined	Schaefer et al. (2008)
	Rhizobium leguminosarum pv. *viciae*	OHtDeHL, HHL, HHL, OHL, OHOHL, OOHL	Growth inhibition, induction of rhi genes, plasmid transfer, nodulation	González and Marketon (2003)
	Sinorhizobium meliloti	OHL, OHOHL, OOHL, DDHL, OtdHL, HDHL, OhDHL	EPSII synthesis, motility, nodulation kinetics, plasmid transfer	González and Marketon (2003)
	Mesorhizobium loti	OHHL, OHL, DHL, dDHL	Nodulation	Yang et al. (2009)
	Rhodopseudomonas palustris	pCHL	Chemotaxis	Schaefer et al. (2008)
Beta-proteobacteria	*Burkholderia glumae*	OHL	Toxoflavin synthesis	Ferluga et al. (2008)
	Burkholderia kururiensis	OHHL, OHL, DHL, dDHL	Not determined	Ferluga et al. (2008)
	Ralstonia solanacearum	OHL	Not determined	Ferluga et al. (2008)
Firmicutes	*Staphylococcus aureus*	AIPs (thiolactone peptides)	Virulence, antimicrobial peptides synthesis, genetic competence	Sturme et al. (2007) and Lyon and Novick (2004)
Gamma-proteobacteria	*Erwinia amylovora*	OHHL	Virulence, EPS synthesis, hydrogen peroxide tolerance	Ferluga et al. (2008)
	Pectobacterium carotovorum	OHHL	Varbapenem production, exoenzymes, hrp secretion system	Braeken et al. (2008)
	Dickeya dadantii	HHL, OHHL, DHL	Not determined	Ferluga et al. (2008)
	Pantoea stewartii	OHHL, OOHL	EPS synthesis, biofilm, adhesion, xylem dissemination, pathogenicity	Braeken et al. (2008)
	Serratia liquefaciens	BHL	Swarming, biofilm, protease	Ferluga et al. (2008)

	Pseudomonas aeruginosa	BHL, OdDHL	Biofilm, elastase, lipase, alkaline protease, HCN, pyocyanin, exotoxin A, swarming, lectins, rhamnolipids, virulence.	Braeken et al. (2008) and Ferluga et al. (2008)
		PQS	Elastase, pyocyanin synthesis, LecA lectin, biofilm, AHL signaling, motility + intrinsic functions (antibiosis, iron chelation)	Dubern and Diggle (2008)
		DKPs (e.g., cyclo (D-Ala-LVal))	Unclear, cross-linked to AHL signaling	Holden et al. (1999)
	Pseudomonas syringae pv. *syringae*	OHHL	Cell aggregation, epiphytic fitness, disease development, hydrogen peroxide tolerance, motility	Elasri et al. (2001) and Quin˜ones et al. (2005)
	Pseudomonas aureofaciens	HHL	Phenazine production, rhizosphere colonization, protease activity	Braeken et al. (2008) and Ferluga et al. (2008)
	Pseudomonas fluorescens 2P24	OHHL, OHL	Biofilm formation, wheat rhizosphere colonization, biocontrol ability	Wei and Zhang (2006)
	Xanthomonas campestris	DSF (cis-11-methyl-2-dodecenoic acid)	Extracellular enzymes, LPS and EPS synthesis, multidrug resistance and detoxification, motility and chemotaxis, HR and pathogenicity (hrp), iron uptake, primary metabolism	He and Zhang (2008)
		DF (butyrolactones)	Xanthomonadin production (light protection), colonization	He and Zhang (2008)

BHL N-butyryl-homoserine lactone, *dDHL* N-dodecanoyl-homoserine lactone, *DHL* N-decanoyl-homoserine lactone, *HHL* N-hexanoyl-homoserine lactone, *OdDHL* 3-oxo-N-dodecanoyl-homoserine lactone, *OHDtDeHL* 3-hydroxy-N-7-cis-tetradecenoyl-homoserine lactone, *OHHL* 3-oxo-N-hexanoyl-homoserine lactone, *OHL* N-octanoyl-homoserine lactone, *OOHL* 3-oxo-N-octanoyl-homoserine lactone, *OtDHL* 3-oxo-N-tetradecanoyl-homoserine lactone, *DKP* diketo-peptides

5.9 Future Prospective and Concluding Remarks

Several studies revealed that QS is playing a vital role in inducing protection against abiotic factors, environmental challenges (Popat et al. 2015), and production of biosurfactant along with plant growth promotion. Biosurfactants produced by the rhizosphere and plant-associated microbes are associated with rhizosphere activity, plant microbe interaction, and plant pathogen elimination, increasing the bioavailability of nutrient for beneficial plant-associated microbes. They are proven effective even in improving the agricultural soil quality through soil remediation. Screening of biosurfactant-producing microorganisms from soil biosphere needs to be accelerated, and the application of advanced methodologies such as functional metagenomics will aid in obtaining unculturable biosurfactant-producing microbes (Sachdev and Cameotra 2013). These studies add more insights into the understanding of the QS mechanisms and their role in soil fertility enrichment.

Agriculture is one of the most significant factors contributing to the economic growth of India, and sustainable agriculture economic development is the need of the hour. Hence, a major focus in the coming decades would be on safe and eco-friendly methods by exploiting the beneficial microorganisms in sustainable crop production. Even genetic engineering of rhizosphere microflora and transgenic plants which can alter quorum sensing in microbes will have several benefits in agriculture including yield enhancement and effective plant pathogen management. Besides the growing information on the production of growth regulators and competitiveness of the microbes in the rhizosphere, microsymbionts, and other factors, their effect upon plant growth will become more evident.

Of the ongoing emergence of antibiotic-resistant pathogens, there is a current need for development of alternative management strategies. An antivirulence approach by which quorum sensing is impeded is caught on as a viable means to manipulate bacterial processes, especially pathogenic traits that are harmful to human and animal health and agricultural productivity (LaSarre and Federle 2013). The identification and development of chemical compounds and enzymes that facilitate quorum sensing inhibition by targeting signaling molecules, signal biogenesis, or signal detection are gaining momentum.

Nowadays, screening for quorum quenching compounds is another interesting area which can be carried out in high-throughput screenings since several assays targeting the formation of autoinducers or their receptors are available (Abraham 2016; Reuter et al. 2016). However, the entire mechanism for quorum sensing is known only for a small number of microorganisms, and still very little is known about interspecies cross talks.

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Horizontal Gene Transfer in Soil and the Rhizosphere: Impact on Ecological Fitness of Bacteria

6

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Abstract

The ecological fitness of soil- and root-associated bacterial communities is a key element for soil fertility and plant health as well as plant stress tolerance. Genetic variability in bacterial populations is maintained through mutation and gene acquisition. Horizontal gene transfer (HGT) is accomplished by conjugation, transformation, and transduction both in vitro and under natural conditions. Mobile genetic elements (MGEs) play a significant role in gene dissemination in bacterial communities and increase their adaptability, survival, and ability to colonize different environmental niches. In this context, bacterial conjugative plasmids encoding resistance genes, degradative genes, and tolerance to stress conditions are of much significance. The biofilm mode of bacterial growth further enhances gene exchange and increase the fitness and competitiveness of bacteria. Microcosm studies reveal a number of factors influencing the HGT process in soil. Considering the importance of HGT, a better understanding of genetic processes in the rhizosphere will further help in effective exploitation of naturally engineered bacteria for sustainable agriculture.

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Bacteria • Horizontal gene transfer • Conjugative plasmid • Microcosm • Biofilm • Rhizosphere • Ecological fitness

6.1 Introduction

Horizontal gene transfer (HGT) refers to the transfer of genetic material between prokaryotes. The process occurs in one of three ways: (1) transformation (the uptake of free DNA by competent bacteria from the surrounding environment), (2) transduction (gene transfer mediated by bacteriophages), and (3) conjugation (gene transfer by means of plasmids or integrative conjugative elements). Conjugation is the process by which a DNA molecule (i.e., plasmid or conjugative transposon) is transferred from a donor cell to a physically attached recipient cell via some conjugation apparatus (Zechner et al. 2000). Although most conjugative plasmids shared common mechanistic principles, e.g., synthesis of conjugative pili, there is a remarkable diversity of conjugative systems in Gram-negative and Gram-positive bacteria, depending on the shape and other characteristics of the plasmid-encoded pili. Nonconjugative plasmids are transferred to recipient cells by mobilizing/helper plasmids (Heuer and Smalla 2007). Transfer of conjugative plasmids or transposons has been demonstrated to occur in various ecological habitats, for example, the plant surface, rhizosphere, surface water, and human and animal intestines (Aminov 2011; Madsen et al. 2012; Huddleston 2014; Juhas 2015; Pinto-Carbo et al. 2016; Sun et al. 2016). In contrast to conjugation, transduction provides a means of DNA acquisition in which nonviral DNA is transferred from an infected host bacterium to a new host via infectious or noninfectious virus particles (Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jaiswal et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a, b).

Defective phage particles released from lysed host cells attach to new host cells and deliver their DNA into the new host. The injected bacterial DNA is subsequently integrated into the recipient genome. Unlike conjugation, transduction does not require cell-to-cell contact; however, most bacteriophages infect only a narrow range of hosts (Wommack and Colwell 2000). Evidence for the importance of transduction as an HGT process in the natural environment arises from studies on the abundance of bacteriophages in different settings, primarily soil (Ashelford et al. 2003) and from bacterial genome sequences (Canchaya et al. 2003). The role of bacteriophages in contributing various genes to bacterial genera of medical and ecological significance is well documented (Weitz et al. 2013; Broszat and Grohmann 2014; Dalmasso et al. 2014; Chen et al. 2015; Obeng et al. 2016).

Horizontal gene transfer plays an important role in formulating bacterial genomes, promoting intra- and interspecies variability and distributing functional genetic modules within communities. HGT provides a means for enhanced understanding of ecological adaptation and bacterial evolution in the biosphere. Extensive gene exchange during bacterial evolution is made evident by the marked similarity of genes among distantly related species, variation of gene content between closely related strains, and incongruent phylogenetic trees. Horizontal gene transfer is a major force in bacterial evolution; a well-documented example of HGT is the spread of antibiotic resistance genes among pathogenic and nonpathogenic bacteria (Barlow 2009; Boto 2010; Davies and Davies 2010; Abulreesh 2011, 2012; Baltrus 2013; Wellington et al. 2013). The driving force for the acquisition of foreign genes via HGT is believed to be the need for bacteria to overcome environmental stresses for survival and to compete successfully in their ecological niches (Hacker and Kaper 2000).

Mobile genetic elements (MGEs) such as plasmids, bacteriophages, integrative conjugative elements, transposons, insertion sequences (IS) elements, integrons, gene cassettes, and genomic islands are the key vehicles among HGT mechanisms. In many species, a high proportion of horizontally transferred genes can be attributed to plasmid-, phage-, or transposon-related sequences, as remnants of these mobile elements have been located adjacent to genes identified as horizontally transferred (Ochman et al. 2000; Brussow et al. 2004; Frost et al. 2005; Gyles and Boerlin 2013). It has been suggested that MGEs add some metabolic burden to their host, and adaptation occurs to minimize this impact (Dahlberg and Chao 2003; Heuer et al. 2007). The prevalence of plasmids, however, indicates that they benefit bacteria and compensate for any burden they might impose on the cell. Plasmids persist because bacterial communities and their environments are continuously changing; the variability carried by these genetic elements increases the speed at which adapted strains arise, and the adapted strains retain the MGE so they can propagate rapidly (Jat et al. 2015; Kumar et al. 2015; Ahmad et al. 2016; Meena et al. 2015f, 2016a; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016).

The MGEs that enhance an organism's adaptability evolve and survive at the expense of those that do not. Thus, MGEs confer an improved fitness to the bacterial community and its ability to colonize different environmental niches. MGEs additionally increase the possibility of new strains arising with novel or increased selective advantages over neighboring communities. Metagenomic approaches have revealed a large and untapped diversity of resident MGEs in soil- and plant-associated bacteria. Approximately 18% of bacterial isolates from the phytosphere of sugar beets was found to contain plasmids (Powell et al. 1993), and a large proportion were able to mobilize non-self-transferable but mobilizable Inc-Q plasmids (Kobayashi and Bailey 1994). The extensive presence of plasmid-related sequences in soil DNA (directly extracted) indicates a significant abundance of plasmids in soil (Heuer et al. 2009). The abundance of transferable plasmids in soil is believed to be related to the presence of contaminants (e.g., antibiotics, xenobiotics). Several studies have indicated that genes encoding the enzymes involved in catabolism of environmental pollutants are present on plasmids (Smets and Barkay 2005; Kopmann et al. 2013).

Different methods involving various molecular techniques have been employed to detect and study soil plasmid structure, organization and function (Heuer and Smalla 2012). Moreover, metagenomics methods such as pyrosequencing of soil DNA have proved to be highly sensitive and have led to the discovery of novel plasmid sequences (Kristiansson et al. 2011). Genome sequencing data have revealed the modular character of conjugative plasmids, where different modules (e.g., a compactly arranged gene) are dedicated toward carrying out specific functions (de la Cueva-Méndez and Pimentel 2007; Norman et al. 2009). The overall genetic makeup of conjugative plasmids can be divided into four distinct categories of modules: (1) modules affecting plasmid replication and copy control, (2) modules affecting plasmid stability, (3) modules affecting plasmid propagation, and (4) modules affecting plasmid host adaptation, along with numerous other subcategories (Norman et al. 2009). The first three categories are considered "plasmid core" or plasmid "backbone" genes. Sequence analysis of plasmid backbone genes is considered a consistent and reliable foundation for plasmid classification, as opposed to traditionally used methods (Heuer and Smalla 2012). Apart from plasmid backbone genes, a highly diverse, accessory, or flexible set of genes within soil plasmids occurs as a fourth module which carries genes responsible for environmental adaptation. These accessory genes often differ greatly among plasmids with identical plasmid backbones and impart the ability to adapt to varied environmental conditions such as exposure to antibiotics, heavy metals, and xenobiotics (Dennis 2005; Schluter et al. 2007; Heuer et al. 2009).

Degradative genes resident on MGEs have been isolated successfully from soil treated with the herbicide 2, 4-D but not from untreated control soil. Similarly, self-transferable plasmids which confer resistance toward antibiotics have been isolated from animal manures used for soil fertilization (Heuer and Smalla 2007; van Overbeek et al. 2002). Sequencing of plant-associated bacteria reveal that many phytopathogenic and symbiotic bacteria carry plasmids (Zhao et al. 2005; Bardaji et al. 2011), pathogenicity islands (Gardiner et al. 2014), or integrons (Gillings et al. 2005). These studies reveal the significance of horizontal gene transfer in bacterial adaptation and evolution under changing environmental conditions (Parewa et al. 2014; Prakash and Verma 2016; Meena et al. 2015e, 2016b; Teotia et al. 2016; Bahadur et al. 2016b; Das and Pradhan 2016).

In recent years, the importance of biofilm formation and its relationship to gene transfer has received significant attention (Burmolle et al. 2014; Stalder and Top 2016). It is well recognized that horizontal gene transfer via plasmids occurs more effectively on surfaces, e.g., in biofilms than among planktonic cells. Biofilms are highly structured bacterial communities embedded in a self-produced matrix composed of exopolysaccharides (EPSs), proteins, and DNA. These films adhere to biological and non-biological surfaces (Hall-Stoodley et al. 2004) and provide a favorable environment for genetic elements to be transferred horizontally. Rhizobacterial biofilms associated with plant roots support bacterial survival and host plant colonization, reduce biotic and abiotic plant stress, and enhance agricultural productivity (Lopez et al. 2010; Yadav and Sidhu 2016; Meena et al. 2016d; Saha et al. 2016b; Verma et al. 2014, 2015b). All these advantages conferred by biofilms are directly or indirectly associated with a high frequency of horizontal gene transfer in the biofilm mode of growth. In this chapter, we focus on horizontal gene transfer in soil- or plant-associated (rhizosphere) bacteria that contribute to

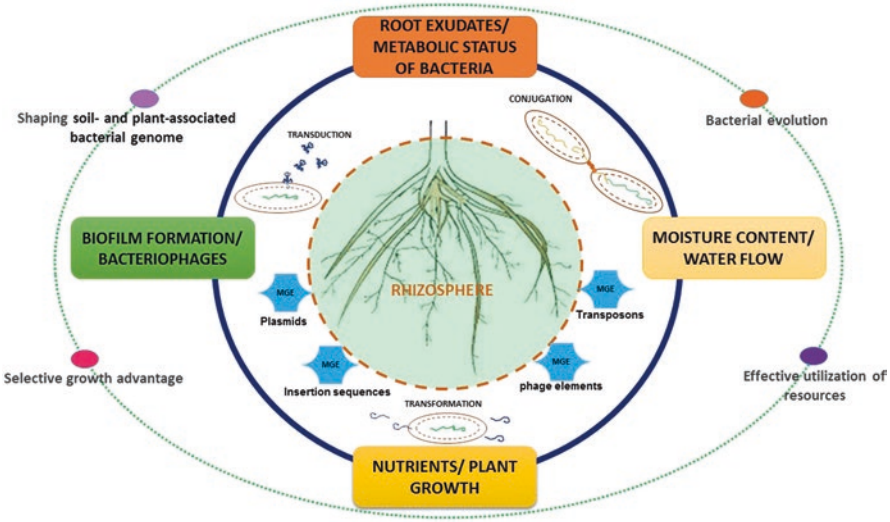

Fig. 6.1 Gene transfer in the rhizosphere: mechanisms, factors, and outcomes

genetic variation in microbial populations and ultimately broaden their range of environmental niches by increasing their fitness and competitiveness (Fig. 6.1).

6.2 HGT in Environment and Its Role in Evolution of the Bacterial Genome

Discovery of the transferable nature of multidrug resistance by Watanabe in 1963 resulted in the recognition of horizontal gene transfer. Since then, HGT has become a topic of extensive investigation worldwide, particularly in medical microbiology. The occurrence of HGT among bacteria in the natural environment was subsequently recognized; such processes are believed to relate to the risk of genetically modified bacteria released into the environment (Heuer and Smalla 2012). In view of the use of genetically modified (GM) crops and microbes in agricultural settings, the role of mobile genetic elements (MGE; plasmids, transposons, bacteriophages, etc.) associated with plant and soil and factors influencing this mobility has received attention from many scientists (Smalla et al. 2000; van Elsas and Bailey 2002). Studies have demonstrated that HGT is a major, if not the dominant force in bacterial evolution (Frost et al. 2005; Davies and Davies 2010; Wiedenbeck and Cohan 2011; Dutta and Sarkar 2015; Navarre 2016). Up to 20% of a typical bacterial genome acquired from other species and MGE acts as a vector for HGT (Ochman et al. 2000).

HGT affects only those bacteria that readily exchange genes, and members of such rapidly exchanging communities have shown similar characteristics such as genome size, GC content, carbon utilization, and oxygen tolerance (Jain et al. 2003).

On the other hand, considerable evidence indicates that HGT is an ongoing process that plays a primary role in real-time ecological adaptations of prokaryotes (Smets and Barkay 2005). MGEs play an essential role in the process by shaping the bacterial genome, promoting intraspecies variability, and distributing functional genetic modules among communities. Consequently, HGT of genetic modules that allows adaptation to rapidly changing biotic interactions has frequently been observed (Smets and Barkay 2005). The interactions include:

1. Antibiotics production by microorganisms
2. Dissemination of antibiotic resistance
3. Release of xenobiotics or new secondary metabolites
4. Dissemination of degradative gene and pathway assemblies (McManus et al. 2002; Top and Springael 2003; Larrain-Linton et al. 2006)
5. Symbiotic or pathogenic interactions and speed of the spread of genomic islands (Arnold et al. 2007; Heuer and Smalla 2012)

The most widely studied examples of genetic exchange through HGT in natural environments is the dissemination of multiple antibiotic resistance via MGE, which allows bacterial populations to adapt rapidly to strong selective pressures (Cordero et al. 2012; Wellington et al. 2013; Ojala et al. 2014). MGEs involved in transmission of antibiotic resistance include combinatorial genetic evolution of MDR facilitated by transposons, IS elements, and integrons. Transposable elements like ISCRs (insertion sequence common regions) mobilize DNA adjacent to their insertion site via rolling circle replication (Toleman et al. 2006). ISCRs are closely associated with antibiotic resistance genes on conjugative plasmids (Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Masood and Bano 2016; Meena et al. 2016e).

It is interesting to observe that under natural conditions, especially in wastewater and soil, the presence of several toxic pollutants (e.g., metals and pesticides) may increase selective pressure and co-selection of resistant strains. These pollutants may further increase the ecological fitness and survivability of bacterial strains (De Lipthay et al. 2008; Imfeld and Vuilleumier 2012). Various degradative plasmids have been characterized from bacteria which degrade PCBs, chloroaniline, and other recalcitrant molecules (Merlin et al. 1999; Boon et al. 2001; Springael and Top 2004). Many self-transferable plasmids participate directly in active gene transfer. Russell et al. (2011) reviewed the evolutionary trends of enzymatic machinery involved in the degradation of xenobiotics and concluded that horizontal gene transfer among bacteria is one of the major determinants in the acquisition of new and efficient enzymatic functions. New enzymatic pathways have emerged from a wide variety of enzyme families.

Metagenomic mapping studies for two discretely located hexachlorocyclohexane (HCH)-degrading strains of *Sphingobium japonicum* (*Sphingobium japonicum* UT26 from Japan and *Sphingobium indicum* B90A from India) have shown that the previous common ancestor was unable to degrade HCH isomers, but descendants acquired degrading genes by transposon-mediated HGT (Sangwan et al. 2014). Likewise, Pearce et al. (2015) showed that different HCH-degrading bacteria yielded a distinct set of metabolites during degradation of HCH isomers. The analysis confirmed the role of horizontal transfer mediated by an insertion sequence in the acquisition of the pathway.

6.3 Gene Transfer in the Rhizosphere

Among the conditions occurring within the phytosphere, the rhizosphere is optimally suited for the growth and intensive interaction among microbial communities. The availability of essential elements (C, N, P, K), moisture, and other critical constituents (e.g., organic acids) in the vicinity of plant roots make the rhizosphere the preferred site for gene transfer, such that it is referred to as a "hotspot" for genetic evolution (van Elsas et al. 2003). The rhizosphere provides an ideal environment for HGT processes and may support rapid adaptation of bacteria against environmental changes as compared with bulk soil. Conjugative plasmid transfer frequency between bacterial species is enhanced under high nutrient availability and water movement (Kroer et al. 1998). Bacterial colonization and adherence to the root surface in response to the presence of root exudates impart significant effects on gene transfer.

Due to intimate contact among cells and higher metabolic activity in response to the presence of an ample nutrient supply, elevated plasmid transfer in the rhizosphere has been observed (Kroer et al. 1998; van Elsas et al. 2003). Musovic et al. (2006) demonstrated the exceptionally broad host range of the pKJK10 plasmid in the barley rhizosphere. They describe the potential of mobile genetic elements, crossing large phylogenetic distances, i.e., gene swapping between Actinobacteria and Proteobacteria, in bacterial evolution. Organic acids and other constituents of root exudates stimulate the transformation in *Acinetobacter* sp. BD413 (pFG4) in sterile soils. The organic acids, acetate, lactate, and alanine, resulted in the highest transformation frequencies (Nielsen and van Elsas 2001). Molbak et al. (2007) studied conjugal transfer in the rhizospheres of pea and barley. The experiments showed that a higher rate of root exudation and root growth rate in pea was responsible for higher conjugal frequency. The distribution pattern of donors on pea roots was shown to affect genetic transfer. Transfer of the plasmid RP4 derivative between *Pseudomonas fluorescens* and *Serratia* sp. was studied in a sand microcosm and found to be related to the availability of root exudates and bacterial metabolic activity (Kroer et al. 1998). Regardless, however, the direct relationship between the metabolic activity of transforming bacteria and gene transfer is in need of further investigation (Meena et al. 2013c, 2015a; Raghavendra et al. 2016; Zahedi 2016; Singh et al. 2015; Bahadur et al. 2016a).

Genetic transfer of various contaminant-degrading genes has also been shown to take place effectively in the rhizosphere and is concurrently responsible for enhanced plant growth (Wang et al. 2007, 2014a, b; Jia et al. 2013). Using an in silico metagenomic prediction method, Cabezon et al. (2015) and Lopes et al. (2016) revealed a significantly higher abundance of predicted genes associated with HGT in the rhizosphere compared with bulk soil. The pilus assembly protein CpaE and type IV pilus assembly protein PilV as well as genes involved in transformation/conjugation, such as the type IV secretion system proteins VirB4, VirB5, VirB6, and VirB9, among other transduction and transformation stimulating genes, were prevalent in the rhizosphere.

Bacteriophages present in the rhizosphere serve as another important agent responsible for genetic variation and evolution of indigenous bacterial communities. Because phage DNA is often packaged in relatively resilient phage coats, it is possible that transducing phages provide a reservoir of bacterial genes under localized conditions where the host may not survive (Van Elsas et al. 2003). Studies have shown that soil conditions affect the burst size of the lytic phage thus indirectly affecting the frequency of gene transfer and lysogeny (Burroughs et al. 2000). One of the mechanisms responsible for interspecies gene transfer in the rhizosphere is the overlapping susceptibility to phages among bacterial communities (Ashelford et al. 2000). Ashelford et al. (2003) highlighted the importance of soil bacteriophages in controlling bacterial populations and in mediating gene transfer in soil. Moreover, studies have shown that the lysogenic mode is preferable and common under different soil environments (Williamson et al. 2007; Ghosh et al. 2008).

Biofilm development and succession of microbial communities are now recognized as an important arena of rhizosphere biology. Different rhizospheric factors are known to influence bacterial biofilm formation. The beneficial effects of root exudates on biofilm development have been extensively investigated and reviewed (Bais et al. 2006; Zhang et al. 2014; Yuan et al. 2015).

6.4 Gene Transfer in Biofilms

Genetic variability among bacterial populations occurs via mutation and acquisition of new genes through various genetic exchange mechanisms. Gene transfer in a single species results in the propagation of specific traits. Interspecies gene transfer may result in an entirely new genetic combination which may be of significance to human health and the environment. The relationship between biofilms and HGT has been investigated by numerous workers (Ghigo 2001; Tormo et al. 2005; Antonova and Hammer 2011; Madsen et al. 2012; Cook and Dunny 2014). In general, HGT rates are higher in biofilm communities compared with those in the planktonic state. Biofilms are also implicated in the promotion of plasmid stability and may enhance the host range of MGEs that are being transferred (Madsen et al. 2012; Broszat and Grohmann 2014).

Several authors have reported enhanced HGT in biofilms via conjugation (Sorensen et al. 2005; Maheshwari et al. 2016); however, certain spatial constraints within biofilms may hinder the dispersal of plasmids (Krol et al. 2011; Merkey et al. 2011). Lili et al. (2007) indicated that plasmids which are maintained through high transfer frequencies may only be able to persist in biofilms. Interestingly, other mechanisms of gene transfer, for example, transformation, occur at higher rates in biofilms. Gene transfer via both small DNA fragments as well as plasmid transformation has been documented (Maeda et al. 2006; Etchuuya et al. 2011). It has been reported that competence of cells in the biofilm mode is triggered by extracellular DNA (eDNA) molecules within the biofilm matrix (Molin and Tolker-Nielsen 2003; Meena et al. 2014a, 2016c; Saha et al. 2016a; Sharma et al. 2016). Thus, transformation triggers and stabilizes biofilms and vice versa.

Conjugative pili formation is best studied among other biofilm-associated factors encoded by backbone genes of plasmids. There is much evidence in support of greater effectiveness of conjugative plasmids, compared to deficient strains, in biofilm formation (Reisner et al. 2006; Burmolle et al. 2008; Roder et al. 2013; Madsen et al. 2016). Other factor encoded by plasmid accessory regions includes different types of fimbriae and conjugative pili. These adhesions play a significant role in cell surface adherence and cell-to-cell contact, mainly in members of family Enterobacteriaceae. Three pathways in enteric bacteria are known for synthesis of surface-associated fimbriae: (1) the type IV pili pathway, (2) the nucleation pathway, and (3) the chaperone/usher pathway (Clegg et al. 2011; Madsen et al. 2012). These fimbriae perform a number of functions, and genes are located both on plasmids and on chromosomes. Several such plasmid-encoding cell surface adhesion factors are known in Gram-negative and Gram-positive bacteria, for example, *Pseudomonas putida* TOL plasmid, *Lactococcus lactis* pAMb1, and *Azospirillum brasilense* plasmids (D'Alvise et al. 2010; Petrova et al. 2010). Thus, the plasmid's role as a social evolutionary platform has been described in accordance to plasmid functions including (a) host fitness, (b) multicopies of gene present on the plasmid, (c) high gene expression rate, (d) mobility of gene, and (e) high turnover of plasmid-encoded gene (Madsen et al. 2012).

The interconnection between biofilm formation and gene transfer has been a topic of investigation in recent years. Madsen et al. (2012) published an excellent article on this issue and concluded that plasmid biology and biofilm community structure and related functions are interconnected through various interactions at both community and genetic levels. Biofilms provide an excellent environment for bacterial interaction due to their high cell density and extensive communication network within the biofilm matrix. Since bacterial communities within biofilms are heterogeneous and often multispecific, variations within specific bacterial lineages have been recorded (Stewart and Franklin 2008). These variations provide recipients that are more accessible for plasmid transfer than in planktonic culture. Thus, bacterial genetic heterogeneity is maintained and promoted by HGT and mutation provided via the biofilm mode of growth (Jefferson 2004; Conibear et al. 2009; Rankin et al. 2011).

6.5 Gene Transfer in the Soil System

Most of our knowledge of gene exchange, however, comes from investigations of the planktonic mode. The study of gene transfer under complex natural conditions such as bulk and rhizosphere soil remains a challenging task. Many factors are known to affect gene transfer occurring in the soil system; therefore, careful investigation using soil microcosms is suggested. Hill and Top (1998) reviewed gene transfer in soil using microcosms with special focus on transfer of broad host range plasmids and catabolic soil plasmids. The importance of gene transfer in soil and other natural habitats has been recognized due to (a) interest in the possible spread of genetically modified microorganisms, (b) spread and exchange of antibiotic resistance, (c) the role of HGT in the evolution of new bacterial traits, and (d) the possible role of introducing catabolic genes to enhance bioaugmentation strategies to enhance bioremediation of soil contaminants.

Laboratory microcosms are used to assess gene transfer for a number of potential benefits as mentioned above. Although microcosms are not exact replicas of the soil system, they possess many of the same chemical and physical attributes. Microcosms must be calibrated to ensure that they reflect natural conditions (Bolton et al. 1991). Microcosms can be used to obtain vital information on (1) survival and dispersal of bacterial strains, (2) ability to compete with indigenous microflora, (3) capacity to exchange genetic information, and (4) stability of heterogeneous DNA in soil. Most of the well-studied examples mainly comprise various conjugative plasmids and their exchange by conjugation using suitable recipient strains. Some of the widely used plasmids described by Hill and Tops (1998) are RP4, RP4p (RP4::pat), pBLK1-2 (pRK2073::Tn5), RP4::Tn4371, pJP4, pEMT3k (pEMT3::mini Tn5), pEMT1k (pEMT1::miniTn) R57.b, R388::Tn1721, pLF40, pFT30, pJB5JI::Tn5, and pIJ673. Other plasmids studied include fluorescent marker-tagged plasmids such as pB10 (De Gelder et al. 2005), pKJK10 (Musovic et al. 2006; Claudia et al. 2013), gfp-tagged IncP-1α plasmid RP4 (Musovic et al. 2010), pBP136, pCAR1, NAH7 (Shintani et al. 2014), and low GC-type plasmid pHHV216 (Jechalke et al. 2013).

Soil microcosms utilized in gene transfer studies vary in complexity from simple closed vessels containing a few grams of soil in a conical flask or falcon tube to more complicated systems including vertical soil columns. Other microcosms include continuous flow reactors through which water or nutrients are percolated. Microcosms for studying bacterial interactions in the rhizosphere/rhizoplane were elaborated by Hill and Top (1998). The microcosm system adopted depends upon the objectives of the study. Care should be taken to assess the desired factors affecting gene transfer in the soil/rhizosphere (Meena et al. 2013b, 2014b, 2015b, c, d; Rawat et al. 2016; Yasin et al. 2016; Verma et al. 2015a; Shrivastava et al. 2016; Velazquez et al. 2016; Sindhu et al. 2016; Singh et al. 2016). Important factors include inoculum treatment and mode of application, concentration and sampling methods, soil temperature, soil depth, concentrations of media, and types and amounts of degradable chemicals (Hill and Top 1998; Wang et al. 2014a, b). Table 6.1 shows the various soil factors affecting gene transfer studies in microcosms.

Table 6.1 Soil factors affecting gene transfer

Factors	Effects/explanation
Drying and sieving	Disturbing the soil results in poor survivability of strains and ultimately poor conjugation
Earthworm activity	Varying influence, depending upon the depth at which earthworms are present
Nutrient availability	Nutrient availability enhances survival and therefore gene transfer
Plant rhizosphere	High concentrations of root exudates and nutrients in the rhizosphere positively affect gene transfer
Selective pressure such as heavy metals or recalcitrant organics	In most of cases, heavy metals/recalcitrant organics enhance the number of transconjugants
Soil type	Soil variables such as types and amounts of clay, organic matter, pH, moisture, and incubation temperature influence gene transfer
Spatial separation between donor and recipient strains	Moisture content helps in movement and survivability of strains thus directly affecting gene transfer
Sterilization	Sterilization of soil increases transfer frequencies
Temperature	Higher transfer frequency observed at environmentally relevant soil temperatures

Adopted and modified from Hill and Top (1998)

6.6 Conclusions

The current state of understanding of HGT in soil and other natural environments demonstrates that HGT is a mechanism of bacterial chromosomal evolution which provides real-time adaptation among bacteria. HGT also provides genetic diversity through its gene pool, which helps bacteria adapt to changing environmental conditions. The availability of nutrients in the plant rhizosphere attracts bacteria, thus offering a greater opportunity for HGT compared to bulk soil. Microcosm and biofilm studies demonstrate that bacteria receive advantages and long-term ecological benefits for survival and adaptation through HGT. However, the exact mechanisms and magnitude of HGT in unsterile soil and in the rhizosphere must be explored further, as factors influencing gene transfer in such situations are complex and multifactorial.

Considering the untapped diversity of MGEs in soil- and plant-associated microbiomes, the impact of HGT on influencing plant-microbe interactions must be further explored for possible exploitation in sustainable agriculture.

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Hairy Root Culture: A Biotechnological Approach to Produce Valuable Metabolites

7

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Abstract

Hairy root (HR) cultures are attracting more attention due to their unique ability in degrading different pollutants and production of metabolites with therapeutic or industrial applications. This specific type of plant cell culture is derived from explants that are infected by *Agrobacterium rhizogenes*. The HR cultures are categorized by their growth rate as well as their genetic and biochemical stability. Progress in design of innovative bioreactors and process intensification for HR growth will allow successful industrial production of metabolites. This chapter will present advances in work on HR cultures related to the detoxification of pollutants, production of valuable metabolites, and their cultivation in large-scale intensified bioreactors.

Keywords

Hairy root • Metabolite • Scale up • Bioreactor • Process intensification

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7.1 Introduction

Plants are able to produce a wide range of primary and secondary metabolites (Yazaki et al. 2008; Sharma et al. 2013). However, the large-scale production of these valuable compounds has been limited by low growth rates, climate dependency, restricted cultivation areas, plant diseases, pests, overharvesting, and intense labor requirement (Sharma et al. 2013; Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2016b; Rates 2001). Moreover, the chemical synthesis of plant-derived metabolites is not a feasible choice due to their complex structures and their specific stereochemical requirements (Sharma et al. 2013; Namdeo 2007). All these issues emphasize the need for developing new methods and protocols for the industrial-level fabrication of plant-derived metabolites.

Suspension culture of plant cells has been considered as another promising source for biosynthesis of valuable secondary metabolites (Sharma et al. 2013). More than 25% of the available pharmaceuticals are either based on originally found compounds in plants or are extracted from them (Giri and Narasu 2000). Production of secondary metabolites by using suspended plant cell culture is usually a challenging task as these compounds produce at distinct developmental stages. Therefore, in vitro studies of differentiated and organized tissues (mainly the roots) have been developed and were reported to be a more predictable approach as compared to cell suspension cultures (Sharma et al. 2013; Kumar et al. 2015; Ahmad et al. 2016; Meena et al. 2016a; Parewa et al. 2014).

The plant roots are suitable for large-scale production since they are the key point for synthesis and/or storage of certain chemicals. The biotechnological fabrication of wide range of valuable secondary metabolites by using plant cultures can be seen as an alternative to the extraction of whole plant material (Namdeo 2007). Several strategies have been investigated in order to further enhance the production of secondary metabolites from medicinal plants. Some of these include high yielding cell line screening, media modification, elicitation, precursor feeding, large-scale cultivation system, plant cell immobilization, hairy root culture, biotransformation, and others (Rao and Ravishankar 2002; Vanisree et al. 2004).

Recently, hairy root (HR) culture has been developed in order to inhibit the use of large volumes of plants that are needed to be purified. Totipotency is among the major characteristics of plant cells; therefore, HRs could successfully produce primary and secondary metabolites similar to intact roots (Giri and Narasu 2000; Qaderi et al. 2016). HR culture is a tool that makes use of soil bacterium *Agrobacterium rhizogenes* ability to transfer genes to the genome of the host plant (Sharma et al. 2013; Thwe et al. 2016). This technique was developed as the innovative path for bulky production of secondary metabolite and phytochemicals which allows developing large amount of roots and secondary metabolites in short time for continuous supply of improved value products (Korde et al. 2016). These HRs have also been used for root physiology and biosynthetic pathway (Giri and Narasu 2000), regeneration of whole plants with desirable phenotypes, and phytoremediation of toxic substances and reactive dyes (Talano et al. 2012; Prakash and Verma

2016; Meena et al. 2015a, 2016b; Priyadharsini and Muthukumar 2016; Kumar et al. 2017). Finally, HR cultures include other aspects such as molecular metabolic engineering, bioreactor design, and optimization (Ono and Tian 2011). In this chapter, we present advances in work on HR cultures related to the detoxification of pollutants, production of valuable metabolites, and fabrication in large-scale intensified bioreactors. A suggestion to overcome current challenges and emerging trends for future progression of research has also been provided.

7.2 Definition and Basic Features of HRs

HR production is carried out through the plant tissue culture technique in order to study the plant metabolic processes or to manufacture precious secondary metabolites with the use of plant genetic engineering. HR culture is also called as transformed root culture from gram-negative soil bacterium *A. rhizogenes* that contains root-inducing plasmids (Ri plasmids) (Korde et al. 2016; Pistelli et al. 2010). It infects roots of dicot, and some monocot plants cause them to produce the opines which is a type of unusual amino acids (octopine, agropine, nopaline, mannopine, and cucumopine). Such opines are used by the bacterium as a carbon, nitrogen, and energy source (Ferdosi and Kashefi 2014).

The morphology of HRs is significantly different from the normal roots as they are much more branched and have much lateral meristematic growth, which will lead to higher biomass. The abnormal roots however are easier to grow in artificial media without hormone, and they are neoplastic in nature, with hazy growth. Fabricated HRs by infection of *A. rhizogenes* have a high growth rate as well as genetic and biochemical makeup (Korde et al. 2016).

However, new techniques are developed in order to make HRs by the use of new plant species (Georgiev et al. 2011). HRs have numerous advantages such as indefinite and fast in vitro growth even in the absence of phytohormones as well as high genotype and phenotype stability (Ono and Tian 2011). HR culture is among the main cultures that are used to investigate metabolic processes of plants, secondary metabolites production, recombinant proteins, plant genetic engineering, phytoremediation, artificial seed production, biofortification, and biopharmaceuticals. Applications of these efficient technologies also include several aspects as metabolic engineering, bioreactor design, and process optimization (Raghavendra et al. 2016; Zahedi 2016; Meena et al. 2015b; Rawat et al. 2016; Kumar et al. 2016a).

7.3 Mechanism of HR Cultures

The interaction between plants and *A. rhizogenes* in HR establishment involves a complex series of events. *A. rhizogenes* is responsible for a neoplastic outgrowth of fine roots at the infection site, and infected plants show reduced vitality. These symptoms came to be known as the hairy root disease. Roots arising at the site of infection can be cultured aseptically, and the resulted transformed root clones may

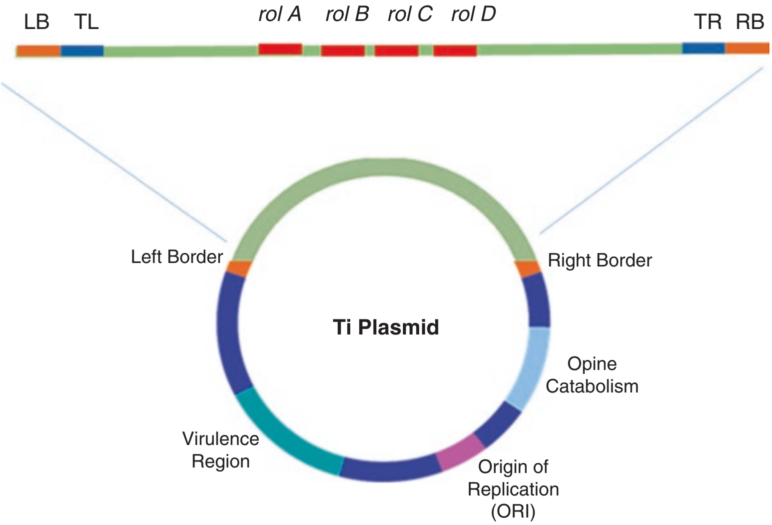

Fig. 7.1 Schematic overview of a Ri plasmid of *A. rhizogenes*

be subcultured indefinitely on basal medium, growing at rates several times quicker than normal roots (Flores and Filner 2012). *Agrobacterium* recognizes various phenolic compounds that have been produced from wounded plant cells, namely, acetosyringone and α-hydroxy acetosyringone.

After microbial colonization, consequently their attachment to plant cells T-DNA will be inserted (Sharma et al. 2013). This T-DNA is a transferable DNA from bacterium to plant cell. The T-DNA has a set of genes that are capable to encode enzymes required for cytokinin biosynthesis, phytohormone auxin control (*iaaM, iaaH, ipt*), and synthesis of sugar and amino acids (unusual amino acids). These segments have eukaryotic regulatory sequences and approximately 10–30 kbp in size and encode for the Ri conjugation, catabolism, opine synthesis, and integration of the T-DNA itself (Pistelli et al. 2010). Genes of T-DNA fragment facilitate the formation of neoplastic crown gall tumor and HR tissues followed by the synthesis of opines (Sharma et al. 2013; Yasin et al. 2016; Meena et al. 2016c; Jaiswal et al. 2016; Jha and Subramanian 2016). Depending on the bacterial strain, these metabolites are used as a carbon and nitrogen source for the bacteria. *A. rhizogenes* strains were categorized into two main classes, namely, Agropine-type and Mann opine-type strains. Among these, agropines are the most often used strains due to their strongest virulence (Sharma et al. 2013). The virulent strains of *A. rhizogenes* contain the Ri plasmids with different gene sequences (Fig. 7.1). Plasmids can be divided in strains producing mannopine and cucumopine with single DNA and strains producing octopine and agropine with two T-DNAs. The two T-DNAs are classified in the T_R-DNA (right DNA) and the T_L-DNA (left DNA). The root-inducing genes (*rol A*, *rol B*, *rol C*, *rol D*) are found in the center of T_L-DNA of the agropine-producing strains. Parts of the T_R-DNA are genes for the biosynthesis of auxins and the synthesis of mannopine and agropine. After the transfer of the T_L-DNA and T_R-DNA, they are integrated in the genome of the plant cell. The T_L-DNA is vital for the hairy root induction (Chandra 2012).

7.4 Establishment of HR Cultures

Successful HR culture system requires several essential check marks, namely, selection of best *A. rhizogenes* strain, appropriate explants and antibiotic, and a suitable culture medium (Sharma et al. 2013). Strains of *A. rhizogenes* are widely varying in their transforming ability. HRs that are fabricated by using different types of bacterial strains show significantly different morphologies. These observed virulence and morphology differences could be justified by the different strain plasmid harbored (Saha et al. 2016a; Yadav and Sidhu 2016; Nguyen et al. 1992; Meena et al. 2015f). Most plant materials like hypocotyl, stem, cotyledon, leaf, tuber, or storage root may be applied to make HRs (Królicka et al. 2001; Sevón and Oksman-Caldentey 2002; Giri et al. 2001). In order to induce HRs, explants should be infected with strains of *A. rhizogenes* either by cocultivation or direct inoculation (Giri et al. 2001; Ur Rahman et al. 2004). Subsequently, roots are subculture using a medium such as MS or B_5 (Fig. 7.2) (Sevón and Oksman-Caldentey 2002; Le Flem-Bonhomme et al. 2004; Palazón et al. 2003a, b).

7.5 Application of HR Cultures

The HR culture shaves diverse and abundant applications (Fig. 7.3). They traditionally have been used to investigate root physiology in conjunction with biosynthetic pathway elucidation (Ibanez et al. 2016). Nowadays, HR culture technique is now being used for the fabrication of bioactive compounds, secondary metabolites, and phytochemicals. HRs are popular for regeneration of whole plants with desirable phenotypes by infection of ornamental plants with *A. rhizogenes* (Meena et al. 2016d; Saha et al. 2016b; Verma et al. 2015b; Bahadur et al. 2016b; Das and Pradhan 2016; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016).

Moreover, HR cultures have been used for phytoremediation of toxic substances and reactive dye. Presently, several high-value bioactives are fabricated by using HRs from various plant sources which have application in pharmaceutical and cosmetic products (Ono and Tian 2011). Furthermore, recombinant protein production using this system was found to be a sustainable method for producing cytokines as well as protein therapeutics (Talano et al. 2012).

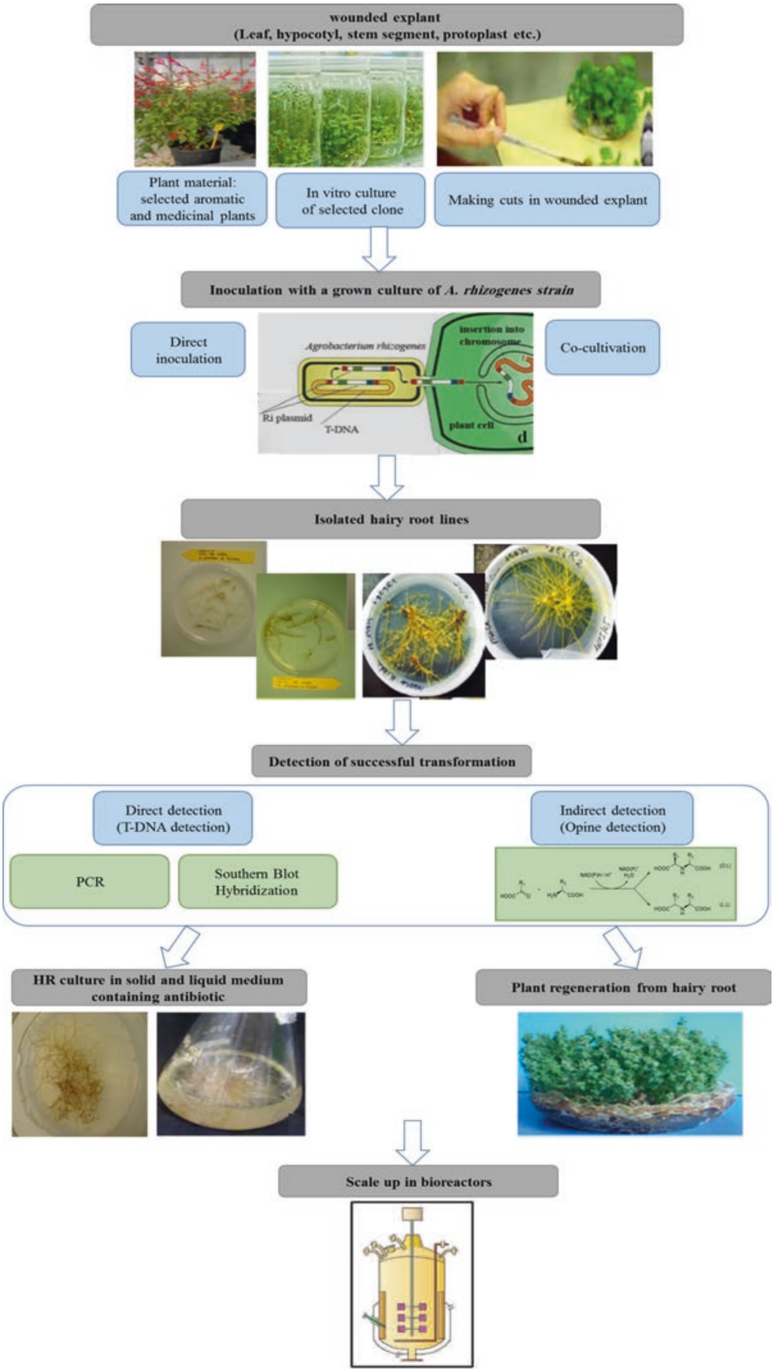

Fig. 7.2 An overview of the HR culture establishment

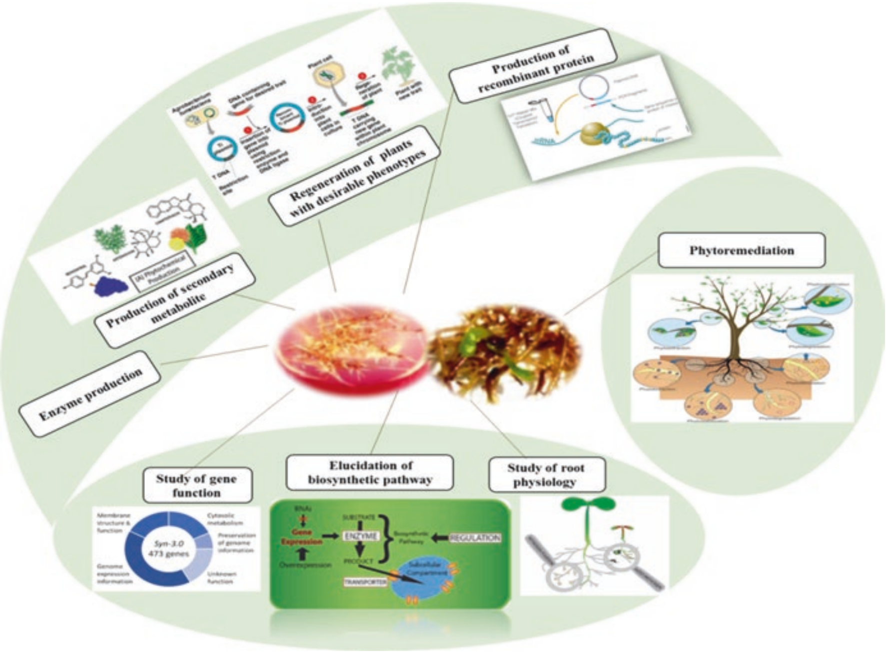

Fig. 7.3 The systematic applications of HR cultures

7.5.1 Application of HR Cultures for Secondary Metabolites Production

Plants are known as chemical factories since they pose the ability to fabricate important phytochemical. However, the major issue is that their growth is dependent to the outside environmental stress. HR cultures are promising source for phytochemical due to sizable biomass production and biosynthetic capacity.

