Rhizosphere Microbiome and Its Role in Plant Growth Promotion

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Abstract

Microbial communities play a vital role in the growth and development of plants by influencing their physiological processes. The role of rhizodeposits to shape the rhizobacterial community structure is well established. Plant roots release various organic chemicals that attract and choose specific kind of microbes within the rhizosphere. In response, the plants associated with microbes enhance plant growth and productivity via different mechanisms. Therefore, in order to develop sustainable farming approaches such as biofertilizers and biopesticides, the study of host plants and associated microbial interactions in the rhizosphere plays an important role. Although plant growth-promoting microbial communities are abundant in the rhizosphere, many plant pathogens are also present that break through the plant defense mechanisms and cause various diseases. Therefore, to promote growth and productivity of crop plants, it is central to know what types of microorganisms are present and what functions they are performing in the rhizosphere. In this chapter, we have discussed the chief components of rhizosphere microbiome and its role in plant growth and management of various phytopathoens. The rhizospheric plant-microbe interactions and function of rhizosphere

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microbiome in agriculture have been described. Finally, we have drawn attention to various approaches to manipulate and redirect the microbial population in rhizosphere to enhance plant growth and crop productivity.

Keywords
Rhizobacteria • Rhizospheric microbiome • Rhizodeposits • Plant growth promoting

3.1 Plant Microbiome: An Introduction

Joshua Lederberg used the term “microbiome” as the microorganisms inhabiting our body as commensals, symbionts, or pathogens (Lynch 1990), and plant microbiome is the dynamic community of microorganisms associated with the plant. Phyllosphere, rhizosphere, and endosphere are the regions of the plant which provide niche for microbial community (Berg et al. 2016).

The aerial portion of plants inhabited by microorganisms is called phyllosphere; the latter is further divided into caulosphere (stems), phylloplane (leaves), anthosphere (flowers), and carposphere (fruits). Conservative estimates indicate that bacteria are the most abundant colonizers of leaf surfaces (Morris and Kinkel 2002). On the basis of degree of sway of diverse leaf exudates or other materials, assorted microorganisms may either die or endure and propagate in contrast to phyllosphere, the belowground portion of plants colonized by microbiome, broadly soil under the sway of roots, is known as **rhizosphere,** whereas the **rhizoplane** encompasses the root surface and its adhering soil. Various compounds are released from plant roots that take part in symbiotic functioning in the soil area under the influence of plant roots (rhizosphere) (Barea et al. 2005). For instance, rhizosphere provides a nutrient-rich environment for diazotrophic bacteria that fix atmospheric nitrogen and made the nitrogen available to plants. Abundance of bacteria, fungi, and archaea is high in the rhizosphere due to the presence of nutrient-rich environment (Egamberdiyeva et al. 2008; Mendes et al. 2011). Based upon the kind of colonization, plant microbiome is classified into epiphytes and endophytes. Microbes living on plant tissues or in close proximity (phyllosphere) and in the rhizosphere are well thought-out as epiphytes, while microbes living within plant tissues (stem, root, leaf tissues) are well considered as endophytes (Turner et al. 2013).

3.1.1 Contribution of Plant Microbiome in Plant Intensification and Health

The combinations as well as concentration of different kind of nutrients in the soil affect plant health and development. Furthermore, owing to immobility of some nutrients, plants frequently face considerable challenges in obtaining an enough provision of these nutrients in order to fulfill the demands of basic cellular processes. Limiting nutrient supply results in decreased plant productivity. Plant roots uptake mineral nutrients from the soil, but several factors influence the effectiveness of nutrient acquisition which includes chemistry as well as composition of certain soils that makes plants difficult to absorb nutrients and that either the nutrients may not be existing in such soils or may be present in forms that the plants cannot use.

As a result, many plant species develop an evolution of the mutually positive symbiotic associations with the soilborne microorganisms termed as plant growth-promoting rhizobacteria. As a consequence of their association, both the plant and the microsymbiont associated with that plant obtain valuable resources that they need for their own productivity and survival.