Furthermore, HR cultures frequently accumulate phytochemical at much higher levels than cell or callus cultures (McCoy and O'Connor 2008; Ono and Tian 2011). Secondary metabolites as summarized in Table 7.1 are naturally more complex as compared to primary metabolites. These compounds have been categorized into terpenoids, phenolics, and alkaloids (Chinou 2008).

Several HR cultures have attracted significant amount of attention due to their potential in production of valuable phytochemical including *Artemisia annua*, *Catharanthus roseus*, *Arachis hypogaea*, and *Camptotheca acuminata/Ophiorrhiza pumila* (McCoy and O'Connor 2008). List of secondary metabolites produced by wild HR cultures is summarized in Table 7.2. Although, non-transgenic HR cultures continue to serve as a good source for phytochemicals and secondary metabolites (Ono and Tian 2011).

However, application of metabolic engineering methods requires acritical understanding about the regulation of secondary metabolite pathways and the metabolic

Table 7.1 Classification of secondary metabolites (Rao and Ravishankar 2002)

Terpenes (composed of C and H)	Phenols (composed of sugars, benzene ring, H and O)	Alkaloids	Steroids
Monoterpenes	Phenolic acids	Acridines	Cardiac glycoside
Sesquoiterpenes	Coumarins	Glucosinolates	Pregnenolone derivatives
Diterpenes	Lignins	Betalains	
Triterpenes	Flavonoids	Quinolizidines	
Tetraterpenoids	Tannins	Furonoquinones	
	Anthocyanins	Harringtonines	
	Hydroxycinnamoyl derivatives	Isoquinolines	
	Phenalenones	Indoles	
	Proanthocyanidins	Purines	
	Stilbenes	Pyridines	
	Tanins	Tropane alkaloids	

phenotype of the HR culture to regulate the dynamic distribution of metabolites between different biochemical pathways (Kruger and Ratcliffe 2009; Talano et al. 2012). Table 7.3 tabulated the common secondary metabolites that are produced by transgenic HRs.

7.5.2 Application of HR Cultures in Phytoremediation

Environmental remediation is a method that deals with the removal of toxins in order to support the environment (Macek et al. 2008). Remediation processes can be expensive; therefore, efficient and inexpensive technologies are still developing to address the needs in the field. Bioremediation includes the environmental treatment with the use of microorganisms and plants (Novakova et al. 2007; Najmanova et al. 2007). In case of using plants, this is so-called phytoremediation (Garbisu and Alkorta 2001; Korde et al. 2016). The use of plants to absorb and accumulate organic and inorganic pollutants or to transform toxic molecules to harmless once has attracted attention (Eapen et al. 2007; Doty 2008; Macek et al. 2008; Ibanez et al. 2016).

Phytoremediation process usually occurs through several complex interactions between the key involved sources (Krystofova et al. 2009; Guillon et al. 2006). Roots are normally the main contact point between contaminants and the plant tissues they are the key point of assessment of the phytoremediation potential (Verma et al. 2014; Meena et al. 2014a, 2015e; Teotia et al. 2016).

However, in this sense HR culture has been found suitable in order to study the xenobiotic detoxification without the soil matrix or microbes interaction (Talano et al. 2012). Figure 7.4 summarizes how a plant deposits the toxin efficiently. Plants are able to chemically modify toxic substances through their direct metabolism (Krystofova et al. 2009). Greater genotypic and phenotypic stability are the

Table 7.2 List of the secondary metabolites that are produced by wild HR cultures

Secondary metabolite	Function	HR	References
Ajmalicine, ajmaline	Antihypertensive	*Rauvolfia micrantha*	Sudha et al. (2003)
Artemisinin	Antimalarial	*Artemisia annua*	Weathers et al. (2005)
Azadirachtin	Biopesticide	*Azadirachta indica*	Srivastava and Srivastava (2012c)
Benzylisoquinoline alkaloids (morphinan, codeine, and sanguinarine)	Analgesic, antibiotic	*Papaver somniferum*	Park and Facchini (2000) and Le Bonhomme et al. (2004)
Betalain	Red pigments for food industry, strong aphrodisiac, laxative	*Beta vulgaris*	Rudrappa et al. (2004) and Pavlov et al. (2003)
Camptothecin	Antitumor, AIDS, falciparum malaria, colorectal and ovarian cancers treatment	*Ophiorrhiza alata* Craib, *Ophiorrhiza pumila*	Ya-ut et al. (2011) and Sato et al. (2001)
3,4-Dihydroxyl-L-phenylalanine	Therapeutic agent against Parkinson's disease	*Stizolobium hassjoo*	Sung and Huang (2006)
Dopa and dopamine	Neurotransmitters	*Beta vulgaris*	Rudrappa et al. (2004)
Flavone glycosides	Anti-inflammatory action	*Catharanthus roseus*	Talano et al. (2012)
Flavonoids	Meant for the treatment of gastric ulcers, anti-inflammatory, and antitussive	*Glycyrrhiza pallidiflora*	Li et al. (2002)
Flavonoids	Antimutagenic, antiulcer, antitumor, antimicrobial	*Glycyrrhiza uralensis*	Zhang et al. (2009)
Glycyrrhizin	Artificial sweetener and pharmaceutical products (peptic ulcers treatment)	*Glycyrrhiza inflate*	Wongwicha et al. (2011)
Glycyrrhizin	Diuretic, tonic, alexiteric, antifertility	*Abrus precatorius*	Dixit and Vaidya (2010)
Hyoscyamine	Narcotic and antispasmodic activity, used against Parkinson's disease	*Datura stramonium*	Pavlov et al. (2009)
Indole alkaloids (vinblastine, vincristine)	Anticancer	*Catharanthus roseus*	Ayora-Talavera et al. (2002)
Iridoid glycosides	Anti-inflammatory, analgesic, antidiabetic	*Harpagophytum procumbens*	Georgiev et al. (2006)

(continued)

Table 7.2 (continued)

Secondary metabolite	Function	HR	References
6-Methoxy-podophyllotoxin	Anticancer	*Linum album*, *Linum persicum*	Wink et al. (2005)
Physalins	Diuretic, febrifuge, vermifuge	*Physalis minima*	Azlan et al. (2002)
Plumbagin	Diuretic, antibacterial and used against leprosy	*Plumbago zeylanica*	Sivanesan and Jeong (2009)
Resveratrol	Anti-inflammatory, antioxidant, anti-infective, anticancer	*Arachis hypogaea*	Kim et al. (2008)
Rosmarinic acid	Astringent, antioxidant, anti-inflammatory, antimutagenic, antimicrobial, antiviral	*Nepeta cataria*	Yang (2010)
Rutin	Antioxidant, anticarcinogenic, antithrombotic, cytoprotective, vasoprotective	*Fagopyrum esculentum*	Kim et al. (2010)
Rutin, hispidulin, and syringin	Anti-inflammatory; antifungal	*Saussurea involucrata*	Fu et al. (2005)
Serpentine	Diabetes treatment	*Catharanthus roseus*	Datta et al. (2010)
Sesquiterpenes	Phytoalexins	*Hyoscyamus albus*	Kawauchi et al. (2010)
Shikonin	Dye for silk and food industry, anti-inflammatory, anti-allergic, and antineoplasic activities	*Arnebia*	Talano et al. (2012)
Stilbenoids (resveratrol, pinosylvin, and derivatives)	Antioxidant, anticancer, antiatherosclerosis, neuroprotective, and estrogenic activities	*Arachis hypogaea*	Medina-Bolivar et al. (2010)
Tropane alkaloids	Narcotic, anticholinergic and antispasmodic activity	*Datura metel*, *Hyoscyamus muticus*	Moyano et al. (2003)
Tropane alkaloids	Narcotic, anticholinergic and antispasmodic activity	*Hyoscyamus niger*	Zhang et al. (2004)
Tropane alkaloids (scopolamine and hyoscyamine)	Narcotic, anticholinergic and antispasmodic activity	*Datura innoxia*	Dechaux and Boitel-Conti (2005)
Tropane alkaloid (hyoscyamine, atropine, and hyoscine)	Used against Parkinson's disease	*Atropa belladonna*	Richter et al. (2005)

(continued)

Table 7.2 (continued)

Secondary metabolite	Function	HR	References
Tropane alkaloids (scopolamine and hyoscyamine)	Parasympatholytic	*Przewalskia tangutica*	Lan and Quan (2010)
Withanolide A	Brain regenerative properties	*Withania somnifera*	Praveen and Murthy (2012)
Xanthotoxin (furocoumarin)	Leucoderma	*Ammi majus*	Krolicka et al. (2001)

important advantages of HR cultures which provide a more promising system over time for phytoremediation (Doran 2009). Additionally, the organized nature of HR cultures offers an added advantage that makes them more useful for cultivation in bioreactors at large scale (Angelini et al. 2011; Bahadur et al. 2017; Verma et al. 2017b; Kumar et al. 2017b). HRs that have been functionalized by genetic engineering are expected to become a new solution for environmental treatment in near future (Guillon et al. 2006).

HRs produced by hyper-accumulators are capable to uptake nickel, uranium, or cadmium from polluted environment (Boominathan and Doran 2003; Boominathan et al. 2004; Eapen et al. 2003; Agostini et al. 2003; Suresh et al. 2005; Gujarathi et al. 2005). Phytoremediation of several environmental pollutants by wild-type and transgenic HR cultures is shown in Table 7.4.

7.6 Recent Advances in HR Cultures Scale-Up

Root tissues are not identical to microbial cultures in many ways. Therefore, bioreactors for HR cultures are more challenging to be controlled, operated, and scaled up. Development of innovative bioreactors and process intensification will allow to optimize cell growth and large-scale production (Sharma et al. 2016; Meena et al. 2013c, 2016e; Verma et al. 2015a; Bahadur et al. 2016a; Masood and Bano 2016).

7.6.1 Development of Groundbreaking Bioreactors in HR Cultures

Design and optimization of bioreactors have been the great advance in HRs for industrial-scale production of metabolites (Huang and McDonald 2012). Production of HRs in bioreactors helps to have a better control on operating conditions and consequently optimize the growth and biosynthesis of the secondary metabolite (Eibl and Eibl 2008). Bioreactor optimization for fabrication of HRs is of critical importance for scale-up strategies.

HR bioreactors can be in general divided into gas or liquid phase. In liquid-phase bioreactors, roots are always placed in the medium; as a result they are called submerged reactors. On the other hand, in gas-phase reactors, the roots are almost exposed

Table 7.3 List of secondary metabolites produced through transgenic HR cultures (Talano et al. 2012)

Secondary metabolite	Function	Transgenic HR	Foreign genes
Solanoside	Antineoplastic agent	*Solanum khasianum*	Gene encoding a specific antibody that binds solanoside
Indole	Beneficial effects on cancer, sedative and hypotensive action	*Catharanthus roseus*	Modified anthranilate synthase (AS) alpha subunit (*trp5*) and tryptophan decarboxylase gene (TDC)
Ginseng	Traditional Chinese medicine, tonic, antiaging, anticancer, and anti-diabetes properties	*Panax ginseng*	*cs* gene for cycloartenol synthase enzyme
Scopolamine		*Hyoscyamus niger*	Putrescine *N*-methyltransferase *pmt*) and hyoscyamine 6ß-hydroxylase (*h6h)* genes
Catharanthine	Anticholinergic agents that act on parasympathetic nervous system	*Catharanthus roseus*	*Geraniol 10-hydroxylase (G10H) and a jasmonate-responsive transcript factor (ORCA3)*
Hyoscyamine, scopolamine		*Scopolia parviflora*	Putrescine *N*-methyltransferase (*pmt*) and hyoscyamine 6ß- hydroxylase (*h6h)*
Anisodamine, anisodine, hyoscyamine, scopolamine		*Anisodus acutangulus*	Putrescine *N*-methyltransferase (*pmt*) and gene codifying tropinone reductase I (TRI)
Glycyrrhizin	Medicine, healthcare products, food (sweetener), and cosmetics	*Glycyrrhiza uralensis*	Chalcone synthase
Flavones: baicalin, baicalein, wogonin	Diuretic, anti-inflammatory, antiseptic, antispasmodic, and anticancer	*Scutellaria baicalensis*	Chalcone isomerase
Vitamin C	Antioxidant properties	*Solanum lycopersicon*	*gal* UR gene
Total sterols	Hypocholesterolemic, anticarcinogenic properties	*Centella asiatica*	Farnesyl diphosphate synthase from *Panax ginseng*

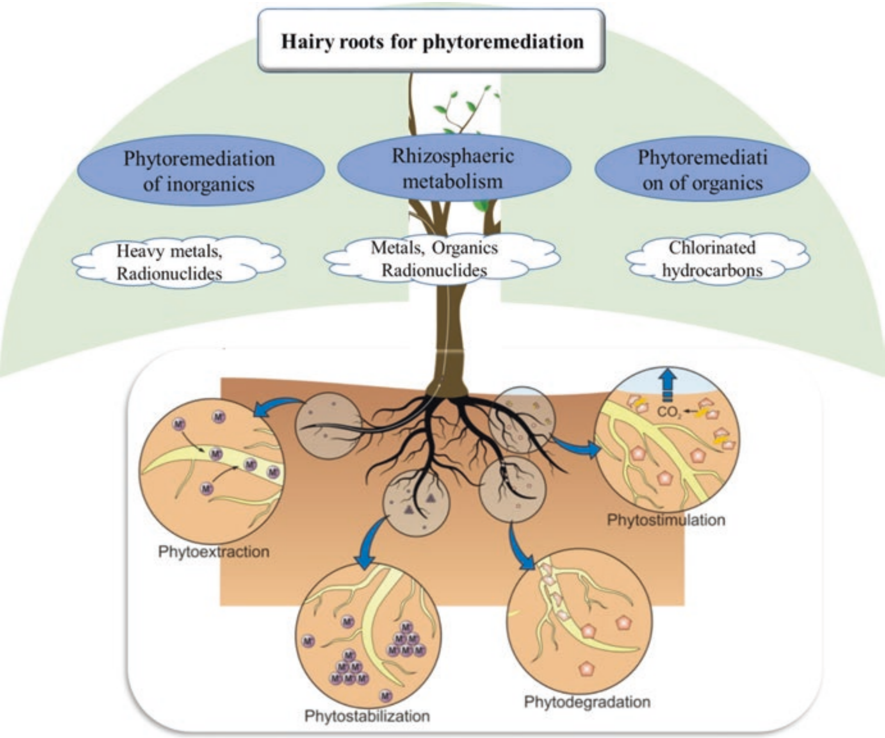

Fig. 7.4 Types of phytoremediation. Plant metabolizes the pollutant via organic and inorganic phytoremediation or rhizospheric metabolism. Phytoremediation includes several approaches, namely, phytostabilization, phytoextraction, phytodegradation, and phytostimulation

to air or another gas mixture (Kim et al. 2002a, b; Stiles and Liu 2013). The design of the reactor also depends on the product location, which is either intracellular or extracellular (Meena et al. 2013b, 2015d; Shrivastava et al. 2016; Singh et al. 2015).

HR cultivation is usually associated with clumps formation that are naturally composed of primary roots and their bridged lateral roots. It is very difficult to find appropriate bioreactor for HR cultures because the rheological properties of HR cultures vary from one species to another and even within clones of a single species. Several bioreactor designs have been reported for HRs (Mishra and Ranjan 2008). Schematic diagrams of promising bioreactor types that have been successfully tested are depicted in Fig. 7.5.

7.6.1.1 Liquid-Phase Bioreactors

In liquid-phase reactors, the culture space is filled up with liquid medium, and several techniques are used to provide the required aeration to the media. Since the roots are submerged, therefore, mixing and mass transfer are the main issues in scaling up the process (Eibland Eibl 2008; Curtis 2000; Nath et al. 2017; Sarkar et al. 2017; Verma et al. 2017a).

Table 7.4 Phytoremediation of several environmental pollutants by wild-type and transgenic HR cultures

Chemical nature of pollutant	Nature of HR	Pollutant	Plant species	References
Inorganic	Wild type	Arsenic	*Nicotiana tabacum*	Talano et al. (2014)
		Cadmium	*Thlaspi caerulescens*	Nedelkoska and Doran (2000)
		Cadmium and lead	*Brassica juncea*	Eapen et al. (2007)
		Chromium	*Brassica napus* and *Pantoea* sp. FC1	Ontañon et al. (2014)
		Nickel	*Alyssum murale*	Vinterhalter et al. (2008)
		Nickel	*Alyssum bertolonii*	Boominathan et al. (2004)
		Uranium	*Armoracia rusticana*	Soudek et al. (2011)
		Uranium	*Daucus carota*	Straczek et al. (2009)
		Zinc and nickel	*Brassica juncea*	Ismail and Theodor (2012)
	Transgenic	Copper	*Nicotiana tabacum*	Ibanez et al. (2016)
Organic	Wild type			
		Explosives (DNT, TNT; ADNTs; DANTs)	*Armoracia rusticana*	Nepovim et al. (2004)
		N-acetyl-4-aminophenol	*Armoracia rusticana*	Huber et al. (2009)
		PCBs	*Solanum nigrum*	Rezek et al. (2007), (2012)
		Phenol and chloro derivatives	*Brassica juncea*	Singh et al. (2006), Coniglio et al. (2008), and Gonza’lez et al. (2012)
			Daucus carota, *Ipomoea batatas* L.	De Araujo et al. (2006)
			Nicotiana tabacum	Talano et al. (2010)
			Helianthus annuus	Jha et al. (2013)
			Nicotiana tabacum	Talano et al. (2010)
			Solanum lycopersicon	Khoudi et al. (2012)
			Solanum lycopersicum	Gonzalez et al. (2006); (2008)

(continued)

Table 7.4 (continued)

Chemical nature of pollutant	Nature of HR	Pollutant	Plant species	References
		Reactive red 198 dye	*Tagetes patula* L.	Patil et al. (2009)
		Tetracycline, oxytetracycline	*Helianthus annuus*	Gujarathi et al. (2005)
		Textile dye: Methyl orange	*Brassica juncea.*	Telke et al. (2011)
		Textile dye: reactive green 19A- HE4BD	*Sesuvium portulacastrum* L.	Lokhande et al. (2015)
	Transgenic	Phenol	*Nicotiana tabacum*	Alderete et al. (2009)
			Brassica juncea inoculated with two rhizobacteria	Gonzalez et al. (2013)
			Solanum lycopersicum	Oller et al. (2005)
			Brassica juncea inoculated with *Pantoea* sp. FC1	Ontañon et al. (2014)
			Nicotiana tabacum expressing *tpx1* and/or *tpx2* genes	Sosa Alderete et al. (2009), (2012)
			Nicotiana tabacum expressing *tpx1* gene + AMF	Ibanez et al. (2011)
		TCE	*Atropa belladonna*	Banerjee et al. (2002)

DNT 2,4-dinitrotoluene, *PCB* polychlorinated biphenyls, *TNT* 2,4,6-trinitrotoluene, *DANTs* diaminonitrotoluenes, *ADNTs* aminodinitrotoluenes, *AMF* Arbuscular Mycorrhizal Fungi, *TCE* trichloroethylene

Design considerations comprise of mechanisms to provide adequate nutrient to the roots. Mixing and aeration strategy represents the main design differences between the various types of liquid-phase bioreactors. The most commonly used liquid-phase bioreactors are, namely, pneumatic reactors and stirred tanks. Methods for immobilizing HRs include cages, meshes, and polyurethane foam (Eibl and Eibl 2008).

Past studies evaluated the use of stirred tank reactors (STR) for HRs cultivation. In order to supply required amount of oxygen, compressed air is always spared into the bioreactor from a placed device in the impeller region. STRs are normally not useful for HR cultures despite their wide range of application in biotechnology. This is mainly because of the callus formation and wound response which are usually a response to the impeller rotation shear stress (Taya et al. 1989; Mishra and Ranjan 2008). Pneumatic bioreactors are the ones that include both airlift and bubble column reactors.

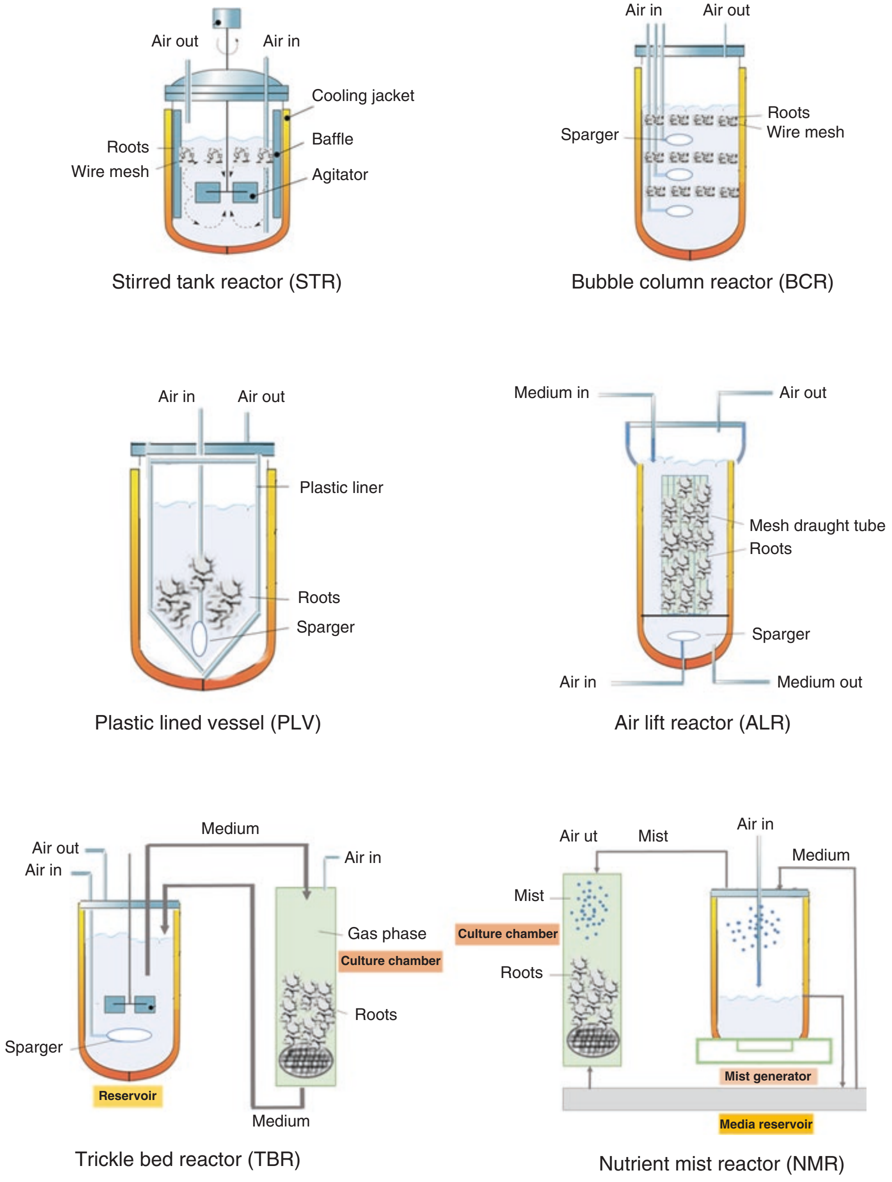

Fig. 7.5 Schematic diagrams of the bioreactors used for HR culture

Bubble column reactors (BCR) are among the simplest bioreactors that are easy to scale up. The use of bubbles instead of mechanical mixers minimizes the shear stress on the cultures (Choi et al. 2008; Huang and McDonald 2012). However, the major drawback with BCRs are the undefined flow pattern of the liquid (Choi et al. 2008) and the reduced growth performance (Kwok and Doran 1995). In the presence of high biomass, the bubbles may coalesce resulting in the reduction of gas-liquid interface area (Huang and McDonald 2012). BCRs are liquid-phase bioreactors in which the roots are submerged in the medium. Liquid mixing is obtained by the upflow of air bubbles generated from an air distributor situated at the bottom of the column. In contrast to BCRs, airlift reactors (ALRs) contain a draft tube (either internal or external) to avoid coalescing bubbles. ALRs distribute shear stress more evenly, reduce shear stress, consume little energy, and promote a cylindrical mixing of the medium (Stiles and Liu 2013).

The draft tube in ALRs prevents bubble coalescence by forcing the bubbles to move in one direction. It also distributes shear stresses equally throughout the reactor. As a result, cells are able to grow in a more stable physical environment than those growing under high shear, a condition causing cell damage and lower productivity in STRs. It has also been shown experimentally that shear stress rates generated in ALRs are lower than those generated in BCRs.

ALRs have been extensively used for HRs since the initiation of HR bioreactor studies for species including *Panax ginseng* (Yoshikawa and Furuya 1987), *Armoracia rusticana* (Taya et al. 1989), *Trigonella foenum-graceum* (Rodriguez-Mendiola et al. 1991), *Lippia dulcis* (Sauerwein et al. 1991), *Lithospermum erythrorhizon* (Shimomura et al. 1991), *Ophiorrhiza pumila* (Sudo et al. 2002), and *Echinacea purpurea* (Abbasi et al. 2009).

Conventional ALRs have been extensively used for scale-up cultures of HR lines; however, they are generally not appropriate for high-density cultures due to inadequate mixing and oxygen mass transfer (Choi et al. 2008). This phenomenon is mainly based on uneven distribution of root tissue at certain regions as well as excessive gas-phase channeling (Taya et al. 1989).

7.6.1.2 Gas-Phase Bioreactors

In gas-phase reactors, roots are exposed to a mixture of air or gas mixture. The liquid nutrient is usually sprayed onto the top of the root bed (Kim et al. 2002a, b). These reactors have been widely used in plant tissue and HR cultures due to their abundant oxygen supply (Stiles and Liu 2013; McKelvey et al. 1993; Katuri et al. 2011; Wyslouzil et al. 1997). However, gas-phase reactors yet require a matrix for anchoring the HRs. These can be mesh trays or mesh cylinders. In addition, these reactors are labor intensive as their requirement for uniform loading (Eibl and Eibl 2008; Choi et al. 2008; Srivastava and Srivastava 2007; Velazquez et al. 2016; Meena et al. 2014b, 2015c; Sindhu et al. 2016; Singh et al. 2016; Ramakrishnan and Curtis 2004).

Nutrient mist reactors (NMRs) are another one of gas-phase-type reactors. In these systems plant organ is usually dispersed in the air phase with the help of a mesh support. NMRs have definite advantages, such as easy operation, high dissolved oxygen tension present in the mist, lack of shear, and ease of scaling up. Whitney (1992) investigated the performance of different types of bioreactors for *D. stramonium* and *Nicotiana tabacum* cultivation. Authors stressed that the growth rate and yield of tobacco HRs were greater in NMRs than in STRs, TBRs, and ALRs. Recently, HRs of *Stizolobium hassjoo* (velvet bean) were cultivated in 3 and

9 l NMRs by Huang et al. (2004) to evaluate the oxygen uptake rate, effects of intermittent medium supply, and other growth-related parameters.

Several other comparative studies also have been evaluated the optimal bioreactor type for a particular species of HRs. The production of *Artemisia annua* HRs was compared both in bubble and mist bioreactors. Based on the results, authors suggested that the overall biomass was higher in the BCR (Kim et al. 2002a, b). However, the mist reactor usually accumulates lower amount of biomass as compared to the BCR. This behavior could be due to insufficient nutrient availability (Choi et al. 2008; Srivastava and Srivastava 2012a, b).

7.6.1.3 Novel Bioreactors

Hybrid reactor can be seen as a method to address this issue, a reactor which allows the roots to attach uniformly to the anchoring system (Stiles and Liu 2013). Disposable bioreactors could also be seen as another alternative to the traditional protocols. These reactors can significantly reduce the operation costs by eliminating the need for cleaning or sterilization though out the process (Eibl and Eibl 2006). Disposable wave bioreactor systems could also be another advancement in the bioreactor design area (Mishra and Ranjan 2008). These systems work on the basis of using wave for agitation purpose which in turn reduces the stress levels (Palazón et al. 2003a, b). Large-scale wave bioreactors having the capacities of up to 600 L are now commercially applicable (Mishra and Ranjan 2008; Eibl and Eibl 2006).

7.6.2 Process Intensification

Process intensification methods could also be utilized in plant and tissue culture works (Stiles and Liu 2013). The ability to exploit HR cultures as a source of bioactive chemicals depends on the development of a suitable bioreactor system where several physical and chemical parameters must be taken into consideration. Selection of highly productive cell lines, manipulation of nutrients, optimizing the culture environment, elicitation, metabolic engineering, in situ product removal, and ultrasound have been applied for process intensification in HR bioreactor cultures (Mishra and Ranjan 2008; Stiles and Liu 2013).

7.6.2.1 Optimization of Bioreactor Parameters

Development of an appropriate bioreactor depends on several physical and chemical parameters, such as optimum pH, sufficient substrate, controlled temperature, salts for nutrition, product and by-product removal, oxygen, inoculation size and density, and product recovery. The agro-bacterial concentration has an important role in the production of transformed roots (Mishra and Ranjan 2008). Dissolved oxygen is another important factor in the bioreactor microenvironment. HRs cultured in bioreactors have the affinity to form clumps which critically inhibits the oxygen transfer (Bordonaro and Curtis 2000). Nutrient availability is also a major point for scale-up, and minerals are an important regulatory factor for HR growth (Sivakumar et al. 2005). Furthermore, periodic measurement of nutrients concentration during periods in bioreactors would provide key information regarding metabolic production (Wilhelmson et al. 2006; Sivakumar et al. 2005).

Light also plays a key role for both growth and production of secondary metabolites. The stimulatory role of light on the production of secondary compounds has been demonstrated using plant species "*Perilla frutescens* and *Artemisia annua*" (Zhong et al. 1991; Wang et al. 2001; Abbasi et al. 2007; Taya et al. 1994; Jacob and Malpathak 2004).

7.6.2.2 Elicitation

Elicitation is the effective technique which is currently used for improving the production of secondary metabolites (Zhao et al. 2005; Baenas et al. 2014). Overall, based on origin, elicitors are classified biotic and abiotic. Basically, biotic elicitors are either physical factors or chemical factors such as ultraviolet light heavy metals and salts (Stiles and Liu 2013). Salts including $AlCl_3$, $AgNO_3$, $CdCl_2$, $CaCl_2$, $CuCl_2$, $CoCl_2$, KCl, $HgCl_2$, $MgSO_4$, $VOSO_4NiSO_4$, and Zn ions have been used to increase the secondary metabolite production in a variety of plant (Ramirez-Estrada et al. 2016; Li et al. 2006; Vasconsuelo and Boland 2007). Abiotic elicitors are usually cheaper than biotic; however, they are not as efficient for the cultivation of the target microorganism (Georgiev et al. 2007). Specificity of the elicitor, culture growth stage, treatment interval, the concentration, medium composition, and light are the main factors that affect the effectiveness of elicitation (Sharma et al. 2013).

7.6.2.3 Metabolic Engineering

Metabolic engineering of biosynthetic pathways has been established recently to enhance the fabrication of secondary metabolites. In this case some general issues have to be taken into account, namely, competing pathways, cofactors for the reaction, and rate-limiting enzymatic steps which are among the major metabolic engineering issues (Ludwig-Müller et al. 2014; Georgiev et al. 2010; Chandra and Chandra 2011).

7.7 Concluding Remark and Future Developments of HR Cultures

To date, significant progresses have been made in the genetic transformation and tissue culture in order to amplify the key pathways for the biosynthesis of targeted metabolites. Commercial production of HRs has attracted much attention recently as compared to the other plant cells. HR cultures are unique due to their much higher genetic and biosynthetic stability. However, exploration into inexpensive novel elicitors and bioreactors are required in order to warrant their industrial implementation. Further, generated knowledge from plant metabolic pathways and advancements in genetic engineering will help HRs to become a promising and sustainable fabrication system in the near future.

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Part II

Beneficial Soil Microbe Interaction in Some Economically Important Crops

Metagenomic Approaches in Understanding the Mechanism and Function of PGPRs: Perspectives for Sustainable Agriculture

8

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and E. Kariali

Abstract

The rationale of this article especially emphasizes the potential contributions of metagenomics to the study of plant growth-promoting rhizobacteria (PGPRs) which play an important role in the sustainable agriculture. Several studies are currently focused to unravel the molecular mechanism implicated in plant–microbe interactions to comprehend the functionality of PGPRs. In this context, researchers are presently using advanced molecular techniques, modern sequencing technologies, and metagenomics, to explore the structural and functional aspects of genes that analyze the protein composition. Metagenomics has a huge prospective to endow with fundamental knowledge on plant–microbe interactions necessary for new innovations to increase sustainable agricultural productivity. This review summarizes the main features of PGPRs in sustainable agriculture and gives a brief outlook on the recent trends in plant–microbe metagenomics. It also critically discusses the current knowledge of plant–soil–microbe-mediated interactions and the impact of enhanced genomic technologies and our perception to understand how these relationships impact plant performance and sustainable improvement of plant productivity. Metagenomic applications in framework of plant–microbe interactions are also highlighted that profit from these novel technologies.

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Plant growth-promoting rhizobacteria (PGPR) • Sustainable agriculture • Crop productivity • Plant–microbe interactions • Metagenomics

8.1 Introduction

The rhizosphere is a biologically dynamic zone of the soil contiguous to plant roots that encompass soilborne microbes, where the biochemical and physical characteristics together influence the roots (Zeyaullah et al. 2009). Studies on the plant–microbe interactions in the rhizosphere are greatly imperative for understanding an array of intrinsic metabolic and physiological processes, such as nutrient geocycling, carbon sequestration, and ecosystem functioning. There are aplethora of reports on the role of rhizosphere–microbe interactions in nutrient cycling; plant diversity and carbon sinks raised noteworthy interest and enthused further researches on plant–microbe interactions (Opik et al. 2003; Bahadur et al. 2017; Verma et al. 2017b; Kumar et al. 2017a). The microbial diversity present in soil is exceptionally incredible, with ~10^9 bacteria per gram of soil representing surplus 5000 bacterial species (Fierer et al. 2012). However, soil microbiome is very essential in shaping the following parameters, viz., plant nutrition plan, health/disease, soil gene pool, pesticide/pollutant decomposition, bioindicators, nutrient cycling, soil fertility, and soil structure. Each gram soil contains $10^{9–10}$ bacterial cells ($10^{7–8}$culturable, 10^4 species).

The soil metagenome has a greater biodiversity than any other habitat, >1,000,000 Gb per gram soil estimated from 10^9 bacterial cells with 5 Mb genomes), when compared to 6 Gb Sargasso sea metagenome sequenced, 3 Gb human genome, gut metagenome 0.5 Gb, 577 Gb sequenced from 124 individual gut microbiomes (Qin et al. 2010). Nonetheless, the ecologists face a colossal challenge to link microbial diversity studies in the rhizosphere. Primarily the molecular interactions between microbes and plants have been contemplated as an effect. However, as indicated in the recent literature, it was recognized as an effective process with high level of complexity wherein at least two genomes share information devoid of sharing the same ecological niches from a cellular perspective (Sharma et al. 2016a, b). More recently, the extent of influence among the organisms involved in the interactions is therefore claimed important that the biotechnological management of microorganisms has evicted to be an indispensable target for improving the functions of plant (Swarupa et al. 2016). Therefore, the technologies that overcome these limitations in agricultural production are highly inevitable. Several solutions that can increase agricultural yield include better agricultural practices and land management, use of biofertilizers, integrated pest management and farm mechanization, transgenic crops, and extended use of plant growth-promoting rhizobacteria (Glick 2014). Numerous approaches will only have short stint benefits as the world is finite with limited resources and, they count to several environmental reparations. Sustainable agriculture devoid of causing environmental damage is one of the key solutions to congregate the augmented food demand. It is worth mentioning that such problems can be achieved by introducing new practices by employing potential PGPR (Nath et al. 2017; Sarkar et al. 2017).

Plant-associated microbes present a striking and promising source to this end but are virtually unexploited. Consequently, bioprospecting of plant microbiomes is gaining progressive attention (Muller et al. 2016). Nevertheless, traditional microbiological approaches present severe limitations, as only a petite portion of the soil bacteria is cultivable by means of standard methods (Torsvik et al. 1996; Verma et al. 2017a). Consecutively to attain sustainable agriculture production and productivity, metagenomics is no doubt a promising tool to comprehend the plant–microbe interaction that aids in sustainable agriculture.

A triumphant metagenomic approach of the plant–microbe interaction that targets a physiological function warrants a befitting experimental design. An interesting analysis of the rhizosphere by comparative metagenomics holds an immense challenge to divulge several important questions apropos the unculturable fraction of the rhizosphere community. Consequently, in the last two decades, numerous molecular approaches were proposed (Bloem et al. 2006; van Elsas et al. 2007; Sorensen et al. 2009), and until recently, the exploration of entire genomes present in a soil sample, metagenomics, also provided a novel approach for comprehensive assessment (Handelsman 2004; Daniel 2005).

In fact, although metagenomics have led to the discovery of novel molecules, meager understanding of soil complexity, practical approach biases, and diverse microbial spatial distribution makes a debatable question on the value of such efforts in linking soil functions with microbial diversity. In recent years, sequencing of soil metagenome provided innovative insights into the ecology of soil microorganisms and proved to be a powerful tool for resurgence of novel genes and biomolecules (Daniel 2005). Apparently, metagenomics is an uncomplicated culture-independent approach and generally consists of cloning and analyzing the microbial DNA extracted directly from an environmental sample. It involves the following main steps: (a) DNA isolation from soil, (b) fragmentation and insertion of DNA into appropriate vectors, (c) cloning of DNA and transformation of appropriate host cells, (d) developing a metagenomic library, and (e) screening of the clone library (Handelsman 2004).

The rapid growth of metagenomics entails an expanded focus on plant microbes in a wide range of basic and applied research fields, ranging from molecular microbiology to agriculture biotechnology. Nevertheless it can be anticipated that the numerous novel genes identified through metagenome technologies will possibly surpass the number of genes identified through sequencing individual microbes (Streit and Schmitz 2004). As a consequence, metagenomic tools shall perhaps facilitate the recovery of a high amount of new antibiotics, enzymes, and other molecules from a small fraction of the soil metagenome (Simon and Daniel 2009) in the near future. Nonetheless these interesting molecules along with their molecular structures and functions hold enormous value to industrial applications. Likewise, the invention of novel genes with PGPR abilities may possibly be applied in agriculture by synthesizing the enzyme of interest in large bioreactors for application to crops. To add impetus to these efforts, bioinformatics-based tools along with advanced software's were of great significance toward the interpretation of the metagenome (Hoff et al. 2008). Metagenomic analysis is a revolutionary technique for understanding the microbiological ecology (Kennedy et al. 2010) and biocatalytic applications (Fernandez-Arrojo et al. 2010). The present review recapitulates the main features of PGPRs in sustainable agriculture and gives a brief stance about the trends in plant–microbe metagenomics. This review also discusses the contemporary knowledge of plant–soil–microbe-mediated interactions and the impact of improved genomic technologies on plant performance which sustainably improve plant productivity. Potential applications in the framework of plant–microbe interactions are also emphasized that yield from the new technologies, focusing on metagenomics.

8.2 Portraying the Mechanistic Insights of PGPRs

Approximately 15% of the root surface is covered by microbes that belong to different microbial species (Haldar and Sengupta 2015). The roots secrete a variety of different sugars produced by photosynthesis (~5 to 30%) which are sequentially utilized by rhizosphere microbes (Glick 2014). Bacteria that efficiently colonize the rhizosphere and stimulate plant growth through direct or indirect mechanisms are referred to as PGPRs (Ahemad and Kibretm 2014). PGPRs include a group of naturally occurring soil microbial flora that inhabit in the rhizosphere and thus inflict beneficial effect on the overall growth of the plant. PGPRs include bacteria that belong to genera *Agrobacterium*, *Arthrobacter*, *Acinetobacter*, *Azospirillum*, *Azotobacter*, *Bradyrhizobium*, *Burkholderia*, *Frankia*, *Serratia*, *Rhizobium*, *Pseudomonads*, *Thiobacillus* and *Bacillus* (Vessey 2003). These bacteria assist the plants by employing nutrient transport of minerals and uptake through roots (Glick 1995). Several researchers are actively involved in understanding the underlying mechanism of plant growth promotion by PGPRs (Fig. 8.1). These mechanics are broadly divided into direct and indirect mechanisms. Nonetheless the direct mechanism involves the straight use of required nutrients and/or growth regulators for promoting plant growth. However, if the plants were protected from various stresses factors (biotic and abiotic stress), their healthy growth may come under indirect mechanics (Prakash and Verma 2016; Bahadur et al. 2016; Masood and Bano 2016; Meena et al. 2015e, 2016e; Teotia et al. 2016).

The direct mechanism of PGPRs includes indole-3-acetic acid (IAA), siderophores (Jahanian et al. 2012), 1-amino-cyclopropane-1-carboxylate (ACC) deaminase, hydrogen cyanate (HCN), nitrogenase (Glick 2012), and phosphate solubilization (Ahemad and Khan 2012). Perhaps some PGPRs also possess more environment-specific PGP traits such as heavy metal-detoxifying activity (Ma et al. 2011), salinity tolerance (Tank and Saraf 2010), and biocontrol of phytopathogens and insects (Hynes et al. 2008). PGPRs have become of interest as inoculants for phytoremediation because of their diverse plant growth-promoting capabilities (Liu et al. 2013). Among these, phytohormone production by PGPRs plays a very

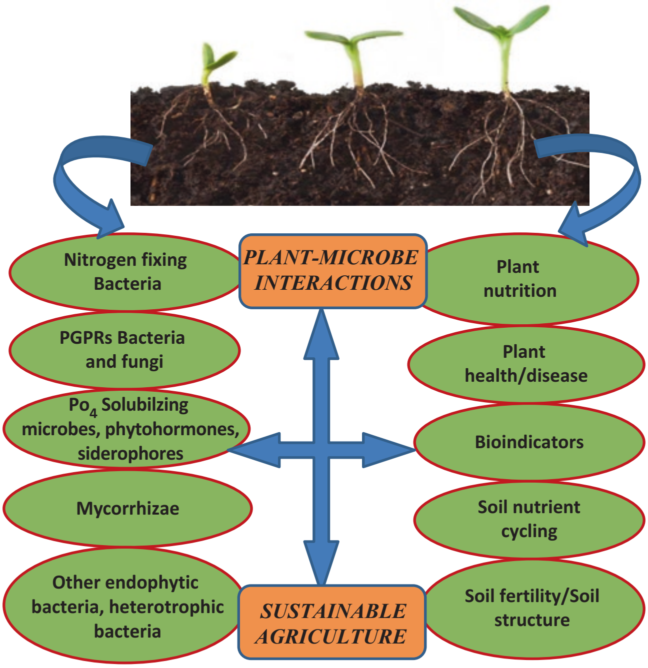

Fig. 8.1 Schematic diagram of plant microbial interactions in the rhizosphere

important role in promoting plant growth as phytohormones can intercede with the processes including cell division, plant cell enlargement, and extension in symbiotic as well as nonsymbiotic roots (Glick 2014). Systematic analysis of whole genome data and the identification of genes that contribute to the beneficial activity of PGPR will aid our understanding of the molecular mechanisms of many bacterial species and also help in the development of PGPR-assisted phytoremediation technology (Fig. 8.1). NGS have recently been employed to study the genomes of several PGPRs such as *Pseudomonas* sp. (Duan et al. 2013), *Bacillus* sp. (Song et al. 2012), and *P. polymyxa* (Li et al. 2014). A thorough understanding of the plant growth-promoting (PGP) metagenomics is highly inevitable to explore the rhizospheric flora in order to maximize the processes that robustly augment plant productivity.

8.3 Role of PGPRs in Sustainable Agriculture

As a consequence of population growth, food consumption is also alarmingly increasing. Conversely, both the cultivable agricultural land and crop productivity are significantly reduced as a result of drought, salinity, global warming, and global industrialization (Gamalero and Glick 2012). Perhaps this sort of setback could only be addressed by practicing the sustainable agriculture that protects the fitness of the ecosystem. It is noteworthy that the vital principle of sustainable agriculture is to significantly minimize the impediments of insecticide and herbicide usage, chemical fertilizers, while reducing the emission of greenhouse gasses. Nonetheless the exploitation of plant microbiome has immense prospective in reducing the incidence of pests and diseases (Van Oosten et al. 2008), promoting plant growth and plant fitness and improved productivity (Lugtenberg and Kamilova 2009). However, the treatment with single strains or mixed consortia was shown to induce resistance to multiple plant diseases (Jetiyanon and Kloepper 2002). Most recently, several microbial biofertilizers and bioinoculants were formulated, produced, marketed, and effectively used by farmers worldwide (Bhardwaj et al. 2014). Even though plants are considered as metaorganisms (East 2013), the concept of understanding of this microbiome on plant health in terms of phenotypes is hitherto scarce. In order to trance for a sustainable agricultural vision, the produced crops need to be operational with disease resistance, salt tolerance, drought tolerance, and heavy metal stress tolerance along with an enhanced nutritional value (Meena et al. 2013c, 2015d, 2016b; Priyadharsini and Muthukumar 2016; Singh et al. 2016; Singh et al. 2015). Despite the accomplishment of above desired crop properties; one possibility of employing soil microbes (algae, fungi, bacteria, etc.) that augment the nutrient uptake competence and water holding efficiency (Armada et al. 2014), among these potential rhizospheric bacteria known as PGPR's are the most promising, despite the fact that PGPR may be used to enhance plant health and promote plant growth rate exclusive of environmental contamination (Calvo et al. 2014). For decades, varieties of PGPRs have been studied, and only a few of them have been commercialized so far, including the species *Pseudomonas*, *Bacillus*, *Klebsiella*, *Enterobacter*, *Azospirillum*, *Azotobacter*, *Variovorax* and *Serratia* (Glick et al. 2012). However, the utilization of PGPR in the agriculture represents only an undersized portion of agricultural practices worldwide (Bashan et al. 2014).

Nonetheless this is attributable to incoherent properties of inoculated PGPR, furthermore, which could influence the crop productivity (Fig. 8.1). The triumphant utilization of PGPR is merely reliant on its survival in soil, the compatibility with the crop on which it is inoculated, the interaction ability with native microbes in soil, and environmental factors (Martinez-Viveros et al. 2010). An additional challenge is that the modes of action of PGPR are diverse, and not all rhizobacteria possess the same mechanisms (Dey et al. 2004; Choudhary et al. 2011). Conversely many achievements have been reached with the application of microbial biotechnology in agriculture, but many challenges as well as opportunities need to be explored for the future sustainable agricultural developments (Kumar et al. 2017b; Meena et al. 2014b, 2015a, b, c; Raghavendra et al. 2016; Zahedi 2016; Shrivastava et al. 2016; Velazquez et al. 2016; Sindhu et al. 2016).

In recent times, there has been enormous surge to comprehend and investigate the genomic prosperity of rhizosphere microbes by linking soil community structure to both the general soil biophysical context and the social science perspective in order to understand human impacts and drivers of human decision-making for sustainable soil management. Therefore, this update in due course will focus on handy knowledge anchored in the root microbiome, its functional importance, and its potential association to the establishment of a host phenome, toward attaining sustainable agriculture. Therefore, by linking the soil biodiversity and functions to the ecosystem services, the soil ecosystem can be better conserved and managed for sustainable agricultural intensification (Rawat et al. 2016; Yasin et al. 2016; Meena et al. 2016c).

8.4 Molecular Sequencing Techniques for Studying Plant Microbiomes

Traditionally, the components of the plant microbiome were characterized by isolating and culturing microbes on different culture media and growth conditions. These culture-based techniques missed out immense preponderance of microbial diversity in an environment or in plant-associated habitats, which is at this time obvious by modern culture-independent molecular techniques for analyzing whole environmental metagenomes. Over the preceding 5 years, these culture-independent techniques have noticeably changed our perception on microbial diversity in a particular environment, from which only <1% are culturable (Hugenholtz et al. 1998). Subsequent to discovering the significance of the conserved 16S ribosomal RNA (rRNA) sequence (Woese and Fox 1977) and the first use of DGGE of the amplified 16S rRNA gene in the microbial community analysis (Muyzer et al. 1993), nevertheless, there was an immediate flare-up of advanced research toward microbial ecology using various molecular fingerprinting techniques. Apart from DGGE, TGGE, and FISH, clone library construction of microbial community-amplified products and DNA sequencing techniques emerged as other supporting tools for the better understanding of microbial ecology (Muyzer 1999). Furthermore, there are many newer techniques to understand the microbiome, from metagenomics to metaproteomics (Rincon-Florez et al. 2013; Schlaeppi et al. 2014; Yergeau et al. 2014) (Fig. 8.2). However, these techniques cover the whole microbiome, instead of selecting particular species, unlike conventional microbial analysis.

8.5 Modern Sequencing Technologies for Studying Plant Microbiomes

In the analysis of whole microbiome, the initial effort was started with the discovery of a conserved 16S rRNA gene sequence and its PCR applications in the identification of microorganisms (Woese and Fox 1977). Thus far, there are meticulous improvements achieved with these techniques, consenting to metagenomics, in order to study and understand the microbiome in a holistic insight in a petite period. The comprehensive assessment of soil ecosystems and more significantly functional genes allied with ecosystem processes are fastly curved into cost-efficient facets. This is primarily through the development of a range of whole metagenome sampling, followed by purification, separation, sequencing, and finally data analysis and interpretation. Particularly, the sequencing technology is going through speedy development, as it provides wide and thorough views of metagenomics, and

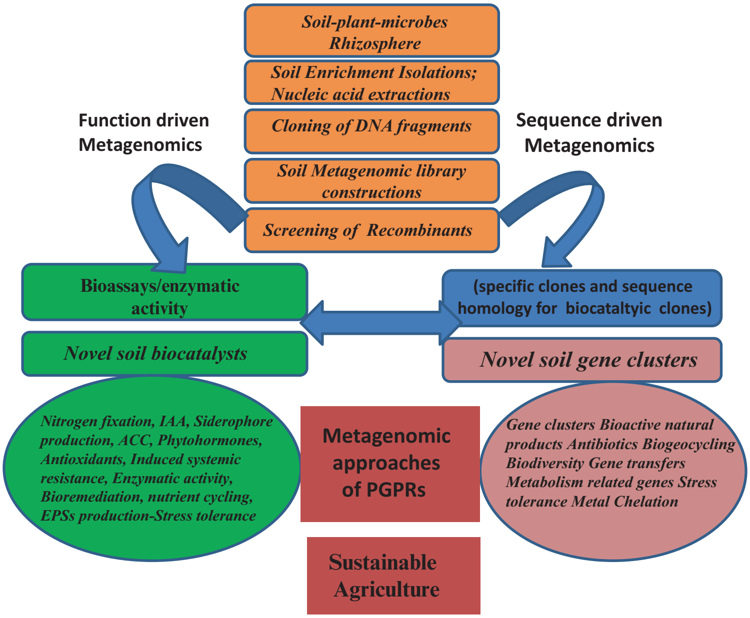

Fig. 8.2 Scheme of metagenomics for the discovery of novel soil biocatalysts and gene clusters from soil microorganisms

nowadays the largely named are (a) high-throughput sequencing (HTS) and (b) next-generation sequencing (NGS) technologies. These HTS techniques include the use of 454 Genome Sequencer (Roche Diagnostics), the HiSeq 2000 (Illumina), and the AB SOLiD System (Life Technologies Rincon-Florez et al. 2013; Yergeau et al. 2014; Saha et al. 2016a; Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b). Furthermore, other advanced techniques, such as DNA/RNA-SIP and DNA arrays (PhyloChip and functional gene arrays), moreover have promising features in the analysis of microbiomes, particularly their functional parts (Rincon-Florez et al. 2013; Uhlik et al. 2013). At present, there is a transition from metagenomics to metatranscriptomics, as the latter answers the diversity and functional part of the microbiome, rather than only showing the diversity. Nonetheless, it was also apparent in recent times that the functional flexibility and function-based diversity of the microbiome may possibly be central factors in niches somewhat than mere diversity (Barret et al. 2011; Chaparro et al. 2012).

However, in metatranscriptomics approaches, RNA-SIP, quantitative reverse transcription-PCR, and complementary DNA analysis coupled with pyrosequencing provide advanced functional insights into microbiome activities in the soil and rhizosphere (Schauss et al. 2009; Uhlik et al. 2013). Predominantly, the significance of RNA-SIP was underlined in forthcoming studies for sequential analysis of the flow of root-derived carbon and differentiation of primary and secondary microbial utilizers, which have elevated rates of labeling than their genes and need not depend on cell division, unlike DNA-SIP (Bressan et al. 2009; Uhlik et al. 2013). In order to surmount the broader constraints of quantitative PCR and microarray technology in analyzing the gene expression of a complex community, these sophisticated technologies still facade enormous challenges in the years to go.

8.6 Understanding the Mechanism and Functions of Plant–Microbe Interactions

A wider variety of novel endophyte phylogenetic lineages were discovered (Sun et al. 2008), underscoring a larger gap in understanding the total endophyte community in plants than previously realized. In addition to that, putative protein coding sequences associated with root colonization competence and PGPR were also explored (Barret et al. 2011; Sessitsch et al. 2012). Interestingly the advent of molecular techniques in microbial ecology has enabled more widespread studies of endophyte abundance, community composition, and functional genetic analysis; genes involved in detoxification of ROS, protein secretion systems, and flagellar motility have been explored as significant determinants for successful plant colonization and microbial competition (Hardoim et al. 2008; Cheng et al. 2010). However, the genes involved in the production of siderophores, abscisic acid, indole acetic acid, and quorum sensing (QS) autoinducer signaling genes were also associated with biocontrol, phytostimulation, and colonization (Forchetti et al. 2007; Ramesh et al. 2009; Faure et al. 2009) (Fig. 8.2). Perhaps this area of research will advance our insight in not only microbial interspecies communication but also the factors influencing the colonization success of potential endophyte inoculants. Undoubtedly, the metagenomic analysis of diverse plant species may signify that bacterial protein families identified to hinder with the plant immune response can distinguish between the rhizosphere and soil microbiota (Bulgarelli et al. 2015), suggesting that immune system mediated microbial insight, at least in part, and bacterial colonization of the rhizosphere. Interestingly the culture-independent approaches evidenced that microbial diversity of soil and rhizosphere microbiomes is highly underestimated. Notably the dawn of next-generation DNA sequencing methods has undeniably sparked a new era in molecular characterization of environmental ecosystems (Yadav and Sidhu 2016; Meena et al. 2014a, 2016d; Saha et al. 2016b; Verma et al. 2014, 2015b). Recent metagenomic studies have also revealed a wide range of antibiotic resistance genes (ARGs) and mobile genetic elements and virulence factors from different ecosystems (Kristiansson et al. 2011; Bengtsson-Palme et al. 2014).

In a very recent study of Mendes et al. (2014), the epiphytic rhizosphere microbiome of soybean was compared to that in bulk soil with regard to taxonomic and functional composition. Likewise, functions that may be of benefit for the plant in terms of growth promotion and nutrition were detected. Unno and Shinano (2013) investigated the rhizosphere metagenome of plants that demonstrated enhanced growth in the presence of phytic acid and detected genes encoding enzymes associated to phytic acid utilization, for instance, alkaline phosphatase or citrate synthase. Chhabra et al. (2013) applied a targeted metagenomic approach by constructing a fosmid library in *Escherichia coli*, which was screened in an assay for mineral phosphate solubilization activity. Interestingly the genes and operons with homology to phosphorus uptake, regulatory system and solubilization mechanisms were investigated.

The phyllosphere metagenomic datasets generated in these studies were additionally characterized in combination with a metagenomic dataset from *Tamarix*-associated phyllosphere bacteria to screen for photosynthetic genes that were further identified from other microorganisms to be involved in light-driven energy generation and diverse microbial rhodopsins (Atamna-Ismaeel et al. 2012a, b). Another metagenomic project was performed with the aim to attain a full sequence of a complete genome sequence of uncultured phytopathogen and insect symbiont *Candidatus Liberibacter asiaticus* which causes citrus huanglongbing disease (Duan et al. 2009).

8.7 Applications of Plant–Microbe Metagenomics in Agricultural Research

In the rhizosphere makes a source of gene pool with a huge potential, particularly for agricultural applications with the aim to improve crop productivity and quality of agricultural products and shield crops from pests. Perhaps this could be performed by exploring the genes responsible for PGPR activities and application of the recombinant molecules to soil. A functionally competent chitinase may perhaps be used as an effective fungicide in a research experiment by Ikeda et al. (2007), who used T-RFLP and clone library analysis to identify chitinase genes in maize rhizosphere. The same group of researchers established novel bacterial chitinase genes and found significantly large differences in chitinase gene diversity between the bulk and rhizosphere soils.

An additional example of Hjort et al. (2010) also explored the potential of chitinases in phytopathogen-suppressive soils. An activity that improves the plant fitness and, hence, improves crop production is apparently ACC deaminase activity. Interestingly Nikolic et al. (2011) also analyzed ACC deaminase genes (*acdS*) of bacterial endophytes colonizing field-grown potato plants and discovered the presence of two unique types of *acdS* genes, the dominant one showing high homology to an *acdS* gene derived from *P. fluorescens* through PCR analysis. The fundamental study on siderophores is mainly fascinating due to its triple function application, nutritional, systemic resistance inductor (ISR) and biocontrol (Bakker et al. 2007; Ramos Solano et al. 2008). Despite its significance in agriculture, the only instance to date that has been reported in marine settings, through expression-dependent methods, and resulted in a cluster composed by five ORFs that synthesized vibrioferrin, a siderophore explored in *V. parahaemolyticus* (Fujita et al. 2011).

The sequencing of whole genomes from a number of species permits to delineate their organization and provides the basis for understanding their functionality (Morrell et al. 2012), as a consequence favoring metagenomic–agricultural practices. Additionally metagenomic analyses also depicted several metabolic processes, adaptations, and plant growth-promoting characteristics in rice (Sessitsch et al. 2012). In a metagenomic analysis of the barley rhizosphere, gluconate production was identified as a key mineral phosphate solubilization mechanism in an uncultivated microbiome (Chhabra et al. 2013). Similarly, the metagenomic characterization of the microbial communities associated with cucumber and wheat roots revealed that genes involved in the microbial degradation of plant cell wall polysaccharides were enriched in both species, and their differential recruitment could be used to classify their associated microbiota (Ofek-Lalzar et al. 2014). Nonetheless, efforts addressed to the success of an apt data of associated molecular information on transcriptome and proteome sequencing are also crucial to depict the gene pool of a genome and its central functionalities. Notably these efforts undeniably led to the most important step forward in biological sciences (Barh et al. 2013) as well as agriculture (Van Emon 2015).

Furthermore, the revelation of the complexity of genes and their networking is also crucial for being translated into breeding practice for crops or livestock, contributing to their health, resistance, and productivity. In actual fact, the contribution of genomics to agriculture spans the identification and manipulation of genes linked to specific phenotypic traits (Zhang et al. 2014) in addition to molecular breeding by marker-assisted selection of variants (Iovene et al. 2004). Eventually in the coming years, the agricultural metagenomics without doubt aims to reveal several innovative solutions through the study of crops or livestock genomes, achieving information for protection and sustainable productivity for food industry, however, for alternative facets like energy production or design of pharmaceuticals (Wilson and Roberts 2014). In a metagenomic assay of the barley rhizosphere, Bulgarelli et al. (2015) identified a positive selection on microbe interaction traits (e.g., type VI secretion system (T6SS) as well as those putatively involved in microbe interactions. Interestingly, T6SS sequences were also found in high abundance in a metagenomic study of the soybean rhizosphere (Mendes et al. 2014).

However, little information is available for microbe–plant communities wherein they are integrated. Seeing that an example, it is accepted that soil is one of the principal carbon reservoirs on earth, and prokaryotes include a significant amount of the soil biomass (Whitman et al. 1998). However, in the last three decades, culture-independent methods showed that, albeit fast-evolving sequencing strategies, the great majority of bacterial species are still unidentified (Rappe and Giovannoni 2003). The application of metagenomics in agriculture also proved to be suitable for depicting the multifarious patterns of interactions occurring among microorganisms in soil (Carbonetto et al. 2014) and in plant rhizosphere (Mendes et al. 2014). Metagenomics are recently revealed to be useful to trace the shift in taxonomic composition and functional redundancy of microbial communities in rhizosphere soils in association to environmental changes (Pan et al. 2014) and agricultural management (Souza et al. 2015).

Metagenomic studies can also help decipher the role of soil microbes in plant nutrition (Pii et al. 2016) or in the cycle of elements (Stempfhuber et al. 2015). Plant, soil, and microbiome also play a crucial role in agriculture provided that it determines plant fitness (Haney et al. 2015) and soil biogeochemical properties (Acosta-Martinez et al. 2014) and affects both yield and quality traits (Deusch et al.

2015). Furthermore, the applications can lead to the discovery of new genes, bioproducts, and plant growth-promoting microorganism consortia, useful for understanding relevant aspects such as response to stresses (Timmusk et al. 2014) or dysbiosis (Handelsman 2004; Vayssier-Taussat et al. 2014). Therefore, the amount of metabolic diversity present in soil to harness novel gene encoding is undeniably vast which could be explored with the help of metagenomic techniques. Interestingly the metagenome represents the genomes of uncultured microbes as a rich source for isolation of many novel genes. In consequence, metagenomics not only provides us innovative insights into microbial taxonomic/genetic diversity life but also access to genes (metabolic diversity) producing novel biomolecules (Fig. 8.2).

8.8 Future Perspectives in PGPR Metagenomics

PGPRs that are difficult to culture are hardly understood and make up a huge part of soil sequencing techniques that allow us to do more researches. Therefore, the translational research like metagenomics is highly indispensable to apply these tools for the benefit of agriculture, particularly by evaluating the effects of decisions on microbes known to have positive or negative effects on productivity and identify microbes that are indicators for higher and lower productivity (Souza et al. 2015). However, preceding works highlighted numerous approaches to harness microbe–rhizosphere interactions for increased farm productivity (Kaymak 2010; Altomare and Tringovska 2011; Shen et al. 2013); nevertheless, how these interactions may perhaps be exploited for biotechnological applications is not completely explored. Remarkably these rhizosphere–microbe interactions are modulated by numerous chemical molecules produced by plant roots which in turn communicate with soil microbes. However, identifying these signal molecules and harnessing them to improve interaction between beneficial microbes and plant roots can further improve resource availability. Interestingly one such mechanism explored so far is the metagenomics of plant microbial signaling that can undoubtedly dole out this rationale. However, using metagenomics it is now possible to identify mechanisms and isolate genetic resources for maximizing nutrient cycling and nutrient use efficiency without cultivating soil microbes (Abhilash et al. 2012).

Nonetheless, utilizing metagenomics to characterize soil microbial communities facilitates regulation of plant performance through enhanced bioavailability of nutrients and secretion of bioactive compounds for pest control and hormones to excite plant growth. In the years to come the plant microbiome may shed light on solutions to modify plant genetics, function, and ecology for survival in unique habitats or environmental conditions (Fig. 8.2). Noteworthy, such resolutions may help to meet rising food demands, curtail land and biodiversity loss, and mitigate the impacts of climate change. Furthermore understanding the physiological interactions among the microbiomes may allow feasible expression of specific bacterial traits, viz., nitrogen fixation, phosphate solubilization, ACC deaminase, quorum sensing, siderophores, chitinases, auxins, gibberellins, or antibiotic production. Eventually detection of novel genes coding for known activities associated to the microbial interaction with plants is undoubtedly a prudent attempt; nevertheless, a real progress is inevitable toward the invention of presently unknown mechanisms of the plant–microbe interactions. However, the application of metagenomic services can perhaps contribute to improved disease detection/protection in crops which may further improve crop health by exploiting the association between microbes and plants. Metagenomics can be applied to the development of next-generation pesticides and fungicides in addition to improving the efficiency of organic agriculture.

8.9 Conclusions

The advanced tools of metagenomics offer many avenues into a broadened view of PGPR and their activities in particular. Quantifying the impacts of plant microbiome has advanced our conceptual understanding in plant–microbe metagenomics, with real-world applications that have the potential to increase crop production during enhanced plant trait expression and/or increased utilization of insignificant habitats. Recent advances in metagenomics augmented our overall understanding of plant–microbe and microbe–microbe interactions in the rhizosphere and also outlined quite a few questions for the future. Notably the field of metagenomics, with reference to soil microbial ecosystems has immense potential, it is hitherto not studied and explored to a great extent. Interestingly, the discovery of novel PGPR activities, either by functional screening or sequence information, will add a great deal to our current understanding of mechanistic variations that exist in PGPR phenotypes. Additionally, metagenomics can also unravel the gene clusters of biosynthetic-related genes, synthesis of antimicrobial compounds. Hoping for further advancement of metagenomics in developing successful research and development, PGPR use will certainly befall a reality and will be helpful to fundamental biochemical and physiological processes that ascertain the stability and productivity of agroecosystems, thus leading us toward an ideal sustainable agricultural system. The use of metagenomics in parallel with established or novel molecular approaches will certainly lead to the discovery of novel mechanisms of PGPR activity, newer types of PGPR identity, and a spanking new look on the biology and practical applications of PGPR.

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Role of Bioinoculants as Plant Growth-Promoting Microbes for Sustainable Agriculture

9

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Abstract

The green revolution bought amazing consequences in food grain production but with insufficient concern for agriculture and environmental sustainability. The efficient biofertilizers are gaining importance in sustaining agriculture. Various complementing combinations of microbial inoculants for management of major nutrients are necessary for agriculture sustainability. In such case, microorganisms are useful for biomineralization of bound soil and make nutrients available to their host and/or its surroundings. Nitrogen and phosphorus are major plant nutrients which occupy a key place in the balanced use of fertilizer. Leguminous crop fixes the atmospheric nitrogen by *Rhizobium* which requires optimum level of phosphorus in plant tissue. Mineral solubilizers play an important role in seedling setting because more of the tropical soils are phosphate fixing and make it unavailable to the plants. Phosphate-solubilizing microorganisms (PSMs) that solubilize bound form of phosphorus and AM fungi act as uptaker of phosphorus and make it available to the host plants. Microorganisms facilitate plant mineral nutrition by changing the amounts, concentrations and properties of minerals available to plants. Because of the various challenges faced in screening, formulation and application, PGPB have yet to fulfil their promise and potential as commercial inoculants. This chapter focuses on some important information

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regarding the various types of biofertilizing potential of some important group of microbes, their formulations, their application for the development of sustainable technology, their scope of improvement by promising new technique and commercially available biofertilizer and its application in India.

Keywords

Beneficial bacteria • Inoculant • Plant growth-promoting bacteria (PGPR) • Sustainable agriculture

9.1 Introduction

In the late 1960s, agriculture system focused on food crop productivity, though high-yielding varieties (HYVs), agrochemicals, irrigation system and chemical fertilizers were extensively used throughout India. About 50% of the yield growth was contributed by the use of fertilizer alone. In fact, India is the world's largest user of chemical fertilizers, consuming each year ~16% of the world's N consumption, ~ 19% of phosphatic and ~15% of potassic nutrients of the global total (Anonymous 2008). As per the Raghuwanshi (2012) report, out of the ~329 M ha of India's geographical area, ~114 M ha are under cultivation. Farmers inoculate the soil with fertilizers in order to reap a better harvest. Fertilizers function as catalysts for growth and development of plants by providing proper nutrients. These can be categorized into chemical and biofertilizer which has its advantages and disadvantages (Tables 9.1 and 9.2).

For the balanced nutrient management for crop growth, these advantages need to be integrated in order to achieve optimum performance by each type of fertilizer. High inputs of chemical fertilizers during the last 150 years left soils degraded, polluted and less productive but have also posed severe health and environmental hazards. The use of biofertilizers would solve these issues and make the ecosystem healthier. It is reported that the ~22 M ha of land are now cultivated organically which represents <1% of the world's conventional agricultural production and ~9% of the total agricultural area (Mishra and Dash 2014).

Essential elements are required for proper growth and functioning of plant. The shortage of any of these essential nutrients to plant, listed in Table 9.3, can lead to damage to crop health. Primary macronutrients or micronutrients such as nitrogen, phosphorus and potassium are required in the greatest quantities, whereas secondary macronutrients or micronutrients are needed in smaller quantities, and are found in adequate quantities in soil, and therefore do not often limit crop growth. Micronutrients, or trace nutrients, are needed in very small amounts and can be toxic to plants in excess. Silicon (Si) and sodium (Na) are sometimes considered essential plant nutrients. Due to their omnipresent nature, they are never in short supply of these nutrients in soil (Parikh and James 2012).

Biofertilizers play an important role in improving the nutrient supplies and their availability in plant which includes selective organisms, like bacteria, fungi and

Table 9.1 Advantage and disadvantage of chemical fertilizer

Advantage	Disadvantage
Nutrients are soluble and immediately available to plants, creating a direct and fast effect	Overuse can result in negative effects such as leaching, pollution of water resources, destruction of microorganisms and beneficial insects, crop susceptibility to disease attack, acidification or alkalization of the soil or reduction in soil fertility, all of which cause irreparable damage to the overall ecosystem
The price is lower and more competitive than organic fertilizer, which makes it more popular with farmers	Oversupply of nitrogen leads to softening of plant tissue resulting in increased susceptibility to diseases and pests
They are quite high in nutrient content; only relatively small amounts are required for crop growth	They reduce the colonization of plant roots with mycorrhizae and inhibit symbiotic nitrogen fixation by *rhizobia* due to high nitrogen fertilization
	They enhance the decomposition of soil, which leads to degradation of soil structure
	Nutrients are easily lost from soils through fixation, leaching or gas emission and can lead to reduced fertilizer efficiency

Table 9.2 Advantage and disadvantage of using biofertilizer

Advantage	Disadvantage
The nutrient supply is more balanced, which helps keep plants healthy	They are comparatively low in nutrient content, so a larger volume is needed to provide enough nutrients for crop growth
They enhance soil biological activity, which improves nutrient mobilization from organic and chemical sources and decomposition of toxic substances	The nutrient release rate is too slow to meet crop requirements in a short time; hence, some nutrient deficiency may occur
They enhance the colonization of mycorrhizae, which improves phosphorus supply	The major plant nutrients may not exist in organic fertilizer in sufficient quantity to sustain maximum crop growth
They enhance soil structure, leading to better root growth	The nutrient composition of compost is highly variable
They increase the organic matter content of the soil, thereby improving the exchange capacity of nutrients, increasing soil water retention, promoting soil aggregates and buffering the soil against acidity, alkalinity, salinity, pesticides and toxic heavy metals	The cost is high compared to chemical fertilizers
They release nutrients slowly and contribute to the residual pool of organic nitrogen and phosphorus in the soil, reducing nitrogen leaching loss and phosphorus fixation; they can also supply micronutrients	Short shelf life, lack of suitable carrier materials, susceptibility to high temperature and problems in transportation and storage are all biofertilizer bottlenecks that still need to be solved in order to promote effective inoculation
They encourage the growth of beneficial microorganisms and earthworms	
They help to suppress certain soil-borne plant diseases and parasites	

Table 9.3 Essential plant nutrient elements and their primary form utilized by plants

Essential plant element		Symbol	Primary form
	Carbon	C	CO_2 (g)
	Hydrogen	H	H_2O (l), H^+
	Oxygen	O	H_2O (l), O_2(g)
Mineral elements			
Primary macronutrients	Nitrogen	N	NH_4^+, NO_3^-
	Phosphorus	P	HPO_4^{2-}, $H_2PO_4^-$
	Potassium	K	K^+
	Calcium	Ca	Ca^{2+}
Secondary macronutrients	Magnesium	Mg	Mg^{2+}
	Sulphur	S	SO_4^{2-}
	Iron	Fe	Fe^{3+}, Fe^{2+}
	Manganese	Mn	Mn^{2+}
	Zinc	Zn	Zn^{2+}
Micronutrients	Copper	Cu	Cu^{2+}
	Boron	B	$B(OH)_3$
	Molybdenum	Mo	MoO_4^{2-}
	Chlorine	Cl	Cl^-
	Nickel	Ni	Ni^{2+}

Parikh and James (2012)

algae. These organisms are capable of fixing atmospheric nitrogen and make it available to the soil for the plant growth. They are eco-friendly, cost-effective and renewable source of plant nutrients. The biofertilizer plays a vital role in maintaining long-term soil fertility (Mishra et al. 2015). Biofertilizers are economical, eco-friendly, productive and accessible to small farmers over chemical fertilizers after the long-term use (Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2016b).

9.2 Types of Bioinoculants and Their Role

The efficient biofertilizers are the outcome of most advance microbial technology required to support sustainable and non-polluting agriculture. The biofertilizers contained living microorganism that, when applied to seed, plant surfaces or soil, accelerate their microbial processes which result in the availability of nutrients for easy assimilation by plants (Sharma et al. 2012; Kumar et al. 2015, 2016a; Ahmad et al. 2016; Meena et al. 2016a; Jha and Subramanian 2016). Since nitrogen is inert in nature, the plants cannot utilize it from the atmosphere. At ambient temperature and pressure, diazotrophs mediate nitrogen fixation under enzymatic reaction by a process known as biological nitrogen fixation (Table 9.4).

Table 9.4 Types of biofertilizers

	Group	Example
Biofertilizer for micronutrients		
	N2-fixing biofertilizers	
(a)	Free-living	*Azotobacter*, *Beijerinckia*, *Derxia*, *Nostoc*
(b)	Symbiotic	*Rhizobium*, *Frankia*, *Anabaena azollae*
(c)	Associative symbiotic	*Azospirillum*, *Gluconacetobacter diazotrophicus*
	P-solubilizing biofertilizers	
(a)	Bacteria	*Bacillus megaterium* var. *phosphaticum*, *Bacillus subtilis*
		Bacillus circulans, *Pseudomonas striata*
(b)	Fungi	*Penicillium sp.*, *Aspergillus awamori*
	P-mobilizing biofertilizers	
Biofertilizer for macronutrients		
(a)	Arbuscular mycorrhiza	*Glomus* sp., *Gigaspora* sp., *Acaulospora* sp.,
		Scutellospora sp. and *Sclerocystis* sp.
	Sulphur oxidizers	*Thiobocblus thioxidans*
(a)	Zinc solubilizers	*Bacillus* sp., *Pseudomonas* sp., *Aspergillus niger*
(b)	Potassium and silicate solubilizers	*Erwinia*, *Pseudomonas* sp., *Bacillus* sp., *Fracturia auerentia*
(c)	Manganese solubilizers	*Penicillium citrinum*
Plant growth-promoting rhizobacteria		
	PGPR	
	Bacteria	*Pseudomonas fluorescens*, *Bacillus* sp., *Burkholderia*
		Herbaspirillum
	Fungi	*Piriformospora indica*
Biofilmed biofertilizers		
	Fungal-bacterial biofilms (FBB), fungal-rhizobial biofilms (FRB)	

9.3 Biofertilizer for Macronutrients

9.3.1 N_2-Fixing Biofertilizers

9.3.1.1 Asymbiotic/Free-Living Nitrogen-Fixing Biofertilizers

Most important bacteria in this group are *Azotobacter*, *Derxia* and *Beijerinckia* which are found in soil system.

Azotobacter *Azotobacter* is a potential biofertilizer in rhizosphere of leguminous and nonleguminous crops due to availability of various readily utilizable carbon compounds. Amutha et al. (2014) worked on mass production of *Azotobacter* and phosphobacteria using specific medium of Pikovskaya's media for phosphobacteria and Ashby's agar for the *Azotobacter* production. Initially, the organism was isolated from the soil sample, and conformation was done using the biochemical test; the cell count reached to 10^8–10^9 cells mL^{-1}, and the broth is used as inoculant. It increases crop yield by 20–30%, replaces chemical nitrogen and phosphorus by ~25% and stimulates plan growth.

Cyanobacteria *Cyanobacteria* are excellent N_2 fixers. Earlier they are known as blue-green algae such as *Anabaena*, *Nostoc*, *Aulosira* and *Tolypothrix*. *Cyanobacteria* include unicellular colonial species in which some filamentous species have the ability to differentiate into different cell types:

(a) *Vegetative cells*: normal photosynthetic cells found under favourable growing conditions.
(b) *Akinetes*: climate resistant spores formed under environmental stress conditions.
(c) *Heterocysts*: thick-walled cells containing nitrogenase enzyme vital for N_2 fixation. Heterocysts are specialized structures for N_2 fixation and able to fix nitrogen (N_2) into ammonia (NH_3^+), nitrites (NO_2-) or nitrates (NO_3-) which can be utilized by plants.

9.3.1.2 Symbiotic Nitrogen-Fixing Biofertilizers

Rhizobium Rhizobia are the most important of all the biofertilizers which fix the atmospheric nitrogen by forming root nodules which act as mini-factories of nitrogen fixation in legume plants. Atmospheric nitrogen fixation is carried out by the enzyme nitrogenase of *Rhizobium* with the help of nodulins (legume plant protein) and transfers to plant for effective symbiosis. It has been shown in recent findings that there are more crop-enhancing and biofertilizer attributes in cereal crops due to rhizobial inoculation. In addition, plant nutrients like P, K, Ca, Mg and even Fe accumulation were observed (Baset Mia and Shamsuddin 2010; Parewa et al. 2014; Prakash and Verma 2016; Meena et al. 2015f, 2016b; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016; Jaiswal et al. 2016).

***Frankia*: *Casuarina* (nonleguminous tree) Symbiosis** Nonleguminous tree nodules with *Frankia* are called actinorhizal plant. Nodules are formed by filamentous spore-forming actinomycetes. The actinorhizal nodules represent the cluster of modified roots with *Frankia*-infected cells found in the cortex. Nodules first appear as swelling and later develop vesicles which are the sites of N_2 fixation.

Anabaena azollae *Anabaena azollae* is a cyanobacterium that forms symbiotic association with a water fern *Azolla* and used as biofertilizer for rice cultivation. Apart from nitrogen fixation, *Azolla* is also known to suppress weed population in wetland rice and provides additional economic advantage to rice cultivation.

9.3.1.3 Associative Nitrogen-Fixing Biofertilizers

Azospirillum *Azospirillum* colonizes the root zone and fixes nitrogen in loose association with C_4 plants such as maize, sorghum, sugarcane, etc. *Azospirillum* fixes atmospheric N_2, mineralizes nutrients from soil, sequesters Fe, survives in stressed environmental conditions and also favours beneficial mycorrhizal plant associations. *Azospirillum* biofertilizers are suitable for C_4 crops such as maize, sorghum and other cereals like rice, wheat, barley and ragi and various horticultural crops.

Gluconacetobacter diazotrophicus Nitrogen-fixing bacteria *G. diazotrophicus* earlier known as *Acetobacter diazotrophicus* were discovered from sugarcane crop. The bacterium colonizes the internal tissues of sugarcane and fixes nitrogen up to 200 kg ha^{-1}. It is an acid and sucrose loving (~30% of sucrose) with highest pH (5.5) and oxygen-tolerant bacterium. An experiment was conducted by Murumkar et al. (2016) who studied the effect of set treatment of *G. diazotrophicus* and PSB on seed yield, quality and saving of chemical N and P fertilizers for sugarcane seed plots. The set inoculation of *G. diazotrophicus* and PSB coupled with ~78% recommended N and 75% recommended P_2O_5 significantly improved the growth, two eye bud-set yield and quality.

9.3.2 Phosphorus Biofertilizers

9.3.2.1 Phosphorus-Solubilizing Biofertilizer

Another plant nutrient such as phosphorus plays an important role for the growth and development of plants. Only 15–20% of applied phosphorus is recovered by the crops and the remaining gets fixed in the soil. Several microorganisms have the ability to solubilize this fixed phosphorus by producing various organic acids (butyric acid, lactic acid, succinic acid, etc.) and enzymes that make them available to the crops (Sharma et al. 2012). Several soil bacteria belonging to genera *Bacillus*, *Aspergillus*, *Penicillium* and *Trichoderma* have the ability to solubilize inorganic phosphate and make it available to plants. The basic mechanism for mineral phosphate solubilization is the production of organic acids and acid phosphates which play an important role in mineralization of organic phosphorus in soil. Vahed et al. (2012) during their study suggested that consumption of biofertilizer was able to stimulate growth and increase grain yield, and it will be decreased in the presence of phosphate-solubilizing bacteria (Priyadharsini and Muthukumar 2016; Kumar et al. 2017a; Meena et al. 2015a; Bahadur et al. 2016b; Das and Pradhan 2016).

9.3.2.2 Phosphorus-Mobilizing Biofertilizer

P mobilizers facilitate mobilization of soluble phosphorus from distant places in soil where plant roots cannot reach. Mycorrhiza is a prominent P mobilizer in a symbiotic association with plant roots. Fungus get benefited by obtaining its carbon requirements from hosts through photosynthates, and the plant in turn gains the much needed nutrients which would otherwise be inaccessible to the host (Bahadur et al. 2017; Verma et al. 2017b; Kumar et al. 2017b). This uptake of nutrients is facilitated with the help of hyphae of the fungus. These fungi are associated with majority of agricultural crops. Probably vesicular-arbuscular mycorrhiza (VAM) is the most abundant fungus in agricultural crops and accounts for 5–50% of the biomass of soil microbes (Raghavendra et al. 2016; Zahedi 2016; Meena et al. 2015b, e; Teotia et al. 2016).

Seven genera of VAM which these fungi produce symbiosis with plants form a large number of spores that penetrate into the plant root and form two types of structures, i.e. vesicles and arbuscules. Vesicles are smooth oval bodies that are most likely storage structures. Arbuscules are formed inside the plant cells. Nutrients travel from soil through fungal hyphae to these arbuscules which gradually degenerate and provide nutrients to plants. Thus, the association helps in higher uptake of P and better utilization of other nutrients like N, Cu, Zn, S, etc. (Sharma et al. 2012).

9.3.3 Sulphur Oxidizers

For the growth of plant and soil health, sulphur is an essential nutrient, and the genus *Thiobacillus* is an important group of sulphur oxidizer. The application of sulphur coupled with thiobacilli renders alkali soils fit for cultivation of crops. The formation of sulphuric acid by *Thiobacillus* in soil increases the level of soluble P, K, Ca, Mg, Al and Mn ion. The sulphuric acid produced in the mixture dissolves the phosphate and thereby enhances phosphorus nutrition of plants (Sharma et al. 2012).

9.4 Biofertilizer for Micronutrients

9.4.1 Zinc (Zn) Solubilizers

Zn is an important element present as cofactor and metal activator. Exogenous application of soluble zinc sources, similar to fertilizer applications, has been advocated to various crops. This causes conversion of ~96 to 99% of applied available zinc to various unavailable zinc that can be reverted back to available forms by inoculating Zn solubilizers like *Pseudomonas* sp., *Bacillus* sp. and *Aspergillus niger* (Sharma et al. 2012). Among fungal genera, *A. niger* possesses immense potential of solubilizing zinc. Vaid et al. (2014) studied the effect of zinc-solubilizing bacteria (ZSB) on zinc nutrition of rice which increased the mean dry matter yield/pot (~13%), productive tillers/plant (~15%), number of panicles/plant (~13%), grains/panicle number (~13%), grain yield (~17%) and straw yield (~12%) over the control and Zn fertilizer treatment.

9.4.2 Potassium- and Silicate-Solubilizing Bacteria

Soil microorganisms have the ability to absorb and mobilize the fixed form of nutrient from trace mineral sources. Silicate bacteria are known to release organic acids during solubilization (Nath et al. 2017; Sarkar et al. 2017; Verma et al. 2017a). It is known to dissolve potassium, silica and aluminium. Soil microorganisms for solubilization of silicate minerals are *Erwinia*, *Pseudomonas* sp. and *Bacillus* sp. (Sharma et al. 2012; Rawat et al. 2016; Yasin et al. 2016; Meena et al. 2016c, e; Saha et al. 2016a; Masood and Bano 2016).

9.4.3 Manganese (Mn) Solubilizers

Penicillium citrinum present in soil is known to solubilize manganese from the low-grade manganese ores from the soil. It produces reductive compounds such as organic acids which help in solubilizing manganese.

9.4.4 Plant Growth-Promoting Rhizobacteria (PGPR) as Biofertilizer

Rhizobacteria aggressively colonize plant roots and multiply and colonize on the roots in the presence of a competing microflora and enhance plant growth. 1-Aminocyclopropane-1-catrboxylate (ACC) deaminase is the PGPR enzyme that is able to hydrolyse ACC by lowering ethylene concentration in seedlings; these PGPR stimulate seedlings' root length (Sharma et al. 2012). Several PGPR inoculants are commercialized which function as bio-protectants, biofertilizers and bio-stimulators (Sharma et al. 2012). Several bacterial species such as *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Klebsiella*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Burkholderia*, *Bacillus*, *Flavobacterium*, *Microbacterium* and *Serratia* have reported as the most significant phosphate-solubilizing bacteria (Saharan and Nehra 2011; Bhattacharya and Jha 2012; Yadav and Sidhu 2016; Meena et al. 2016d; Saha et al. 2016b; Bahadur et al. 2016a).

Piriformospora indica *Piriformospora indica* is a wide-host root-colonizing endophytic fungus which promotes plant growth and performance. The use of *P. indica* as a growth and biomass-stimulating fungus in agriculture is well known because:

(a) Single infection processes are sufficient for the efficient root colonization.
(b) It can survive under adverse environmental conditions, viz. such as cold (<0 °C), extreme heat (>45 °C), salt and heavy metal-polluted soils and soils with varied pH values (3.3–9.2).
(c) It promotes micro (e.g. Fe)- and macro (such as P, S and N)-nutrient uptake from soil.
(d) It confers resistance to root and leaf pathogens through induced systemic resistance (ISR).
(e) It stimulates plant growth and biomass though root exudates.

9.4.5 Biofilmed Biofertilizers

Recently, application of developed biofilm as biofertilizer has a great potential in crop production; biofilm is an assemblage of microbial cells (algal, fungal, bacterial and/or other microbial biopolymer (EPS) produced by the cells). Fungal-bacterial biofilms (FBBs) enhanced metabolic activities compared to monocultures. Beneficial biofilms developed in vitro-cultured conditions in both fungal and bacterial strains were used as biofertilizers for nonlegume species with good efficacy results (Verma et al. 2014, 2015b; Meena et al. 2013c, 2014a; Singh et al. 2015). Recently, Hettiarachchi et al. (2014) worked on the fungal-bacterial interaction as biofilmed biofertilizers (BFBFs) in *Hevea* seedlings and observed that BFBF application increased root growth of the seedling rubber plants.

9.5 Mode of Action of Biofertilizer

Several mechanisms encourage the crop growth by the use of biofertilizers. The mode of action of commercially available biofertilizers is not always understood; growth promotion has been identified as the result of indirect or direct mechanisms. Conversely, direct growth promotion mechanism may provide some compounds essential for crop growth which stimulate nutrient uptake. Biofertilizers solubilize the insoluble forms of phosphates like tricalcium, iron and aluminium phosphates into available forms (Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b).

Biofertilizers compose organic matter and help in mineralization in soil. Core mechanism for mineral phosphate solubilization is the production of organic acids and acid phosphatases. It is generally accepted that the major mechanism of mineral phosphate solubilization is the action of organic acids synthesized by soil microorganisms (Shrivastava et al. 2016; Velazquez et al. 2016; Meena et al. 2015c; Sindhu et al. 2016). The production of organic acids results in acidification of the microbial cell and its surroundings. The most frequent mean of mineral P solubilization is gluconic acid and ketogluconic acid. Other organic acids, such as glycolic, oxalic, malonic and succinic, have also been identified among P solubilizers. Chelating substances and inorganic acids such as sulphideric, nitric, and carbonic acid are considered as other mechanisms for P solubilization. However, the efficacy and their contributions to P release in soils seem to be less than organic acid production. In recent years, the use of artificially produced inoculum of mycorrhizal fungi has increased its significance due to their varied role in plant growth and yield and resistance against climatic and edaphic stresses, pathogens and pests (Meena et al. 2014b; Singh et al. 2016).

9.6 Types of Biofertilizer Formulation

Various industries and research institutes are involved in a formulation containing an effective bacterial strain (Bashan 1998). A microorganism which is optimally functional under laboratory conditions might not be able to produce same efficacy under field conditions after formulation production. Once an inoculant formulation which works in situ has been developed, it must be allowed for the sophistication of the end user (Stephens and Rask 2000).

9.6.1 Carriers

The delivery vehicle of live microorganisms from the factory to the field is called carrier (Trevors et al. 1992). A good carrier should therefore possess as much of the following properties:

(a) Excellent moisture absorption capacity
(b) Lump-free forming materials
(c) Easy to sterilize by autoclaving
(d) Low cost and availability in adequate amounts
(e) Good p^H buffering capacity

In case the inoculant is used as seed coating, the carrier shall assure the survival of the PGPM on the seed. A good carrier should have one essential characteristic: the capacity to deliver the right number of viable cells in good physiological condition at the right time (Trevors et al. 1992; Meena et al. 2015d).

9.6.2 Peat Formulations

Peat formulations have been the carriers of choice and are the most commonly used in the *rhizobia* inoculation industry (Kaljeet et al. 2011). Peat inoculant applied to the seed as slurry is the most commonly used method to inoculate grain legumes with rhizobia (e.g. *Bradyrhizobium* sp., *Mesorhizobium* sp., *Rhizobium* sp., etc.). Peat slurry inoculants are made using finely milled peat that has been sterilized by gamma irradiation, and these sterilized inoculants can support high concentrations of rhizobia, generally 10^9–10^{10} cells g^{-1} peat at manufacture (Hartley et al. 2005).

9.6.3 Vermiculite Formulation

Vermiculite is a naturally occurring layer silicate mineral.

For example, increased amount of N and P availability in the final product can be achieved by adding N-fixing and P-solubilizing bacteria to a vermicompost (Vassileva et al. 2010). Vermiculite has become a very attractive material for the inoculant production due to the various properties exhibited by it like antic-rusting (Hemphill 1982), moisture-holding and plant growth-promoting (Lima et al. 1984; Reid et al. 1983) abilities.

9.7 Talc Formulation

Talc, chemically referred as magnesium silicate [$Mg_3Si_4O_{10}(OH)_2$], is used as a carrier for formulation development due to its inert nature and easy availability as raw material from soapstone industries. The potential of talc to be used as a carrier was demonstrated by Kloepper and Schroth (1981). Rhizobacteria could survive in talc for 2 months. The *fluorescent pseudomonads* after storage for 2 months in talc mixture with ~20% xanthan gum at 4 °C did not decline in number. While *P. fluorescens* isolate Pf1could survive up to 240 days in storage (Vidhyasekaran and Muthamilan 1995), *P. putida* strains 30 and 180 could survive up to 6 months (Bora et al. 2004), and *B. subtilis* survived up to 45 days in talc-based formulations (Amer and Utkhede 2000). Saravanakumar et al. (2007a) demonstrated that application of talc-based bioformulation of *P. fluorescens* Pf1 consistently reduced the blister blight disease and increased the yield on tea plants. The same research group has demonstrated that *P. fluorescens* Pf1 effectively controlled the dry root rot disease on mung bean plants (Saravanakumar et al. 2007b). Further, seed treatment, soil application and seedling dip of talc-based bioformulation of Pf1 effectively reduced the sheath rot disease on rice plants under glasshouse and field conditions (Manikandan et al. 2010).

9.8 Press Mud Formulation

Press mud is a by-product of sugar industries. Its usefulness as fertilizer is based on the nutrient content of the mud. It is rich in micronutrients and can reduce the requirement of chemical fertilizers. It also provides suitable conditions to bacteria for carrying out nitrogen fixation and phosphate solubilization that keep the soil healthy and develop the self-reclamation cycle.

The fertilizer produced is free from all pathogens, harmful bacteria, weeds and seeds due to the high temperature produced during bio-composting. Fertilizer is easy to handle, to pack and to transport. The biocompost contains 25–30% organic carbon, 1.2–2.0% nitrogen, 1.5–2.0% phosphorus and 2.5–3.0% potash (Partha and Sivasubramanian 2006). This carrier maximizes the survival of *Azospirillum* sp. by providing favourable conditions in comparison to lignite, which is predominantly used as a carrier material in India (Muthukumarasamy et al. 1999).

9.9 Promising New Technologies

A popular method for storing and delivering microorganisms through liquid formulations is water-in-oil emulsions (Vandergheynst et al. 2006). This formulation slows down water evaporation as the oil traps the water around the organism which is particularly beneficial for organisms that are sensitive to desiccation. Thickening the oil phase using hydrophobic silica nanoparticles significantly reduced cell sedimentation and improved cell viability during storage (Vandergheynst et al. 2007).

Recently, a new process named PGSS (particles from gas saturated solutions), based on the application of supercritical fluid properties, is used which is carried out at low temperatures and uses carbon dioxide as a supercritical fluid. Another new technology is proposing the exploitation of the natural production of bacterial biofilms as a possible carrier. Application of a biofilmed inoculant containing a fungal rhizobia consortium significantly increased N_2 fixation in soybean compared to a traditional rhizobium inoculant (Jayasinghearachchi and Seneviratne 2004).

Interestingly, beneficial endophytes were observed to produce higher acidity and plant growth-promoting hormones than their mono- or mixed cultures with no biofilm formation (Bandara et al. 2006). Wheat seedlings inoculated with biofilm-producing bacteria exhibited an increased yield in moderate saline soils (Ashraf et al. 2004). Inocula made with biofilms were shown to allow their rhizobia survive at high salinity (400 mM NaCl) by 10^5-fold compared to rhizobial monocultures (Seneviratne et al. 2008). Bio-nanotechnology applications which employ nanoparticles made of inorganic or organic materials could also provide new avenues for the development of carrier-based microbial inocula (Malusa et al. 2012).

9.10 Commercially Available Biofertilizer in India and Its Application

Around 170 organizations in 24 countries are engaged in commercial production of biofertilizers. NifTAL (USA) has played a major role in the popularization of *Rhizobium* inoculants. The Philippines implemented the National *Azolla* Action Programme (NAAP) in 1982 to develop farm-based technology for the use of *Azolla* fertilizer for rice. The current global market for organically raised agricultural products is valued at ~US$ 30 billion with a growth rate of ~8%. The organic cultivation represents less than 1% of the world's conventional agricultural production and ~9% of the total agricultural area (Mishra and Das 2014). The Government of India and the different state governments have been promoting the use of biofertilizers. The GOI has been providing the National Biofertilizers Development Centre act Ghaziabad with six regional centres at Bangalore, Bhubaneswar, Jabalpur, Hisar, Imphal and Nagpur. Different commercial available biofertilizers in India are listed in Table 9.5.