3.1.1.1 Mechanisms of Improving Plant Growth and Health

1. Direct mechanisms

   Plant microbiome may unswervingly assist the proliferation of their host plant through various methods:

   (a) Fundamental macronutrient for plant growth and health is nitrogen (N). Although, an approximate of 78% by volume of the atmosphere is occupied by nitrogen, but because of its inert form growing plants are incapable of nitrogen uptake. Diazotrophic bacteria have capability to convert atmospheric inert form of N_2 to the plant utilizable form (ammonia) by the action of intricate enzyme: nitrogenase (Kim and Rees 1994).

   (b) Phosphorus next to nitrogen is an essential macronutrient which is recognized as one of the vital elements that limit plant development (Feng et al. 2004). Preponderance of phosphate is fixed in soils, and hence, plant available P is barely accessible even though the copiousness of phosphorus (both organic and inorganic) in soils. Some bacterial species have solubilization potential for inorganic phosphorus through the release of metabolites such as organic acids (Rodríguez et al. 2006; Bianco and Defez 2010; Shahid et al. 2012), the functional groups (hydroxyl and carboxyl)of organic acids are responsible for chelation the phosphate cation and convert it into soluble form (Chen et al. 2006; Vyas and Gulati 2009; Lavania and Nautiyal 2013). *Pseudomonas putida*, *Pantoea agglomerans*, and *Microbacterium laevaniformans* are some common examples of inorganic phosphate-solubilizing bacteria (Park et al. 2011).

   Organic phosphorous is available to plants in mineralized form, and the process of mineralization is carried out by some bacterial genera through the liberation of phosphatase enzyme that catalyzes dephosphorylation of chemical bonds (phosphoester or phosphoanhydride) present in organic phosphorus (soil phytate) (Jorquera et al. 2008).

   (c) Some bacterial genera associated with plants, particularly the rhizobia, are known to produce several plant hormones like indole-3-acetic acid (IAA) (Ghosh et al. 2011), and some of the *Bacillus* spp. produce gibberellins (Gutierrez-Manero et al. 2001). Some strains of *Pseudomonas* produce hormone analogs that induce jasmonate and ethylene signaling within the plants resulting in plant defense responses against different plant pathogens (Melotto et al. 2006). Some bacterial genera have also been documented for hormone precursor degradation or degradation of hormones. For instance, deamination of ACC catalyzed by ACC deaminase of bacterial origin prevents ethylene signaling in plants that results in increased tolerance of plants to environmental stress (Glick 2005).

2. Indirect mechanisms:
   Preclusion from deleterious effects of plant pathogens on plants via increasing natural resistance of host plant or through the synthesis of several inhibitory compounds involves in indirect mechanisms (Nehl et al. 1997). Generally, these mechanisms include niche exclusion and production of antifungal metabolites: HCN, viscosinamide, phenazines, pyrrolnitrin, tensin, and pyoluteorin (Bhattacharyya and Jha 2012). In addition, many rhizobacteria have also been reported for the production of siderophores that prevent the proliferation of plant pathogens by limiting the supply of iron required for their growth (Ali and Vidhale 2013). **Induced systemic resistance** is the outcome of interaction of some microbial strains that induces impedance against several pathogenic microbes to host plant (Lugtenberg and Kamilova 2009).

3.2 Bioprospecting Microbes Along with Metagenome of Plant Rhizosphere

Rhizosphere provides a suitable environment for the growth of microorganisms. Multiple numbers of beneficial microorganisms are also residents of rhizosphere which are responsible for multiple biological as well as ecological processes that are essential for plant health (Kent and Triplett 2002). The abundance of plant growth-promoting microorganisms assumes a natural importance from agriculture point of view. The diversity of such microorganisms in soil is much higher than any other habitat; therefore (Delmont et al. 2011; Janssen 2006), rhizosphere ecosystem is a great pool for discovering novel microbes and their products; the term used to denote the discovery of novel microbes from natural system is “bioprospecting” (Lee and Lee 2013).