9.11 Conclusions

Microbial inoculants have long been incorporated into field practices worldwide. The demand for natural biofertilizers is rising steadily in all parts of the world. Public awareness about the environment is increasing, while the apprehension about pollution and health hazards due to synthetic chemicals especially in rich countries is growing. Significant advances have been made by some Asian countries in the development and use of biofertilizers, but their potential remains largely underutilized due to the difference in efforts and experiences in different countries. Peat

Table 9.5 Microbial biofertilizer available in India

Biofertilizer	Active ingredient	Mode of action	Dose	Manufacturer
A. Phosphate-solubilizing microorganisms				
Grotop PSB powder	Phosphate-solubilizing microorganisms (*Bacillus* sp.), powder 10^7–10^9 CFU g^{-1} and liquid 10^9 CFU ml^{-1}	Solubilize unavailable organic and inorganic forms of phosphorus (80%)	*Seed*: 5–10 g kg^{-1} seed	MD Biocoals Pvt. Ltd., Haryana
			Soil: 0.5–1 kg $acre^{-1}$ along with 40–50 kg manure	
			Foliar: 3 ml l^{-1} water	
Mani Dharma's biopromoter	*Bacillus megaterium* + *Aspergillus niger*	Biopromoter facilitates root formation and plant growth	*Foliar*: 200 g/ 200 ml^{-1} of 'rice kanji' or 5% jaggary water	Mani Dharma Biotech Private Limited, Tamil Nadu
		It improves soil quality with subsequent uses. It should not be mixed with antibacterial agents and inorganic fertilizers		
Multiplex Nalapak	Homogenous mixture of *Azotobacter* + *Azospirillum* + phosphate solubilizer + potash mobilizer	It produces amino acids, vitamins and growth-promoting substances like IAA, GA and cytokines, which help in better growth and development of crop plants. Improves physical, chemical and biological properties of the soil	*Soil*: 500 ml 5 kg^{-1} $acre^{-1}$ along with 100 kg well decomposed FYM	Multiplex Bio-Tech Pvt. Ltd., Karnataka
			Foliar: 10 g l^{-1} water	
Ambiphos	Phosphate-solubilizing microorganism (*Aspergillus niger*)	PSM secretes organic acids, which dissolve unavailable phosphate into soluble form and make it available to the plants	*Foliar*: 3-5 ml l^{-1} water	Ambika Biotech & Agro Services, Madhya Pradesh

Biophos	*Bacillus megaterium* var. *phosphaticum*	PSM secretes organic acids, which dissolve unavailable phosphate into soluble form and make it available to the plants	*Seed*: 5–10 ml kg^{-1} of seed	Biotech International Limited, Delhi
			Seedling: 125–250 ml in 25–50 litre of water as coating, sett treatment 125–250 ml in 60–80 l ha^{-1} for 30 min	
			Soil: 500–625 ml ha^{-1} mixing with 250–375 kg FYM	
BioP-P	Phosphate-solubilizing microorganism (2×10^8 CFU g^{-1})	PSM secretes organic acids, which dissolve unavailable phosphate into soluble form and make it available to the plants	*Foliar*: 3–5 ml l^{-1} water	Sundaram Overseas Cooperation, Gujarat
PSM	Phosphate-solubilizing microorganisms	PSM secrete organic acids, which dissolve unavailable phosphate into soluble form and make it available to the plants	*Soil*: 0.5^{-1} kg $acre^{-1}$ along with 40–50 kg FYM	Shree Biocare India, Shree Biocare Solution Pvt. Ltd., Gujarat
PSM	Phosphate-solubilizing microorganisms	PSM secretes organic acids, which dissolve unavailable phosphate into soluble form and make it available to the plants	*Soil*: 0.5^{-1} kg ha^{-1} along with 100 kg FYM	KRIBHCO, UP

(continued)

Table 9.5 (continued)

Biofertilizer	Active ingredient	Mode of action	Dose	Manufacturer
B. Phosphate-mobilizing biofertilizer				
Mani Dharma VAM	Vesicular-arbuscular endomycorrhiza (VAM)	Solubilize phosphate and supplies P, Zn, Mn, Fe, Cu, Co and Mo to the plants. Increases the plant vigour by inducing drought resistance in young seedlings. Protects the plants from the fungal pathogens	*Soil*: 200 g/m^2 or 2–5 g seedling^{-1}; 50–200 g trees^{-1}; 3–5 kg acre^{-1} (2–3 cm depth)	Mani Dharma Biotech Pvt. Ltd., Tamil Nadu
Ecorrhiza-VAM/ Nurserrhiza-VAM	Arbuscular mycorrhiza	Improved uptake of nutrients, root development and growth in plant	*Soil*: 3–5 kg acre^{-1} with the 200–250 kg FYM, one tablet plant^{-1} in 2–4 inch deep hole near the plant root	TERI, New Delhi
Root care	Mycorrhiza (*Glomus intraradices*)	Improved plant health, uptake of nutrients and reduction of environmental stress	*Soil*: 5 kg acre^{-1}.	Ambika Biotech, MP
Mycorrhizae	105 propagules/kg with carrier material (talc powder/vermiculite)	Mobilize major nutrients like phosphorus and potassium and certain micronutrients like zinc, calcium, etc.	*Soil*: 5–10 kg of VAM ha^{-1} is recommended along with the 1 q of FYM; 25 g plant^{-1}	Dr. Rajan Laboratories, Tamil Nadu
JOSH Super/JOSH Plus	Mycorrhiza (*Glomus intraradices*)	Root development in plant enhance growth	*Soil*: 5 kg acre^{-1} for all crops, 60 infective propagules g^{-1}	Cadila Pharmaceuticals Limited, Gujarat

Shubhodaya	Vesicular-arbuscular mycorrhiza (with three species – (1)isolated from desert and adoptable to harsh water strained condition, (2) adoptable to water lodging conditions and (3) adaptable to general and acidic/basic soil conditions)	Improved uptake of nutrients	*Soil*: 5–10 kg $acre^{-1}$	Cosme Biotech, Goa
TARI VAM	Vesicular-arbuscular mycorrhiza	Mobilize nutrients like phosphorus and zinc	*Soil*: 5–10 kg $acre^{-1}$	TARI Biotech, Tamil Nadu
BioCarry	Vesicular-arbuscular mycorrhiza (VAM)	Helps in efficient mobilization and uptake of fertilizers and other nutrients by plants	*Soil*: 5 kg $acre^{-1}$	Sundaram Overseas Operation, Gujrat
Symbion VAM	Solid formulations of arbuscular mycorrhiza	Improved uptake of nutrients, root development in plant and growth	*Soil*: 5 kg $acre^{-1}$	T. Stanes and Company Limited, Tamil Nadu
CAMBAY's VARDHAK	Arbuscular mycorrhiza (powder and tablets)	Helps in efficient mobilization of nutrients	*Soil*: 5 kg $acre^{-1}$; one tablet $plant^{-1}$	Neesa Agritech Food and Limited
Mycorrhiza – VAM	Arbuscular mycorrhiza	Mobilize nutrients like, P, Zn, Cu and B	*Soil*:10 kg $acre^{-1}$	KCP Sugar and Industries Corporation Ltd
Mycorrhiza-AM Biofertilizer	Arbuscular mycorrhiza	Helps in efficient mobilization of nutrients and improved plant growth	*Soil*: 5 kg $acre^{-1}$	Majestic Agronomics Pvt. Ltd., HP
Colonizer	Arbuscular mycorrhiza (powder)	Colonizes living plants roots. Improves phosphorus uptake and imparts stress and disease resistance	*Soil*: 2–3 kg $acre^{-1}$	Krishidhan Seeds Pvt. Ltd., Maharashtra

(continued)

Table 9.5 (continued)

Biofertilizer	Active ingredient	Mode of action	Dose	Manufacturer
C. Enriched compost				
Multiplex Sagar (Compost Poly Culture)	Homogenous mixture of *Azospirillum* + *Trichoderma* + *Pleurotus*	Nitrogen-fixing potential, biopesticidal activity, enhances compost degradation	*Soil*: 1 kg acre^{-1} along with 1000 kg well decomposed FYM *Foliar*: 100 ml 10 l^{-1} water	Multiplex Bio-Tech Pvt. Ltd., Karnataka
Enriched compost culture	*Trichoderma harzianum*+ *Aspergillus*+*Penicillium*	Enhances compost degradation	*Foliar*: 100 ml 10 l^{-1} water	Organic Biotech Pvt. Limited, Maharashtra
Bio-manure culture	*Trichoderma harzianum*+*Aspergillus*	Enhances compost degradation	*Foliar*: 100 ml 10 l^{-1} water	Uno Natural and Greens Private Limited, Tamil Nadu
LignoBiocompost culture	*Trichoderma reesei*, *Phanerochaete chrysosporium* and *Aspergillus awamori*	Enhances compost degradation	*Foliar*: 75–100 ml 10 l^{-1} water	Peak Chemical Industries Limited, West Bengal

formulations have been developed into effective carriers which are accepted worldwide, but their development has almost reached its limits. It is quite early to declare these carriers as potentially universal due to the lack of information about new developments from research institute. Special attention should be paid to the needs and constraints of developing countries that need easy-to-use and inexpensive formulations as agriculture in developed countries is the major promoter of microbial inoculants that are environmentally friendly. For the future, more research should be focused on the development of better and more economical feasible, synthetic inoculant carriers, while sustaining peat-based inoculant production for agriculture.

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Microbial Diversity of Tropical Andean Soils and Low-Input Sustainable Agriculture Development

10

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and Pablo Quichimbo

Abstract

The Tropical Andes spans over 1,540,000 km^2 from western Venezuela to northern Chile and Argentina and is currently considered the most biologically rich and diverse region on Earth. The rural populations from the Andean highlands depend largely on agriculture and related activities for their livelihoods. In spite of a long history of agriculture in the region, crop production in these highlands is constrained by adverse natural factors such as low soil fertility, rugged terrains, water deficit, and cold climates. In the last decades, a better understanding of the functioning of microbial communities in agricultural soils has led to the development of technologies that could alleviate some of these natural constraints and increase productivity sustainably. A promising approach to take advantage of the functioning of these microbial communities is the development of *bioinoculants*, products containing live or latent cells of agriculturally beneficial strains of microorganisms. When applied to seeds or soils, these bioinoculants boost the populations of beneficial microorganisms in the rhizosphere and accelerate certain microbial processes that result in increased nutrient acquisition by plants and in augmented antagonism to pathogens. A key step in the process of developing this kind of bioinoculants is the study of the indigenous microbial

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biodiversity of the agricultural and natural ecosystems in which these inoculants will be applied, in order to select microbes that are well adapted to the particular conditions of these ecosystems. Here we review the most recent descriptions of the microbial diversity of Tropical Andean soils, the potential use of these microbes for improving the functioning of crop production systems, and important experiences in the development of inoculant technologies in the region.

Keywords
Bioinoculants • Plant growth-promoting microorganisms • Tropical Andes • Sustainable agriculture • Biofertilization • Biocontrol

10.1 Introduction

The Tropical Andes is a vast and diverse territory spanning north to south from western Venezuela to northern Chile and Argentina, next to the Pacific coast of South America. Home to ~70 million people – almost half of the population of the Andean countries – the region represents a melting pot of cultures in which both ancient and modern traditions hybridize (Sandor and Eash 1995; Stanish 2007) (Fig. 10.1a). The livelihoods of the people living in the Tropical Andes are strongly linked to agriculture. Indeed, mixtures of indigenous and introduced crops are cultivated by Andean farmers to satisfy national food demands, in agricultural production systems mostly dominated by smallholders and family farmers (Fonte et al. 2012) (Fig. 10.1b, c).

During the last decades, a tremendous demographic growth in the region has led to unprecedented pressures on natural resources and to an increase of rural poverty and hunger. To satisfy food demands of this growing population, the use of natural resources has been intensified in an attempt to achieve higher productivities. Alas, agriculture in the Andean highlands faces several challenges that limit productivity gains. For instance, besides lacking the financial resources needed to afford fertilizers, pesticides, irrigation systems, machinery, and/or improved crop varieties, small Andean farmers must frequently deal with harsh climate conditions and nutrient-limited soils (Fonte et al. 2012). These production conditions have caused many farmer families to suffer food shortages of varying degrees, exacerbating the poverty-resource degradation-scarcity-poverty cycle (Jodha and Shrestha 1993; 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).

It is, therefore, imperative to explore new options aimed at increasing the productivity and carrying capacity of farms, in order to improve the livelihoods of Andean farmers and allowing them to compete favorably in the modern world without causing further environmental degradation (Partap 1999). Among these options, the Food and Agriculture Organization of the United Nations identified the following: (1) cultivation of high-value cash crops (like fruits and vegetables), (2) adoption of sustainable farming practices (which avoid the abuse and misuse of synthetic

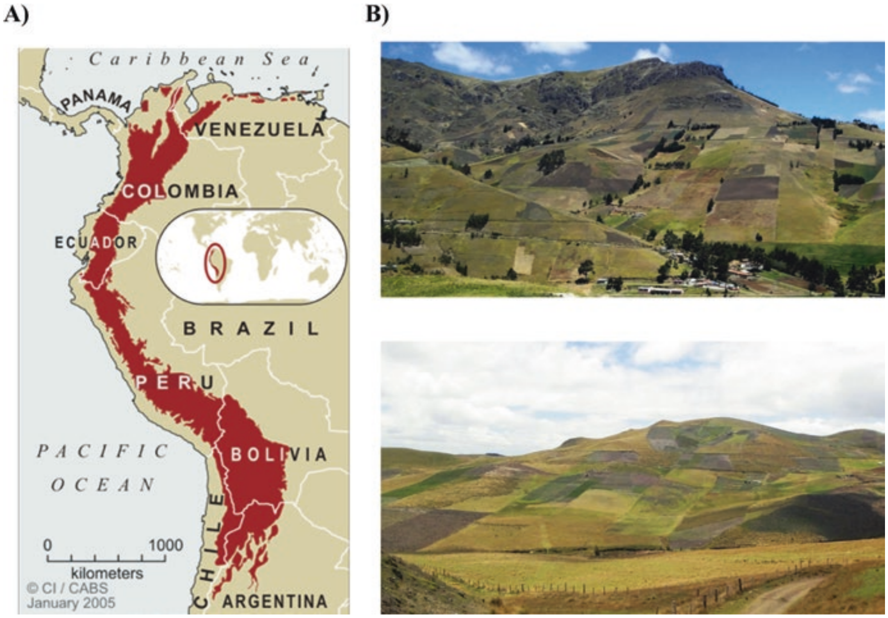

Fig. 10.1 (**a**) The Tropical Andes Region. ©2005 CI/CABS (Reproduced with permission of Critical Ecosystem Partnership Fund). Available at: http://www.cepf.net/where_we_work/regions/south_america/tropical_andes/Pages/default.aspx. (**b**) Small farms in the Andean region of Ecuador (Highlands or Páramos). Copyright: Luis Andrés Yarzábal (Reproduced with permission)

agrochemicals and fertilizers), and (3) rescue of native species, varieties, and breeds known as neglected crops, which have played an important role in the human diet and traditional cultures for millennia (FAO Reports 2003, 2013).

A complementary and promising strategy for improving the agricultural productivity of Andean farms – without serious social, economic, or environmental impacts – is the proper use of biotechnological products, such as *bioinoculants* (also termed microbial inoculants). A bioinoculant can be defined as a product containing individual strains or consortia of known microbes that have plant growth-promoting effects (plant growth-promoting microorganisms; PGPM) when added directly to the soil or as a seed coating during planting (Owen et al. 2014). Among currently used bioinoculants, we can mention commercial formulations containing nitrogen-fixing bacteria (NFB or N-fixers), phosphate solubilizing bacteria (PSB), and/or mycorrhizal fungi (MF).

The use of such kind of bioinoculants has allowed to increase agricultural productivity and sustainability worldwide, without harming the environment (Fuentes-Ramírez and Caballero-Mellado 2006; Singh et al. 2011a; Velivelli et al. 2014a), thus becoming a real alternative to synthetic agrochemicals. Contrary to the general opinion, adoption of bioinoculants by the local farmers in underdeveloped countries, particularly in the Andean region, can be achieved successfully and perceived favorably if adequately planned and addressed. More importantly, in the long-term, the use of bioinoculants, together with appropriate land management and selection of suitable cultivars, may positively impact the livelihoods of individual farmers and their families (Meena et al. 2016a, b; Parewa et al. 2014; Prakash and Verma 2016; Jha and Subramanian 2016; Kumar et al. 2016a).

10.2 The Agricultural Landscape of the Tropical Andes

The Tropical Andes hold an old and rich tradition in agriculture. Alongside Central America, the Tropical Andes are considered the cradle of agriculture in the Americas, with archeological evidence of farming dating back to ~9000 years before the present (Dillehay et al. 2007; Piperno 2011). Dominated mainly by the influence of the Inca Empire (*Tawantinsuyu*) formed by the assimilation of different peoples, just prior to the arrival of European conquistadores, agriculture in the Tropical Andes exhibited an advanced degree of ecological specialization and technological intensification that allowed cultivation on steep mountain slopes. Inca agriculture took advantage of the natural altitudinal gradient formed in the slopes of the Andes, to cultivate crops with different temperature requirements in a highly organized fashion that allowed feeding a population of about eight million at its height (Borsdorf and Stadel 2015).

Water and soil management was an important issue in Inca agriculture, and several strategies such as long-distance irrigation canals (*acequias*), raised bed (*waru-waru*), sunken fields (*qochas*), and field terraces (*andenes*) were used to conserve these resources (Borsdorf and Stadel 2015). Incan farmers managed also practices such as intercropping (*chacras*), crop rotation, and planned fallows to maintain and restore soil fertility and point manage the incidence of pests (Borsdorf and Stadel 2015; Pestalozzi 2000). To date, many of these traditional agricultural practices are still commonly used among Andean farmers.

Modern agriculture in the Tropical Andes is hard to define because of the diversity of technologies and traditions it is made of. Different criteria could be used to classify these production systems (Borsdorf and Stadel 2015; Mulligan et al. 2009); however, by integrating several of these criteria, three broad categories can be identified, namely, (1) smallholder commercial and subsistence farms, (2) large-scale commercial export-oriented farms, and (3) managed pastures and rangelands. These three systems are roughly distributed along an altitudinal gradient, with large farms located at lower altitudes, where soils are more fertile, and small farms and pastures located at higher altitudes, on marginally fertile lands. These systems also differ among themselves in terms of their demand for external inputs, their impact on natural resources, their productivity and their level of technological intensification (Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Meena et al. 2015a; Jaiswal et al. 2016).

By large, agriculture in the Tropical Andes is dominated by smallholder commercial and subsistence farms. These farms concentrate around towns and cities, in the valleys, on hillslopes, and in the high plateaus (*altiplanos*) up to ~4200 m asl (Borsdorf and Stadel 2015; Mulligan et al. 2009) (Fig. 10.1b, c). Agricultural

Table 10.1 Commercially cultivated crops in Tropical Andean agricultural production systems

Smallholders farms		Large-scale farms	Pastures and rangelands	
Native cultivars	Introduced cultivars		Forages	Livestock
Corn	Tomato	Rose	Kikuyu	Cattle
Bean	Peppers	*Gypsophila*	Ryegrass	Sheep
Potato	Broccoli	*Hypericum*	Alfalfa	Goats
Squash	Cauliflower	Tomato	Clover	Llamas
Quinoa	Cabbage	Broccoli		Alpacas
Amaranth	Radish	Alcachofa		Vicuñas
Oca	Spinach	Sugarcane		
Mashwa	Onion			
Ullucus	Lettuce			
Chili pepper	Carrot			
	Coffee			

production in these farms is devoted to local and national markets and to self-consumption by farmer families. In general, a greater share of agricultural production is used for self-consumption in upland communities that are farther away from urban centers (Mulligan et al. 2009).

Although productivity in these smallholder farms is low compared to large-scale commercial farms, they supply most of the national demand of fresh fruits and vegetables in their corresponding countries and, thus, have a significant socioeconomic impact (Devenish and Gianella 2012). Crops cultivated in these small farms are highly diverse and represent a mixture of native and introduced crops (Table 10.1), which are cultivated using a combination of traditional practices and modern technology. However, low productivity, inappropriate adoption of production practices and technologies, and lack of research oriented to understand and improve these production systems threaten the sustainability and environmental health of these small farms (Bojaca et al. 2010; Cole et al. 2011).

In contrast with smallholder farms, large-scale commercial and export-oriented farms in the Tropical Andes are concentrated almost uniquely in the warmer valleys. The main crops cultivated in these systems are vegetables (e.g., broccoli, artichoke, tomato, peppers, lettuce), cut flowers (e.g., roses, *Gypsophila*, *Hypericum*), and sugarcane. The production of these systems is destined in part to supply national supermarket chains, but the majority of it is exported to foreign markets. These systems exhibit high productivity and intensification and contribute to rural economies by providing rural employment and generating external revenue; however, they generate a larger environmental impact than small farms and increase the dependence on external inputs (Mulligan et al. 2009). In the last decades, market preferences and environmental regulations have promoted the introduction, in many of these large-scale operations, of practices that reduce the negative impacts they generate on the environment (Raghavendra et al. 2016; Zahedi 2016; Meena et al. 2015b, f; Rawat et al. 2016; Yasin et al. 2016).

The third type of agricultural production system in the Tropical Andes is the managed pastures and rangelands for livestock grazing. These systems can be found typically at greater elevations (>3000 m asl) on mountain slopes and high plateaus up to ~4500 m asl (Borsdorf and Stadel 2015). The most common species managed in these systems are dairy cattle, sheep, goats, and Andean cameloids (llamas, alpacas, and vicuñas) (Borsdorf and Stadel 2015). Among these species, dairy cattle are the most commercially important species in the Tropical Andes. Both large and small dairy cattle farmers (2–30 cattle) with different levels of technological intensification coexist in the Tropical Andes (Aubron et al. 2009). Most of the dairy cattle are fed on rangelands or on crop residues, with few farmers actually establishing and managing pastures and fodder crops (Aubron et al. 2009).

In certain parts of the Peruvian and Bolivian Andes, elaborated long rotations (~12 years) of crops (potato, quinoa, oats, barley) and fallows are used (Pestalozzi 2000). Common fodder crops used by dairy cattle ranchers are kikuyu, ryegrass, clover, and alfalfa, whereas common breeds include Holstein, Brown Swiss, and Criollos (Aubron et al. 2009). Historically, cattle farming in the Tropical Andes has been one of the main drivers for the deforestation and ecosystem degradation since native forests are normally cleared to create new rangelands and later abandoned when productivity starts to decrease (Lozada 2006). These abandoned rangelands are difficult to recover either to reestablish commercial production or for restoring the original ecosystem (Posada et al. 2000).

Agricultural production systems in the Tropical Andes are also strongly influenced by local natural and cultural factors. Depending on their location and the scale of operations, different systems show different levels of sophistication in terms of cultural practices and inclusion of technology, which in turn affect the sustainability of these systems. Being the most numerous, a better understanding of the functioning of smallholder production systems, as well as their optimization and sustainable intensification, would have a greater overall impact on the sustainability of agriculture in the Tropical Andes in the face of emerging challenges (Devenish and Gianella 2012; Fonte et al. 2012; Haller 2014; Mulligan et al. 2010).

10.3 Andean Soils

The Tropical Andes exhibits a high diversity of soil types (Gardi et al. 2014), whose detailed description goes beyond the scope of this chapter. However, considering that the most vulnerable population (small farmers) are established in the Andean highlands (over 2500 m asl) (Fonte et al. 2012) and that they depend mostly on agriculture for their livelihoods, it is of the utmost importance to describe some characteristics of the most representative soils in this region.

Soils in the Tropical Andes can be defined as those located between the Tropic of Cancer (23°26′16″N) and the Tropic of Capricorn (23°26′16″) (Gardi et al. 2014) and above 2500 m asl. Alpine soils dominate above the tree line and, among them, páramo soils stand out, with Andosols as the most extended soil type (Poulenard and Podwojewski 2006; Podwojewski and Poulenard 2006). Nevertheless, Histosols, Leptosols, and Regosols are also present (Buytaert et al. 2011), mainly in large extensions at the Puna highland region of the Central Andes (Gardi et al. 2014; Ochoa-Tocachi et al. 2016).

Andosols are, in essence, volcanic ash soils (Shoji et al. 1993). These soils exhibit different features depending on the factors present during their formation. For example, zones of Holocene (with materials from recent glaciations) and Pleistocene (older glaciers) deposits have promoted the development of allophanic and non-allophanic Andosols, respectively (Poulenard et al. 2003; Harden 2007). Topography and vegetation are other important key factors involved in the formation of these soils: for instance, according to Zehetner et al. (2003), additions of high amounts of organic matter from the páramo vegetation in combination with its slow decomposition rate promoted the presence of allophanic materials over 3200 m asl in the Ecuadorian Andes. However, as altitude decreases, those allophanic materials transformed into other types of colloids – like halloysites – thus modifying the properties of Andosols to such a degree that they transformed into Entisols or Inceptisols.

Human activities commonly performed in Andean páramos – such as burning, grazing, cultivation, and afforestation – also affect the variability of Andosols. Although Andosols present a good physical fertility due to their high water retention capacity, good hydraulic conductivity, and low bulk density (Podwojewski and Poulenard 2006; Buytaert et al. 2011), they seriously limit agriculture development owing to their strong capacity to fix phosphate ions, their low pH, and their high aluminum content (Saigusa and Matsuyama 1998; IUSS Working Group WRB 2014).

10.4 Soil Microorganisms and Agriculture

According to Rajendhran and Gunasekaran (2008), microbial communities are the *architects* of soils. Indeed, the formation of fertile soils from bedrock implies a complex interaction of physical, chemical, and biological processes, with microbes playing a paramount role catalyzing the weathering of mineral surfaces. Soil microorganisms play also a significant role in the major global biogeochemical cycles, regulating the dynamics of organic matter decomposition and – consequently – the availability of plant nutrients such as N, P, and S (De La Peña and Loyola-Vargas 2014).

Even though many such microorganisms are found in the bulk soil, the majority of them thrive in the rhizosphere (i.e., the zone surrounding and influenced by root exudates). In fact, plant roots are able to recruit soil bacteria by secreting a panoply of molecules (sugars, amino acids, flavonoids, etc.) that act as attracting signals (Zhang et al. 2014). In this densely populated environment, microorganisms interact with plants in several ways: whereas some of these microorganisms are pathogens that cause plant diseases and consequently reduce productivity, many others act positively on plant growth and development, through direct or indirect mechanisms, and are collectively known as “plant growth-promoting microorganisms” (PGPM). While some PGPM exert their positive effect by inhibiting or antagonizing plant pathogens (termed "bioprotectants" or "biocontrollers"), others promote plant growth either by releasing phytohormone-like metabolites ("biostimulants"), by mobilizing mineral nutrients such as N and P ("biofertilizers"), or by activating the plant defense systems ("bioelicitors") (Glick 2012). Another group of microorganisms promote indirectly plant growth by degrading toxic xenobiotics ("bioremediators"). Very often, a single microorganism can stimulate plant growth by a combination of these activities (Meena et al. 2016c, d; Saha et al. 2016a; Yadav and Sidhu 2016; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016).

Although there are still many uncertainties on the exact mechanism through which PGPM promote plant growth in different crops and under different environmental conditions, it is supposed that this effect might be based on interactions among biotic (nutrient supply, competitiveness, rate of multiplication, etc.) and abiotic (temperature, humidity, soil pH, etc.) factors (Lucy et al. 2004). It is also becoming clear that the plant growth-promoting traits involved do not work independently of each other but additively (Ahemad and Kibret 2014).

The rational use of PGPM in the field of agriculture is nowadays a well-established technology that has permitted to reduce significantly the use of fertilizers and pesticides – and, consequently, drastically lowered production costs – but also minimized the risk of deleterious and hazardous environmental impacts caused by the misuse and abuse of agrochemicals (Adesemoye et al. 2009). In this context, PGPM are of paramount importance for the development of sustainable agriculture practices. For example, nitrogen-fixing bacteria (NFB) are widely used to enhance crop yield, particularly through the improvement of root nodulation and biological fixation of N_2 in legumes (Herridge et al. 2008). Another important group of PGPM, phosphate solubilizing bacteria (PSB), is also used, but less frequently. These bacteria have the ability to readily and efficiently solubilize mineral forms of P making them available for plant uptake (Saha et al. 2016b; Verma et al. 2014, 2015b; Meena et al. 2014a, 2015e; Teotia et al. 2016; Bahadur et al. 2016b; Das and Pradhan 2016).

Several mechanisms are employed by PSB to perform this inorganic P solubilization, although the details are beyond the scope of this chapter. However, it is important to highlight the production and excretion of large amounts of organic acids like gluconic and keto-gluconic acids (in the case of Gram-negative bacteria, mainly produced through the direct oxidation pathway of glucose) or citric acid (in the case of fungi) (Jones 1998; Rodríguez and Fraga 1999). These acids mobilize P from Fe or Al oxides by efficiently chelating the metal ions, particularly in acidic soils (Johnson and Loeppert 2006).

When considering P mobilization in the rhizosphere, another very important group of PGPB has to be mentioned: organic P-mineralizing microorganisms. These microbes hydrolyze organic forms of P (phosphate esters, phosphonates, and anhydrides) by secreting specific enzymes (mainly phosphatases) to release PO_4^{2-} (Turner et al. 2006; Richardson and Simpson 2011). This process, called "substrate mineralization," is very often underestimated in spite of being essential to release plant-available orthophosphate. Some microorganisms are capable of simultaneously solubilizing inorganic P and mineralizing organic P (Oliveira et al. 2009).

Among the many microorganisms able to promote plant growth and development, arbuscular mycorrhizal fungi (AMF) deserve a special place. Estimated to be present in up to 80% of all terrestrial plant species, arbuscular mycorrhiza is the most frequent type of symbiosis established between plants and members of the *Glomeromycota* phylum (Wang and Qiu 2006; Brundrett 2009). More than 225 species in this phylum have been described; however, it is likely that this number does not reflect the actual richness of AMF (Kivlin et al. 2011).

AMF colonize cortical cells of the roots of vascular plants where they develop their characteristic arbuscular structures that allow nutrient exchange between the host plant and the fungus. By extending the volume of soil that can be explored by AMF hyphae (*soil scouting*), these fungi help their host plants to reach distant nutrients – primarily phosphorus but also sulfur, nitrogen, and micronutrients – and to uptake and transfer water (Parniske 2008; Baum et al. 2015). Additionally, they can alleviate plant biotic and abiotic stresses (Gianinazzi et al. 2010; Singh et al. 2011b) and also act as biocontrollers of a wide range of pathogens, mostly fungi but also bacteria and nematodes (Harrier and Watson 2004; Whipps 2004; Jung et al. 2012; Schouteden et al. 2015). In addition to the direct benefits provided to their host plants, AMF also favors plant growth and development by improving soil structure and aggregation through the formation of an intricate network of hyphae and an abundant secretion of exopolysaccharides (Wright and Upadhyaya 1998) (Fig. 10.2).

10.5 PGPM Prospection in the Tropical Andean Region Context

Many of the abovementioned types of PGPM have been tested both in greenhouse and field trials and proven to be very efficient at promoting plant growth (Glick 2012). Consequently, numerous commercial PGPM-based biofertilizers have been developed and are currently marketed worldwide. However, their effectiveness in the soil-plant system is uncertain, particularly under field conditions. Still, they remain a very attractive alternative to chemical fertilizers and pesticides, particularly in less developed regions (Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b, 2016e; Masood and Bano 2016).

Often, commercial products formulated from exogenous PGPM result in poor performances when applied to different crops. This is frequently due to a low survival rate of exogenous microbial strains when applied to soils different than those from which these strains were isolated. Among the reasons explaining this phenomenon, we can mention (1) the different edaphic characteristics or climatic conditions these microorganisms encounter, (2) a fierce competition by better-adapted indigenous microorganisms during plant colonization, and/or (3) predation by other microorganisms (Bashan 1998). Therefore, in order to guarantee an adequate performance of bioinoculants, isolation and screening of indigenous PGPM strains are more than justified (Shrivastava et al. 2016; Velazquez et al. 2016; Meena et al. 2015c; Bahadur et al. 2016a).

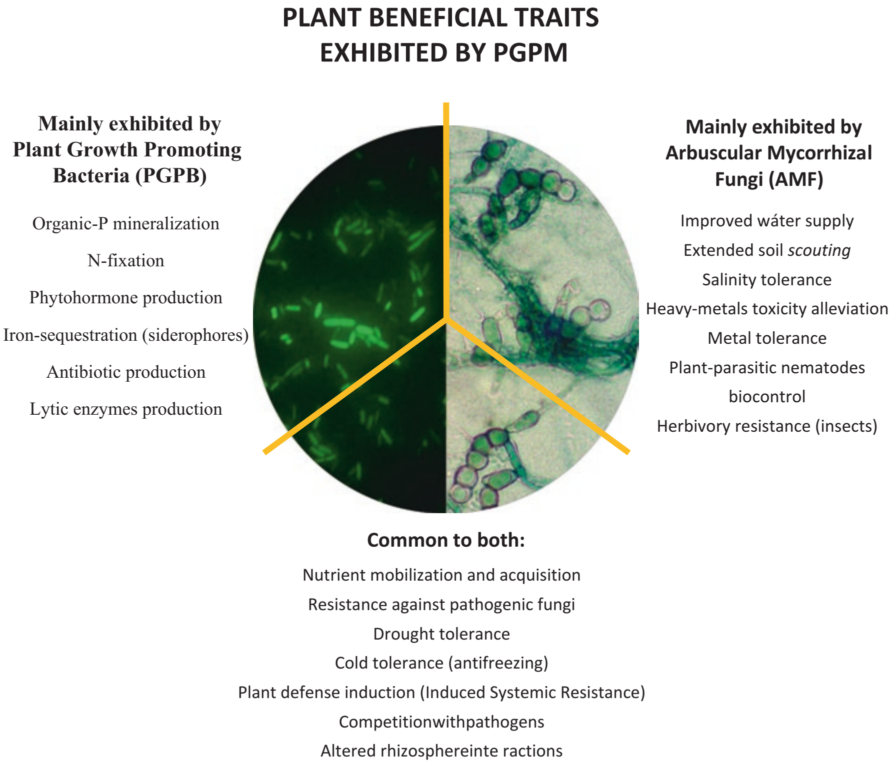

Fig. 10.2 Prominent plant-beneficial traits exhibited by rhizospheric soil microorganisms. Some of the most important functions performed by these microorganisms are also included

Traditionally, this prospection has been performed by first analyzing the soil characteristics where the plants will be grown and taking into consideration their specific requirements, to identify then the required bacterial traits that might be beneficial to these particular conditions. Following such a scheme, Andean environments have been increasingly prospected during recent years to isolate and characterize potential indigenous PGPM in order to develop new biotechnological products, well fitted to increase crop yields under the particular environmental conditions of the Andes. Since most of these microorganisms are frequently associated with plant roots, several research groups have focused on studying the microbiology of the rhizosphere of the most important food crops in the Central Andes. The cases of potato and quinoa are reviewed in the following pages considering their relevance in terms of global markets, food security, and tradition (Sindhu et al. 2016; Meena et al. 2014b, 2015d; Singh et al. 2015, 2016; Meena et al. 2013c).

10.5.1 PGPM and Potato

With a worldwide annual production of ~385 Mt per year (FAO Stat 2014), potato (*Solanum tuberosum*) is the fourth most important food crop after maize, wheat, and rice and is considered critical for food security in an increasingly populated world (Birch et al. 2012). Potato, which originated in the highlands of Peru and Bolivia, has been cultivated locally by farming communities for centuries (Spooner et al. 2005) and is nowadays the main staple crop in the Andes Mountains.

Potato plants are often grown at high altitudes under harsh climatic conditions and in fields where nutrients are often unavailable due to high soil acidity, which may explain why their average production yields are so low. Because it requires large inputs of expensive chemical fertilizers, the productivity of potatoes in small farms is severely constrained. Additionally, fungal diseases that affect potato yield and tuber quality (such as late blight, black scurf, and dry rot) are still common in the Andes (Finckh et al. 2006). The aforementioned reasons explain why researchers have devoted great efforts to characterize the microbes colonizing potato root system in order to search for potential growth promoters and biocontrollers.

The International Potato Center – founded in 1971 with the aim of delivering sustainable solutions to the pressing world problems of hunger, poverty, and the degradation of natural resources (www.cipotato.org) – implemented in 2005 a strategy directed toward exploring the use of rhizobacteria to improve potato production in a sustainable way. The final goal of this project was to develop biofertilizers for small-scale farmers in the Central Andean Highlands. Initial studies were performed with commercial products based on either a Peruvian strain of *Azotobacter* sp. (Azotolum from Peru) or a *Bacillus subtilis* strain from Germany (FZB24). In a field trial performed at 4000 m asl, biofertilization of three Peruvian potato varieties – Yungay, Putis, and Queccorani –increased tuber yields by up to 25% compared to the control plants (Oswald et al. 2007). In a second field trial, performed at 3200 m asl, a total of 23 potato varieties – mainly Peruvian potato landraces – were planted and biofertilized. The results were not as clear-cut as the previous ones, and different responses to PGPB were observed depending on the potato variety (Oswald et al. 2007).

Following these encouraging results, bacteria colonizing the rhizosphere of potatoes were subsequently isolated from rhizospheric soils sampled in different provinces of the Peruvian Andes, tested in vitro for their PGP abilities, and inoculated to potatoes grown in aeroponic systems (Calvo-Vélez et al. 2008; Calvo et al. 2009). The results obtained showed significant increases in tuber numbers per plant, ranging from 40% to 100%, depending on the potato cultivar (Oswald and Calvo 2009). In a follow-up of this work, Oswald et al. (2010) isolated bacteria from the rhizospheric soil of potatoes cultivated in Huancavelica and Puno, at locations situated between 3900 and 4200 m asl in the Central Andean Highlands of Peru.

On the basis of the PGP activities recorded in vitro, 56 isolates – belonging to the genera *Bacillus* and *Azotobacter* and actinomycetes – were selected for a pot experiment conducted under greenhouse conditions and including seven commercial potato varieties. Inoculation of plants with more than 80% of these strains increased total plant and tuber weights between 50% and 200%. Using some of these strains, a field trial was conducted in Puno (3820 m asl), where the authors recorded higher tuber yields in inoculated potato plants than those obtained in the uninoculated controls.

The characterization of bacteria colonizing the rhizosphere of potato was also performed by other research groups in Peru. For example, Calvo and Zuñiga (2010) and Calvo et al. (2010) studied the PGP abilities of several *Bacillus* sp. strains, formerly isolated in the highland Peruvian regions of Huancavelica and Puno – Titicaca Lake – at 3900–4200 m asl by Calvo-Vélez et al. (2008). Besides exhibiting several PGP characteristics in vitro, the isolates inhibited growth of *R. solani* and *F. solani.* Taken together, the results showed the potential of these strains to develop PGP inoculants.

More recently, Ghyselinck et al. (2013) investigated the bacterial communities colonizing potatoes grown at different altitudes in the Central Andean Highlands of Peru and Bolivia. Fifty eight strains out of 585 isolates exhibited antagonism against *R. solani* and *P. infestans*. Additionally, 14 isolates (belonging to the *Pseudomonas koreensis* subgroup, the *P. fluorescens* subgroup and the *Bacillus* genus) protected potato plantlets challenged with *R. solani*. On the other side, 12 strains significantly increased plant growth and development when tested in vitro. These results clearly indicated that some of these isolates might be used to develop new biocontrol products.

Field trials to investigate the effects of PGPM on potato productivity were also conducted in the Andean region of Bolivia, particularly at Lope Mendoza (3440 m asl, Carrasco Province), Tiraque highlands (3453 m asl, Tiraque Province), La Villa (2650 m asl, Cochabamba Province), and Colomi (3200 m asl, Chapare Province) (Franco et al. 2011). In these trials, native isolates of *B. amyloliquefaciens* and *B. subtilis*, as well as a commercial *B. subtilis* strain (FZB 24WG), were tested as single microbial treatments on the native potato cultivar Waycha (*S. tuberosum* sub-sp. *andigena* Hawkes) with the participation of local farmers. Treatments combining native *B. subtilis* strains with organic amendments resulted in superior and uniform plant emergence, higher plant vigor and development, improved plant health, and higher yield of tubers. Also, a suppressive effect on the incidence of *R. solani* in tubers was observed. The commercial *B. subtilis* strain did not perform well in regard to plant growth and yield.

Aside from the beneficial effects of PGP bacteria on potatoes, it has been repeatedly shown that AMF can also promote potato production (Hijri 2016). These benefits do not only rely on the ability of AMF to increase nutrient uptake (mainly P) by plant roots, but also has to do with an enhanced water uptake, a greater disease resistance, and a significant alleviation of cultural and environmental stresses (Berruti et al. 2015). However, these benefits depend on several factors among which we can mention the potato genotype (Vosatka and Gryndler 2000), the AM fungal species or strain (Davies et al. 2005a), and the soil P levels (Herrera-Peraza et al. 2011).

Whatever the case, positive responses of *S. tuberosum* were recorded by McArthur and Knowles (1993) after inoculation with AMF, in experiments conducted in growth chambers under P deficiency. Following these initial observations, some early studies were performed in Peru and Colombia (Moreno Díaz 1988; Sieverding et al. 1991). The results confirmed the positive effects of AMF inoculation on potatoes; however, at least in one of these studies, nonnative AMF isolates were used.

In which can be considered as the first report of its type, Davies et al. (2005a) used a mixed inoculum of Andean native strains of *Acaulospora* sp., *Glomus* sp., *Scutellospora* sp., *Gigaspora* sp., and *Sclerocystis* sp. as biofertilizers to inoculate plants derived from minitubers of Yungay potatoes – an important Peruvian cultivar. The mycorrhizal inoculation resulted in enhanced growth and yield of plants at low P supply as compared to uninoculated controls. Furthermore, direct application of a flavonoid produced by a number of plants (formononetin), previously shown to enhance AMF sporulation and effectiveness of mycorrhizal plants, induced greater extra-radical hyphae formation and a better development of plants and tubers.

The positive effect of formononetin on potato production was further assessed in a field study conducted at 3900 m asl in San Jose de Aymara (Department of Huancavelica), in the central highlands of Peru (Davies et al. 2005b). The production site had very acidic soil (pH 3.6), with low P availability and high Al content. In this case, six Andean potato cultivars were treated directly with formononetin applied as a soil drench when shoots began to emerge from tubers. The treatment did not only induce greater soil sporulation levels of naturally occurring AMF (predominantly *Gigaspora*, *Glomus*, and *Scutellospora*) but also increased tuber dry mass and/or grade quality in three out of six cultivars. This particular form of *biostimulation* demonstrated the possibility of using a radically different approach to reach more cost-effective levels of AMF inoculums, rather than solely relying on indigenous AMF present in the soil of the crop production site.

The development of mixed bioinoculants, combining the PGP abilities of bacteria and the biocontrol capacities of some particular fungi, is another promising approach to increase the yields of different crops. For instance, co-inoculation trials of potato cultivars Waycha (*S. tuberosum* sub-sp. *andigena* Hawkes) and Desiree (*S. tuberosum* sub-sp. *tuberosum*) with *B. subtilis* and the AMF *Glomus fasciculatum* allowed a significant increase in tuber yield and a suppressive/inhibitory effect on soilborne diseases, when assayed in the field (Franco et al. 2011).

The positive effect of mixed bioinoculants was also demonstrated by Pérez et al. (2015). In this work, the authors monitored the effect of bioinputs on 15 native potato cultivars' tolerance to drought stress, at 3309 m asl in Cochabamba (Bolivia). Even though application of poultry manure to potatoes during planting reduced the severity of drought injure and increased the yield, the combined use of earthworm humus and Mibac (a commercial product that combines native strains of *B. subtilis* and *G. fasciculatum*) permitted also to record satisfactory results on both parameters, even though some of the responses were cultivar dependent.

In light of these results and in collaboration with PROINPA, a Bolivian national foundation dedicated at promoting the sustainable use of natural resources through research and innovation, a biofertilizer was formulated with a native isolate of *B. amyloliquefaciens* and used by farmers dedicated to organic production both as a single treatment or mixed with *G. fasciculatum* and vermicompost.

10.5.2 PGPM and Quinoa

Quinoa (*Chenopodium quinoa* Willd.) is another economically important and ancestrally grown crop in the Central Andes. Exceptionally rich from a nutritional point of view, this seed crop – whose grains may even surpass the nutritional values recommended by the World Health Organization (WHO) (Hirose et al. 2010) – has been cultivated in the Andes for thousands of years. It is currently considered a food security crop, especially in the face of the predicted future world scenario of increasing salinization and aridity. Indeed, owing to its exceptional tolerance to abiotic stresses – including frost, salinity, and drought – quinoa is remarkably well adapted to the harsh conditions prevailing in the high Andean mountains (Ruiz et al. 2014). Quinoa grows satisfactory in Andean poor soils; however, to reach adequate levels of production, some amendments are applied including animal and green manures (Jacobsen 2011). The crop has been traditionally grown by small farmers in the Andes and the ancestral knowledge is passed through generations from parents to children. However, in recent years, increasing worldwide demand for quinoa and the subsequent industrial development associated to it are putting in danger this cultural and biodiversity legacy (Jacobsen 2011).

Preservation of small-scale farming in order to continue cultivating quinoa in a sustainable way requires a multidisciplinary approach. Even though according to some authors quinoa is an under-researched and neglected crop (Rojas et al. 2009), some efforts have been made in order to promote organic production of this grain in Andean countries like Bolivia. For instance, Ortuño et al. (2013) reported the development and successful use of bioproducts consisting of mixtures of biofertilizers and biocontrollers, to reduce the harmful effects of chemical fertilizers and pesticides in the environment and to produce quinoa free of contaminants and at lower costs.

In which can be considered the first report on its type, suitable microbes for stimulating quinoa production were isolated and characterized by Ortuño et al. (2013, 2014). Two microbial strains (*Bacillus* sp. and *Trichoderma* sp.), exhibiting PGP- and antagonistic abilities, were large-scale produced in simple and inexpensive culture media and then formulated to obtain bioproducts that were distributed among local farmers. When tested in the field, the bioproducts increased quinoa yield compared to the untreated controls. Besides, inoculated plants exhibited a healthier and more vigorous appearance than untreated plants.

10.6 *Omic* Technologies and Agriculture Development in the Andean Region

Until now, prospection of the microbial communities colonizing Andean crops has relied on culture-based techniques. Consequently, the major flaw in these studies is that the great majority of microbes – the *unculturable* ones – remain to be identified and their functions revealed. Therefore, our understanding of these communities and their changes over time, plant species and age, soil properties, and/or management is at its infancy.

Phenotypic and genotypic approaches are currently available to characterize soil microbial community structures. *Metagenomics*—defined as the direct genetic analysis of genomes contained within an environmental sample—provides access not only to the microbial diversity of a given community (the so-called phylogenetic surveys) but, more importantly, also to the functional gene composition of microbial communities (Thomas et al. 2012). For example, in a recent study based on pyrosequencing, Barnett et al. (2015) studied the variability of the potato root-associated bacterial community with regard to different locations and potato clones. From a total of 26 potato clones collected at three sites, 123 bacterial operational taxonomic units (OTUs) were correlated with tuber yield and/or tuber nutrient content, a majority of them belonging to the order *Rhizobiales*. Interestingly, 23 of these bacterial OTUs were present in at least 50% of samples at each site and, therefore, were considered as part of a core *bacteriome* likely involved in supporting potato crop health.

With a similar objective in mind, two studies were conducted in three different Andean countries (Peru, Bolivia, and Ecuador), at different altitudes (from 2658 to 4075 m asl), and at three potato plant developmental stages (emergence, flowering, and senescence) (Senés-Guerrero et al. 2014; Senés-Guerrero and Schüssler 2016). In both studies, the AMF communities associated with potatoes were described, although the methods used differed: the first report relied on soil DNA extraction, PCR amplification, cloning and sequencing of selected molecular markers (SSU, LSU, and ITS region), while the second report was based on metagenomic analyses of LSU rRNA gene PCR amplicons by pyrosequencing methods (454-GS FLX+).

According to the results of the first study, potato plants were colonized by diverse species from 8 of the 11 *Glomeromycota* families, a much higher AMF diversity than those reported for potato in other ecosystems (Senés-Guerrero et al. 2014). Besides, the composition of the AMF community was affected by potato plant developmental stages, and most of the AMF species detected in potato roots at the emergence stage did not persist during later stages. Contrary to what is characteristic in other alpine environments, the highest AMF diversity occurred at the highest altitude (4075 m asl) in both soil and root samples. The study also highlighted the importance of three OTUs – namely, *Funneliformis mosseae*, an unknown *Claroideoglomus* sp., and *Rhizophagus irregularis*, easily cultivable generalists which colonize early plant developmental stages, as promising candidates for the development of biofertilizers for sustainable potato agriculture.

The second work cited analyzed in depth, for the first time, the composition of the AMF community colonizing Andean potatoes (Senés-Guerrero and Schüssler 2016). In this study, the SSU-ITS-LSU rRNA gene region used was defined as an extended DNA barcode which allowed resolving closely related AMF species (Stockinger et al. 2010; Schoch et al. 2012). Following this methodology, the results showed that almost 92% of the individual root systems studied contained between 1 and 25 AMF species. Additionally, OTU analyses clearly revealed that the AMF community structure varied according to altitude, plant stage, or plant variety.

Of the 41 species detected in total, *Acaulospora* spp. were identified as dominant colonizers (present in 85% of the samples); it was also established that species of this genus co-occurred with *Cetraspora nodosa* and certain *Claroideoglomus* and *Rhizophagus* species in most potato root samples. Surprisingly, these species were relatively conserved throughout the rhizosphere of plants collected in the studied region, even though some samples were collected at distant locations (>3000 km distance). Therefore, as stated before, these AMF species were considered as belonging to a conserved core-species community of native potatoes in the Andes. According to the authors, identification and characterization of some of these yet unnamed AMF species would facilitate the selective design of AMF-based bioinoculants with the purpose of improving sustainable agricultural practices.

Even assuming that the great majority of microorganisms colonizing the rhizosphere of important crops belong to the unculturable category, there is no doubt that the information gained through metagenomic approaches will certainly shed more light on the potential use of this microbial source for biotechnological purposes. In fact, it is increasingly acknowledged that these so-called unculturables might be cultured in vitro if key factors influencing colony formation are appropriately optimized (Stewart 2012). Improvement of culturability of these hitherto-unculturable microorganisms will presumably reveal a range of novel important functions in the rhizosphere, including functions involved in enhancing crop growth and development as well as rhizosphere competence of microbes (Nunes da Rocha et al. 2009).

Among the *omic* technologies, ***metabolomics*** – defined as the systematic identification and quantification of all low molecular weight molecules present in the cells in a particular physiological or developmental state and which constitute the end products of cellular processes – can also play an important role in identifying potentially useful microbes to develop bioinoculants. Besides allowing understanding, at least in part, the complex interactions and chemical *conversations* and *warfare* established among the biological partners which colonize the rhizosphere (Persello-Cartieaux et al. 2003), metabolomic techniques also allow to detect microbial metabolites involved in the biocontrol of phytopathogens.

Some of these metabolites are soluble and have been thoroughly studied in the past; in recent years, however, there has been an increased interest in understanding the effects of microbial volatiles on plants and pathogens (Schmidt et al. 2015). By making use of such an experimental metabolomic approach, Velivelli et al. (2014b) identified the microbial volatile organic compounds (mVOCs) of 27 potato rhizobacterial isolates. Analysis of the complex mixture of mVOCs emitted by the rhizobacteria tested confirmed the presence of some organic volatiles previously shown to act as antifungal; in vitro experiments confirmed the antifungal activity of these mVOCs against *R. solani*. The authors also showed that volatiles able to stimulate plant development or trigger induced systemic resistance (e.g., acetoin and 2,3-butanediol) were present as well.

10.7 Does Biotechnology (and Bioinoculants) Represent a Real Alternative for Small Andean Farmers?

The practical implementation and social acceptance of modern biotechnologies remain a subject of heated debates. Although there has been a strong academic, scientific, and technological development in underdeveloped countries (Eakin and Lemos 2006), typically the development, promotion, and marketing of these technologies have been controlled by large corporations. Consequently, in order to avoid what Rosset and Altieri (1997) termed the threat of *input substitution* in smallholder sustainable agriculture, it is necessary to transfer the technologies to local stakeholders and/or small farmer's cooperatives. On the other hand, the knowledge and confidence of farmers concerning the use of agricultural biotechnological products are also fundamental in order to achieve an adequate perception of their usefulness. Thus, an objective and transparent communication of knowledge in the area as well as a fluid exchange of information between academia, government, business, and farmers is absolutely necessary (Wolt and Peterson 2000). Furthermore, if the impact of biotechnology on the livelihoods of Andean smallholders is to be maximized, then accessibility and costs of development/implementation should be considered alongside technical optimization.

It is also important to emphasize that a change in the scheme of development of agricultural biotechnologies will not only benefit the farmers as final users of these technologies but could also foster – with the cooperation of academia, government, and business – diversification of the rural economies in the Andes through the creation of small and medium biotechnological enterprises able to develop, adapt, and optimize biotechnological solutions for local problems.

Recently, Barragan-Ocaña and del Valle Herrera (2016) investigated the impact of endogenously generated technologies on the lives of farmers from underdeveloped countries. The results obtained confirmed that (1) it is possible to generate technologies in local areas of knowledge, and (2) when managed by small national or local companies, such technologies can contribute to the sustainable development of economies and better conditions for rural producers. Irrespective the fact that this study was conducted in Mexico, their main conclusions do certainly apply to other Latin-American regions. Indeed, there have been some promising results in the Andean region in this way: for instance, Davies et al. (2005a) developed local, on-farm methods for inoculating Andean crops with AMF using roots of infected crops that often performed better than commercial inoculants.

Another good example of success in this area would be the projects developed by the Foundation for Research and Promotion of Andean Products (PROINPA). Together with the International Potato Center (IPC), PROINPA launched several studies aimed at evaluating the potential use of indigenous microorganisms for potato production (Ortuño et al. 2010; Oswald et al. 2007). Some microbial isolates were subsequently tested in Bolivia and Peru in a collaborative project financed by the European Union, COMMINANDES, among whose objectives were stimulating local collective capacities to develop composting systems and management of microbial inoculants to reduce chemical dependence of small-scale farmers. Later in this project, massive culture media were developed, and subsequently liquid and solid formulations were produced. All the bioinoculants developed were tested in farmers' fields to verify their actions and application forms (Ortuño et al. 2010). Some of these microbial resources were used to formulate commercial products currently commercialized by BioTop, a private company based in Cochabamba (Bolivia) that acts as the commercial branch of the PROINPA Foundation (PROINPA/BioTop catalog). A similar approach was followed also by PROINPA researchers to develop bioinoculants that improve quinoa production in the altiplano region (Ortuño et al. 2013). Native microorganisms were prospected, characterized, selected, and used to develop the bioinoculants to reduce the disturbance of the altiplano soil ecosystem and to keep the technology as simple as possible, in order to provide cost-effective technologies for Andean farmers.

Following these successful experiences, an ambitious initiative was launched that deserves to be considered with some detail: the VALORAM project (http://valoram.ucc.ie/). This EU-funded project – whose acronym highlights the importance of exploring and valorizing Andean soil microbial diversity to develop alternative, efficient technologies to intensify potato-based farming systems in a sustainable way – was a collaborative effort between five European and three Latin American partners. Besides isolating, identifying, and characterizing indigenous microbes colonizing the potato rhizosphere in traditionally managed fields, the VALORAM project aimed at assessing and comparing these microbial communities using metagenomic techniques. Furthermore, one of the main objectives of this project was to test and evaluate selected microbial isolates for their plant growth-promoting and protecting properties in field trials, studying their interactions with potato varieties and native rhizosphere microorganisms (VALORAM Report 2015).

According to the participants, several of these objectives have been achieved so far. For instance, as already stated, from an initial collection of ~600 rhizobacterial strains, isolated from eight different potato fields from the Central Andean Highlands of Peru and Bolivia, 23 exhibited antagonistic abilities against *P. infestans* and *R. solani* and were associated with plant growth-promotion and/or disease suppression, during growth room experiments (Ghyselinck et al. 2013). Five of these strains were later shown to increase potato tuber number and yield – depending on the inoculant – when applied to soils amended with organic manure in field trials conducted in Bolivia, Peru, and Ecuador (Velivelli et al. 2014b). Additionally, a suppressive effect of one *Pseudomonas* strain against *R. solani* was also observed in a field trial conducted in Bolivia. In a similar study performed in Bolivia, 17 bacterial strains showing PGP abilities in vitro were tested in potato fields. Even though the potato tuber yield did not vary significantly among plants treated with these microbial inoculants, two *Pseudomonas* sp. isolates and one *Bacillus* sp. isolate appeared to promote potato growth (Franco et al. 2015).

At the time this chapter was written, the results of several of these studies have not yet come to light. However, detailed preliminary information is available from the VALORAM Final Report (2015). According to this report, several assays were conducted in Bolivia, Ecuador, and Peru to evaluate the potential of Andean microorganisms to increase the productivity and health of potato plants grown under high- and low-input cropping systems. These assays did not only include the pilot-scale production of AMF and PGPR inoculums, but were followed by participatory field trials conducted with local farming communities and NGOs. The farmers themselves were asked to evaluate the success or failure of these trials and selected the most accepted technologies in each community. As can be deduced from these results, the VALORAM experience, as a whole, seems to confirm that when a biological approach is combined with suitable plant genotypes, appropriate land management, and inoculation with beneficial microorganisms, then a valuable opportunity results for the sustainable intensification of potato-based farming systems in the Andean region (VALORAM Final Report 2015). Furthermore, preliminary cost-benefit analyses indicate that farmers may reduce their expenses to almost 50% – for example, by reducing their dependence on agrochemicals.

10.8 Concluding Remarks and Future Perspectives

The use of microbial inoculants in modern agriculture represents an extremely important tool that may not only increase the productivity of crops at much lesser costs but also reduce concomitantly the environmental impacts that result from farming activities. The literature is full of reports confirming at different levels of experimentation – laboratory, greenhouse, experimental plots, and open field – that such expectations can be met. However, the use of bioinoculants remains well below its full potential, a fact that can be attributed to several factors among which the correct choice of suitable microbial strains is one of the most important. As already stated by Trivedi et al. (2012) the ecological specificity associated with the naturally occurring microorganisms must orient the efforts of the scientific community in order to end with successful inoculants. Consequently, it is not only necessary to prospect for microorganisms exhibiting remarkable PGP traits, but also to select those able to colonize the rhizosphere of crops and to resist the challenges imposed by the particular climatic conditions that prevails in the Andean mountains. That means that, besides the abilities mentioned in the previous pages concerning the selection of appropriate microorganisms, care must be taken in selecting cold-tolerant or cold-adapted strains, as already established for the Indian Himalayan region (Yarzábal 2014).

On the other side, before engaging in the process of developing and producing of a given bioinoculant, it is necessary to fully understand the ecology of plant-microbe interactions and to apply these ecological lessons throughout the process. As we have seen, it is also absolutely necessary to establish a proactive interaction with the potential users of such technological assets, during experimentation and adaptation to local needs, in order to maximize the chances of a successful incorporation of such resources in their agricultural practices.

In their paramount work on alternative pathways to intensify soil fertility management by smallholder farmers in the Andean highlands, Fonte et al. (2012) insisted on developing proper strategies for taking full advantage of the functioning of soil microbial communities, either by adequately managing the soil or by inoculating beneficial microbes. In order to achieve this goal, one of the steps has been precisely the subject of this chapter, namely, the development of microbial inoculants well suited to each plant crop and properly adapted to the local conditions; the other fundamental step, namely, the characterization of the microbial communities colonizing different Andean agro ecosystems and their shifts owing to alternative management strategies, still needs much work to be accomplished. The possibility of using next-generation sequencing technologies, together with more classic molecular biology techniques, will certainly boost such detailed characterization.

Historically, the Andean region and the population settled in these mountains have dealt with challenges that will certainly increase in the coming years. Nevertheless, it is also true that this region offers unique attributes that, if adequately exploited, may allow a successful intensification of agroecological practices and an improvement of the livelihoods of mountain farmers (Fonte et al. 2012). As pointed by Sinha (1997) and by Trivedi et al. (2012), the experience gained during the past decade in the Indian Himalayan Region – in many aspects similar to the Tropical Andean region – shows that it is indeed possible to reconcile agricultural production and nature, through a harmonic relationship that results in an increased sustainability of the former and a decreased entropy of the latter.

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Entomopathogenic Bacteria and Biorationals in Chickpea Organic Crop Protection

11

S.P. Shanthakumar

Abstract

Global food produce is contributed largely by agriculture and agro-based industries which is crucial for food security. But importance given to the organic crop protection for sustainable farming and land use is trivial across the countries. Recent upgradation in agro-farming systems by techno-crafts for higher yield and crop protection should also place microbes as an important entity in pest management. Development of new biocontrol agents from the microbial community is being reported which should gain lead in organic product development. Earlier microbial pesticide was found to be a slow action pest control or prevention tool in biological control approach. Many target-specific pest control agents like entomopathogenic bacteria and virus were found to be swift in action when compared with entomopathogenic fungi; henceforth, product developers and biocontrol specialists have reclaimed the hope on biological pest control because they could reduce pest population instantly and ecofriendly. In present articles focus on various examples, process and related information on entomopathogenic bacteria for development of biocontrol products against major chickpea crop pest *Helicoverpa armigera*. Special reference is given to chickpea crop since India is the largest producer of chickpea facing the highest crop loss due to pod borer.

Keywords

Insect pathology • Bacteria • Arthropods • Rhizosphere • Non-target organisms

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11.1 Introduction

Global food production of all types stood at ~5.2 billion tons, representing some ~2.7 billion tons of edible dry matter, of which legumes and oil seeds contribute gross tonnage of ~165 Mt. with maximum of ~39 Mt. of dry protein (Borlaug 2003). The Indian agriculture is at the crossroad; our population may reach ~1750 million by 2050. Per capita cropland will then be 0.089 ha, and per capita fresh water supply will be ~1190 m^3/year. Food grain production must be doubled, and the area under irrigation should go up from the current ~60–114 M ha by 2050 (Swaminathan 2010).

Major investment of the farmers in agriculture is on pesticides for control of pest. Achieving sustainable pest control and finding equilibrium levels often take many years, and the result is not the instant pest 'extermination' that is wished for by many farmers (Neuenschwander 2004). Low crop productivity is related to abiotic and biotic factors, viz. damage caused by insect pests, which are realized as a major biotic constraint to sustainable crop production (Sharma and Yadav 2001). Crop loss due to insect pests is estimated to ~14% of the total agricultural production. The global monetary loss due to insect pests accounts to US$ ~90 billion in rice, wheat, maize, potato, cotton, soybean, barley and coffee (Andersen and Cohen 2000). India has the distinction of world's largest producer of pulses, but the average productivity of ~614 kg/ha is very low because of biotic stress in terms of insect infestation. Among all the insect pests, the lepidopteran insect, *H. armigera*, poses a serious threat to the pulses especially to chickpea and pigeon pea (Rabindra et al. 2005; Behere et al. 2013). Not all pests are amenable to classical biological control; many more biocontrol agents should be identified and explored. Parasitoids, predators, pathogens and nematodes have all been used for control of pestiferous arthropods (Figs. 11.1 and 11.2).

11.2 Chickpea Production: Global, National and State Prospects

The chickpea (*Cicer arietinum* L.) is the third most important food legume grown in the world. In India, chickpea is an important pulse crop in terms of both area and production. India is the largest producer of chickpea in the world sharing the range between ~65% and 66% (FAOSTAT 2008) of the total area of ~12 M ha and production of ~9 Mt., respectively. As per FAO report, Mexico has registered highest productivity (~1809 kg/ha) followed by Canada (~1580 kg/ha) and Australia (~1268 kg/ha). In India, chickpea cultivation is being done in ~6 M ha with the production of ~4 Mt. of the grains during 2002–2003. During 2008–2010, chickpea production reached to ~7 Mt., and it was ~71% production at global scenario (FAOSTAT 2010). Madhya Pradesh, Uttar Pradesh, Rajasthan, Maharashtra, Gujarat, Andhra Pradesh, Tamil Nadu and Karnataka are the major chickpea-producing states in India. Coimbatore, Erode, Perambalur and Dindigul are the highest chickpea-producing districts in Tamil Nadu (INDIASTAT 2012).

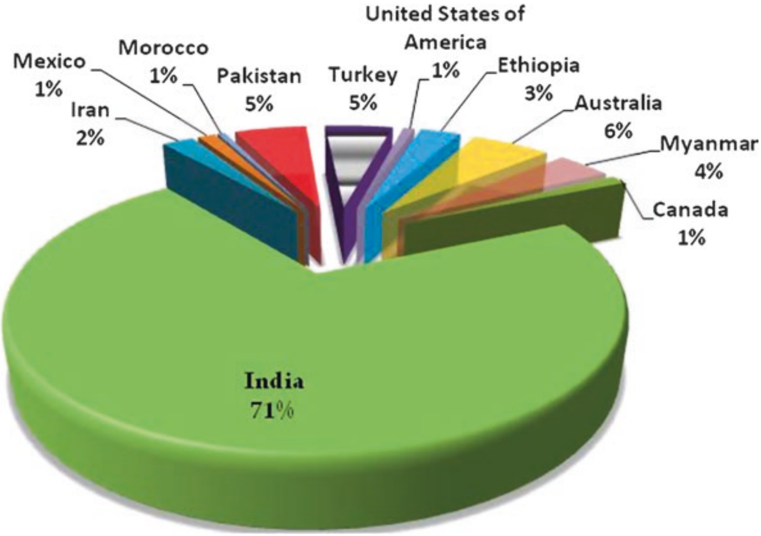

Fig. 11.1 Global status in chickpea production (FAOSTAT 2010)

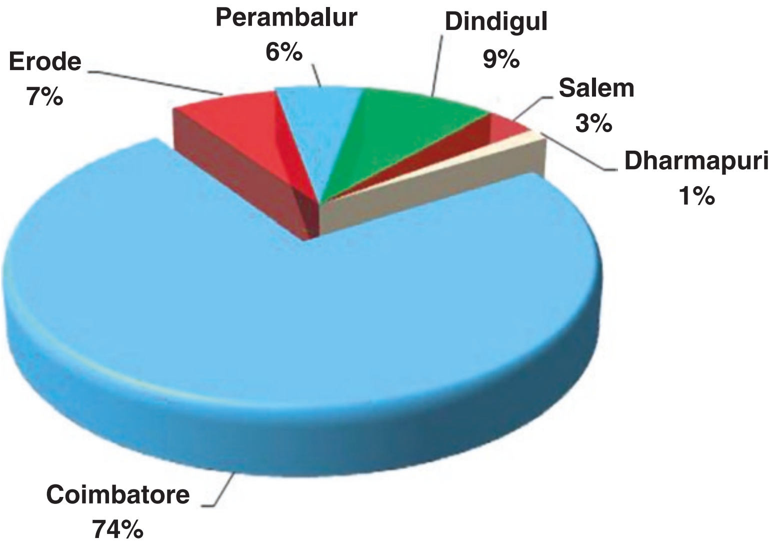

Fig. 11.2 Chickpea production status in Tamil Nadu (INDIASTAT 2012)

In the case of Dindigul district, more than 500 acres of cultivable land is being used for chickpea cultivation, and an average of 203 tonnes of chickpea production per year is the statistical projections by national database (INDIASTAT 2012).

11.3 Crop Loss and Economical Impact Due to *H. armigera*

Insects are the most widely distributed and successful animal class in the world. The indispensable reasons for this phenomenon are rapid reproduction, short life cycle and a robust immune system (Kranthi and Kranthi 2004; Gayatri Priya et al. 2012; Behere et al. 2013). The crop production losses have shown an increasing trend over the years. In 1983, the losses due to insect pests were estimated worth Rs. 6000 crores (Krishnamurthy Rao and KSRK 1983) which increased to Rs. 20,000 crores in 1993 (Jayaraj 1993) and to Rs. 29,000 crores in 1996 (Dhaliwal and Arora 2010). Birthal and Sharma (2004) have reported that *H. armigera* alone causes an annual loss of about Rs. 1000 crores in India. The American bollworm, *H. armigera*, is a polyphagous pest of worldwide occurrence inflicting annual crop damage in India worth US $1 billion (Subramanian and Mohankumar 2006). Global crop losses due to *H. armigera* are estimated to be over US $ 2 billion annually, of which 50% loss occurs in India, causing widespread misery and frequent crop failures (Subramaniam Gopalakrishnan et al. 2011).

In India, this insect occurs as a major pest in many economically important crops, including cotton, pigeon pea, chickpea, tomato, lady's finger and black gram (Ge et al. 2003; Subramanian and Mohankumar 2006; Nguyen et al. 2012; Guo et al. 2012). Severe outbreaks were recorded on soybean and mustard in Madhya Pradesh (Singh 2005), pigeon pea in Karnataka and Andhra Pradesh (Singh 1994), black cumin and strawberries in Himachal Pradesh (Singh 1999), finger millet and sweet orange in Andhra Pradesh (Reddy and Reddy 1999) and chickpea, linseed and mustard in Orissa (Patnaik and Lenka 2000).

It has also been observed that *H. armigera* attacks few new host plants such as rose and gherkin (Malarvannan 2004). During the off season, *H. armigera* is observed to survive on few weeds like *Abutilon indicum*, *Achyranthes aspera*, *Cleome monophylla*, *Solanum viarum*, *Datura metel*, *Acanthospermum hispidum* and *Gynandropsis gynandra* (Rao et al. 1991).

In Tamil Nadu, the data collected on cotton from 1985–1986 to 1987–1988 revealed that *H. armigera* reached the economic threshold level of 10% damage to fruiting parts. The districts of Coimbatore, Erode and Salem had a higher incidence in 1987–1988, and to some extent, a similar trend was noticed in the earlier 2 years (Jayaraj et al. 1990). Intensive field surveys on *H. armigera* incidence in southern districts (Aruppukottai, T.Kallupatti and Thirumangalam) of Tamil Nadu, India, in different rainfed cotton cropping systems (cotton alone and cotton intercropped with cow pea, black gram, green gram, sun flower and sorghum systems) recorded maximum *H. armigera* under pure cotton (Saminathan et al. 2003; Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2016b).

11.4 Chemical Control of *H. armigera*

In the Indian conditions, most of the farmers use insecticides as a dominant tool among the various options for the management of the insect pest. However, the indiscriminate use of insecticides has resulted in resistance development of *H. armigera* to almost all groups of insecticides. In India, resistance was first reported in cotton-growing belt of Andhra Pradesh in 1987 (Reddy 1988). Low to moderate levels of resistance have been reported in Maharashtra; moderate to high in Tamil Nadu, Uttar Pradesh, Gujarat and Punjab; and high in Andhra Pradesh and Madhya Pradesh (Kranthi et al. 2006). Excessive use of insecticides has resulted in an increase in severity of sucking pest which was considered as minor pests in addition to environmental pollution. In order to avoid the development of insecticide resistance, it is essential to curtail the indiscriminate use of the insecticide (Nimbalkar et al. 2009; Kumar et al. 2015, 2016a; Ahmad et al. 2016; Meena et al. 2016a; Parewa et al. 2014; Jaiswal et al. 2016; Jha and Subramanian 2016).

The pest is primarily controlled by biological and chemical means, yet the insect's wide-ranging host preference, high population density throughout the breeding season and tendency to develop resistance to insecticides hamper attempts to overcome the damage it causes (Gunning and Moores 2002; Landers 2007). However, increased use of chemical pesticides has posed serious health hazards and widespread ecological damage (Rejaul Hassan and Karim 2005). Though chemical insecticides have contributed largely in the management of pest, it has resulted in a number of ecological and health hazards due to the accumulation of undesirable residues in the food crops besides promoting insecticide resistance of pests with negative impact on non-target species (Arti and Sujoita 2009).

India produces more than 200 pesticides and formulations, the largest in Asia and twelfth in the world. The agricultural sector consumes ~67% of the pesticides produced, with two-third alone taken by crops like cotton, paddy, vegetables and a fruit; the largest usage is recorded in Andhra Pradesh followed by Tamil Nadu. The insecticides chlorpyriphos, phosalone and malathion were also highly superior in reducing the pest incidence (Biradar et al. 2001). Bioassay against *H. armigera* on pigeon pea revealed that fenvalerate and monocrotophos are more toxic, followed by endosulfan and dimethoate (Sharma and Yadav 2001). On chickpea, the efficacy of acephate alone and in combination with other synthetic pyrethroids was superior against *H. armigera*. Similarly, deltamethrin resulted in lowest fruit damage due to *H. armigera* on tomato followed by cypermethrin and acephate (Mehta et al. 2001; Prakash and Verma 2016; Meena et al. 2015a, f, 2016b; Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Dotaniya et al. 2016).

A troublesome aspect of *H. armigera* is their ability to develop resistance to insecticides. The pest has build-up resistance to commonly used pesticides methomyl, chlorpyriphos, quinalphos, acephate, fenvalerate, endosulfan and monocrotophos and synthetic pyrethroids up to 20- to 60-folds depending on the location (Singh et al. 2002). Resistance to DDT, organophosphorus insecticides and synthetic pyrethroids has bedevilled chemical pest control application and, in some cases, has forced abandonment of cropping due to inability to control the pest (David 1997).

11.5 Biological Control of *H. armigera*

Farmers mainly use inorganic pesticides against insect pests (Malik et al. 2002). The outbreak of *H. armigera* has been attributed to the development of insecticide resistance and the use of broad spectrum insecticides, which are known to have a detrimental effect on populations of its natural enemies and nutritional and bioclimatic factors in host plants (Naseri et al. 2009). Therefore, alternative measures have been adopted, and considerable attention has been directed towards ecofriendly insecticides in the past few years (Arti and Sujoita 2009). In Indian agriculture, the IPM programme has commenced during the last decade, and one of the important steps in biocontrol is using beneficial organisms for the control of insect pest (Prasad et al. 2007; Raghavendra et al. 2016; Zahedi 2016; Meena et al. 2015b; Rawat et al. 2016; Das and Pradhan 2016; Dominguez-Nunez et al. 2016).

11.6 Microbial Pesticides

India has been bestowed with varied diversity, rich in beneficial bacterial, viral, fungal and entomopathogenic nematodes. This, apparently, offers a greater scope for microbial control making it more feasible and cost-effective to the resource-poor farmers. Microbial pesticide would help to manage insecticide-resistant pest population of *H. armigera*, prevent the rise of secondary pest problems and fit well in agriculture (Zhou et al. 2013; Pawar and Borikar 2005). Microbial pathogens are distinguished from commensal microorganisms by their ability to enter, proliferate, persist and disseminate from host sites that are inaccessible to commensal organisms (Finlay and Falkow 1997).

Almost half (~49%) of the total introductions of traditional fungi for biocontrol of insect pests were conducted (Hajek et al. 2007). The most commonly introduced species were *Metarhizium anisopliae* and *Beauveria bassiana* in India (Hajek and Delalibera 2010). However, ~700 products of different microbial are currently available worldwide. Thirty-eight fungal formulations based on *Metarhizium*, *Beauveria* and *Lecanicillium* and ~45 baculovirus-based formulations for the control of *Helicoverpa* and *Spodoptera* are available (Vasantharaj and Ramamurthy 2008). Fungal pathogens particularly *Beauveria bassiana* (Saxena and Ahmad 1999; Uma Devi et al. 2008), *Metarhizium anisopliae* (Gopalakrishnan and Narayanan 1989; Khaderkhan et al. 1993; Shanthakumar et al. 2009), *Lecanicillium lecanii* and *Nomuraea rileyi* (Lingappa et al. 2005; Shanthakumar et al. 2010b) have been widely used as insecticides globally.

Next important microbial agent is the entomopathogenic virus. The most prevalent viruses in the environment, three families (*Baculoviridae*, *Polydnaviridae*, *Ascoviridae*), are specific for insects and related arthropods. The most widely exploited virus groups for biocontrol of insects pests are the baculoviruses (Evans 2000; Monobrullah and Nagata 2000). Some of the viral organisms pathogenic to *H. armigera* are nuclear polyhedrosis virus (NPV), cytoplasmic polyhedrosis virus (CPV) and granulosis virus (GV).

The average mortality of *H. armigera* due to the above pathogens was ~21% and could reach ~57% in an epidemic year (Fan et al. 1999). Application of different doses of *Splt* MNPV showed dose-related mortality on final instars of *Spodoptera litura* (Mohammad and Uma 2008). Entomopathogenic viruses are generally considered to be environmentally safe and do not leave toxic residues (Morris 1980; Monobrullah 2003). However, widespread use of viruses for pest management has been hampered by their relatively high cost, slow activity and susceptibility to UV degradation (Moscardi 1999).

Followed by entomopathogenic virus, entomopathogenic nematodes are other important biocontrol agents for agricultural insect pest management. It is well known that entomopathogenic nematodes, which are classified into Steinernematidae and Heterorhabditidae families, have great potential as biological control agents in plant protection (Klein 1990). Their activity against different pest insects is already well studied (Ebssa 2005; Laznik et al. 2008; Forst et al. 1997). Endemic nematode was tested successively against various insect pests at the laboratory and field (Ehlers 1995; Woodring and Kaya 1988 and Legaspi et al. 2000). Virus and nematodes even though perform well in controlling insect but when it comes to product development at large scale for growing demand, both the group have some limitations as they need living host system which is not required in case of bacterial entomopathogens (Yasin et al. 2016; Meena et al. 2015e, 2016c, d; Saha et al. 2016a, b; Yadav and Sidhu 2016; Teotia et al. 2016; Bahadur et al. 2016b).

Thus bacterial entomopathogens are versatile and can be produced in large scale in fementers with limited resource which is economical and time saving in terms of mass production. Naturally available soil bacteria from plant rhizosphere can be chosen for a simple ecological compatibility reason to make the product effective in field condition after augmentation. Many studies on soil bacterial insecticides were carried out and reported against a wide range of pests as discussed in the following chapters.

11.7 Role of Soil and Rhizosphere Entomopathogenic Bacteria

Rhizobacteria have been studied as plant growth promoters for agricultural production as well as biocontrol agents against both diseases and pests (Kloepper and Beauchamp 1992). A few bacterial isolates with pesticidal activity against Lepidoptera, Coleoptera and Diptera (Shah and Goettel 1999) are commercially available. Notably the soil-dwelling insect pathogen, *B. thuringiensis*, is suitable for use in biological control, and certain strains have been developed as commercial bioinsecticides (Clara et al. 2004).

Different isolates of *B. thuringiensis* have been proven to be successful against various insects and nematode pests under field conditions. *Pseudomonas gladioli* showed antifeedant activity and growth reduction of *H. armigera* that fed on *P. gladioli*-treated cotton plants (Qingwen et al. 1998). The diet contaminated with the bacteria, *Pseudomonas maltophilia*, *B. subtilis*, *Escherichia coli* and *Staphylococcus epidermidis*, showed insecticidal potential against *Helicoverpa zea.* Among the four species, *P. maltophilia* caused severe losses in all stages of *H. zea*, with the larval stage being the most susceptible which led to more than a 60% loss in adult emergence (Bong and Sikorowski 1991). *Pseudomonas fluorescens* and *Pseudomonas chlororaphis* harbouring the *Fit* gene cluster colonize and kill *S. littoralis*, *H. virescens* and *Plutella xylostella* via oral infection (Beat et al. 2013).

Similarly, rhizobacteria isolated from cotton roots exhibiting antagonism towards seedling blight and leaf blight of cotton were tested for their efficiency against *H. armigera*. The bioformulation developed using *B. subtilis* (isolate DGL9) + chitin was found to be detrimental to the developmental stages of *H. armigera* (larva, pupa and adult) by causing larval mortality and pupal and adult malformation with reduced adult emergence (Ayyathurai et al. 2009). Maria et al. (2008) have shown the first evidence that the two root-associated bacteria, *P. fluorescens* strains CHA0 and Pf-5, also exhibit potent insecticidal activity and kill larvae of *Manduca sexta* and *Galleria mellonella* within time frames that were comparable to those of the known insect pathogens, *Photorhabdus* and *Xenorhabdus.* Zehnder et al. (1997) evaluated induced resistance in cucumber by plant growth-promoting rhizobacteria (PGPR) *P. putida*, *S. marcescens*, *Flavimonas oryzihabitans* and *B. pumilus* on the spotted cucumber beetle *Diabrotica undecimpunctata* and striped cucumber beetle *Acalymma vittatum.*

Ramamoorthy et al. (2001) reviewed that certain fluorescent pseudomonads are effective rhizosphere colonizers and are endophytic in nature in the plant system. Genetically engineered fluorescent pseudomonads with the insecticidal crystal protein effectively control lepidopteran insect pest. Transgenic *P. cepacia* strain 526 with the crystal protein gene has consistently shown insecticidal activity against tobacco hornworm (Stock et al. 1990). Thus, PGPR treatment of crops can be effective for insect pest management and has a great potential for future use. The increase in hymenopterous parasitoid and spider population in the crop because of bacteria *Pseudomonas* is reported and synergistically was found responsible for the reduced incidence of leaf folder under field conditions (Radjacommare et al. 2002). The increased natural enemy population might have associated with host-bacteria-based pathways (octadecanoid pathway) leading to the production of volatile compounds, which attract the natural enemies. The activation of octadecanoid pathway and increased amount of volatile substance have been reported (Bell and Mullet 1993).

11.8 Molecular Characterization and Identification of Entomopathogenic Bacteria

Comparison and analysis of the 16S rRNA gene has been extensively used as a diagnostic method to determine phylogenetic relationships of bacterial isolates. Moreover, this gene is characterized by having areas of secondary structure which have also proven useful for diagnostic purposes. The size of this gene is approximately 1.6 kb and is composed of regions with different levels of variability thus providing valuable information for differentiation of taxa (Stackebrandt and Goebel 1994). The study of the genetic diversity among bacterial species and strains has also had an impact in assessing relatedness among species and understanding their diversity (Boemare and Tailliez 2009). Bacteria are characterized by having single chromosome within the nucleoid. The size of this chromosome varies among species. For example, the bacterial genomes of *B. thuringiensis* (the widely studied insect pathogen), *B. cereus* and *B. anthracis* are around 5.4 Mb (Carlson and Kolsto 1993 and Ivanova et al. 2003). Other species such as *B. subtilis* and *B. licheniformis* have a smaller chromosome (4.2 Mb) (Rey et al. 2004).

Entomopathogenic nematode symbiotic bacteria *Photorhabdus luminescens* have a genome size of 5.7 Mb (Duchaud et al. 2003). Many bacteria also contain extrachromosomal elements (plasmids), which are smaller double-stranded DNA (dsDNA) molecules that replicate independent of the chromosomal DNA. Genes located in bacterial plasmids usually code for proteins that determine specific phenotypes but do not code for products needed for bacterial survival and growth. Bacterial genes are organized in operons or cassettes that consist of a promoter, a series of genes and a transcription terminator (Verma et al. 2014, 2015b; Meena et al. 2014a, 2016e; Bahadur et al. 2016a; Masood and Bano 2016).

11.9 Microbial Mode of Action and Active Principle

The microbial entomopathogenic agents like bacteria and fungi infest the insect primarily, and then after colonization, they secret toxins which curtails the normal metabolism and decease. Entomopathogenic fungi like *Beauveria* sp. produce several metabolites, including bassianin, beauvericin, bassianolide, beauveriolide, bassiacridin, oosporein and tenellin (Vining et al. 1962; Strasser et al. 2000; Quesada–Moraga and Vey 2004). Beauvericin is toxic to *H. zea*, *Culex pipiens*, *Aedes aegypti* and *Calliphora erythrocephala* rupturing the midgut epithelium and dissolving the ribosomes (Zizka and Weiser 1993; Grove 1985; Champlin and Grula 1979). *Metarhizium* sp. produces destruxins and cytochalasins (Roberts 1981); *P. tenuipes* produces tenuipesine (Kikuchi et al. 2004); *Akanthomyces gracilis* produces akanthomycin (Wagenar et al. 2002); *Cordyceps pseudomilitaris* produces coryanhidrides (Isaka et al. 2000); *Tolypocladium* spp. produce efrapeptins (Krasnoff and Gupta 1992); *Aschersonia aleyrodis* produces destruxins and homodestruxins; and *Aschersonia tubulata* produces dustanin (Krasnoff et al. 1996).

Different types of *Cry* proteins isolated from *B. thuringiensis* could directly bind to peritrophic membrane and disintegrate the columnar cells and microvilli and cause imbalance in gut pH and kill the lepidopteran insects (Garczynski and Siegel 2007). Oral injection with *P. entomophila* bacterial cells and monalysin toxin isolated from *P. entomophila* could cause significant mortality in *Drosophila melanogaster* (Takayuki Kuraishi et al. 2011). Novel toxin complexes (Tc) A and (Tc) B from bacterium *Yersinia entomophaga* against *Plutella xylostella* were reported by Landsberg et al. (2011).

11.10 Bacterial Source for Insect Toxins and Biopesticides

The entomopathogenic toxins in the form of proteins and secondary metabolites were reported from many bacterial species. As far as the protein insecticidal toxins are concerned, it is the crystal insecticidal proteins or cry toxins and corresponding Cry genes that were reported from the spore-forming bacterial genus, *B. thuringiensis*. The presence of Cry genes is not unique to *Bt*, but also several other bacterial species including *B. sphaericus*, *P. popilliae*, *P. lentimorbus* and *Clostridium bifermentans* produce Cry proteins (Barloy et al. 1998; Zhang et al. 1997; Yokoyama et al. 2004). *Pseudomonas fluorescens* CH0 and the related strain Pf-5 possess an insecticidal toxin named fluorescence insecticidal toxin (Fit) reported by Maria et al. (2008) on lepidopteran insect pest, *Manduca sexta*. The Fit toxins produced by the above two *P. fluorescens* strains were similar to the MCF (makes caterpillar floppy) toxin produced by the entomopathogenic bacterium *Photorhabdus luminescens* (Daborn et al. 2001). Currently, 145 holotype crystal protein genes have been assigned to 50 sets at the primary rank (*cry*1–50), and 9 *cyt* genes have two primary ranks (*cyt*1–2).

In addition to the ICPs, 21 holotype vegetative insecticidal protein (*vip*) genes with three primary ranks (*vip*1–3) have been classified. *Bacillus thuringiensis*, *B. sphaericus*, *B. cereus*, *Brevibacillus laterosporus*, *Clostridium bifermentans* and *Paenibacillus popilliae* are important entomopathogenic bacteria which was reported for the presence of toxin-producing genes, viz. Cry1A(a-i), Cry1B(a-g), Cry1C(a-b), Cry1D(a-b), Cry1E(a-b), Cry1F(a-b), Cry1G(a-c), Cry1H(a-b), Cry1I(a-f), Cry1J(a-d), Cry1Ka, Cry1La, Cry2A(a-e), Cry9Aa, Cry9B(a-b), Cry9Ca, Cry9E(a-d), Cry15Aa, Cry26Aa, Cry28Aa and Cry32Aa (Garczynski and Siegel 2007).

The action potential of the above-mentioned active principles was proved against different ecological population of *H. armigera* across India. The baseline susceptibility of Indian populations of *H. armigera* to the insecticidal protein Cry1Ac from *B. thuringiensis* was determined through bioassays conducted in 1999 and 2001. Populations of *H. armigera* were collected from cotton fields of nine major cotton-growing states in India, which included Punjab (Bathinda), Haryana (Sirsa), Rajasthan (Sri Ganganagar), Madhya Pradesh (Barwaha and Khandwa), Gujarat (Rajkot, Vadodara and Anand), Maharashtra (Jalgaon, Jalna, Akola and Yavatmal), Andhra Pradesh (Adilabad, Warangal, Khammam and Guntur), Karnataka (Raichur, Davangere and Ranebennuru) and Tamil Nadu (Coimbatore and Dindigul) and were found susceptible to crystal protein toxins (Jalali et al. 2004).

Secondary metabolite produced by bacteria for their insecticidal activity was not much explored, and only few studies were taken up in the recent past. Detailed analysis of liquid cultures of the entomopathogenic bacteria (Brachmann et al. 2006; Lang et al. 2008) showed that these bacteria are in fact very important secondary metabolite producers that can produce several structurally diverse compounds. Therefore entomopathogenic bacteria can be regarded as a novel source of potential biocontrol products which have been studied only recently. Eleftherianos et al. (2007) show that *Photorhabdus* species produced a small-molecule (E)-1,3-dihydroxy-2-(isopropyl)-5-(2-phenylethenyl)benzene (ST) that acted as an inhibitor of phenoloxidase (PO) in the insect host *Manduca sexta.*

The entomopathogenic bacteria *Xenorhabdus* and *Photorhabdus* produce phage-derived bacteriocins (Thlaer et al. 1995), colicin E3-type killer proteins (Singh and Banerjee 2008) and insect toxin complexes (Ffrench-Constant and Waterfield 2006) as well as several other secondary metabolites (Piel 2004). Insecticidal compounds from bacteria described in the literature represent mostly small molecules like benzylideneacetone (Ji et al. 2004), iodinine (Fodor et al. 2004), phenethylamines and indole derivatives (Li et al. 1995; McInerney et al. 1991a), and comparatively less number of complex compounds like the xenorhabdins and xenorxides (Li et al. 1998) and xenocoumacins (XCNs) (McInerney et al. 1991b) was reported.

Despite their simple structure, different biological activities have been described for these compounds, and their biosynthesis genes have not been identified yet except for the XCNs (Helge and Bode 2009). Additionally, it should be mentioned that other entomopathogenic bacteria reported have not been analysed for secondary metabolites and/or genes encoding the corresponding biosynthesis genes but are members of well-known insecticidal genera like *Serratia entomophila* and *Erwinia carotovora* (Grimont et al. 1988; Vallet-Gely et al. 2008). Entomopathogenic activity of *E. carotovora* has been reported only under lab conditions and has to be proven for its insecticidal activity under field conditions.

11.11 Frontiers of Microbial Pesticides in Field Application

The definite evaluation of the efficacy of an entomopathogen attacking a pest is often the determination of the reduction of pest damage and increase in crop yield (Hajek and Goettel 2007). Naturally, the most useful information on the effects of pathogens on non-targets is gained from field studies. By knowing the physiological host range of a pathogen, we can attempt to predict its ecological host range. However, it is fairly typical that hosts can be infected in the laboratories that are never found infected under field conditions (Hajek and Butler 1999).

On contrary, few reports on microbial biocontrol agents which were found successful at laboratory level also performed well at field scale as reported by Radjacommare et al. (2002) which demonstrated that the talc-based formulation of two *P. fluorescens* strains (PF1 and FP7) and its mixture (with and without chitin) were tested against sheath blight and leaf folder in rice. The application of talc formulation through seed, root, soil and foliar spray significantly reduced the sheath blight and leaf folder incidence both under greenhouse and field conditions. Several *Pseudomonas* strains have been found to control many fungal, bacterial, viral and insect pests at laboratory level (Ramamoorthy et al. 2001). The laboratory biocontrol efficacy and PGPR activity of fluorescent pseudomonads were further increased by mixing two or more strains of *Pseudomonas* species (Garica and Sarmiento 2000; Nandakumar et al. 2001; Nakkeeran et al. 2004) or in combination with other bacterial or fungal antagonists (Duffy et al. 1996) or mixed with chitin or other substances (Benhamou et al. 1998). Even though many reports on the entomopathogenic bacteria have been recorded, only limited studies were made on its efficacy at field level which should be given importance in future studies for sustainable organic crop protection (Shanthakumar et al. 2010a; Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b, c; Singh et al. 2015).

11.12 Biosafety of Microbial Pesticides on Beneficial Insects

Beneficial microbes proposed to have biocontrol potential against various pests should pass through various regulations for commercial product development. The major criterion in the regulatory forum is nothing but the biological safety of the microbes against higher animals, and human must be tested safer according to standard protocol. Protocols for testing the effects of pathogens on non-targets have been suggested for a few specific entomopathogen/host systems (Hokkanen and Hajek 2003). Studies of potential effects of entomopathogens on non-target organisms generally begin with laboratory assays for host specificity. Bioassay methods for different groups of pathogens are described in detail by Lacey (1997). Insect pathogens may have indirect effects on non-target organisms, and consequently impacts could also occur at the field level. In addition, such community level influences may occur across time and space. To investigate non-target effects on communities, standard ecological measurements, such as diversity indices, would be appropriate (Magurran 2004).

The microbial pesticides developed should be safer against beneficial insects as they were used worldwide to control pests. As deployment of beneficial insect predators and parasitoids against the insect pests has been found as an effective and feasible method of augmentative biological control in several countries (Gurr and Wratten 2000; Gurr et al. 2000; Shanthakumar et al. 2010b), the entomopathogens should be evaluated for its non-specificity against natural predatory insects like green lacewings (*Chrysoperla* sp.), true bugs (*Geocoris*, *Orius* and *Nabis* sp.), various predatory beetles (*Cheilomenes* sp. and *Coccinella* sp.) and spiders.

Advantage of bacterial insect pathogens is that they are naturally less harmful to Hymenopteran families like Ichneumonidae, Braconidae, Trichogrammatidae and Tachinidae which are common natural enemies of insect pests in all agro-systems (Luttrell et al. 1994). Generally, entomopathogens appear to be harmless against natural enemies. *Bt*s and baculoviruses are safe to natural enemies, while fungi and nematodes may affect some natural enemies. These effects are usually limited to some natural enemies and are minor. Many studies have been published on compatibility of entomopathogens and natural enemies; however, reports on greenhouse and field evaluations are limited (Ravensberg 2011; Shrivastava et al. 2016; Velazquez et al. 2016; Meena et al. 2014b, 2015c, d; Sindhu et al. 2016; Singh et al. 2016).

If the product developed does not pass through these safety parameters, it will have deleterious effect on habitat management which is directly linked to the disturbances in diversity of natural enemies and the quality of the environment in which they occur. As a result of frequent and intense disturbance regimes, many agricultural systems are recognized as particularly difficult environments for natural enemies (Landis and Marino 1999). This is significant for annual monocultural cropping systems where the rates of establishment of imported natural enemies, and their success in controlling the target pest are lower than in more stable cropping systems (Hall et al. 1980).

Beneficial organisms are generally considered to be more susceptible to chemical insecticides than their hosts. Croft (1990) studied interactions between beneficial insects and pesticides intensively in field crops, orchards, vineyards and glasshouses. Most microbial control agents are generally considered to be host specific and pose a lower risk than associated with many chemical pesticides (Goettel and Roberts 1992). Exposure of honey bees to high inoculum densities of *B. bassiana* resulted in very low mortality that was not different from the control suggesting that *B. bassiana* can be applied for pest control in fields where honey bees are used for pollination (Al mazrawi 2007).

Earlier report on non-infectivity of HaNPV to *Bombyx mori* was confirmed by Sanjay et al. (1991), where they found that *B. mori* fed on HaNPV-infected leaves did not affect larval weight, larval duration, cocooning percentage, weight of cocoons and percentage adult emergence of silkworm, thus reported to be non-infective. Neem extract did not affect the parasitization of *Trichogramma pretiosum* and *T. principium* (Klemm and Schmutterer 1993) as same as oils from neem, citronella and lemon grass were not repellent to *Coccinella undecimpunctata* (Matter et al. 1993) and hence can be used as biorationals in combination with bacterial insect pathogens.

11.13 Rationale and Future Prospects

Microbial contrivances shows selective sweep in insect pest population without any negative impact on environment and crop production. Need for laboratory and field evaluation on the active microbes is felt necessary for product development to validate their ecological impact precisely other than target pest control. This review highlights the bright scope for bacterial entomopathogens both in action potential and low-cost production over the entomopathogenic fungus, virus and nematodes. Moreover, the secondary metabolite produced by the entomopathogens should be given importance rather than protein toxins for future product development as the bacterial system is good source for production of life-sustaining concentrations of target-specific metabolites. Composite cultures and use of safer insecticidal biorationals like neem and other plant-based products are highly recommended as organic pest control strategy.

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Bio-stimulants: An Approach Towards the Sustainable Vegetable Production

12

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Abstract

In the context of changing climatic scenario, depletion of natural resources and increasing hunger and malnutrition, it is necessary to ensure sustainable agricultural production and resource utilization. Bio-stimulants are a viable alternative in this condition. Bio-stimulant consists of various substances and microorganisms which have found to be effective in enhancing plant growth enhance nutrition efficiency, abiotic stress tolerance and crop quality traits. Vegetables are a rich and relatively cheaper source of vitamins. Consumption of vegetable provides palatability and taste, increases appetite, supplies fibre for digestion and helps in preventing malnutrition. To enhance the sustainability of vegetable production, bio-stimulants can be effectively used. In this chapter, status of vegetable production worldwide and in India, categories of plant bio-stimulants and its importance in vegetable production enhancement and factors contributing towards the expansion of the bio-stimulants market in the world have been discussed. The impact of PGPR carrying plentiful multifunctional plant growth-promoting activities on vegetable crops is discussed. Furthermore, this chapter

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has summarized recent advancement in bio-stimulant commercial products and vegetable disease interaction and has drawn lines of future research that can aid to improve the effectiveness of the use of bio-stimulants in sustainable quality vegetable production.

Keywords

Microorganism • Horticultural crops • Biofertilizers • Nutrients • Food security

12.1 Introduction

The decline of natural resources and environmental misbalance inflicted by current agricultural practices has posed a severe challenge to the sustainability of food and nutritional drift. Global population has been constantly rising (1.13% per annum), resulting in the steady demand for food. The adverse impact of ecological threats as a result of the nonjudicial use of chemical fertilizers and pesticides and the sustainable management of soil fertility have become a major concern nowadays (Wezel et al. 2014). Undesirable changes in soil biological and chemical properties have not only questioned the sustainable food production but alarming malnutrition too. Apart from this, the changing climatic scenario has added huge unforeseen costs in cultivation practices. Today growing food is much costlier economically and environmentally than the last decades. To combat with such situations, cost-effective and environmentally friendly agricultural practices are essential. In such context, bio-stimulants are a viable alternative (Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jat et al. 2015; Kumar et al. 2015, 2016b).

Bio-stimulant is an organic material neither a plant nutrient nor a pesticide but has a positive impact on plant health when applied in small quantities. The level of response from bio-stimulants cannot be attributed to the application of traditional plant nutrients (Gallant 2004). Bio-stimulant consists of various substances and microorganisms (microbial inoculants, fulvic acid humic acid, seaweed extracts, trace minerals, protein hydrolysates, amino acids), which have found to be effective in enhancing plant growth (du Jardin 2012; Calvo et al. 2014).