Amann et al. (1995) reported that 99% of microbial population in soil cannot be cultured under laboratory conditions. Therefore, utilization of non-culturable microbial assets would provide inimitable prospect to find novel microbial resources (Lee and Lee 2013). A total microbial genome which is directly isolated from microbial habitat known as metagenome is a rich source for bioprospecting (Berry et al. 2003; Zhou et al. 1996; Bertrand et al. 2005). For this metagenome from rhizosphere is cloned in a suitable host to comprise metagenome library (Rondon et al. 2000; Kim et al. 1992). This cloned library is either used for analysis of microbial community through direct sequencing of whole genome or used for selecting novel genetic resources for non-culturable rhizosphere microbiome.

Some common examples of bioprospecting potential of rhizosphere metagenome

1. Novel genus ***Swaminathania*** *salitolerans* from the mangroves
   A variety of bacterial strains belonging to taxa *Swaminathania*, *Vibrio*, *Bacillus*, *Enterobacter*, and *Azospirillum* were recovered from *Porteresia coarctata* Tateoka. Among these bacterial genera, *Swaminathania salitolerans*—a novel salt-tolerant strain—possess nitrogen-fixing activity along with phosphate solubilization. Likewise *Mangroveibacter plantisponsor*, a novel diazotrophic strain, was recognized as new genus in *Enterobacteriaceae* (Loganathan and Nair 2004).

2. Novel *Vibrio* associated with the mangroves
   Four new species (*Vibrio rhizosphaerae* sp. nov., *Vibrio porteresiae* sp. nov. (Rameshkumar et al. 2008), *Vibrio mangrovi* sp. nov (Rameshkumar et al. 2010), and *Vibrio plantisponsor* sp. nov (Rameshkumar et al. 2011)) isolated from the rhizosphere of mangrove define innovative ecological function of *Vibrio* as a rhizosphere-associated heterotrophic nitrogen-fixing bacteria.

3.3 The Rhizosphere Microbiome

The soil fraction under the sway of root secretions is termed as rhizosphere, this zone of soil can hold approximately 10^{11} microbial populace per gram of soil sample (Egamberdiyeva et al. 2008) as well as more than 30,000 species of prokaryotes (Mendes et al. 2011). A diverse array of compounds are accumulated and secreted through plant roots that will attract a diverse group of microorganisms that are metabolically active (Lugtenberg and Kamilova 2009). All this activity makes the rhizosphere the most dynamic environment in the soil (Walker et al. 2003). Rhizosphere consists of plant beneficial as well as plant pathogenic microbial species. Beneficial microbial community includes nitrogen fixers, mycorrhizae, plant growth-promoting rhizobacteria (PGPR), antagonistic microorganisms, as well as protozoa (Bonkowski et al. 2009; Buée et al. 2009; Raaijmakers et al. 2009). Pathogenic fungi, some bacterial species, and nematodes are deleterious to plant health.

3.4 Composition, Abundance, and Diversity of Rhizospheric Microbiome

It has been recognized that microbial life is present in a trifling area of soil which is localized in hot spots like rhizosphere, where microorganisms have continuous access to the flow of various plant root-derived organic substrates (Nannipieri et al. 2003). Flow of such nutrients together with physicochemical and biological factors can influence microbial community structure and function of rhizosphere (Sorensen 1997; Brimecombe et al. 2001). Microbial community and its abundance present in rhizosphere are represented in Fig. 3.1 as follows:

3.4.1 Bacteria

Wide variety of bacterial genera are present in rhizosphere whose composition differ among different plant species, root zone as well as plant phonological phase (Rovira 1965; Hinsinger et al. 2009; Marschner et al. 2011). Mendes et al. (2011), Weinert et al. (2011), and Yang et al. (2012) reported that the most dominant bacterial groups present in rhizosphere of sugarcane, pea native hardwood forest, and conifer plantations belong to *Proteobacteria*, *Firmicutes*, *Actinobacteria*, *Bacteroidetes*, and *Acidobacteria*. Among them, *Proteobacteria* are considered to be the most abundant bacterial group in