12.2 Importance of Vegetable in Food Basket

Vegetables are a rich and relatively cheaper source of vitamins. The consumption of vegetable provides palatability and taste, increases appetite, supplies fibre for digestion and helps in preventing constipation. It plays a key role in neutralizing the acids produced during digestion of pretentious and fatty foods and also provides valuable roughages which help in the movement of food in the intestine.

Some of the vegetables are good sources of carbohydrates (leguminous vegetables, potato, sweet potato, garlic, onion and fenugreek), proteins (peas, leafy vegetables, beans and garlic), vitamin A (carrot, drumstick, tomato, leafy vegetables), vitamin

B (garlic, peas and tomato), vitamin C (drumstick leaves, green chillies, leafy vegetables, cole crops and leaves of radish) and minerals (leafy vegetables, drumstick pods). As per nutritionist, the daily requirement of vegetables is 75–125 g of green leafy vegetables, 85 g of other vegetables and 85 g of roots and tubers with other food.

All these vegetables are important dietary sources of micronutrients. The World Health Organization (WHO) approximates that less fruit and vegetable intake contributes to ~16 million disability-adjusted life years (DALYs). The DALYs is a measure of overall disease burden expressed as the potential life lost through premature mortality and the years of productive life lost through ill-health and disability. The approximately 1.7 million losses of life worldwide are attributable to low fruit and vegetable consumption (FAO STAT 2014). In this regard, WHO recommended the dietary allowance of 400 g of fruit and vegetables per day – excluding starchy root crops for the prevention of chronic diseases like diabetes and obesity, heart disease and cancer and for the prevention and relief from several micronutrient deficiencies, especially in developing countries (WHO 2003). There is a huge gap in the recommended dietary allowances and actual intakes in fruits and vegetables worldwide due to lack of availability and accessibility for the poor masses. A low production trend has been observed worldwide.

12.3 Status of Vegetable Production

The annual growth rate of vegetable in the world has been declined from 6.7% in the decade 1990–2000 to 3.4% in 2000–2011. The trend is applicable to nearly about all countries in Asia and Pacific region except Iran (Table 12.1). Due to the increased resource use efficiency, Iran has maintained increasing return.

India is the second largest producer of vegetables in the world (next to China) and produces ~15% of the world's vegetable biomass. It produces over ~90 Mt vegetables in ~6.2 M ha which are ~3% of the total area under cultivation in the country. In India, more than 40 types of vegetables belonging to different groups are commercially cultivated. These include solanaceous, cucurbitaceous, *Allium* groups,

Table 12.1 Vegetable producers and their productivity in major countries in Asia and Pacific region

	Area		Production		
Countries	('000 ha) 2011	Growth percent (2000–2011)	('000 tonnes) 2011	Growth percent (1990–2000)	Growth percent (2000–2011)
China	24,213	2.9	562,596	10.7	4.2
India	7571	3.0	105,795	4.0	3.5
Asia	40,228	2.6	802,500	8.4	4.0
Iran	885	4.3	23,764	1.2	6.7
Africa[a]	5388	2.1	36,846	4.7	3.4
World	56,734	2.1	1,090,425	6.7	3.4

[a] Regional Office for Africa; (Source: FAO STAT 2014)

leguminous, cruciferous, root crops and leafy vegetables. Among these the five crops, viz. potato (*Solanum tuberosum*), tomato (*Solanum lycopersicum*), onion (*Allium cepa*), cabbage (*Brassica oleracea* var. *capitata*) and cauliflower (*Brassica oleracea* var. *botrytis*), account for ~60% of the total vegetable production in the country. Vegetables including root and tuber crops occupy an important place in the diversification of agriculture and have played a pivotal role in food and nutritional security of the ever-growing population of our country (Maity et al. 2013). Still, the sector is surrounded by some issues that hinder the sustainable development of the vegetable sector of India. The major issues are described below.

12.3.1 Use of Quality Inputs

The vegetable sector suffers from a lack of availability of good quality seeds, planting material (Shubha and Shridhar 2016; Shubha et al. 2016), fertilizer and plant protectants. Availability of critical inputs is very much essential for achieving a good harvest. Bio-stimulants can complement the fertilizers and plant protection material.

12.3.2 Ecological Issues

Indiscriminate use of fertilizers and agrochemicals in vegetable crops has challenged the environment and ecological balance. To restore the ecological balance, bio-stimulants can help in promoting conservation agriculture.

12.3.3 Quality Control

Although India produces ~15% of vegetables but hardly 1% of the produce is exported. The main constraint is the quality of vegetables. The quality requirements for export differ from those for domestic needs. Nevertheless, uniformity in size and colour is a universally accepted attribute; there are quite a lot of other specific quality requirements for the world market. The export consignments are rejected at the destinations for not meeting the recommended international standards due to pesticide residues and contamination with fungicides and other agrochemicals. Different markets require different qualities. For example, in onion Japan and European markets demand yellow or brown varieties, while Southeast Asian and West Asian countries require light to dark red varieties. The season of demands also differs in several countries as per climate and consumers' preferences.

12.3.4 Post-harvest Management

Vegetables are highly perishable in nature, ~25–40% of the produce get wasted due to lack of sufficient post-harvest handling measures, which cuts down the export quantities and increases competitiveness.

This issue can effectively be resolved by using the bio-stimulants as it can supplement the inputs like fertilizer and agricultural chemicals and is safe to the environment. It enhances the quality and quantity of produce which helps to fetch better market.

12.4 Bio-stimulant and Its Importance in Vegetable Production Enhancement

Bio-stimulants are mixtures of one or more things such as microorganisms, trace elements, enzymes, plant hormones and seaweed extracts rather than chemical fertilizers, which meant to correct severe nutrient deficiency. It has shown to influence several metabolic processes such as photosynthesis, respiration, ion uptake and nucleic acid synthesis. Bio-stimulants enhance nutrient availability, increase antioxidants, enhance metabolism water-holding capacity and increase chlorophyll production. Besides many advantages, the use of bio-stimulants in agricultural practices is proposed as a safe tool to enhance the nutritional properties of food crops (Ahmad et al. 2016; Meena et al. 2016a; Parewa et al. 2014; Prakash and Verma 2016; Kumar et al. 2016a).

Agricultural bio-stimulants comprise diverse formulations of substances, compounds and microorganisms that are applied to plants or soils to improve crop vigour, quality, yield and tolerance to abiotic stresses. It promotes plant growth and development throughout the crop life cycle from germination to maturity in a number of established ways. Better germination and root development, greater vigour and stress resistance, more efficient energy and nutrient uptake and transport are possible through the use of bio-stimulants (Fig. 12.1). By improving the efficiency of the plant’s metabolism to induce yield increases and enhance crop quality, it helps in increasing plant tolerance to abiotic stresses and recovering from stresses; facilitates nutrient assimilation, translocation and use; enhances quality attributes of produce, viz. sugar content, colour and fruit seeding; and enhances soil fertility, mainly by fostering the growth of complementary soil microorganisms (Meena et al. 2015a, f, 2016b; Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Raghavendra et al. 2016; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016; Jaiswal et al. 2016; Jha and Subramanian 2016).

The bio-stimulants are established as ecofriendly compounds having beneficial effects on plants (Schiavon et al. 2008). In particular, they decrease the use of chemical fertilizers by escalating the amount of macro- and micronutrients taken up by plants, positively influencing root morphology and plant growth (Nardi et al. 2009; Ertani et al. 2013). They exhibit hormone-like activity and influence plant metabolism through interacting with the biochemical processes. The manipulation of physiological mechanisms, such as nitrogen assimilation and glycolysis are induced to enhance plant quality parameters (Ertani et al. 2009). The mechanisms behind the biochemical and physiological effects of bio-stimulants on vegetable are often unidentified. It is because of the heterogeneity of the raw materials constituents used for vegetable production (Zahedi 2016; Meena et al. 2015b, 2016c; Rawat et al. 2016; Yasin et al. 2016; Saha et al. 2016a; Yadav and Sidhu 2016; Bahadur et al. 2016b; Das and Pradhan 2016).

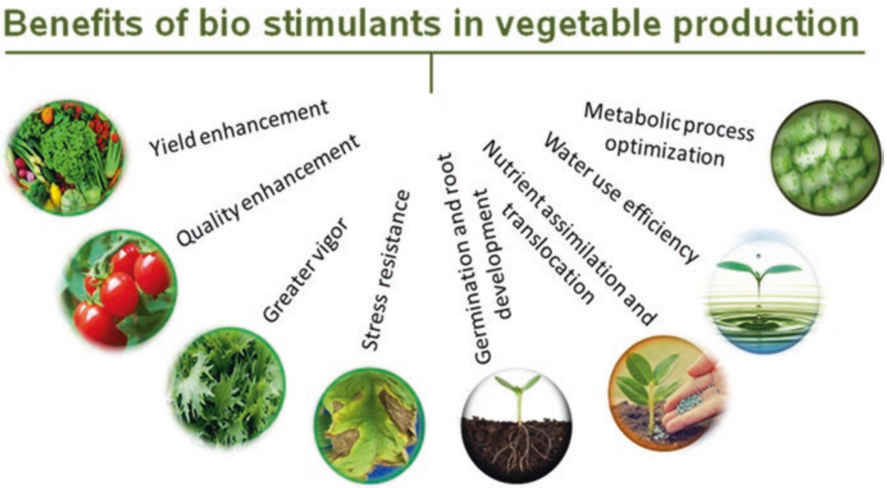

Fig. 12.1 Benefits of bio-stimulant in vegetable production

These effects are influenced by many components that may act synergistically in different ways. Current studies suggest that the active molecules in bio-stimulants can promote assimilation of nitrogen through stimulation of the activity and transcription of nitrogen assimilation and Krebs' cycle enzymes (Schiavon et al. 2008). The induction of the metabolic pathway linked with the synthesis of phenylpropanoids in plants treated with bio-stimulants may explain the reason behind the plants to overcome stress situations (Ertani et al. 2013).

Pepper is an important agricultural crop known for the nutritional value. It is an excellent source of a wide range of phytochemicals with renowned antioxidant properties. The major antioxidant compounds include capsaicinoids, carotenoids and phenolic compounds, particularly quercetin, flavonoids and luteolin (Howard et al. 2000). In recent studies, the application of certain bio-stimulant to pepper plants was found to exert affirmative effects on plant growth and yield devoid of fruit quality degradation (Azcona et al. 2011; Meena et al. 2014a, 2016d; Saha et al. 2016b; Verma et al. 2014, 2015bVerma et al. 2014; Meena et al. 2014a).

Bio-stimulants improve nutrient availability at root rhizosphere, enhance water-holding capacity, increase antioxidant activities and proliferate metabolism and chlorophyll production (EBIC 2013). It distinguish themselves from traditional crop inputs in three ways: (1) operate through different mechanisms than fertilizers, no matter the presence of nutrients in the products, (2) act only on the plant's vigour and do not have any direct actions against pests or disease and (3) play a complementary role in cropping nutrition and crop protection (EBIC 2013).

Bio-stimulants have a significant impact on crop yield, thereby helping nations cater to the surging demand for food. Keeping this in mind, the global population explosion is one of the foremost factors driving the bio-stimulants market. The

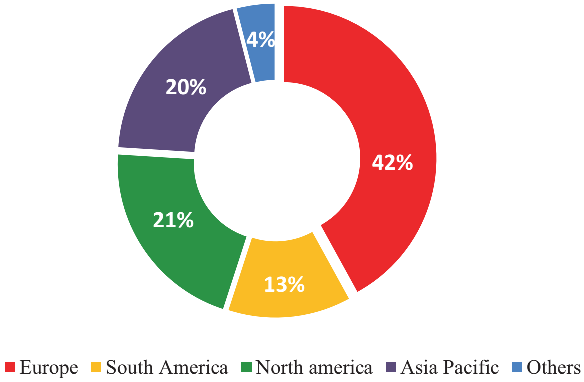

Fig. 12.2 Global bio-stimulant market share

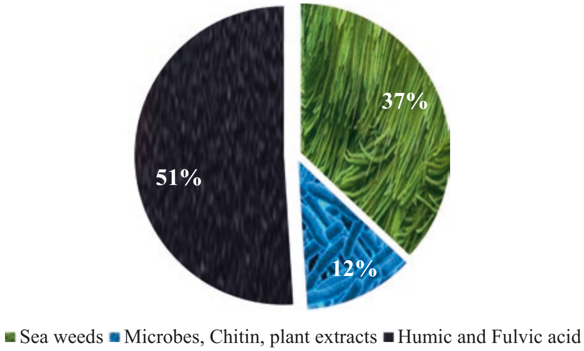

Fig. 12.3 Bio-stimulants active ingredient sources

bio-stimulants can increase crop yield by 5–10% while increasing the fertilizer use efficiency by at least 5–25% and reducing the cost of pesticides ~10–15% (EBIC 2013). The global market of bio-stimulant was mainly concentrated in Europe (Fig. 12.2), although is projected to be spread across the world and will reach from $1.69 billion in 2016 to $2.24 billion by 2018 (Calvo et al. 2014) and $3.08 billion by 2022 at 10.50% CAGR (Anonymous 2016).

12.5 Categories of Plant Bio-stimulants

The bio-stimulant includes a diverse group of products, technologies that have different modes of action and are derived from naturally occurring microorganisms, plant extracts or other organic matter. Worldwide the bio-stimulants' active ingredient sources are majorly classified in three as humic acid and fulvic acid (~51%), seaweed extracts (~37%) and microbes, and chitin and plant extract (~12%) (Figs. 12.3). The details are presented below.

12.5.1 Humus and Humic Acids

Humic substances are natural elements of the soil organic matter, consequential to the decompositions of the animal, plant and microbial residues as a result of the metabolic activity of soil microbes by means of these substrates. The best sources of humic acids are found in layers of leonardite. It is an organic matter alike the soft brown coal but differs by its degree of oxidation. Both the humic acid and fulvic acid have been shown to possess an affirmative impact on plant growth through providing an effective growing environment for plants by increasing surface water infiltration, penetration and soil water-holding capacity. They also enhance the availability of phosphorus potassium and some essential micronutrients (Gallant 2004). Humic acids play an important role in physiological and morphological effects on plants (Eyheraguibel et al. 2008) The humic acids retain nutrient ions and thus prevent them from leaching. They also act as a buffer for plants from too high concentrations of fertilizer salts. Other than these the humic acids have been shown to boost germination rates and promote greater fibrous root growth (EBIC 2013).

The bio-stimulants act in synergy with plant nutrients. The application of humic acid and nitrogen in combination has promoted better root growth than with only nitrogen. They also enhance chlorophyll content of plant leaves and improve stand uniformity by influencing metabolism (Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b, 2015e; Teotia et al. 2016).

12.5.2 Fulvic Acids

The fulvic acids are a kind of humic substances recognized to be powerful organic electrolytes which help to dissolve soil minerals and metals (Huang and Deller 1970). Fulvic acids transform minerals to readily available form for easy absorption by plants (Jackson 1993). They act more in the plant than in the soil and enhance vitamins, coenzyme, auxin, nutrient and metabolism, which help significantly to plant health. Furthermore, the fulvic acids help plants to resist wilting indirectly by raising the amount of carbohydrates which results in soluble sugars accumulation in the cell. To deal with drought stress, they increase the osmotic pressure on the cell walls. Finally, fulvic acids help to enhance the nutrient uptake by increasing the permeability of the cell membrane.

12.5.3 Cytokinins

Cytokinins promote cell division in plants. They have been reported to promote cell expansion, enlarge leaf surface area that results in more chlorophyll production and amplify photosynthesis. A low concentration of cytokinins has been used as a seed treatment to promote lateral root development in young seedlings (Laplaze et al. 2007; Werner et al. 2010). They also have the ability to promote nutrient translocation within plants which is responsible for increased plant metabolism (Chang et al. 2013).

12.5.4 Protein Hydrolysates and Other N-Containing Compounds

Protein hydrolases are actually amino acids and peptide mixtures which are obtained by enzymatic and chemical protein hydrolysis produced from agro-industry as by-products, from both animal (e.g. epithelial tissues, collagen) and plant sources (crop residues) (Calvo et al. 2014; Halpern et al. 2015). In biostimulants some other nitrogenous molecules like polyamines, betaines and 'nonprotein amino acids' are there (Vranova et al. 2011). Protein hydrolysates are established for having a role in increasing microbial biomass and activity, soil respiration and thus overall soil fertility. Significant improvements in yield and quality traits have been reported in agricultural and horticultural crops (Calvo et al. 2014). A number of commercial products prepared from protein hydrolysates of animal and plant origins are available in the European market (Table 12.2).

Table 12.2 Examples of commercialized bio-stimulants and their use in vegetable disease management

Products	Product origin	Manufacturer	Crop	Disease targets
Vacciplant®	Laminarian extract from brown algae, *Laminaria digitata*	Laboratoire Goemar, France	Tomato	Bacterial spot, bacterial speck, grey mould, powdery mildew, *Phytophthora* blight, early blight, Anthracnose
			Egg plant	Powdery mildew, *Phytophthora* blight
			Cucurbits	Powdery mildew, *Phytophthora* blight
			Zucchini	
			Cucumber	
			Watermelon	
			Melon	
			Leafy vegetable	Downy mildew
			Lettuce	Grey mould
			Spinach	
			Cabbage	Downy mildew
				Grey mould
Elexa® 4PDB	Chitosan-based natural product	Plant Defence Boosters Inc., USA	Cucumber, melon, pumpkin, squash	Downy mildew
				Powdery mildew
			Peas	Powdery mildew
Milsana®	Alcoholic extract from dried plant part of a weed giant knotweed (*Reynoutria sachalinensis*)	KHH Bioscience, USA; BIOFA AG, Germany	Greenhouse as well as open field cucumber	Powdery mildew
			Tomato and pepper	Powdery mildew
ChitoPlant ®	Chitosan-based natural product	ChiPro GmbH, Germany	Tomato	Powdery mildew Scab
			Potato	
			Cucurbits	Downy mildew

12.5.5 Beneficial Bacteria

The bio-stimulants, in agriculture point of view, can be considered of two types within the taxonomic, functional and ecological diversity: first mutualistic endosymbionts like *Rhizobium* and second mutualistic, rhizospheric-like 'plant growth-promoting rhizobacteria' (PGPR). *Rhizobium* and related taxa are commercialized as biofertilizers. The PGPRs are multifunctional and influence all aspects of plant life: morphogenesis and development, nutrition and growth, interactions with other organisms in the agroecosystems, response to biotic and abiotic stress, etc. (Bhattacharyya and Jha 2012; Gaiero et al. 2013; Vacheron et al. 2013; Shrivastava et al. 2016; Velazquez et al. 2016; Meena et al. 2015c). Plant growth-promoting rhizobacteria (PGPR) are now increasingly applied in vegetable crops (Table 12.3).

PGPR inoculants are nowadays regarded as some type of plant 'probiotics', i.e. efficient contributors to plant nutrition and immunity (Berendsen et al. 2012). Plant growth-promoting rhizobacteria (PGPR) is such group of microorganisms that act as a bio-stimulant in a wide range of soil and plant interactions including improvement

Table 12.3 Plant growth-promoting rhizobacteria (PGPR) application in vegetable crops

PGPR spp./strain	Crop	Effect on plant growth	References
Rhizobium und Nicola; Rhizobium spp. Mesorhizobium, R.leguminosarum, Bradyrhizobium, Sinorhizobium meliloti	Broccoli, carrot, lettuce	Increased yield, enhanced macro and micronutrient uptake,	Yildrim et al. (2011), Bhagat et al. (2014), and Ghosh et al. (2015),
Azotobacter chroococcum, Azotobacter spp. A. vinelandii Azospirillum lipoferum, A. brasilense,	Cucumber, lettuce	Increased germination, increased length and weight of roots, improved vigour index of germinating seeds	Fasciglione et al. (2012) and Mangmang et al. (2015),
Pseudomonas P. aeruginosa, fluorescens, P. putida, Pseudomonas sp.	Broccoli, cucumber, lettuce,	Enhanced nutrient uptake, increased plant growth, increased dry matter and mineral content of fruits, increased yield in terms of number of fruits and weight	Kohler et al. (2009), Dursun et al. (2010), and Tanwar et al. (2014)
Achromobacter xylosoxidans, Stenotrophomonas maltophilia, Achromobacter sp., A. xylosoxidans	Cucumber, potato	Increased plant height, dry weight, fruit yield, tuber dry matter	Egamberdieva et al. (2011) and Dawwam et al. (2013)
Bacillus subtilis, B. Megaterium, B. cereus, B. amyloliquefaciens, Bacillus sp.,	Cucumber, pepper	Induced systemic tolerance to drought stress, increased root vigour, increased fresh root and shoot weight and their length	Wang et al. (2012), Kokalis-Burelle et al. (2002), and Lim and Kim (2013)

in the availability of nutrients, production of volatile organic compounds, hormone release or hormonal changes within plants, enhancement of tolerance to abiotic stresses and much more. Beside these low cost, easy access and simple mode of application have attracted the agrarian stakeholders (Sindhu et al. 2016; Meena et al. 2014b, 2015d, 2016e; Singh et al. 2016; Masood and Bano 2016).

12.6 Strategies for Bio-stimulants Adoption

The farmers of developing countries will not adopt bio-stimulant and biocontrol management practices until and unless the successes are guaranteed. The small-scale farmers in developing countries do not always welcome the suggestion of using alternative methods with much enthusiasm (Bashan et al. 2014). Among the bio-based products, majority of the farmers are using bio-stimulants and biopesticides. In North America, it represents ~40% of the biocontrol market as compared with ~25% in Europe, ~20% in Asia, ~ 10% in South America and ~5% in the rest of the world (Cox and Wong 2013).

The main reason for farmer's laggardness about these alternative methods of agro-ecological management is the variable efficacy in the field as compared with conventional chemical inputs (Arora et al. 2011; Walters et al. 2013). These products have shown variable field performances as compared with the laboratory or in greenhouse condition. Such inconsistency in practical conditions made this technology not fully reliable does the farming community (Gozzo and Faoro 2013).

Naturally, the bio-stimulants depend on the concentration and interaction with the environmental condition. As, for example, the PGPR, bacteria concentrations in commercialized products may fall below the desired threshold level (10^8–10^{11} cells/mL). The concentration varies under a long term or in any inadequate storage conditions. Similarly, the performance of bio-stimulants greatly depends on the field environmental condition (temperature, relative humidity, the intensity of sunlight, concentration of UV radiation, disease pressure), crop systems (nutritional requirements, plant genotype, physiology) and the formulation (Walter et al. 2014).

The farmers' adoption decision depends mainly on the label of change that they want from the current agricultural practices and the potential of a new technology. The level of change can be manipulated by creating a need for development through effective utilization of extension strategies. The benefits of the technology have to be clearly demonstrated to educational programmes, awareness campaigns obviously backed by pragmatic field results. Development of detailed package of practices about the agronomic parameters crop management techniques, the time and frequency of dosage application procedures and other important practices (Singh et al. 2015; Meena et al. 2013c; Bahadur et al. 2016a).

In developing countries like India, certain other things have to be considered for successful transfer of technology. The first is the availability of the product in the right time at the right place. It has been reported that the basic input like the seed, fertilizer is still partially available to the farmers. In such a condition the products like bio-stimulants have to be readily available in local markets during the pick application period. Agricultural Extension strategies required here to demonstrate the beneficial elements of the technology and convince the farmers about the better return on investment by means of better resource use efficiency and good environmental benefits.

12.6.1 Factors Contributing Towards the Expansion of the Bio-stimulants Market in the World

- Rising global population and food demand
- The need for sustainable increase in the crop yield
- To minimize the abiotic stress in plants
- The growing concerns about sustainable agriculture
- Eco-friendly properties of bio-stimulants over pesticides and fertilizers
- The increase in government grants and funding to encourage the use of bio-stimulant products
- Proven performance and acceptance from NGOs, governmental bodies and academia
- The rising awareness regarding the use and benefits of bio-stimulants
- The growing popularity of natural and organic ingredient-based agriculture
- Effort on the part of the market players to develop cost-effective products
- Demand from farmers and consumers for environmentally safe and organic products that provide alternatives to synthetic inputs

There are two indispensable factors for effective adoption of any particular technology knowledge about technology and compatibility of the technology with local condition. This is true for bio-stimulants too. The knowledge factor can be taken care of through research in applications of bio-stimulants in vegetable crops, types of vegetable crops may be covered with the level of concentration, etc. Agronomic field research in vegetable crop particular to Indian condition is very less which needs to be promoted.

The compatibility of a technology depends on several other factors such as the cost of the product, ease of application and efficiency. For that purpose, detailed studies are required for (1) long-term survival and good shelf-life of bio-stimulant, specificity in applications in a wide range of agroecological conditions in the vegetable crop, (2) cost reduction mechanisms, (3) suitable conditions dosage, concentration and (4) farm machinery applications of bio-stimulants.

Presently, India does not have much production units of bio-stimulants. It majorly depends on imports. In 2016, India has imported 492 tonnes of bio-stimulants worth $ 15.78 Million. The United States is the largest supplier of bio-stimulants accounting for imports worth $ 9.75 Million followed by Mexico and Israel which exported bio-stimulants worth $ 2.93 Million and $ 1.37 Million, respectively (Zauba.com 2016). Although very less amount is used for plant growth promotion. Efforts are required to production, promotion and adoption of bio-stimulants. In such a condition, public-private partnership and convergence approach are required (Mukherjee et al. 2012a; Mukherjee and Maity 2015).

A strong extension strategy is required which shall be focused on the promotion of bio-stimulants and its use in vegetable production. Development of strong hub and spoke model like some private extension system (Mukherjee et al. 2011) is required for effective delivery of bio-stimulants products at farmers' doorsteps. Targeting large farmers can be another option. Large farmers and the progressive have greater risk-absorbing capacity in case of inadvertent loss. Study depicts that marketing orientation, education, economic motivation, social participation, family size and extension agency contact are such factors that can influence farmers progressiveness (Mukherjee et al. 2012b). Large-scale and progressive farmers can be motivated towards the adoption of bio-stimulants which further be upscaled as per the theories of diffusion. Farmers are facing severe losses due to unseasonal rains, the risk of droughts and natural calamities (Mukherjee 2015) which can be addressed to some extent by the use of bio-stimulant technology.

12.7 Conclusions

In order to enhance the sustainable food production, food and nutritional security with a significant reduction of synthetic fertilizers, agrochemical use and environmental pollution and natural resource productivity enhancement through the use of bio-stimulants in the vegetable are essential. It promotes plant growth and development throughout the crop life cycle from germination to maturity in a number of established ways. Better germination and root development, greater vigour and stress resistance, more efficient energy and nutrient uptake and transport are possible through the use of bio-stimulants. India is a larger import of plant bio-stimulants. For better adoption of bio-stimulants, research and extension are both required. Especially the knowledge and awareness about the bio-stimulant technology and compatibility of the commercial product which Indian farmers' condition are necessary.

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Efficacy of Biological Soil Amendments and Biocontrol Agents for Sustainable Rice and Maize Production

13

Manoj Kaushal and Suhas P. Wani

Abstract

Exploiting the agroecosystem services of soil microbes appears as a promising effective approach to alleviate the negative impacts on soil systems and crop production. Lack of soil organic matter (SOM) is a prevalent feature of degraded soils. Different biological soil amendments, such as organic manure, compost, vermicompost, indigenous microbes, and crop residues, are widely used in reclamation of degraded soils. The biological soil amendments also furnish a valuable source of fertilizer for growing rice and maize and also boost physicochemical and biological parameters of soil such as water holding capacity, moisture content, electrical conductivity, organic carbon content, and population of beneficial microbes which directly correlates to soil health and fertility. However, efficiency of amendments applied based on variety of factors including the composition and characteristics, soil microflora, and environmental conditions can accelerate initial reclamation and lead to self-sustaining primary productivity of crops. On the other hand, high cost of chemical fertilizers, pesticides, and other agricultural inputs and their harmful environmental legacy have encouraged researchers to explore the use of microbial-mediated amendments to play a central role in raising productivity and inhibition/suppression of pathogenic population below levels at which they cause economic and other effects to the crops as well as the environment. Biological control can be achieved through one or more mechanisms, viz., antibiosis, competition for nutrients and/space, induced resistance, plant growth promotion, and rhizosphere colonization ability. Potent biocontrol agents such as *Bacillus* sp., *Pseudomonas* sp., and *Tricoderma* sp. prove to be very promising in controlling soilborne diseases of rice and maize crops employing both antibiosis and induction of host resistance. Determination of the

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modes of action of biocontrol agents is obligatory to provide higher level of protection to crop under a particular environmental condition that exists in divergent agroecosystems. This chapter reviews an insight of mechanisms of biological soil amendments and biocontrol agents and their emphasis on soil amelioration with the goal of a sustainable agricultural system.

Keywords
Biological soil amendments • Biocontrol mechanisms • Intermediate metabolites • Induced systemic resistance • Rhizobacteria • Sustainable agriculture

13.1 Introduction

Rice (*Oryza sativa* L.), a widely grown crop in tropical and subtropical regions, is the most important staple foods for ~50% of the world's human population and requires ~10 Mt. of N fertilizers every year (Zhang et al. 2014). N source supplied to crop is usually by commercially available N fertilizers such as urea, which results in a substantial amount of loss through different mechanisms and thus becomes one of the predominant factors for environmental hazards and deterioration of soil fertility as well (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 sustainable maize production systems also face major challenges of appropriate management of N fertilizers to maximize economic return while minimizing environmental pollution. Maize, grown in rotation with legume crops (alfalfa or soybeans), often yields more, so organic N in crop residues derived from biological N_2 fixation by legume crops has been an effective alternative to meet this challenge (Raaijmakers and Lugtenberg 2013). Increase maize yield from ~5 to 20% attributed to the beneficial effect of crop rotation including improved soil physical properties (Barea 2015), a better balance of plant nutritional factors, increased root activity, a shift in soil mycorrhizal populations, lessen disease severity (Reid et al. 2001), and magnified seasonal N mineralization (Browne et al. 2013). A large effort has been devoted to the studies of legume effects on subsequent cereal crops grown in rotation systems (Barea et al. 2013a; Lugtenberg 2015). The use of biological soil amendments such as manure and compost improves soil fertility and soil quality as well as enhances the population of beneficial microbes in rice and maize fields.

Biological soil amendments of animal origin such as manure and compost that include animal waste and human waste serve as a potential vector for soil- and root-borne pathogens and also critical in sustainable farming systems and certified organic production. Addition of dairy farm manure provides partial or complete N and other nutrient elements, as well as increases soil N release through seasonal N mineralization and availability to the plant (Zolla et al. 2013). However, nutrient (N) availability from manure varied greatly due to source of manure, method of storage (Eghball 2000), and time and method of application. Manure application usually increases crop yield due to plant nutrient availability (Ma et al. 1999b) and improved

Table 13.1 List of major rice diseases and their causal organisms

Disease	Causal organism	Biocontrol agents
Bacterial blight and leaf streak	*Xanthomonas oryzae*	*Streptomyces* sp.
Blast	*Pyricularia grisea*	*P. fluorescens*
Brown spot	*Bipolaris oryzae*	*P. aeruginosa*
Crown sheath rot	*Gaeumannomyces graminis*	*P. fluorescens*
False smut	*Ustilaginoidea virens*	*Pseudomonas* sp.
Foot rot	*Erwinia chrysanthemi*	*Azotobacter* sp.
Grain rot	*Burkholderia glumae*	*Bacillus* sp.
Leaf scald	*Rhynchosporium oryzae*	*Pseudomonas* sp.
Leaf smut	*Entyloma oryzae*	*Pseudomonas* sp.
Pecky rice (kernel spotting)	*Curvularia* sp.; *Fusarium* sp.	*Pseudomonas* sp.
Root rots	*Pythium spinosum*	*P. fluorescens*
Seedling blight	*Sclerotium rolfsii*	*B. glumae*
Sheath blight	*Rhizoctonia solani*	*P. fluorescens*
Sheath brown rot	*Pseudomonas fuscovaginae*	*B. amyloliquefaciens*
Sheath rot	*Sarocladium oryzae*	*P. aeruginosa*
Sheath spot	*Rhizoctonia oryzae*	*Pseudomonas* sp.
Stem rot	*Sclerotium oryzae*	*P. fluorescens*
Seed-rot and seedling disease	*Fusarium* sp.; *Pythium* sp.	*Pseudomonas* spp.

soil structure (Spence and Bais 2013). The N fertilizer application can be reduced by the use of biological N_2 fixation technology which further minimizes environmental risks (Raimam et al. 2007).

N-fixing bacteria may be free-living or symbiotically associated to rice plants mostly species of *Alcaligenes*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Herbaspirillum*, *Klebsiella*, *Pseudomonas*, and *Rhizobium* (Hirsch et al. 2013b). The most serious constraint on high productivity of rice (Table 13.1) and maize (Table 13.2) crop is the diseases caused by fungi, bacteria, viruses, or nematodes (Manandhar et al. 1998) causing annual yield losses in very high amount. Beyond good agronomic practices (resistant cultivars and application of pesticides), a wide variety of approaches may be used to prevent, mitigate, or control rice diseases such as heavily use of chemical fertilizers and pesticides.

However, many resistant cultivars have very short life span due to the breakdown of the resistance in high pathogenic variability of the pathogens. Also, the environmental pollution caused by excessive use of agrochemicals as well as strict regulations on chemical pesticide has led to considerable changes in attitudes of people's toward the use of more pesticides in rice and maize crops. Among the alternatives, a variety of biological controls are available for use in rice as well as maize crops, but their effective adoptions will require a greater understanding of the complex interactions among plants, soil, and microbes (Meena et al. 2016a; Parewa et al. 2014; Prakash and Verma 2016; Jaiswal et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a). This article presents an advanced survey of biological soil

Table 13.2 List of major maize diseases and their causal organisms

Disease	Causal organism	Biocontrol agent
Anthracnose leaf blight	*Colletotrichum graminicola*	*Torulaspora globosa*
Aspergillus ear	*Aspergillus flavus*	*Streptomyces* sp.
Bacterial leaf spot	*Xanthomonas campestris*	*B. subtilis*
Bacterial stalk and top rot	*Erwinia carotovora*	*B. subtilis*
Bacterial stripe	*Pseudomonas andropogonis*	*Microbacterium maritypicum*
Black bundle disease	*Cephalosporium acremonium*	*Glomus fasciculatum*
Charcoal rot	*Macrophomina phaseolina*	*Trichoderma* sp.
Cladosporium rot	*Cladosporium herbarum*	*Trichoderma* sp.
Fusarium ear	*Fusarium subglutinans*	*T. harzianum*
Holcus spot	*Pseudomonas syringae*	*M. maritypicum*
Leaf spots, minor	*Alternaria alternata*	*Pseudomonas* sp.
Penicillium ear rot	*Penicillium* sp.	*Trichoderma* sp.
Seedling blight	*Gibberella fujikuroi*	*Bacillus* sp.
Sheath spot	*Rhizoctonia solani*	*T. harzianum*
Smut	*Ustilago maydis*	*T. viride*
Stalk rot	*Physoderma maydis*	*T. machilonis*
Stewart's disease	*Erwinia stewartii*	*M. maritypicum*
Yellow leaf blight	*Phyllosticta maydis*	*Pantoea ananas*

amendments and biocontrol agents applied to the suppression of plant diseases for sustainable rice and maize production (Zancarini et al. 2013).

13.2 Biological Soil Amendments (BSAs)

Any material of plant or animal origin added to the soil to brush up its physicochemical and biological properties in relation to plant growth or ameliorate the WHC, avoiding contamination of pathogens, is considered as biological soil amendments (BSAs). The BSAs consist of whole or a part of materials of animal/plant origin, such as manure, blood meal, and fish emulsion and human waste, compost, or table waste, used alone or in consortium. Moreover, BSAs increase soil microbial activity, uptake of nutrients, decomposition rate, and crop vigor and yield while reducing fertilizer need leading to maximize yields (Fig. 13.1). However, there is still lack of information available with regard to utility of BSAs, organic amendments, growth regulators, and other biological stimulants. BSAs may be treated or untreated and transform depleted soil into healthy soil (Zolla et al. 2013; Meena et al. 2015a, f, 2016b; Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Dotaniya et al. 2016).

Treated BSAs are substitute in which microbial/bacterial inoculums are added that have been isolated from highly fertile soils and exhibit optimum abilities to produce organic nutrients and beneficial enzymes. This can increase availability of labile organic carbon and more accumulation of soil organic carbon such as azolla-algal biofertilizers which increases accumulation of ferric iron oxide in soil and

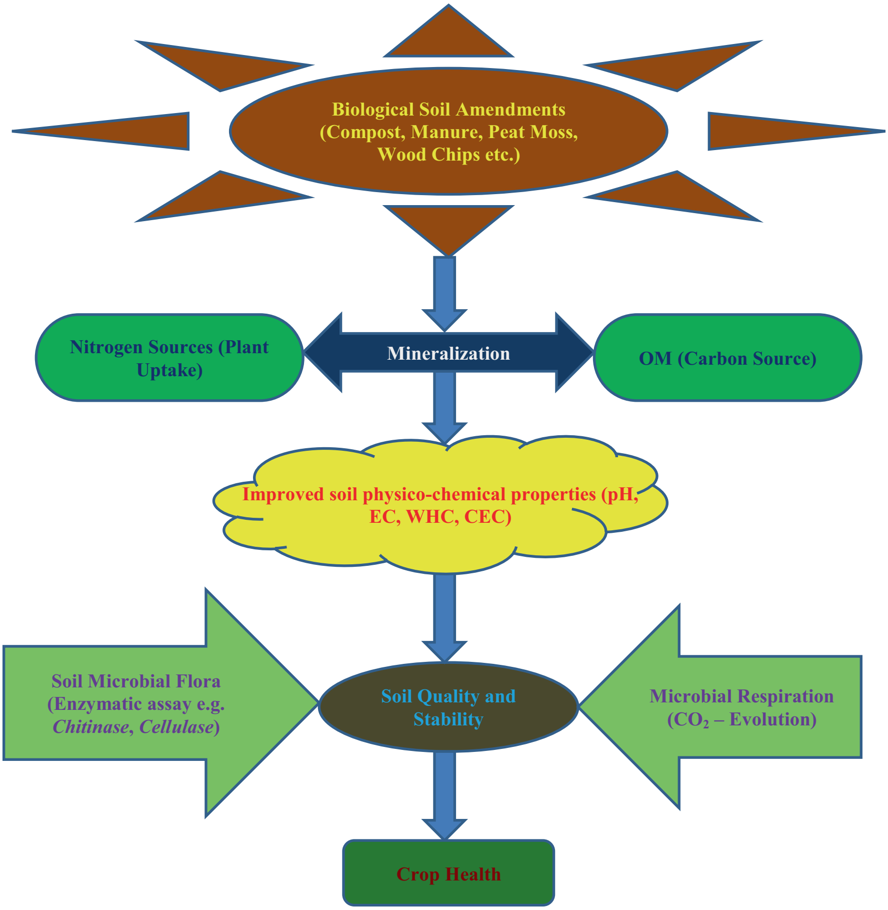

Fig. 13.1 An overview of biological soil amendments (BSAs) and their role toward the soil sustainability

ultimately increases soil redox value and soil porosity in rice cropping system. Azolla anabaena treatment also diminishes CH_4 emission rate during the rice growing seasons due to the lower C/N ratio (14:1) and maximizes cellulose and lignin content. Agnihotri et al. (1999) also reported that rice straw application before flooding and the biofertilizers after flooding enhanced CH_4 efflux from rice fields, while CH_4 fluxes were decreased by composts of cow dung. Composted livestock manure application in rice field increased rice yield by ~30% and dwindle CH_4 emissions 56% per unit of grain yield compared to the non-fertilized control treatment. Availability of major nutrients such as N, P, K, Ca, Mg, Si, soluble Fe, etc. can also be increased to rice and maize plants by adding BSAs, organic materials, inorganic fertilizer, and other amendments (Ali et al. 2012), which further stimulated plant growth and yield (Hu and Wang 1995; Lee et al. 2004).

Overall BSAs such as straw compost, cattle manure compost, green plant biomass, and azolla anabaena improve soil quality parameters such as porosity, total nitrogen, MBC, MBN, SOM, CEC, and nutrient availability to plants in paddy and maize fields alone or as consortium or in combination with other chemical fertilizers. In addition to nutrients released from the added BSAs, they also accelerate the rice and maize plant growth, photosynthetic carbon assimilation and root exudation, and microbial activity and increased the MBC that eventually resulted in organic C accumulation in soil (Ali et al. 2012). Conclusively, to minimize the use of conventional NPK fertilizers, reducing CH_4 emissions and sustaining rice productivity, BSAs could be introduced in rice and maize cropping systems.

13.2.1 Beneficial Soil Microorganisms

Naturally occurring soil microbes are nature's most constructive fertilizer producers and serve as supreme agents of BSAs. Thus, BSAs are adopted for their multiple benefits to sustained plant growth and overall soil productivity and disease suppression. They are also effective in different soil conditions and provide unique propensity to fix both atmospheric and chemical nitrogen and thus selected for utmost adaptability. These rhizospheric bacteria are ruling in this category due to their natural enzyme production capabilities which transform insoluble form of phosphorus and potassium to soluble form. Besides they also produce antibiotics and other plant hormones that stimulate root and shoot growth of rice plants. These microbes are isolated, screened, and grown in the laboratory under aseptic conditions to provide a pure microbial culture.

Thereafter, pure microbial culture is combined with other BSAs and applied to soil so that indigenous bacteria multiply, grow, and get adapted to conditions rapidly. BSAs improve the biological health of soil, thereby increasing nutrient uptake by 150–250% and reducing volatilization (gaseous escape) and leaching run off and seepage. Increasing BSAs of a soil makes the soil more permeable to absorb additional water and healthy populations of microbes metabolizing nutrients, making them available to plants (Duarte et al. 2006).

13.2.2 Humus

Decomposed parts of plant and animal organic matter within the soil that resists further decomposition are called humus, and the process of formation is called humification. Humus profoundly improves soil structure and permeability, enhances water holding capacity of soil, and naturally chelates unavailable micronutrients. Active humus within the soil is created by both biological and chemical processes and is composed largely of three organic acids: humic acid, humin, and fulvic acid (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).

These small organic materials join together to form complex chemical structures called polymers. Chemically, these are polyphenolic acids, and synthesis of these polymers results from primary transformative mechanism, i.e., release of enzymes from different microbes. Humus is considered as "Black Gold" of soil as it darkens soil color and increases absorption of organic compounds that aid plant nutrition, buffering capacity of soil, thereby helping to stabilize the soil's pH and thus plants for absorbing mineral nutrients as well in cleaning of toxic materials in the soil (Mercado-Blanco 2015).

13.2.3 Biostimulants

Biostimulants include diverse formulations, microorganisms, plant extracts, and other bioactive compounds applied to improve crop yields, quality, and tolerance of biotic and abiotic stresses in a cheaper way. They are used as BSAs (microbial inoculants, humic and fulvic acids, seaweed extracts, protein hydrolysates, amino acids) to escalate plant growth. Moreover, these BSAs also increased leaf pigments (chlorophyll and carotenoids) and stimulate root growth and enhance the antioxidant potential of plants (Nardi et al. 2009; Ertani et al. 2013). Biostimulants influence biochemical and physiological mechanisms (glycolysis and nitrogen assimilation) and thus sway plant metabolism (Ertani et al. 2009; Vaccaro et al. 2009; Azcona et al. 2011). In maize plant, a protein hydrolyzate-based fertilizer was proved to overcome salinity stress through stimulation of enzymes, enhancement of phenylalanine ammonia-lyase (PAL) activity and transcription, and increase of flavonoid synthesis (Ertani et al. 2011; Saha et al. 2016a, b; Yadav and Sidhu 2016; Meena et al. 2015e, 2016d; Verma et al. 2015b; Teotia et al. 2016; Bahadur et al. 2016b).

13.2.4 Intermediate Metabolites

This category of BSAs is derived from plant and animal soluble comprising simple and complex sugars, amino acids, carbohydrates, peptides, lignin, and cellulose. They help to break soil compaction, improve CEC, and serve as an immediate source of energy for soil microbes and plants.

13.3 Biological Control and Its Mechanisms

The rhizosphere region of plants is surrounded by diverse types of microbes which can contribute to biological control due to secretion of a variety of root exudates in higher amount. Biological control refers to the inhibition/suppression of activities and populations of one or more plant pathogens through introduced or native microbial species. Microbes that contribute most to disease control are most likely genera of bacteria (*Bacillus*, *Pseudomonas*, *Burkholderia*, *Lysobacter*, and *Streptomyces*),

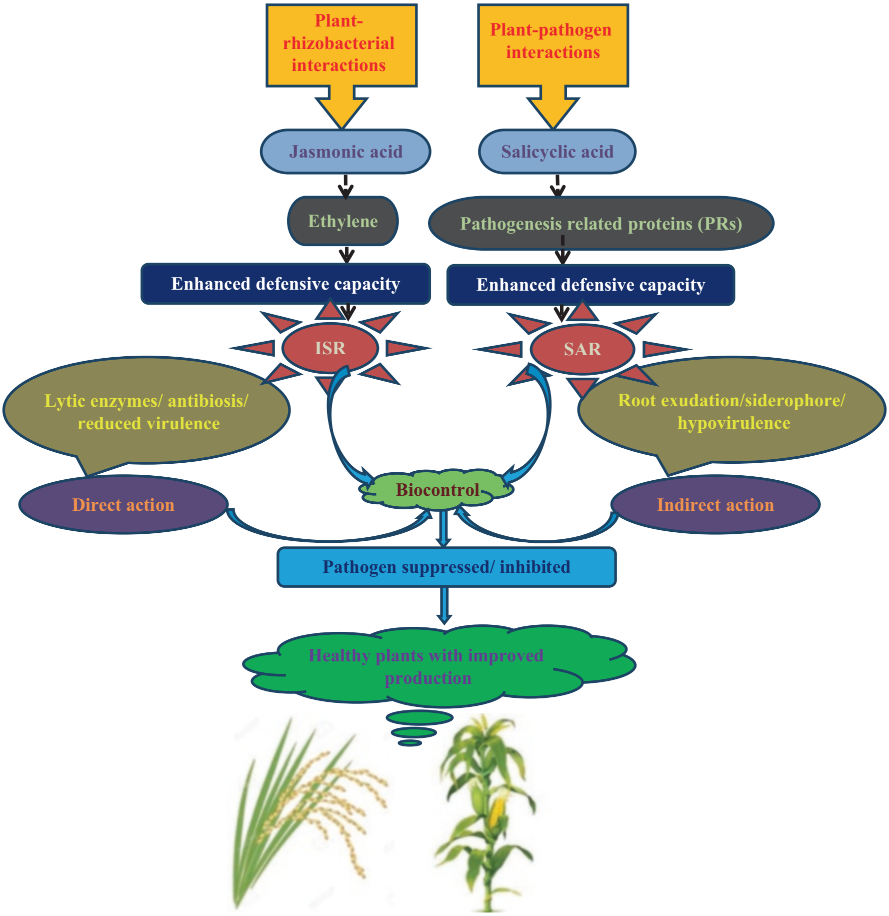

Fig. 13.2 Different mechanisms carried out by BCAs leading to biological control (mainly rice and maize crops)

fungi (*Trichoderma*, *Gliocladium*, *Dactylella*, and *Paecilomyces*), and some VAM fungi (*Glomus* sp.) considered as biocontrol agents (BCAs). These microbes provide biological control in a variety of ways (Fig. 13.2), including niche exclusion, bio-antagonism, and induction of induced systemic resistance (ISR) against infection by fungal, bacterial, and viral pathogens in different plant species (Compant et al. 2005).

Plant diseases may be suppressed by one or more microbes and codified as general and specific suppression. When inoculation of a biocontrol agent results in substantial levels of disease suppression, it leads to specific suppression. Biocontrol agents are also responsible for depletion of available soil nutrients making less available to the pathogens for their proliferation and becomes as causal agents for plant disease. Selection and desired effects of applying microbial cultures may vary based on their adaptability to new ecological and environmental conditions, so they are applied in soils as single inoculation or repeated applications to produce the anticipated results. Also in rice cropping system, more than 95% of the agricultural land devoted to crop production worldwide can be classified as having disease-inducing soils, which have poor physical properties, and large amounts of energy are lost as greenhouse gases (Verma et al. 2014, 2015a; Meena et al. 2013b, 2014a, 2016e; Sharma et al. 2016; Shrivastava et al. 2016).

Biological factors have been identified as the most important element disease suppressive soils (Mazzola 2002). Disease suppressive soils are the soils in which the pathogen may persist in the soil but causes little or no damage to crops. A prominent example of disease suppressiveness is *Pseudomonas fluorescens* producing 2, 4-diacetylphloroglucinol (Raaijmakers and Weller 1998); siderophore-mediated competition for iron has been studied in detail over the last three to four decades (Weller 2007).

16S rRNA-based techniques have also been used to identify additional bacterial taxa such as *Pseudomonas*, *Azospirillum*, *Gluconacetobacter*, and *Burkholderia* that are involved in take-all decline (Sanguin et al. 2009; Schreiner et al. 2010). Fusarium wilt suppressiveness (Alabouvette 1999), tobacco black root rot disease suppressiveness (Kyselkova et al. 2009), and *Rhizoctonia solani* suppressiveness (Mendes et al. 2011) are other well-examined examples of disease suppressive soils. Besides good cultural practices (soil and water management), commercialization of biocontrol agents governed by several factors such as stability, efficacy, specificity toward host, and reliability has also a number of constraints. Significant biological control arises from manipulating different associations/interactions between microbes and host plants or antagonisms between microbes and pathogens. Plants, pathogens, and BCAs interact in a variety of ways for successful biological control in rice and maize cropping system.

Microbial interactions are comprehensive analyses of symbiotic microorganisms (bacteria, fungi) interacting with plants, viz., competition, mutualism, commensalism, antagonisms, predation, and protocooperation. Mechanism of both beneficial and antagonistic functions exhibited by symbiotic microbes toward their hosts could enable the development of microbe-based sustainable agriculture (Velazquez et al. 2016; Meena et al. 2014b, 2015c; Sindhu et al. 2016; Singh et al. 2016; Masood and Bano 2016).

13.3.1 Antagonism

Interaction involving physical contact of the pathogen with BCAs and other organisms would be required to exert a suppressive effect referred to as direct antagonism. Indirect antagonisms do not involve targeting a pathogen by BCAs, for example, stimulation of plant host defense pathways by nonpathogenic ones.

13.3.2 Mutualism

Mutualism is an obligatory interaction between two or more species in which both species are benefitted such as mycorrhizal association between higher plants and fungi. For example, bacteria in the genus *Rhizobium* can reproduce in mutualistic association with legume plants and *Glomus* and *Gigaspora* sp. with some horticultural plants. In this type of mutualism, BCAs stimulate host defense and improve nutrition to plants which can contribute to biological control (de Bruijn 2015).

13.3.3 Commensalism

Some microbes live in a symbiotic interaction with plants, where one gets the benefit and the other is neither harmed nor benefitted creating challenges to soilborne pathogens. Increasing iron uptake efficiency of the commensal microbes is also an important factor to colonize plant roots which leads to the displacement of pathogens from infected areas/sites.

13.3.4 Protocooperation

Both partners count in association do not depend on each other for survival. Some microbes isolated and classified as BCAs are involved in protocooperation depending on environmental conditions leading to disease suppression.

13.3.5 Competition

The rhizosphere region of plant secretes root exudates such as flavonoids, sugars, carbohydrates, proteins, amino acids, etc. for which competition exists between pathogens and BCAs, thus becoming an important factor for limiting disease incidence and severity. For example, soilborne pathogens (*Fusarium* and *Pythium*) infect through mycelial contact and are more susceptible to competition than other microbes. These microbes produce secondary metabolites that suppress soilborne fungal pathogens. Another example of biological control is iron limitation in the rhizosphere region which depends on soil pH to support the growth of microorganisms, generally iron (ferric form) which is insoluble in water (pH 7.4) needed with concentrations of 10^{-6} M. However, highly oxidized and aerated soil contains much lower concentration (10^{-18} M) (Barea and Richardson 2015).

13.3.6 Antagonism

Microbes produce lytic enzymes which hydrolyze compounds such as cellulose, hemicellulose, proteins, and DNA. Secretion of lytic enzymes resulted in suppression of plant pathogens directly by lyse cell walls and act to decompose plant residues. For example, *Lysobacter* and *Myxobacteria* are known to produce lytic enzymes and thus suppress fungal plant pathogens. *Serratia marcescens* produce chitinase for the control of *Sclerotium rolfsii* (Ordentlich et al. 1988), and a b-1, 3-glucanase significantly contributes to biocontrol activities of *Lysobacter enzymogenes* strain C3. Microbes also produce hydrogen cyanide (HCN) which effectively blocks the cytochrome oxidase pathway and is highly toxic to all aerobic microorganisms and thus suppresses plant pathogens. HCN production by fluorescent pseudomonads is involved in the suppression of root pathogens. *P. fluorescens* CHA0 produces antibiotics, siderophores, and HCN and inhibits the growth of *Thielaviopsis basicola* (Olivares et al. 2013). *Enterobacter cloacae* suppress *Pythium ultimum*-induced damping-off by producing volatile compounds such as ammonia.

13.3.7 Predation

Predation mediated by microbes (BCAs) is pathogen nonspecific and provides disease control at different levels under nutrient-limited conditions. For example, chitinase enzymes produced by *Trichoderma* attack cell walls of fungi (*Rhizoctonia solani*) by decreasing the concentration of cellulose. BCAs directly attack the fungal pathogen that kills it or its propagules. Obligate bacteria (*Pasteuria penetrans*) are the prominent example to be used as BCA against fungal parasites (*Coniothyrium minitans* that attacks sclerotia and *Pythium oligandrum* that attacks living hyphae) of plant pathogens. Fungi (*Acremonium alternatum*, *Ampelomyces quisqualis*, and *Cladosporium oxysporum*) are some of the other examples that attack powdery mildew pathogens (Meena et al. 2013c, 2015d; Singh et al. 2015; Bahadur et al. 2016a).

13.4 Induced Systemic Resistance (ISR)

It is the state of enhanced defensive capacity developed by a plant when appropriately stimulated (Van Loon et al. 1998), where plants trigger biological or chemical inducers for protection of nonexposed parts against attack by pathogenic microbes. Both biotic and abiotic agents protect crops against pathogens by eliciting induced systemic resistance (Da Rocha and Hammerschmidt 2005; Reglinski and Walters 2009). Bacteria such as *Bacillus* spp., *Pseudomonas* sp. (Bakker et al. 2007), and *Serratia* sp. (Press et al. 1997; Schuhegger et al. 2006) and fungi like *Trichoderma* sp. (Segarra et al. 2009), *Piriformospora indica* (Shoresh et al. 2010), *Penicillium simplicissimum* (Elsharkawy et al. 2012), *Phoma* sp. (Sultana et al. 2009), nonpathogenic *Fusarium oxysporum* (Fravel et al. 2003), and arbuscular mycorrhizal fungi (Pozo et al. 2009) have been implicated as BCAs to elicit induced systemic resistance (ISR). ISR elicitors identified include flagella (Meziane et al. 2005), iron-regulated metabolites (Audenaert et al. 2002; Meziane et al. 2005; Ongena et al. 2005; Ran et al. 2005; De Vleesschauwer et al. 2008), the antibiotics

2,4-diacetylphloroglucinol (Iavicoli et al. 2003; Weller et al. 2012) and pyocyanin (Audenaert et al. 2002; De Vleesschauwer et al. 2006), biosurfactants (Ongena et al. 2007; Tran et al. 2007), and volatile organic compounds (Ryu et al. 2004).

Siderophore, flagellar peptides and lipopolysaccharides, 2, 3-butanediol, cyclic lipopeptides, and other volatile substances are some of the other chemical elicitors of ISR produced by the rhizobacterial strains (Van Loon et al. 1998; Ryu et al. 2004; Compant et al. 2005; Van Wees et al. 2008). Kloepper et al. (1980) were the first to demonstrate the importance of siderophore production as a mechanism of biological control of *Erwinia carotovora* by *Pseudomonas fluorescens* strains A1, BK1, TL3B1, and B10. Also, a direct correlation was established in vitro between siderophore synthesis in fluorescent pseudomonads to inhibit germination of chlamydospores of *F. oxysporum*.

Siderophore-producing PGPR have also been identified as molecules able to activate ISR for protection of plants against diseases (Leeman et al. 1996a; Audenaert et al. 2002; Meziane et al. 2005). An important determinant of ISR siderophore pseudobactin was developed against blast disease in rice (De Vleesschauwer et al. 2008).

BCAs and other nonpathogenic microbes stimulate the pathways of ISR as a result of infection by a pathogen, upon colonization or after treatment with specific chemicals. ISR is mediated by a network of interconnected signaling pathways such as jasmonic acid (JA) and/or ethylene produced by some nonpathogenic rhizospheric bacteria. Another systemic acquired resistance (SAR) is mediated salicylic acid (SA)-dependent induced resistance triggered by a localized infection and leads to the expression of pathogenesis-related (PR) proteins produced by pathogen infection (Fig. 13.2).

Generally, ISR is not accompanied by the activation of PR genes, but enhanced defensive capacity of SAR is associated with the accumulation of PRs (Van Loon 2007). SA accumulation occurs locally and at lower levels with the development of SAR, and its application induces SAR in many plant species (Van Loon et al. 1998). Tissue necrosis development is a necessary feature for SAR activation (Vleesschauwer and Hofte 2009), but SAR can also be triggered without tissue necrosis in *Arabidopsis thaliana* (Mishina and Zeier 2007). PR proteins include some enzymes that acts directly to reinforce cell wall boundaries to resist infections lyse invading cells and induce localized cell death. In general, ISR-mediated protection is significantly less than that of SAR (Van Loon 2000); however, combination of ISR and SAR provides a better protection indicating that they act additively in inducing resistance to pathogens (Van Wees et al. 2000). Despite local site of induction, induced resistance is expressed systemically in plant parts that are separated from the inducer conferring an enhanced level of protection against a broad spectrum of pathogens. Root-colonizing microbes having biocontrol strains (*Pseudomonas* sp. and *Trichoderma* sp.) are known to strongly induce plant host defenses (Harman et al. 2004).

To overcome the SA-mediated pathway, pathogenic strains of *Pseudomonas syringae* produce JA. Sometimes absence of production of inducing components in the rhizosphere or an inability of the particular plant species to perceive such compounds leads to the failure to elicit ISR in certain hosts (Van Loon 2007). *P. putida* WCS358r and *P. fluorescens*WCS374r act differently depending on the plant species: in *Arabidopsis*, WCS358r elicits ISR, but not in radish and carnation plants (Van Peer et al. 1991; Van Peer and Schippers 1992; Leeman et al. 1995; Van Wees et al. 1997).

13.5 Suppression by Antibiotics Production

Antibiotics are one or more compounds secreted by one microbial species at low concentrations to inhibit/kill other microbial species. BCAs must produce antibiotics biosynthesized by different genes in sufficient quantities near the pathogen to induce positive biological control. Several BCAs that produce in situ antibiotics have been measured (Thomashow et al. 2002); however, the effective quantities are still required to be estimated because of the presence of other organic compounds. Few examples of BCAs that are known to produce multiple antibiotics are *Bacillus cereus* strain UW85 that produces both zwittermicin (Silo-Suh et al. 1994) and kanosamine and can suppress one or more pathogens. This ability of producing different antibiotics by single bacterial species suppresses diverse plant pathogens and thus enhances biological control in rice and maize cropping systems.

13.6 Conclusions and Future Prospective

An ideal agricultural system is considered as sustainable if it supports and improves soil health as well as fortifies the environment while fulfilling the world's food demand for increasing population. Biological soil amendments offer an environmentally sustainable approach to increase crop production and good soil health. The utilization of BSAs can decrease the use of synthetic fertilizers, prevent the exhaustion of soil organic matter, and diminish environmental pollution, thus enriching soil fertility and enhancing rice and maize yield. Also, biological control led by BCAs offers excellent model systems that furnish novel genetic constituents and bioactive compounds with multifold use in agriculture and environmental sustainability. Current and future progress in our understanding of BCAs and mechanisms of actions, formulations, and applications could facilitate their development as the reliable components in management of sustainable agroecosystems. The use of molecular tools has enhanced our capacity to understand and manipulate the different biocontrol products with improved effectiveness. Genetic enhancement of BCAs with native microbial strains may involve addition of one or more traits associated with effective disease control and plant growth promotion. Genetic manipulation of native microbes from rice and maize cropping systems to enhance establishment and proliferation of beneficial microorganisms is being pursued.

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14

Bacterial-Mediated Selenium Biofortification of *Triticum aestivum*: Strategy for Improvement in Selenium Phytoremediation and Biofortification

Zain ul Abadin, Muhammad Yasin, and Muhammad Faisal

Abstract

The increasing world population has forced the world to improve the productivity of crops. Among other important cereals, wheat is one such a crop which has increasing demands all over the world. It provides ~20% of caloric and protein needs worldwide. Although the use of modern technologies enhanced the production of wheat, it also resulted in decreased mineral content of crops, which include Ca, K, Na, Zn, Fe and Se. The selenium (Se) content in wheat is highly variable ranging from 5 to 720 μg Se/kg. Meanwhile the Se distribution is highly uneven worldwide, ranging from a low value of 0.01 mg Se/kg of soil to a higher value of 1200 mg Se/kg of soil in seleniferous soils. Wheat is among one of the major sources of Se supply for humans in areas where wheat is an important component of daily diet, so it must be maintained in healthy concentration to ensure adequate supply of Se to humans. The use of selenate and selenite with urea crystals and foliar application proved to enhance selenium content, but these measures have their own drawbacks. Bacterial inoculation to wheat resulted in remarkable increase in the accumulation of selenium in wheat plant along with Ni, Mn, P, Mo, K, Fe and Ca. Selenium-fortified wheat is a best option for the daily intake of selenium by humans.

Keywords

Biofortification • Phytoremediation • Wheat • Selenium • Bacteria

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14.1 Introduction

The selenium (Se) is a metalloid, which belongs to the group VI-A of the periodic table. Selenium shows several beneficial as well as toxic effects on organisms that depend on the quantity of available Se in soil for plant uptake, accumulation in food stuff and its daily intake by humans and other organisms. Selenium requirement for humans is ~55 to 60 μg day^{-1}; however, daily intake of <40 μg Se may lead to Se deficiency, and daily intake of ~400 μg Se may cause toxic effects in humans (WHO 1996). Se exists in six isotopes with ^{80}Se as the most abundant one. In nature, Se is found in four different oxidation states, 2 in halides, 0 in elemental form, 4^+in selenite and 6^+in selenate. It belongs to group VI-A, and its chemical properties are very similar to sulphur (S). In environment, Se occurs in both inorganic and organic forms in soil, water and air. Inorganic forms include selenite/selenate salts, while organic forms are the Se products from decomposition of Se-rich plant material (Barceloux and Barceloux 1999). Shale rock-derived soils are one of the natural rich sources of Se. Selenium distribution is highly uneven worldwide, and Se quantity in soil may vary from a low value of 0.01 to 2 mg Se kg^{-1} to a high value of 1200 mg Se kg^{-1} of soil (Mayland 1994). Anthropogenic activities are one of the major factors for the imbalance of Se in the environment, e.g. the use of Se metalloid in metallurgy and glass manufacturing industry constitutes ~60% of the total Se used (USGS 2011).

Selenium plays a significant role in the biological systems, as it is the main component of many selenoproteins in living organisms. About 30 selenoproteins are encoded by 25 human genes. Glutathione peroxidases (GPxs) are such eight proteins (GPx1-GPx8) having antioxidant properties with multidimensional roles in living cells, ranging from H_2O_2 homeostasis to regulation of apoptosis (Brigelius-Flohe and Maiorino 2013). Other selenoproteins are deiodinases and thioredoxin reductases which play a significant role in thyroid hormone metabolism, intracellular redox potential, DNA synthesis, cancer prevention, fertility and reproduction (Suttle 2010). Selenium in combination with vitamin E plays a synergistic effect on muscle activity as it improves endurance and recovery of muscles cells (Cabaraux et al. 2007).

Low Se content in diet may reduce the efficiency of immune system which may result in occurrence of various diseases, both in animals and humans (Table 14.1). In animals, deficiency of Se affects the heart, skeletal muscles and liver. White muscle disease, a degenerative myopathy, is a common disease of animals due to Se deficiency. Commonly cattle, poultry and horses are affected by this disease. In humans Se deficiency results in Keshan disease (cardiomyopathy) and Kashin-Beck disease (osteoarthropathy). Investigations showed that these diseases are common in areas where daily intakes are between 10 and 15 μg Se day^{-1}.

On the other hand, high Se intake may result in low haemoglobin level, decreased sperm motility and increased incidence of pancreatic and skin cancer. It is estimated that over 800 million people worldwide might have been affected due to selenium deficiency (Fordyce 2013; 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).

Table 14.1 Impact of Se deficiency on various organisms

Organism	Effects	References
Mouse	Se deficiency causes increase in inflammatory lesions caused by *S. aureus* mastitis	Gao et al. (2016)
Chicken	Low Se intake results in an increase in NO and Hsps which may play special role in chicken erythrocyte injury	Zhao et al. (2016)
Rats	Low selenium concentration in the kidney of a growing rat leads to damages of the ultrastructure and extracellular matrix (ECM) of the kidney	Han et al. (2016)
Chicken	Se deficiency caused changes in autophagy-related genes, which increased the autophagic process and also caused structural damages to the immune organs of chickens	Khoso et al. (2016)
Chicken	Se deficiency decreases the expression of selenoproteins, reduces antioxidant function, and increases the expression of inflammatory factors in chicken aorta vessels	Du et al. (2016)
Human	A low concentration of selenium in blood serum in the early stage of pregnancy has been proved to be a predictor of low birth weight of a new born baby	Pieczynska and Grajeta (2015)

It is very important to address new strategies to manage Se status in human's population. Various strategies can be used to cope up with Se deficiency in food such as Se foliar application in crops and Se-enriched fertilizers (urea granules) which showed improved Se content of food crops. Selenium biofortification, a process in which agronomic practices like conventional plant breeding or modern biotechnology are applied to produce crops with greater nutritional value, can enhance Se content of food crops. Plants with the ability to store and volatilize Se can be used for removing excess Se from seleniferous or contaminated areas (phytoremediation) and produce Se-enriched dietary material to eliminate Se deficiency in areas with low Se (biofortification) content in food. The three important components for a successful biofortification strategy include (1) increase in nutrient content as well as yield of the crop; (2) increased efficacy, i.e. improvement in nutrient status of mineral; and (3) the adoptability of the strategy by the farmers. Additionally, the rhizospheric plant growth-promoting microbes can perform a significant role in absorption of nutrients by plant roots, through plant root growth promotion especially root elongation and increasing its number (Ker et al. 2014). Previous studies showed that Se biofortification coupled with microbes is an effective strategy to enhance Se content in plants (Table 14.2).

14.2 Worldwide Importance of Wheat (*Triticum aestivum*) as Food Crop

Wheat is one of the oldest forms of nutrition available to humans and considered to be one of the main crops to ensure global food security. Introduction of new technologies in agriculture sector and development of high-yield strains of crops had helped a lot to reduce hunger and poverty worldwide. In developing countries, it is

Table 14.2 Bacterial-associated Se biofortification in different crops and its effects on Se uptake in plants

Crop	Mineral for biofortification	Bacteria used	Results	References
Wheat	Selenium	*Paenibacillus* sp.; *Bacillus* sp.	Se associated with STB was translocated into the leaves	Acuña et al. (2013)
Wheat	Selenium, iron	*Bacillus* sp.	Increase in Se and Fe amount in wheat kernels Enhanced growth of plants	Yasin et al. (2015a)
Wheat	Selenium	*Bacillus* sp., *Paenibacillus* sp., *Klebsiella*, *Acinetobacter* sp.	P-solubilization, high IAA production	Duran et al. (2014)
Wheat	Iron, copper, zinc	*Providencia* sp., *Anabaena* sp., *Calothrix* sp.	Increased protein content	Rana et al. (2012)
Saltmarsh bulrush, rabbitfoot grass	Selenium, mercury	Rhizosphere bacteria	Se and Hg were accumulated in wetland plants	De Souza et al. (1999)
Wheat	Selenium	*Stenotrophomonas* sp., *Enterobacter* sp., *Bacillus* sp., *Pseudomonas* sp., *G. claroideum*	Rise in selenium content of wheat grains	Duran et al. (2013)
Chickpea	Iron	PGPR	Increase in iron content of grain and shoot	Khalid et al. (2015)

projected that the demand will increase by ~60% till 2050 (Nelson et al. 2010). To meet this increasing demand, several developing countries are importing colossal amounts of wheat, and it is estimated that wheat has the highest percentage (~46%) out of total food imports (Dixon et al. 2009).

Wheat is an important source of calories and proteins. It helps to meet one fifth of daily calories and proteins to human population. According to the available data, ~19% of daily caloric needs and ~21% of daily protein intake globally are met by wheat consumption. Developing countries have higher demand for wheat. In Central Asia ~47% of the daily calories and proteins are provided by wheat intake; on the other hand this percentage falls dramatically to ~20% in high-income countries (Parewa et al. 2014; Prakash and Verma 2016; Meena et al. 2015f, 2016b; Priyadharsini and Muthukumar 2016; Jaiswal et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a).

However, the ~2.5 billion deprived people of the world are dependent on wheat as the main component of their diet. With regard to wheat as an important cereal crop worldwide, Se-supplemented or Se-rich wheat grains can be an important

Table 14.3 Percentage dependence of people on wheat in different regions of the world

Region	Share in cereal intake	
	Calories (%)	Proteins (%)
Australia	78	85
Central Asia	89	91
Eastern Europe and Russia	81	84
High-income countries	70	79
North Africa	66	71
North America	73	80
West Asia	78	84

source of Se supply to humans, Table 14.3 shows the dependence on wheat as the main constituent of the food of the world populations (Shiferaw et al. 2013).

14.3 Content of Se in Wheat Under Natural Conditions Worldwide

Selenium content of the soil varies significantly across the globe, which in turn affects the Se content of crops growing in those regions. Studies show that selenium content of wheat varies from as low as 0.001 mg/kg in the areas of southwestern Australia to as high as 30 mg/kg in some areas of South Dakota, whereas the world's average wheat content is between the range of 0.02 and 0.60 mg Sekg^{-1}. A study conducted by Lyons et al. (2005a) in different areas of Mexico and Australia showed the variation of the Se content of wheat varieties in these regions. The results of the study provided a range 5–720 μg Se kg^{-1} in wheat samples. Survey conducted to find out Se content of wheat grown at Centro Internacional de Mejoramiento de Maiz y Trigo (International Maize and Wheat Improvement Centre) showed a range from 9 to 244 μg Se kg^{-1} in hundred wheat samples, whereas at the same place, field trials showed a range of 40–110 μg Se kg^{-1}.

Field trials of wheat grown at three different soils near Tamworth, New South Wales, over a period of 27 years also showed large variations in Se content. Neutral soils showed large amount of Se in wheat ranging from 61 to 510 μg Sekg^{-1} in 27 samples of wheat during the year of 1971. This range narrowed in 1996 and became 140–490 μg Sekg^{-1}. While for black cracking soil with slightly acidic pH, the range almost remained the same, i.e. from 35 to 210 μg Se kg^{-1}, over the period. For more acidic soil, Se content of wheat was very low it ranged from 18 to 22 μg Se kg^{-1}. These results also supported the idea that Se absorption by plants decreases in acidic soils (Lyons et al. 2005a). Selenium concentrations determined in different areas of the world are shown in Table 14.4.

Table 14.4 Concentration of Se in wheat worldwide

Country	Selenium (mg/kg)
Algeria	0.021–0.153
Belgium	0.003–0.303
China	Deficient 0.001–0.105
Colombia	180
Greece	0.019–0.528
India	Seleniferous 0.742
	Non-seleniferous 0.010
Ireland	0.060–0.069
Russia	0.044–0.557
Scotland	0.003–0.006
World (average)	0.1–1.9

Adopted from Fordyce (2013), Hira et al. (2004) and Fordyce et al. (2000)

14.4 Factors Influencing Selenium Availability in Soil

There are many factors which determine availability of Se in soil (Fig. 14.1). These factors include organic matter content, pH of soil, redox conditions in the crop field, speciation of Se, soil texture and mineralogy, etc. (Fordyce 2013).

In natural conditions, the inorganic form of Se, i.e. selenite (SeO_3^{-2}), is more stable because it is absorbed by ligand exchange which is pH dependent. Decrease in pH increases adsorption by ligand exchange. This adsorption and formation of insoluble iron oxide and oxyhydroxide makes selenite less available for absorption by plants (Fig. 14.1). On the other hand, selenate (SeO_4^{-2}) is more soluble and mobile at neutral and alkaline pH, that is why it is easily taken up by plants. This is also supported by comparing uptake of selenate and selenite by plants (Alloway 2013; Kumar et al. 2017; Meena et al. 2015a, b; Raghavendra et al. 2016; Zahedi 2016; Rawat et al. 2016; Yasin et al. 2016; Das and Pradhan 2016; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016).

Other inorganic forms of Se present in soil are selenides (Se^{2-}) and elemental selenium (Se^0), which are present in acidic and organic-rich environment. These forms of Se are less available to plants due to their low solubility and oxidation potential. Organic forms of selenium in soil are selenomethionine ($C_5H_{11}NO_2Se$) and selenocysteine ($C_3H_7NO_2Se$). Both of these organic forms are readily available to plants. Order of Se bioavailability of these forms of Se, starting with the most soluble and mobile forms are as follows: selenate (Se^{+6}) > selenomethionine > selenocysteine > selenite (Se^{+4}) > selenium (Se^0) > selenide (Se^{-2}) (Jacobs 1989; Neal 1995; Yanai et al. 2015).

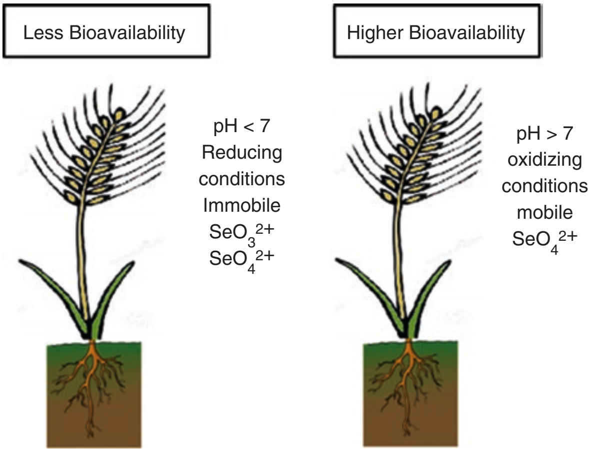

Fig. 14.1 Factors influencing Se availability in soil (Fordyce 2013)

14.5 Plant-Microbe Interaction (PMI) and Plant Growth

To meet the ever-increasing demand of food, it is important to increase per hectare yield of staple food crops; current strategies include the use of fertilizers and chemical pesticides. Although these techniques helped to achieve the target of enhanced production, it also resulted in environmental and health-related problems (Leach and Mumford 2008). So there is a need to introduce ecologically favourable methods to cope up with these nuisances. In this regard, application of plant-microbe interaction can be a good strategy to meet these challenges of high-yield, less pollution, eco-friendly and cost-effective production of food. The rhizosphere microbes (bacteria, fungi, algae, etc.) interact with plant roots and can improve nutrient uptake in plant through root growth promotion, solubilize inorganic nutrients in soil as well as protect plants from various pathogens (Ehlers 2006; Berendsen et al. 2012).

The microbes improve plant growth by the production of different phytohormones such as cytokinins, ethylene, gibberellins and IAA. Although these hormones are also synthesized by plants, these microbes, in particular, play a role for balanced quantity of these hormones in plants, for instance, the role of these microbes in balancing ethylene, inhibitor of plant growth, by controlling its precursor 1-aminocyclopropane-1-carboyclic acid (ACC) (Glick 2005). Besides this balancing of hormones, nutrient acquisition helps in direct growth enhancement. One such example is nitrogen fixation by bacteria. These are plant growth-promoting rhizobacteria (PGPR), which use root exudates and metabolize it to provide nitrogen to plants in turn. Free-living bacteria in soil such as *Azospirillum*, *Burkholderia* and *Stenotrophomonas* also have the capacity to fix nitrogen. Sulphur is also such a nutrient which is provided to plants through oxidation by these microbes (Banerjee and Yesmin 2009).

Another mechanism of supporting plant is by microbial antagonism which includes secretion of diffusible antibiotics, biosurfactants and volatile organic compounds (VOCs) to inhibit pathogenic microorganisms, degradation of toxins and pathogenicity factors and competition for minerals like iron through synthesis of competent siderophore uptake systems. These microbes can help plants by induced systemic resistance (ISR), a phenomenon by which microbes activate the plant to defend itself (Van Loon 2007).The inoculation of efficient microbe in soil and plant systems has a number of advantages when compared to synthesized pesticides and fertilizers. These microbes are safer, because they create less damage to environment and pose less risk to human populations. They are more specific in their activity as small quantities can show high effectiveness with high decomposition rates and can be good candidates for integrated pest management (Berg 2009; Meena et al. 2015e, 2016c, d; Saha et al. 2016a, b; Yadav and Sidhu 2016; Bahadur et al. 2016b).

14.6 Role of Selenobacteria (Se-Tolerant Bacteria) in Wheat Growth Promotion and Selenium Uptake

Numerous studies (Yasin et al. 2015a; Duran et al. 2014) in the last two decades support the idea of microbe-supplemented biofortification of wheat. Selenobacteria (Se-tolerant bacteria) isolated from different ecological niches have been explored and studied for their potential in the bioremediation and biofortification of soils (Eswayah et al. 2016). Duran et al. (2013) showed that inoculation of bacteria enhanced translocation of Se to shoots and ultimately increased the Se content of the wheat grain. Another study conducted by same research group shows that ACC deaminase activity of selenobacteria not only protects plant against stress but also improves the Se content of plant and eliminates stress produced due to Se toxicity (Acuna et al. 2013).

Studies conducted by Yasin et al. (2015a) on wheat also showed strong relation between selenobacteria (Fig. 14.2) and wheat growth and their positive role in biofortification of Se and other essential mineral elements in plants. *Bacillus* strains with high tolerance for Se showed significantly improved Se uptake in wheat plants and different plant growth-enhancing attributes including auxin production, more differentiated roots, greater number of leaves, greater dry weight and increased shoot length and higher acid phosphatase activity (Yasin et al. 2015b). Another study by our group showed that bacterial inoculation increased acid phosphatase activity in *T. aestivum* by ~40% (Yasin and Faisal 2013).

Fig. 14.2 Pure culture of selenium-resistant bacteria showing characteristic red colonies on LB agar supplemented with sodium selenite (Na_2SeO_3)

14.7 Uptake of Selenite and Selenate in Microbes and Plants

Less work was carried out on the transport of selenate and selenite into the bacterial cells. Available data showed that two different mechanisms are used by bacteria for uptake of these oxyanions. Selenate ions are transported by sulphate ATP-binding cassette transporter complex (consists of five proteins) which is encoded by the *cys*AWTP operon (Sirko et al. 1990). This complex includes two CysA, which are ATP-binding proteins; CysT and CysW, which are transmembrane proteins; and CysP which is periplasmic sulphate-binding protein. While selenite is transported by sulphate permease in *E. coli* along with ABC transporter complex, blocking of transport complex does not completely prevent the selenite uptake (Turner et al. 1998; Rosen and Liu 2009).

As discussed earlier, Se has similar properties as that of S, so they have some common enzymes for their metabolism. Selenium non-accumulator plants cannot tolerate high Se, and they contain generally less than 25 μg Se gramme^{-1} dry weight (DW) of the plant (White et al. 2004), whereas hyperaccumulator species of plants have high selenium content of 10–15 mg Se gramme^{-1}dry weight of plant. One hypothesis is Se hyperaccumulator plants have the ability to bear high Se content due to their capability to restrict integration of selenomethionine and selenocysteine (SeCys) into cellular proteins (Brown and Shrift 1982; El Mehdawi and Pilon-Smits 2012). This restriction is achieved by conversion of SeMet into amino acids which are not involved in protein formation like ɣ-glutamyl-Se-methylselenocysteine, Se-methylselenocysteine and selenocystathionine (Burnell 1981). The available data shows that Se is not required by plants as there is no codon found for SeCys in plants. However, plants are ought to be significant sources of Se for animal and humans (Sors et al. 2005a, b).

Three readily available forms of Se in soil are selenate, selenite and organic compounds of Se. Uptake of these compounds depends on physiochemical status of soil, i.e. amount of phosphate and sulphate ions and pH. Selenate and sulphate ions compete for transport into the cell; however, these ions are transported against their electrochemical gradients, by cotransport of three protons against one ion (Boldrin et al. 2016). Sulphate is transported via high- and low-affinity sulphate transporter proteins. Literature review showed that high-affinity sulphate transporters are responsible for selenate transport into the plant (Shibagaki et al. 2002). On the other hand, selenite and organic Se compounds have different mechanisms for their transport into the cell. There uptake is passive as compared to selenate which is taken actively (Abrams et al. 1990; Supriatin et al. 2016).

Experiments with wheat showed similar results for the transport and assimilation of Se, and selenate uptake was through high-affinity sulphate transporters in wheat, because S starvation increased selenate uptake. Similarly, selenite uptake in wheat roots is through phosphate transporters, and it is metabolically dependent active process. Assimilation of these two oxyanions is also different as selenate remains in roots and shoots, especially in xylem sap, because its assimilation into organic compounds is quite low, whereas selenite is rapidly metabolized into organic forms in plant tissues. Furthermore, studies show that selenite presence in the soil inhibits selenate uptake (Li et al. 2008; Verma et al. 2014, 2015a, b; Meena et al. 2013b, 2014a, 2016e; Sharma et al. 2016; Masood and Bano 2016; Teotia et al. 2016).

14.8 Selenium Fortification Strategies and Their Worldwide Application

There are various methods and strategies to improve Se content in food and its consumptions by humans. One way is to take Se directly either by supplementation of livestock or by Se pills, while the other way, as discussed in this chapter, is to use agronomic biofortification strategies. Agronomic biofortification is an important tool to enhance Se status of crops. Several recent studies proved that this strategy enhances Se content of crops (Ros et al. 2016). Another strategy is to apply Se fertilizers directly to the soil; however, Se uptake in plants may be affected by various factors such as application time of specific fertilizer, chemical speciation and type of Se in soil. Among the inorganic anions such as selenate and selenite, supply of selenate to plants results in the highest crop response regarding Se uptake in plants (Cartes et al. 2005).

Another strategy is the foliar application of Se fertilizer. This strategy is more effective as compared to Se application through soil, as studies showed that it almost doubles the Se content of the crop. A study by Ducsay and Lozek (2006) showed that the foliar application of 10–20 g Se hector^{-1} increased the Se content of wheat grains. Se content in unfertilized samples was 0.045 mg/kg^{-1}dry weight, whereas when 10 g Sehector^{-1} was applied, this content was raised to 0.088 mg/kg dry weight. It was a combination of foliar and soil-applied Se because the foliar fertilizers are applied before extensive leaf cover. Such fertilizers showed different crop responses when applied on different times of the season. However, Se application through foliar sprays lasts for shorter time in comparison to Se application through soil. Other strategies include granule fertilizers, liquid fertilizers, seed enrichment and use of organic Se fertilizers, but these techniques produce less significant results as compared to the two techniques discussed earlier (Ros et al. 2016; Shrivastava et al. 2016; Velazquez et al. 2016; Meena et al. 2014b, 2015c; Sindhu et al. 2016; Singh et al. 2016).

The Finnish government made it compulsory to include Se in all multi-nutritional fertilizers since 1984. As a result, an increase in Se content of ~125 analysed food items was noticed, and daily human intake was also increased from just below 25 μg day^{-1} in 1975 to a slightly above 124 μg day^{-1} (Eurola et al. 1991). In Australia, the addition of selenate at a rate of 4–120 g Se hector^{-1} resulted in 133-fold rise in the Se concentration of crops (Lyons et al. 2005b; Meena et al. 2013c, 2015d; Singh et al. 2015; Bahadur et al. 2016a). Similarly, in Romania this technique was also applied because of low levels of Se in the soil, and selected plant growth-promoting bacteria were inoculated to enhance Se concentration in crops (Oancea et al. 2014).

14.9 Conclusions

As selenium is an essential micronutrient for animals and humans. Above certain level it is toxic to the biological system. Several strategies are adapted to overcome the deficiency of selenium in human diet. The use of wheat and other crops which accumulate selenium in association with selenium-resistant bacteria not only boosts the selenium accumulation by plant but may also be a way to amend the selenium-deficient soil with considerable amount of this metalloid. Selenium-biofortified crops can be a good and cheap source of selenium for daily requirements of human population.

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Role of Vesicular-Arbuscular Mycorrhizae in Mobilization of Soil Phosphorus

15

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Abstract

The microorganisms play a vital role in sustaining the crop production through improving the soil properties and plant nutrition. Among the microorganisms VAM (vesicular-arbuscular mycorrhizae) is a beneficial fungus that plays an important role in soil nutrient dynamics and improving soil physical, chemical and biological properties. Though phosphorus is the second macronutrient required in relatively large amounts by plants next to nitrogen, it is one of the most difficult nutrients for plants to acquire because of its low solubility, low mobility and fixation in soil. The mycorrhizal symbiotic association between fungi and plants plays an important role in the uptake of phosphorus. Many experiments have specified that VAM is able to alter mobilization of soil phosphorus of its host plants. The paper summarizes about mycorrhizal symbiosis of VAM involving multistep colonization process, soil phosphorus dynamics in the rhizosphere and mycorrhizal mechanism and pathways involved in phosphorus availability and uptake.

Keywords

Vesicular-arbuscular mycorrhizae • Colonization process • Soil phosphorus dynamics • Phosphorus availability and uptake

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15.1 Introduction

The microorganisms play a vital role in sustaining the crop production through improving the soil properties and plant nutrition. Though the agricultural production has been continued to increase to feed the blooming population in one side, the soil fertility has attained the statue and started to decline because of faulty agricultural practices. Because of that fertile lands are going out of cultivation and increased degradation results increased area under current fallows. In this situation, we must go for a combined use of both organic and inorganic fertilizers in judicious combination based on soil nutrient status to improve and sustain the soil fertility and productivity which is called as integrated nutrient management (INM). One of the major components in INM practices is the use of bio-fertilizers which are prepared from many beneficial microbial inoculants (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).

The main beneficial activities of microorganisms are increased availability of plant nutrients, improvement of nutrient uptake, production of plant growth regulators, plant protection against root pathogens etc. According to their relationships with the plant, the microorganisms can be divided into saprophytes, parasitic symbionts (pathogen) and mutualistic symbionts (symbionts). The mutualistic symbionts are commonly used in bio-fertilizers because it carries out functions for the plants that they are unable to perform for themselves. For example, the host plant receives mineral nutrients by the organisms, and the microorganism obtains photosynthetically derived carbon compounds from the host plant (Finlay 2008). Among these the microorganism VAM is a beneficial fungus that plays an important role in soil nutrient dynamics and improving soil physical, chemical and biological properties (Parewa et al. 2014; Prakash and Verma 2016; Meena et al. 2016b; Jaiswal et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a).

15.2 Mycorrhizal Symbiosis

Frank was the first person to coin the term “Mykorrhizen” in the year 1885 for fungal association in the trees of pines. Mykorrhizen is a Greek term meaning “fungal root”. Paleobotany dates these associations to the Devonian era (~400 million years back). These mycorrhizal associations played predominant role in the transformation of primitive aquatic plants to highly evolved terrestrial plants during the course of evolution. Today, mycorrhiza is the most widespread symbiotic association existing in the ecosystems throughout the world (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).

Members of several fungal taxa are involved in mycorrhizal associations and possess a few common characteristic features such as ubiquitous distribution, strong biotrophic dependence on host plants and rarely free-living saprophytes. To date, seven types of mycorrhizae are recognized, viz. ectomycorrhiza, ectendomycorrhiza, endomycorrhiza, arbutoid mycorrhiza, monotropoid mycorrhiza, ericoid mycorrhiza and orchidoid mycorrhiza (Smith and Read 1997). Allen (1991) defined a mycorrhiza as a mutualistic symbiosis between plant and fungus localized in a root or root-like structure in which energy moves primarily from plant to fungus and inorganic resources move from fungus to plant (Rawat et al. 2016; Yasin et al. 2016; Meena et al. 2016c; Saha et al. 2016a; Bahadur et al. 2016b; Das and Pradhan 2016).

15.2.1 Vesicular-Arbuscular Mycorrhizae

Among the mycorrhizal associations, VAM is most widespread in their distribution both genetically and geographically. These fungi lacks sexual reproduction and are classified on the basis of their characteristic chlamydospore size, shape, colour and wall characters. This group includes members of order *Glomales* in class *Zygomycotina.* It encompasses seven genera, viz. *Glomus*, *Gigaspora*, *Modicella*, *Acaulospora*, *Sclerocystis*, *Endogone* and *Glaziella* with more than 150 species. VAM is beneficial symbionts that colonize a wide range of host roots that include both agricultural and horticultural plants. However, a few plant families such as Amaranthaceae, Brassicaceae, Cruciferae, Chenopodiaceae, Caryophyllaceae, Juncaceae, Cyperaceae and Polygonaceae do not exhibit any association (Smith and Read 1997; Brundrett 2009).

15.2.2 Multistep Colonization Process

Mycorrhiza formation is the multistep colonization metabolic process, which involves plant fungal colonization followed by a series of root-fungus interactions. The results give way to the integration of both organisms and development of a well-adapted unity (Fig. 15.1). This efficient mycorrhizal colonization begins with hyphae that arise from soil borne propagules which are called large resting spores of the mycorrhizal plant or mycorrhizal root fragments. Upon the arrival of the fungal hyphae at the root surface, an appressorium is usually formed on the epidermal cells. The appressoria facilitate the hyphae to pass through the intercellular spaces and then enter into root tissues through cortical root layers. Once the hyphae reach the inner cortex, they will grow into the cells as repeated dichotomous branching which forms tree-like structures called arbuscules (Garg and Chandel 2010).

The lifespan of individual arbuscules is about 4–14 days. Arbuscule formation therefore represents a large surface of cellular contact between both symbionts. This facilitates the exchange of metabolites between host and fungus. In fact, the arbuscule is probably the main transfer site of mineral nutrients from the fungus to the plant and C compounds to the fungus (Smith and Smith 1990). This mycelial network could extend several centimetres outside the root surface and bridge the nutrient depletion zone around roots with the bulk soil to absorb low-mobile ions (Yadav and Sidhu 2016; Saha et al. 2016b; Verma et al. 2014, 2015b; Meena et al.

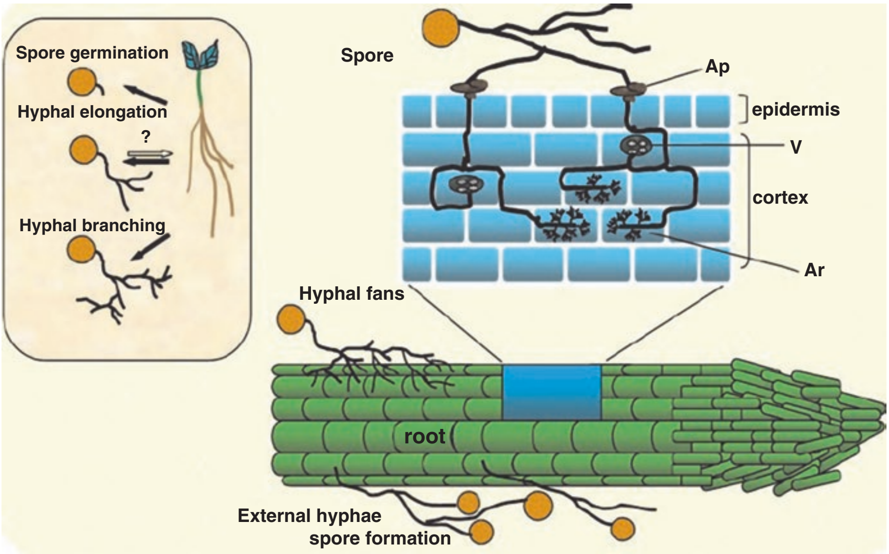

Fig. 15.1 Mycorrhizal multistep colonization (Adapted from Gadkar et al. 2011)

2013b, 2014a, 2015e, 2016d, e; Sharma et al. 2016; Verma et al. 2015a; Shrivastava et al. 2016; Bahadur et al. 2016a; Masood and Bano 2016; Teotia et al. 2016). The factors which influence the mycorrhizal association are host plant, mycorrhizal fungi, soil and environmental conditions (Barea 1991). If any one of these factors is inhibitory to mycorrhizal fungi, the symbiosis will be inhibited even if other factors are optimum (Liu et al. 2000).

15.3 Soil Phosphorus Dynamics in the Rhizosphere

The adequate amount of soil phosphorus is required to enhance shoot and root growth and promote early maturity which in turn help to increase water use efficiency (WUE) and yield potential because it is the element, which helps to store and transfer energy produced by photosynthesis (Tairo and Ndakidemi 2013). Though phosphorus is the second macronutrient required in relatively large amounts by plants next to nitrogen, it is one of the most difficult nutrients for plants to acquire because of its low solubility, low mobility and fixation in soil (Balemi and Negisho 2012).

The availability of soil phosphorus is affected by the presence of Fe and Al oxides which fix phosphorus as Fe and Al phosphates and clay minerals in highly weathered alfisol, ultisol and oxisols and as Ca phosphates under calcareous soils (Amanullah et al. 2010). Despite its availability, the phosphorus uptake is influenced by the rooting type, soil properties and soil moisture availability. Since the P availability depends on many factors, most of the plant phosphorus requirement has been met by diffusion process rather than by mass flow and root interception. In the diffusion process, once the phosphate is adsorbed strongly by the soil, its effective diffusion coefficient value becomes low, which creates a steep concentration gradient in the soil (Kanno et al. 2016). Hence the soil phosphate near the root zone only could reach the root surface to meet the plant requirements and ultimately plant express phosphorus deficiency when the demand is more than the availability exist in soil.

15.3.1 Mycorrhizal Effects on Phosphorus Availability Mechanism

The mycorrhizal symbiotic association between fungi and plants plays an important role in the uptake of phosphorus. Phosphorus has very limited mobility in soils and despite of its low availability it has been utilized quickly around roots and form depletion zones. Thus to obtain more phosphorus, plants must bypass these depletion zones by further root activity. The increased P uptake of mycorrhizal plants is mainly due to absorption and translocation of P from distant areas, which are otherwise inaccessible to plant roots. Hyphae absorb P in the form of orthophosphate and transported actively as polyphosphates (Tinker and Nye 2000; Hinsinger 2001; Plassard and Dell 2010).

The increase in absorption of P by mycorrhizal plants has been attributed to increase in surface area for absorption (Smith and Read 2008; Smith and Smith 2011a). The fineness of hyphae has twofold advantages over root hairs by increase in the surface area of hyphae for greater absorption of nutrient and increase the area of exploration by enabling the entry of hyphae into soil pores which cannot be entered by root hairs. Rapid absorption of soluble form of P by the extra radical hyphae leads to a shift in the equilibrium towards the release of bound P from the soil reserves. It has often been observed that mycorrhizal roots on a unit weight basis absorbed much higher amounts of P than non-mycorrhizal plants. This suggests that mycorrhizal fungus hyphae have higher affinity for phosphate ions at lower threshold concentration for absorption than do plant roots (Bolan 1991).

15.3.2 Mycorrhizal Pathway of Phosphorus Uptake

There are two possible ways in which soil phosphorus has been taken up by the plants: (i) direct pathway and (ii) AM pathway (Smith et al. 2011). Generally plants uptake phosphorus through direct pathway as negatively charged $H_2PO_4^-$ ions which increase negative electric potential inside the cell membrane because of high cell concentration compared to soil solution. Hence an additional metabolic energy required for the Pi uptake, and it needs high-affinity transporter proteins. So the pathway is more effective in the root apex which has high-affinity transporter proteins (PiTs) in the epidermis. But after a certain period of time, two things will happen. The first is when loss of root hairs started, the transporter protein (PiT)

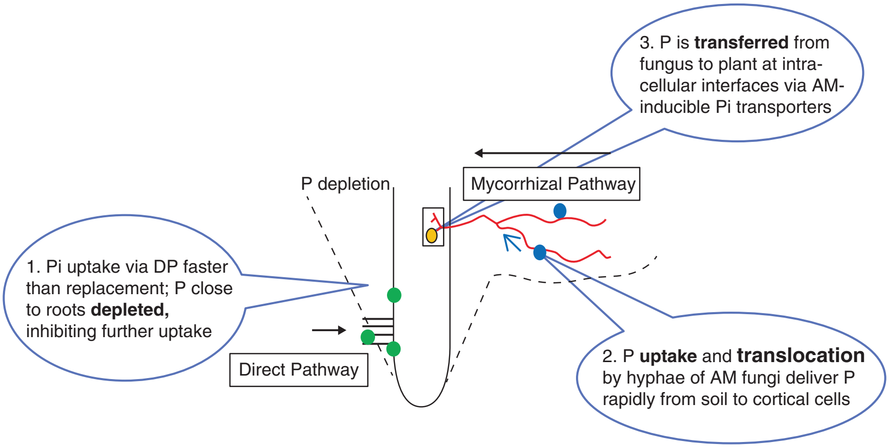

Fig. 15.2 The phosphorus uptake pathways of mycorrhizal root (Adapted from Smith et al. 2011)

activity will reduce, and certainly direct uptake will decline. Second, the uptake of phosphorus as orthophosphate (Pi) by root epidermal cells leads to lower the Pi concentrations in the root rhizosphere making zone of depletion (Smith and Smith 2011b; Balzergue et al. 2011).

Accordingly plants developed a range of strategies to enhance Pi uptake capacity (Marschner 1995) and among one is AM pathway (Fig. 15.2) in which soil phosphorus is foraged from large volumes of soil and transported to cortical cells evaded direct uptake. In the mycorrhizal pathway AM fungal hyphae uptake the orthophosphate (Pi) by fungal Pi transporters from the root and directly translocated into the intracellular fungal structures of arbuscules and hyphal coils which is present in root cortical cells (Smith et al. 2011). The fungal Pi transporters are specific to AM pathway, and it is different from the direct uptake expressed exclusively in the colonized cortical cell. The plant Pi transporters induced in colonized cells transfer Pi from the interfacial apoplast to the plant cortical cells and meet the plant requirement (Velazquez et al. 2016; Meena et al. 2013c, 2014b, 2015c, d; Sindhu et al. 2016; Singh et al. 2015, 2016).

15.4 Mycorrhiza and Soil Phosphorus Uptake

The association between concentrations of extractable soil phosphate and the extent of mycorrhizal colonization in plants are ambiguous. Sites with large amounts of extractable phosphate may have high levels of infection and large numbers of spores, whereas sites with small amounts of extractable phosphate may have low levels of colonization or low numbers of spores (Gianinazzi-Pearson et al. 1980; Almagrabi and Abdelmoneim 2012). In contradictory Rathore and Singh (1995) and Ezawa et al. (2005) reported that plant inoculation with VAM in the absence of added P significantly increased the available soil P because of the release of organic

Table 15.1 Available soil phosphorus (mg kg^{-1}) under maize crop at 45 DAS as influenced by VAM inoculation

	Phosphorus doses (kg ha^{-1})					
Mycorrhizal strain	0	15	30	45	60	Mean
Uninoculated	5.1	6.5	8.3	8.8	10.5	7.9
G. margarita	5.8	6.5	8.8	10.6	11.4	8.6
G. fasciculatum	6.5	7.5	8.8	11.3	12.6	9.4
VAM mixed endophyte	6.0	7.5	8.4	10.9	11.5	8.9
CD($P = 0.01$)	M 0.1		P 0.1		M × P 0.2	

Rathore and Singh (1995)

exudates in the rhizosphere and concluded that mycorrhizal inoculam may substitute phosphatic fertilizer equivalent of 30 kg P ha^{-1} (Table 15.1).

However, in some studies a negative association has been found between the amounts of extractable phosphate in soils and the abundance of VAM fungi as assessed by infection (Liu et al. 2000). Adding phosphate fertilizers has been shown either to have no effect (Kahiluoto et al. 2001) or to decrease (Ryan and Graham 2002) the level of mycorrhizal infection in a range of agricultural crops. This relationship is probably correlated with effects of phosphate on lengths of root colonized. The low percentage of root length colonized at high phosphorus availability does not necessarily imply plant suppression or control of fungal activity; there may be no effects of high phosphorus on the fungus per se (Marschner 1995; Mathimaran et al. 2005; Beauregard et al. 2010). But very high phosphorus application can definitely alter root colonization particularly reducing arbuscule development and decrease mycorrhizal fungal biomass per plant (Smith and Read 2008).

In addition reductions in appressorium formation were also observed in *Pisum sativum* roots at high phosphorus which was arbitrated by internal plant-derived signals (Balzergue et al. 2011). When phosphorus is abundant, a direct possibly less costly uptake pathway is preferred and the rate of root colonization also low (Nagy et al. 2008). However, a group of secondary metabolites called strigolactones which mediate signalling necessary for root colonization has strong negative effect with high phosphorus supply in various species (Lopez-Raez et al. 2008) which is also one of the reasons for the less colonization. Furthermore, the effect of soil phosphorus on mycorrhizal fungal diversity is also confounded by factors such as host species (Gosling et al. 2013).

15.4.1 Rate and Source of P Application vs. VAM Colonization

The sources of different phosphorus fertilizer do not have any significant effect on mycorrhizal infection when it was applied in low rate. The effect of phosphorus source is evident where the rate of fertilizer application is high. The high root length infection is always associated with rock phosphate compared to superphosphate. Phosphate in the soil solution derived from the Ghafsa phosphate rock source is expected to be different from the superphosphate source, and so the difference in infectivity associated with the higher rate of superphosphate application could also have been due to the differences in the rates of dissolution of superphosphate and phosphate rock to provide phosphorus in the soil solution over a given period (Asmah 1995).

15.4.2 Phosphorous Interaction with Zn

It is believed that soil phosphorus has antagonistic interactions with Zn, when any one of the nutrients available in soil is in excess (Gianquinto et al. 2000), and such a relationship is a result of the dilution effect of plant growth due to improved P nutrition. Further a study by Lu et al. (1998) demonstrated an increase in P availability caused no significant change in Zn concentrations of *Brassica napus*, and interactions of P and Zn in *Oryza sativa* and *Triticum aestivum* were additive and beneficial to the concentrations of P and Zn (Islam et al. 2005). The interaction remains uncertain, and the presence or absence of mycorrhizal association on the relationship was hypothesized, despite the fact that much literature has indicted that mycorrhizal fungal colonization promotes P or Zn nutrition of host plants independently. The high avaialble P (P addition up to 40 mg kg^{-1}) in soil has increased plant available zinc, whereas at higher P levels, the zinc translocation was inhibited (Rupa et al. 2003) (Table 15.2).

There was a synergistic interaction between P and Zn, which had resulted in extensive root growth in colonized plants. There is a strong positive relationship between Zn and P contents in the roots (r = 0.95; P < 0.001) and also in shoots (r = 0.96; P < 0.001) (Subramanian et al. 2008).

Table 15.2 Effects of different rates and sources of phosphorus application on root infection, nutrient concentration and uptake of soil phosphorus in maize crop (Asmah 1995)

Soil	Treatment	Root infection (%)	Nutrient concentration (μg g^{-1})	Nutrient uptake (mg/pot)
Paleustal	Control	47.50	1.26	1.65
	TSP1	78.30	1.27	2.58
	TSP2	52.30	2.18	4.38
	PR1	68.90	1.61	2.71
	PR2	75.00	1.61	3.73
Haplustoll	Control	58.00	0.99	1.12
	TSP1	63.80	1.40	2.81
	TSP2	50.00	1.37	3.21
	PR1	77.60	1.12	2.18
	PR2	80.25	1.16	2.33
	LSD (P < 0.01)	16.48	0.39	0.68

TSP1 triple superphosphate at 44 kg P ha^{-1}, *TSP2* triple superphosphate at 22 kg P ha^{-1}, *PR1* rock phosphate at 44 kg P ha^{-1}, *PR2* rock phosphate at 22 kg P ha^{-1}

15.4.3 Phosphatase

Soil phosphatase plays an important role in the P nutrition of plants because it mediates the release of inorganic phosphorus from organically bound phosphorus. Mycorrhizal colonization has been shown to influence the phosphatase activity, particularly the increased alkaline phosphatase activity in the presence of mycorrhizal hyphae (Tarafdar and Marschner 1994). Acid phosphatases have also been reported in mycorrhizal fungi, and although their function is unclear, they may be associated with the growth and development of the fungus within the host tissue as well as with phosphorus acquisition in the rhizosphere. Subramanian et al. (2009) reported that acid phosphatase activity of VAM-colonized soils was higher irrespective of the stages of observation, but the increase was well exhibited at early stages than in the later stages.

15.5 Phosphorus Uptake Under Drought

Plant water use efficiency has been accounted to decrease, increase or remain unchanged with mycorrhizal colonization depending on plant or fungal species combination considered (Auge 2001). The positive effects of mycorrhizal colonization on plant water relations could be explained simply in terms of the improved phosphorus nutrition and larger biomass size of mycorrhizal plants. Increased phosphorus uptake promoted root growth, which in turn enhanced the hydraulic conductivity and transpiration rate in mycorrhizal colonization plants (Bethlenfalvay et al. 1988). Hence the contribution of mycorrhizal colonization towards plant drought tolerance may be due to the impact of accumulative physical, nutritional, physiological and cellular effects imposed by vesicular-arbuscular mycorrhizae (Davies et al. 1992).

15.6 Conclusions

The fertilizer phosphate is becoming one of the most expensive commodities, and its availability is uncertain; the crop production will be critical, particularly in rainfed regions, where the fertilizer application is mainly based on rainfall distribution. In this situation mycorrhizal plant colonization is very useful in conserving energy by reducing fertilizer requirement of crops and in meeting the production targets in nutritionally deficient soils. The omnipresent nature, increased phosphorous uptake, drought tolerance and increased plant growth benefit by mycorrhizal colonization, which is important to increase the absorption of other relatively immobile elements in soil and a step towards the sustainability of the healthy soil and plant ecosystem.

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The Role of Soil Microbes in Crop Biofortification

16

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Abstract

Agronomic practices across the planet are becoming largely unsustainable in their current forms. With a growing population expected to reach ~9 billion by the year 2050, more sustainable ways to produce the world's main crops are needed. The main focus of current agronomic practices, especially in the case of cereal crops, is increased grain number and weight sometimes at the expense of nutritional content leading, in some instances, to micronutrient deficiencies. Micronutrient deficiencies are often termed *hidden hunger*, giving the false appearance that an individual is consuming sufficient amounts of nutrients. To counteract this problem, it is crucial that a sustainable solution to increase micronutrient concentration in a diverse range of crops is found. Plant growth-promoting microbes (PGPM) represents a sustainable solution to this problem. These PGPM can be divided into two main groups: plant growth-promoting rhizobacteria (PGPR) and plant growth-promoting fungi (PGPF). These microbes are capable of increasing micronutrient concentrations in many crops worldwide. This chapter will focus on the use of these microbes to increase micronutrient content, in particular selenium, iron and zinc, using studies conducted over the last two decades right up to the present day, revealing how plant-microbe interactions and our ever-growing knowledge of these interactions can aid in the micronutrient biofortification of crops in a sustainable and environmentally friendly way.

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16.1 Introduction

The pressure to produce sufficient nutritionally rich food in a sustainable manner has never been greater. With a growing global population (~9 billion by 2050), changing demographics and climate, pressure on resources such as water and land use, emergence of novel and more virulent pests and pathogens and changes in regulations with respect to the use of agrichemicals, food security is predicted to become increasingly vulnerable (FAO 2016). The United Nations through the 'Sustainable Development Goals Project' (UN 2015) has identified 17 goals to transform our world. Second on this list is the goal to 'end hunger, achieve food security and improve nutrition and promote sustainable agriculture'.

Nowadays, ~800 million people are undernourished with the vast majority living in developing countries. It is estimated that malnutrition contributes to the death of ~3.0 million children annually. Micronutrient deficiencies also known as hidden hunger where the intake of various vitamins and minerals (e.g. iron, iodine, selenium, zinc, folic acid and vitamin A) is too low for optimal health are a global issue affecting ~2 billion people (Trijatmiko et al. 2016). Nutritional deficiencies not only impact on an individual's health but also on their economic prosperity. The economic cost of micro- and macronutrient deficiencies has been estimated at ~2 trillion US dollars annually. Therefore, improving nutritional health is probably the major socio-economic challenge of this century. The nutritional content of our food crops can be enhanced in various ways. This enhancement is termed 'biofortification' which according to the World Health Organization (WHO) is defined as 'the process by which the nutritional quality of food crops is improved through agronomic practices, conventional plant breeding, or modern biotechnology' (WHO 2016a).

Probably the most famous biofortification project using genetic modification is the production of Golden Rice (Golden Rice 2016), whose benefits although clearly identified has faced much public opposition where it is perceived by many as the 'Trojan horse' for genetically modified crops. Genetic modification, particularly in Europe, is anathema to many, and as a consequence, Golden Rice is still not commercially available (International Rice Research Institute 2016). Besides genetic transformation approaches to biofortification, other biofortification strategies, including initiatives such as those followed in programs by HarvestPlus (2016) for the biofortification of rice, involve a combination of conventional breeding strategies for the exploitation of existing genetic variation in crop germplasm coupled with agronomic strategies, e.g. foliar and soil application of fertilizers (Nakandalage et al. 2016; Amanullah et al. 2016; Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Kumar et al. 2016c).

More recently, an understanding of the complex interactions between plant roots and microbial communities in the rhizosphere has fuelled research into the role and application of soil microbes in the biofortification of crops. There are many reports in the literature on the role of bacteria and mycorrhizal fungi in the mobilization of micronutrients in plants (Wu et al. 2015; Wang et al. 2014; Krishnakumar et al. 2013; Berruti et al. 2016). This chapter will focus in particular on crop biofortification by bacterial- and mycorrhizal-mediated mobilization of the micronutrients iron (Fe), zinc (Zn) and selenium (Se) from the rhizosphere (Jat et al. 2015; Kumar et al. 2015, 2016b; 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).

16.2 The Application of Plant Growth-Promoting Rhizobacteria for the Biofortification of Crops

The rhizosphere, an important interface between plant roots and the soil, can contribute to sustainable agriculture when the interaction between plants and beneficial bacteria is exploited. It has been ~35 years since Kloepper first described the role of plant growth-promoting rhizobacteria (PGPR) in plant growth and defence (Kloepper et al. 1980). PGPR when associated with rhizosphere/plant roots play a major role in the direct or indirect promotion of plant growth. The direct plant growth promoter mechanisms, biofertilization and phytostimulation, are two examples of methods that simultaneously minimize the use of chemical fertilizers and promote plant growth, and bacteria with both biocontrol and biofertilization/phytostimulation properties offer advantage to plants in terms of both enhanced nutrient supply and control of disease (Adesemoye and Kloepper 2009; Lugtenberg and Kamilova 2009; Glick 2012; Velivelli et al. 2014).

The recent work in the area of plant-microbe interactions has focused on the biofortification of staple crops using these PGPR, showing significant results. The WHO has identified micronutrients which are essential to the correct functioning of the human body, i.e. selenium (Se), iron (Fe) and zinc (Zn), and these constitute a significant portion of the current research on PGPR-mediated biofortification (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). These three micronutrients will be discussed further in relation to the biofortification of crops using PGPR.

16.2.1 Selenium

16.2.1.1 The Importance of the Trace Element Selenium in the Human Diet

Selenium (Se), a significant trace element in the human diet, is classified as a metalloid and occurs in the environment in different valences as selenide ($^{2-}$), selenite ($^{4+}$), selenate ($^{6+}$) or elemental Se (0). Se has implications for biological processes, such as anti-oxidation and prevention of certain cancers, e.g. liver cancer (Carlson et al. 2012) and colorectal cancer (Meplan and Hesketh 2012). Selenoproteins, i.e. proteins that contain a selenocysteine amino acid residue, facilitate adequate DNA synthesis, protection against diseases such as HIV, reproduction and thyroid hormone metabolism (Sunde 2012; Hatfield et al. 2014). A delicate balance occurs in humans between having too much and too little Se in the diet. Se levels that are too high can lead to selenotoxicity, resulting in symptoms ranging from nervous system disorders to nail and hair loss (Li et al. 2012), and selenium levels that are too low can lead to inadequate levels of protection against radioactive damage to DNA, which can result in micronuclei formation and potentially cancer (Baliga et al. 2008).

16.2.1.2 The Role of PGPR in the Mobilization of Selenium for the Biofortification of Plants

Plant roots have the capacity to absorb Se as selenate, selenite or organo-selenium compounds such as selenocysteine and selenomethionine, but lack the ability to absorb metal selenides or elemental Se (White et al. 2004, 2007). Generally, Se concentrations found in plants grown in seleniferous soils are less than 25 mg kg^{-1} dry weight (Bell et al. 1992; Terry et al. 2000; Yasin et al. 2015a, b), but in the case of a few hyperaccumulator species, these values can reach over 1000 mg kg^{-1} dry weight in plant material (Ellis and Salt 2003).

Selenate is the most widely utilized form of Se by plants, and in non-hyperaccumulators selenate is transported across the plasma membrane of root cells by high-affinity sulphate transporters (Terry et al. 2000; White et al. 2004, 2007; Sors et al. 2005; Broadley et al. 2006; Hawkesford and Zhao 2007). Plant growth-promoting rhizobacteria (PGPR) have the potential to increase plant Se levels and subsequently benefit the Se status of humans and livestock in areas of the world which may be Se-deficient. Over the past two decades, a number of studies have examined the potential of PGPR to act as Se-biofortification agents. A study by de Souza et al. (1999) found that Indian mustard (*Brassica juncea* L.) can be supported by PGPR to enhance selenium accumulation and volatilization (Rawat et al. 2016; Yasin et al. 2016; Meena et al. 2016c, d; Saha et al. 2016b; Yadav and Sidhu 2016; Bahadur et al. 2016b; Das and Pradhan 2016).

In *B. juncea*, dimethyl selenide is the predominant volatilized form of Se and is typically 500–700 times less toxic than inorganic forms of Se (McConnell and Portman 1952; Ganther et al. 1966; Wilber 1980) making it a suitable vector for biofortification of the human food chain with Se. A number of Se-tolerant rhizobacterial isolates from the rhizosphere of a range of Se-accumulating plants were used in this study. Antibiotic experiments using ampicillin revealed that bacteria were the key factor in enhanced Se uptake by Indian mustard (de Souza et al. 1999). When added to the plant nutrient solution, ampicillin inhibited Se volatilization by ~35% and tissue Se accumulation by ~70%.

The rhizobacterial strains designated BJ2 and BJ15 were used in axenic plant experiments to examine the role of rhizobacteria in Se accumulation and volatilization. When these two strains were inoculated within the rhizosphere of axenic Indian mustard plants, the Se volatilization rate from selenite was four times higher than that of axenic control plants, and plants accumulated more Se in their tissues when compared to axenic controls. Both BJ2 and BJ15 rhizobacterial strains increased Se concentrations in shoots and roots 1.4-fold and fivefold, respectively. As with many PGPR species, these isolates were thought to increase Se uptake via enhanced root hair production. In addition, seedlings with PGPR had a significantly higher Se tissue concentration of 1.3–2 times greater than axenic plants across the spectrum of Se concentrations tested (de Souza et al. 1999).

Acuña et al. (2013) investigated ash-derived volcanic andisol soil in Southern Chile, which is characteristically low in Se content, for the presence of PGPR with the ability to supply increased Se to host plants. Inoculation with two isolates, namely, *Pseudomonas* sp. R8 and *Stenotrophomonas* sp. B19, in the rhizosphere of wheat resulted in higher Se content in roots and leaves compared to uninoculated controls. When plants were inoculated with B19 in soils where the Se concentration was 5–10 mM, a significantly higher Se content was observed in wheat root and leaf tissues compared to plants grown in soil containing 2 mM Se (Acuña et al. 2013). In the same region, Durán et al. (2014) isolated endophytic bacteria from Se-supplemented wheat that shows potential for plant growth promotion, biofortification and biocontrol in wheat cultivation (Saha et al. 2016c; Verma et al. 2014, 2015b; Meena et al. 2014a, 2015e; Teotia et al. 2016).

Endophytic bacterial strains were isolated from both uninoculated control and Se-supplemented wheat plants from the genera *Bacillus*, *Paenibacillus*, *Klebsiella*, *Enterobacter* and *Acinetobacter* and 15 strains selected according to tolerance of high Se levels (~50 mM). A number of these endophytes are highly tolerant to Se, ranging from 60 to 180 mM, and thus have the potential to be used as biofortification agents in areas of the world with low soil Se concentrations. Furthermore, some of these isolates displayed the ability to act as biocontrol agents for the endemic soilborne fungal pathogen *Gaeumannomyces graminis* var. *tritici* that causes take-all disease, one of the most severe wheat diseases in Southern Chile. Isolates from the genera *Acinetobacter* (strain E6.2), *Bacillus* (strain E8.1), *Bacillus* and *Klebsiella* (strains E5 and E1) inhibited the growth of *G. graminis* var. *tritici* mycelia by ~100%, 50% and 30%, respectively, *in vitro*; this adds to the potential of PGPR for biofortification agents that not only increase Se concentration in the plant but also act as sustainable crop protectants (Durán et al. 2014).

Two studies by Yasin et al. (2015) investigated the potential for Se biofortification in crop plants. First, an experiment with *B. juncea* to investigate the potential of two Se-tolerant rhizobacterial consortia to increase plant Se uptake using naturally seleniferous soil containing ~8 mg Se kg^{-1} was carried out with both rhizobacterial consortia consisting of four to five strains each, designated G1 and G2. *B. juncea* accumulated Se to 358 mg kg^{-1} in seeds, 711 mg kg^{-1} in leaf dry weight (DW) and 276 mg kg^{-1} in pod husks. Inoculation of G1 had a positive effect on plant growth compared to controls but did not accumulate Se with a significant difference compared to the control. G1-incoulated plants produced 40–45% more leaf and seed biomass compared to controls however; therefore, these plants were more effective in extracting Se from the soil compared to control plants. G2-inoculated plants had an overall decreased plant growth compared to control plants. However, nonprotein thiol levels were increased threefold in G2-inoculated plants compared to controls. Nonprotein thiols are often used by plants as antioxidant defence compounds, and it may be the case that one or more members of the G2 consortia initiated this response to a perceived bacterial threat (Yasin et al. 2015a). In a second experiment using two individual isolates, namely, *Bacillus cereus* YAP6 and *Bacillus licheniformis* YAP7, inoculation of wheat plants with either bacteria increased Se concentration in the grain by up to 375% compared to uninoculated Se-treated plants (Yasin et al. 2015b).

As mentioned previously, plants grown in seleniferous soil that can accumulate very high tissue levels of Se are termed ‘Se hyperaccumulators’. This poses the question of whether this hyperaccumulation of Se can be attributed to any specific microbe associated with Se-hyperaccumulating plants. Given the current depth of knowledge in plant-microbe interactions, we might reasonably expect such a microbe would be identified. The answer appears to be ‘no’. An experiment by Sura-de Jong et al. (2015) compared the endophytic population of both non-hyperaccumulating and hyperaccumulating plants, with two plant families per grouping, Brassicaceae and Fabaceae growing on the same seleniferous site (Sharma et al. 2016; Verma et al. 2015a; Meena et al. 2013b, 2016e; Shrivastava et al. 2016).

Terminal restriction fragment length (T-RFLP) analysis of bacterial isolates identified equal T-RF diversity between hyperaccumulators *Stanleya pinnata* and *Astragalus bisulcatus* and related non-hyperaccumulators *Physaria bellii* and *Medicago sativa*. Cultivable endophytes from hyperaccumulators were isolated, and of the 66 morphotypes isolated, seven were selected to be co-cultivated with *B. juncea* and *M. sativa*. Although plant growth promotion occurred in both plants, there was no effect on their Se status, suggesting that hyperaccumulation cannot be induced by the application of Se-tolerant PGPR alone (Sura-de Jong et al. 2015). Studies like these highlight the importance of understanding the complex interactions between all constituents of the plant-microbe interaction and how not all bacteria can benefit plant biofortification (Velazquez et al. 2016; Meena et al. 2015c; Sindhu et al. 2016; Bahadur et al. 2016a; Masood and Bano 2016) (Fig. 16.1).

16.2.2 Iron

16.2.2.1 The Importance of Iron in the Human Diet

Iron (Fe) is arguably one of the most important micronutrients in the human diet; it is the basis for the correct function of haemoglobin, and deficiency in iron can lead to anaemia. According to the World Health Organization (WHO), Fe deficiency is the only micronutrient deficiency that is prevalent in both the developing and developed worlds (WHO 2016b). In developing countries, up to ~50% of pregnant women and ~40% of preschool children suffer from anaemia (Beard 2008).Values for recommended daily intake are displayed in Table 16.1. In children under 5 years of age, 0.2% of deaths can be linked to deficiency in iron (Bhutta 2008). Children suffering from anaemia and Fe deficiency are better protected against mortality or

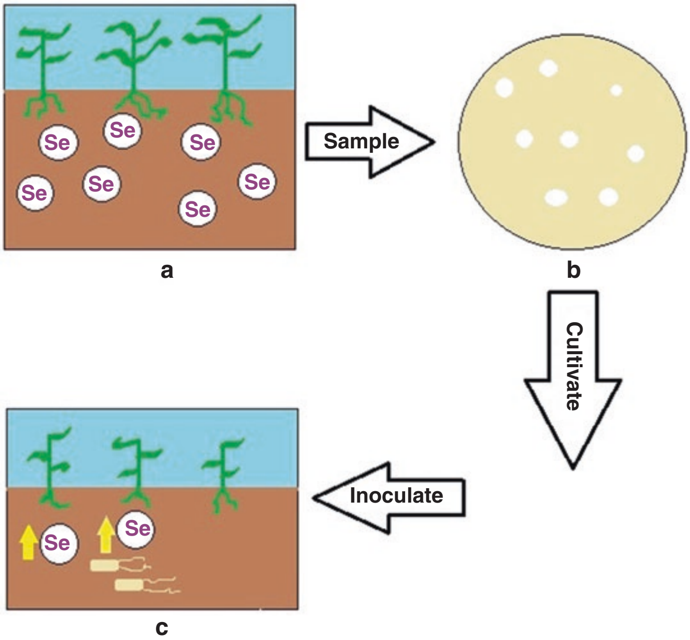

Fig. 16.1 Rationale for selection of PGPR involved in biofortification taking Se as an example. (**a**) Se-enriched soils. (**b**) Isolation of bacteria from (**a**) on Se-supplemented growth media to identify Se-tolerant bacteria. (**c**) Inoculation of PGPR from Se-enriched soils to Se-deficient soils to aid Se biofortification in plants

Table 16.1 Recommended daily dietary intake of Se, Zn and Fe, WHO (2006)

	Se	Zn	Fe
Category	mg		
Infants (1–3 years)	17	2.4–8.3	3.9–11.6
Children (4–6 years)	22	2.9–9.6	4.2–12.6
Adult female	26	3–9.8	19.6–58.8
Adult male	34	4.2–14	9.1–27.4
Pregnant women	28	4.2–14	>50
Lactating women <3 months	35	5.8–19	10–30

Values for Zn and Fe run from low to high as bioavailability increases in the diet. A diet of low bioavailability is defined as a diet low in vitamin C and animal protein; the opposite is true for a diet with high bioavailability. Socioeconomic and dietary factors play a major role in the potential uptake of micronutrients in the human body

hospital admission when supplemented with iron; however, supplementation with iron to the point where children become iron replete and no longer iron deficient may be harmful as in the case of malaria, whereby the causative agent, *Plasmodium*, can benefit from excess iron levels in the blood (Sazawal et al. 2006; Weinberg

1999; Nuberger et al. 2016). So, as for all (bio)fortification strategies, the relative benefits and risks must be balanced (Meena et al. 2013c, 2014b, 2015d; Singh et al. 2015, 2016).

16.2.2.2 The Acquisition of Iron by Plants

Plants acquire Fe via one of two strategies, depending on whether the plant is monocotyledonous or dicotyledonous. Appreciating these different mechanisms in the overall process of Fe acquisition by plants can help in the optimization strategies of Fe translocation from the rhizosphere to the plant. The reduction strategy, used by dicotyledonous plants, involves the secretion of H^+ and organic acids to acidify the rhizosphere which reduces Fe^{3+} to Fe^{2+} and make it available for uptake into the plant. The chelation strategy, used mainly by monocotyledonous plants, involves the secretion of phytosiderophores (e.g. mugineic acid) that can bind Fe^{3+} which is subsequently taken up by the root cells (Gamalero and Glick 2011; Bulgarelli et al. 2013).

16.2.2.3 The Role of PGPR in Iron Acquisition and Plant Biofortification

The enzymes involved in the mugineic acid pathway were deduced from sequence comparison with bacteria, as it is now well known that bacteria can also act to help plants acquire Fe (Crowley 2006; Saha et al. 2016a). In one of the early experiments to determine microbial contribution to plant Fe acquisition, Masalha et al. (2000) experimentally determined that soil microbial activity was enhancing Fe acquisition using sterile and non-sterile soil as growth media. Non-sterile soil was associated with increased Fe uptake, suggesting that the microbial community of the soil may be contributing to Fe uptake in the plant. In sunflower (*Helianthus annuus* L.), root dry weight Fe concentrations were ~1748 ± 48 $\mu g\ g^{-1}$ for non-sterile soil, whereas in sterile soil, Fe concentration was ~248 ± 29 $\mu g\ g^{-1}$, suggesting microbial activity was enhancing Fe translocation from the soil to the plant (Masalha et al. 2000).

The microbial siderophores can be classified into four groups; the most common are the hydroxamate siderophores, followed by catecholates, carboxylates and pyoverdines. Examples of siderophores within these four respective groups include ferribactin, pyoverdine, enterochelin and rhizobactin; these are produced by *P. fluorescens*, *P. aeruginosa*, *E. coli* and *R. meliloti*, respectively (Maurer and Keller-Scheirlin 1968; Smith and Neilands 1984; Schalk and Guillon 2013; Vansuyt et al. 2007). Upwards of ~500 different siderophores have been reported to date, with ~270 being well characterized (Boukhalfa et al. 2003).

Siderophores can also be involved in a biocontrol capacity, sequestering iron away from the rhizospheric soil and making it inaccessible to any potential pathogens (Siddiqui 2006). These microbes can further enhance Fe acquisition in plants by inducing Fe-deficient responses, such as the production of hormonal compounds analogous to plant hormones, which microbes can produce independently. *B. subtilis* GB03 has the ability to enhance Fe acquisition in *Arabidopsis* via transcriptional upregulation of the Fe deficiency-induced transcription factor 1 (FIT1) which is required for induction of ferric reductase FRO2 and the IRT1 iron transporter to acquire Fe in the plant (Zhang et al. 2009).

A group of major microbial-derived plant growth-promoting (PGP) hormones called auxins have been implicated in enhanced Fe uptake. The ratio of auxin-producing microorganisms in soil that contains phenolic root exudates of Fe-deficient red clover (*Trifolium pratense* L.) is higher than that observed in phenolic-free soil solution controls, thus indicating that Fe deficiency in plants may contribute to the abundance of auxin-producing microbes in the rhizosphere. Not only the increase of auxin-producing microbes was observed, but the plant phenolics also inhibited the growth of the majority of microbes, suggesting iron-deficient plants can select for organisms which have the ability to produce auxin and siderophores, ~71% and 86% of the total microbial population, respectively (Jin et al. 2006, 2008). Exogenous application of the major auxin, indole-3-acetic acid (IAA), enhances Fe deficiency-induced reduction of ferric Fe and expression of FRO2 and IRT1, which are critical for enhanced Fe uptake in the plant and growth of lateral roots and root hairs to provide increased surface area for Fe uptake (Jin et al. 2008; Chen et al. 2010; Wu et al. 2012). IAA also contributes extra nutrients for rhizobacterial growth by modulating the quantity of root exudation via an increase of porosity in the cell wall of plants (Glick 2012).

Utilizing two of the most important cereal crops, rice (*Oryza sativa* L.) and wheat (*Triticum aestivum*) in a rice-wheat cropping system, Rana et al. (2015) demonstrated that PGPR and cyanobacteria led to both higher macro- and micronutrient concentration in cereal grain. In rice, bacterial-cyanobacterial consortia increased Fe concentration from ~4 to 14% over the fertilizer-only control. While bacterial-cyanobacterial consortia had a significant Fe increase over uninoculated controls, isolate *Providencia* sp. PW5 alone increased the Fe concentration by ~45% compared to the fertilizer-only control in wheat grains. Adak et al. (2016) also observed increased acquisition of Fe through cyanobacteria inoculation in rice of ~13 to 46% compared to uninoculated controls.

Recent publications from India on the biofortification of chickpea (*Cicer arietinum* L.), a major pulse crop grown under semiarid conditions, have highlighted the potential for Fe biofortification in chickpea. Nineteen *Acinetobacter* isolates statistically significantly increased mineral content in PGPR-inoculated chickpeas compared to uninoculated controls; Fe in plants varied from ~10 to 38% higher (Sathya et al. 2016). All 19 isolates increased Fe in the plant within the range of ~10 to 38%. Gopalakrishnan et al. (2016) also recorded increases in Fe concentration following PGPR treatment. Fe concentration in chickpea grain was increased up to 18% with isolates *E. ludwigii* SRI-229 and *P. monteilii* SRI-360, the two strains displaying the greatest performance over uninoculated controls (Gopalakrishnan et al. 2016). It is important to note that postharvest processing and cooking can affect micronutrient concentrations in the grain. Both Saytha et al. (2016) and Gopalakrishnan et al. (2016) reported that Fe concentration can be affected by cooking and can reduce from 5 to 30% and in some cases gain ~21% (Sathya et al. 2016; Gopalakrishnan et al. 2016).

16.2.3 Zinc

16.2.3.1 The Importance of Zinc to Human Health

Zinc (Zn) is typically the most abundant transition metal in living organisms after Fe and is the only metal resident in all enzyme classes (King 2006; Broadley et al. 2007). Zn plays a critical role in human health and is involved in correct functioning of the immune system to fight infections such as pneumonia (Black et al. 2008). Zn is also involved in protein synthesis, metabolic homeostasis and modulation of gene expression through Zn-containing proteins (Welch 2001) and plays a critical role in male fertility with Zn deficiency resulting in inhibition of spermatogenesis and abnormal sperm production (Prasad 2008). In contrast to Fe, Zn is not stored in the human body in sufficient amounts and as a result must be ingested daily (King 2011). Zn, along with Fe, iodine (I) and Se, i.e. the major micronutrients, is often found in insufficient quantities in plant staple foods to meet human nutritional requirements, and as a consequence, nearly half the global population suffers from Zn micronutrient deficiency (White and Broadley 2009; Cakmak 2008).

16.2.3.2 The PGPR-Mediated Biofortification of Plants with Zinc

Processing of staple grains such as rice and wheat decreases the micronutrient concentration of the grain, especially in the case of Zn in wheat (Zhang et al. 2010; Kutman et al. 2011). Grain concentration of Zn is also hindered by the presence of the well-documented ‘anti-nutrient’ phytic acid, which reduces mineral bioavailability because it can form insoluble complexes with essential minerals such as Zn^{2+} and Fe^{3+} (Urbano et al. 2000; Srivastava 2016). Tariq et al. (2007) investigated the potential of a PGPR consortium to increase Zn concentration in rice; the consortium, named ‘BioPower’, consists of two *Azospirillum lipoferum* strains, two *Pseudomonas* sp. strains and one *Agrobacterium* sp. strain (Hafeez et al. 2002; Tariq et al. 2007).

Rana et al. (2012) showed that inoculation of wheat with *Providencia* sp. + $N_{60}P_{60}K_{60}$ significantly increases grain Zn accumulation to ~42 mg kg^{-1}, along with a threefold increase in the concentration of Fe compared to control plants. Zinc-solubilizing bacteria (ZSB) have also been shown to increase Zn concentration in shoots and roots of soybean and wheat (He et al. 2010). Rana et al. (2015) documented an increased Zn concentration in wheat and rice grains over a 2-year-long rice-wheat cropping sequence. In wheat grains, Zn concentration was ~41 mg kg^{-1} post-treatment with $N_{60}P_{60}K_{60}$ and a bacterial consortium consisting of *B. pumilus* PW1, *Providencia* sp. PW5 and *B. diminuta* PW7.

Zinc concentration in the wheat grain was measured at ~38 mg kg $^{-1}$ post-treatment with $N_{60}P_{60}K_{60}$ only and was measured at ~33 mg kg^{-1} for the control without the application of fertilizer or bacteria. At the end of the 2-year cycle, Zn concentration in wheat grain had increased 1–7% overall in plants that had been treated with both fertilizer and bacteria compared to fertilizer-only controls.

In rice, Zn concentration in grain increased by ~14% when treated with $N_{90}P_{60}K_{60}$ and a PGP bacterial consortium consisting of the strains *Providencia* sp. PR3, *Brevundimonas diminuta* PR7 and *Ochrobactrum anthropi* PR10 (Rana et al. 2015).

Table 16.2 A selections of microbes which have been shown to contribute to the process of micronutrient biofortification

Microbe	Micronutrient	Reference
Bacillus subtilis (GB 03)	Fe	Zhang et al. (2009)
Pseudomonas sp. R8	Se	Acuña et al. (2013)
Stenotrophomonas sp. B19	Se	Acuña et al. (2013)
Providencia sp. PW5	Zn, Fe, Mn, Cu	Rana et al. (2012)
Pseudomonas sp. Z5	Zn	Yasmin (2011)
Flavobacterium sp.	Zn	He et al. (2010)
Anabaena sp.	Fe	Manjunath et al. (2016)
Azotobacter sp.	Fe, Zn	Manjunath et al. (2016)
Calothrix sp.	Zn	Manjunath et al. (2016)
Pseudomonas fluorescens C7	Fe	Vansuyt et al. (2007)

Manjunath et al. (2016) recorded increased Zn concentration in okra (*Abelmoschus esculentus* (L.) Moench). During midcrop stage, Zn concentrations were ~60 to 70% higher in plants treated with *Azotobacter* sp. and a cyanobacterium (e.g. *Calothrix*), compared to uninoculated controls (Majunath et al. 2016). Shakeel et al. (2015) observed that zinc-solubilizing bacteria (ZSB) increased zinc translocation in two rice varieties, basmati-385 and super basmati. A consortium of *Bacillus* sp. SH-10 and *B. cereus* SH-17 yielded a Zn concentration in grain of ~31 mg kg^{-1} compared to a concentration of ~18 mg kg^{-1} in the basmati-385 control. Application of ZSB with Zn fertilizer did not increase Zn concentration in the grain; this may be due to the increased Zn uptake potential of the varieties tested (Shakeel et al. 2015) (Table 16.2).

Isolates hail from diverse genera based on respective abilities to fix or solubilize nutrients within the rhizosphere for plant growth promotion (Fig. 16.2).

16.3 The Application of Arbuscular Mycorrhizal Fungi (AMF) to Biofortification in Crops

Most plants, including all major food crops, form a symbiotic below-ground association with AMF that supplies the host plant with water and mineral nutrients, such as phosphorus (Senés-Guerrero et al. 2014). Plants colonized by AMF can effectively acquire nutrients from a larger soil volume, beyond the nutrition depletion zone to where the plant roots cannot extend. Thus, AMF helps the plant to grow better and increase its productivity. In return, the host plant provides AMF with carbohydrates required to complete its life cycle (Zhang et al. 2015).

The AMF acquire essential nutrients such as P, Zn, Cu, Fe, N and K from the soil, and thus AMF contact with roots provides the plant with access to essential nutritional elements, leading to solubilization, mobilization and uptake of the essential nutrients needed by plants for their growth (Clark and Zeto 2000; Kumar et al. 2016a). Plants colonized with AMF have significantly greater zinc concentrations in all tissue types compared to non-mycorrhizal plants, although the effect is primarily

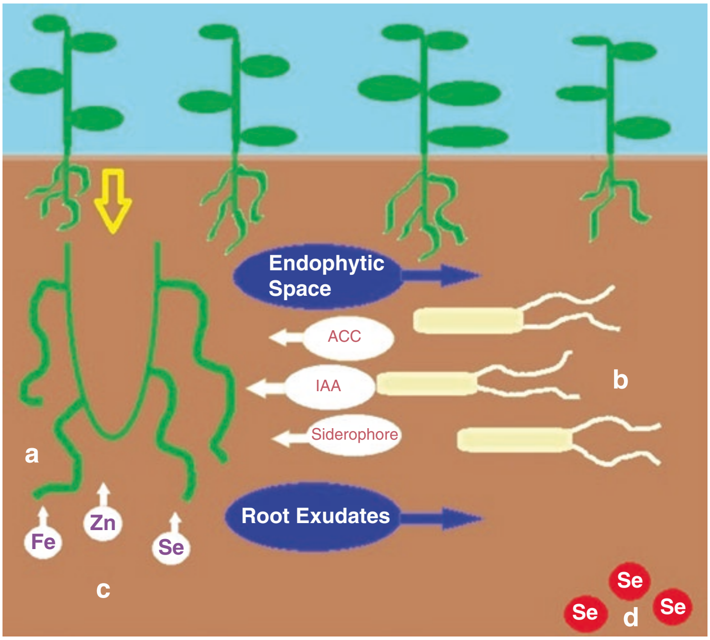

Fig. 16.2 Schematic representation of the reciprocal relationship between PGPR and the host plant; (**a**) represents the plant rhizospheric space, (**b**) represents beneficial PGPR. The plant provides root exudates which are consumed by bacteria as a carbon source, and endophytic PGPR have the option to potentially colonize the plant and avoid adverse environmental conditions. (**c**) Represents the increased uptake of micronutrients in the rhizosphere where PGPR activity leads to micronutrient biofortification of the plant. (**d**) Represents micronutrients in the soil which would be either unavailable or diminished in available supply to the plant without PGPR. Based on numerous PGP activities, PGPR can increase the translocation and concentration of key micronutrients which would otherwise be unavailable to the plant. Especially in the case of siderophore-producing PGPR, which can have a beneficial effect on Fe sequestration from the soil and subsequent transfer to the plant. In return, the plant can supply the PGPR with a carbon source in the form of root exudates and where there are endophytic PGPR present; the plant endosphere can act as a suitable environment for endophytic proliferation

due to soil property differences (Lehmann et al. 2014). Improved total uptake of N-P-K was observed in both shoots and roots of *Plantago minuta* under variable soil water conditions, when inoculated with AMF (Shi et al. 2015). Under field conditions, inoculation of AMF in the soil of chickpea plants increased plant biomass and yield, and also increased the nutritional value of the legume, leading to Fe and Zn biofortification (Pellegrino and Bedini 2014).

In addition, AMF increases positive interactions with rhizobacteria, including beneficial rhizobacteria known to induce spore germination of AMF and root colonization directly. AMF hyphal exudates influence surrounding microbial communities and may drive beneficial bacterial-plant interactions and consequently improve plant fitness and productivity (Scheublin et al. 2010; Cruz and Ishii 2011; Qin et al.

2016). Co-inoculation of AMF and beneficial bacteria, such as *Pseudomonas* strains, substantially increases wheat yield and mineral nutrient concentrations of P, K, Cu, Fe, Zn and Mn in wheat grains (Mader et al. 2011). The co-inoculation of selenobacteria and AMF significantly improves selenium (Se) content in wheat grain, suggesting a synergistic effect between these microbes (Durán et al. 2013). Dual inoculation of AMF and *Rhizobium* in the soybean/maize intercropping system significantly increased the efficiency of N fixation of soybean and enhanced the transfer of N from soybean to maize, leading to the yield enhancement of both crops (Meng et al. 2015).

Another important benefit of AMF is its secretion of a high molecular weight glycoprotein that helps in soil aggregation stability, promotes a better soil structure and healthy plant-soil system (Wu et al. 2014) and mitigates against phytoremediation of Al, As, Cd, Hg and Pb (He and Nara 2007). The AMF also show resistance to several biotic (e.g. pathogen) and abiotic stressors (e.g. drought). Under drought stress, a significant increase in plant growth and photosynthesis was observed when citrus plants were colonized by AMF (Wu et al. 2013). In another study, the AMF-inoculated strawberry has shown enhanced tolerance to drought stress (Boyer et al. 2015). AMF are capable of significantly improving plant innate system, mainly through the priming mechanism (Gallou et al. 2011).

The tomato plants colonized with AMF showed increased plant resistance to early blight, which requires JA signalling pathway (Song et al. 2015). Beneficial microbes provide plants with essential nutrients through a variety of mechanisms, and microbe interactions with plant roots are critical for nutrient uptake and crop productivity. Hence, a better understanding of microbial interactions and subsequent controlling of pathogens are essential for the use of microbes in agriculture.

The role of AMF in nutrient uptake and crop production is a key factor for biofortification of crops using essential mineral elements from the soil. With plant-microbial interactions, crops benefit through symbiosis with AMF, and this could help minimize the application of chemical fertilizers and improve nutrient availability. As a result, AMF could play a vital role in biofortification of crops with essential nutrients, thereby contributing to sustainable crops with improved nutrition that could curb global malnutrition (He and Nara 2007). Increasing the nutritional levels of economically important food crops, without requiring the consumption of more food, is achievable through the use of AMF and other beneficial microbes. Thus, unravelling the potential of AMF as a biofortification agent to increase the nutritional content in edible tissue plant parts is essential in the context of modern agriculture. As such, biofortification using AMF and other beneficial microbes in agriculture is important, including an increase of iron biofortification, zinc biofortification, provitamin A carotenoid biofortification and amino acid and protein biofortification of economically important crops, such as potato, sorghum, cassava, rice, wheat, maize, etc. (Mayer et al. 2008; Khush et al. 2012).

16.4 Conclusions and Future Perspectives

The threats to global food security have been highlighted by many authors to date (Tai et al. 2014; Sundström et al. 2014). National governments through the international forum of the United Nations have agreed on 17 goals to be achieved by 2030 (Sustainable Development Goals project), amongst them the eradication of world hunger and improved nutrition (FAO 2016). A number of these goals, particularly in relation to food security, can be addressed by crop biofortification. Many successful strategies for biofortifying crops are detailed in the peer-reviewed literature with the most famous biofortification project concerning the expression of provitamin A in Golden Rice which was based on a genetic engineering strategy. Even though the Golden Rice project was awarded the Patents for Humanity prize by the United States Patent and Trademark Office (USPTO) in 2015 in recognition of this lifesaving technology and the humanitarian nature of the project, the product is still not available on the market due to public opposition, in the main led by Greenpeace. This year (2016), 121 Nobel Laureates called on Greenpeace to end its opposition to this lifesaving technology (Support Precision Agriculture 2016).

Aside from genetic modification, other successful strategies including conventional breeding strategies have been utilized for crop biofortification. This year (2016), the World Food Prize was awarded to a group of scientists in recognition of their role in crop biofortification using breeding strategies to increase provitamin A in sweet potato by incorporating germplasm from the Andean region in South America to generate orange-fleshed sweet potatoes suitable for Africa (ISAAA 2016). This breeding strategy is reliant on natural diversity in the germplasm of a crop for the production of a particular vitamin or micronutrient.

In the absence of natural germplasm diversity, other strategies for crop biofortification can be utilized including foliar application of micronutrients and/or the exploitation of the natural microbial diversity in soils, i.e. plant growth-promoting microbes (PGPM) most especially bacteria and mycorrhizal fungi. Being environmentally safe and cost-effective are major advantages to the proliferation of PGPM throughout agriculture. Indeed this can be seen by the vast number of commercially available PGPM products released in recent years with up to 4% of the global biocide share being directly related to microbial volatile organic compounds (mVOCs) isolated and synthesized from PGPM (Glare et al. 2012; Wilson et al. 2013; Velivelli et al., 2014; Kanchiswamy et al. 2016), and this trend is set to continue. A historic problem in the biofortification of crops using foliar and soil application of micronutrients particularly in relation to Fe has been the low uptake of the micronutrient post-application. This has been highlighted recently by Kromann et al. (2016) with regard to Fe and Zn biofortification of Andean potatoes. It was found that both foliar and soil application of Zn fertilizers led to a ~three- and twofold increase, respectively, in tuber Zn concentration. However, there was no increase in Fe tuber concentration post-application. In this instance, it can be suggested that application of Fe fertilizer in conjunction with a PGPM capable of increasing Fe translocation and concentration in the tuber could be tested. The study also highlights the need to understand soil parameters within diverse environments, as these can have a significant effect on crop biofortification (Kromann et al. 2016).

Regulatory mechanisms in the plant-microbe micro-/macronutrient cycling pathways and their reciprocal interactions need to be further elucidated to determine the best course of action for formulation of appropriate treatments to specific soil/climate/temperature/crop scenarios. Indeed, this can be further seen in the observation that nitrogen status of the plant can have a positive correlation on the content and translocation of Fe and Zn in plants (Kutman et al. 2010, 2011), and many plant growth-promoting microbes are capable of fixing atmospheric nitrogen (Prasanna et al. 2012). Genome mining of selected PGPR or wild relative/stress-tolerant cultivars of major crops may reveal genes involved in nutrient cycling pathways that, through GM technology, could be incorporated into agriculturally important crops to optimize delivery of micronutrients to deficient populations in the developing world.

Using genomics, identifying changes in gene expression during microbial interactions is critical to understanding the role of microbes in biofortification. In particular, more attention needs to be focused on the following research questions: how microbes influence the nutritional content of economically important crops; identifying appropriate microbial strains; exploiting synergistic microbial activity, e.g. between AMF and other beneficial bacteria; and assessing constant field efficacy under different environmental regimes, to ensuring adequate uptake by plants and improving crop quality. Supplying essential nutrients using beneficial microbes naturally found in soils across the planet, such as AMF and PGPR, will help to alleviate the problem of *hidden hunger* and provide a promising sustainable agricultural strategy for improving current crop micronutrient content and in developing future biofortified crops.

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