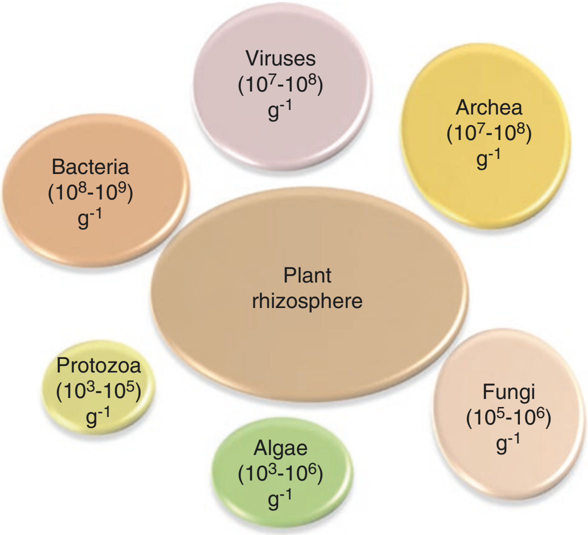

Fig. 3.1 Generalized diagram showing abundance of microorganisms present in the rhizosphere. The size of the circle is a measure of abundance of group of particular microbial community

the rhizosphere due to their ability to respond to labile C sources, showing fast growth and adaptation to the diverse plant rhizospheres. *Proteobacteria* is followed by *Acidobacteria*, which have been attributed to carbon cycle in soils because of their cellulose and lignin degradation capabilities (Ward et al. 2009). In relation to *Actinobacteria*, they have been linked with disease stifling soils and increasing root nodulation in plants thereby contributing in plant growth promotion (Mendes et al. 2011; Tokala et al. 2002). Due to fast growth and response to labile carbon sources, *Proteobacteria* is known to be the most abundant group of bacteria adapted to diverse plant rhizospheres (Bulgarelli et al. 2013; Chaparro et al. 2012; Peiffer et al. 2013). Due to the ability of *Acidobacteria* to degrade cellulose and lignin (Ward et al. 2009) which has also been attributed to carbon cycle, *Acidobacteria* is dominant in soil next to *Proteobacteria*. *Actinobacteria* has been found dominant in disease-suppressive soils, and these bacteria have also been found to increase root nodulation and hence plant growth promotion (Mendes et al. 2011; Tokala et al. 2002). *Rhizobium*, *Azospirillum*, *Burkholderia*, and *Pseudomonas* are the rhizobacterial genera acknowledged from the GenBank database contributing to plant growth promotion. Moreover, a less dominant group of rhizobacteria which do not play a role in plant growth and development includes *Verrucomicrobia*, *Sphingobacteria*, *Flavobacteriia*, *Deinococcus*, and *Epsilonproteobacteria*.

3.4.2 Archaea

Archaea are common but not major inhabitants of rhizosphere; also less information is acknowledged for Archaea from soil. On the basis of earlier 16S rRNA gene amplification, Crenarchaeota has been isolated from tomato rhizosphere which constituted of about 4–16% (relative to bacteria) (Bintrim et al. 1997; Borneman and Triplett 1997). It has also been reported that archaeal abundance is decreased by root exudates due to lower competitiveness than bacteria as well as slower growth rate (Karlsson et al. 2012).

3.4.3 Fungi in the Rhizosphere

The presence of organotropic fungi in the rhizosphere has been shown by both cultivable and non-cultivable techniques (Smit et al. 1999; Viebahn et al. 2005; De Boer et al. 2008; Zachow et al. 2008). Fungi as a member of the rhizosphere microbiome are termed as "mycorrhiza." The representatives of fungi in the rhizosphere include both yeast and filamentous fungi (*Ascomycota* as well as *Basidiomycota*) (Renker et al. 2004; Berg et al. 2005; Vujanovic et al. 2007). Joergensen (2000) reported that grassland plant rhizosphere consists of large amount of fungal biomass, i.e., average of 39% and range of 20–60%. The chief role of mycorrhiza is to increase nutrient uptake by extending the reach of plant root systems as well as the decomposition of root exudates containing simple or complex organic compounds (Butler et al. 2003; Treonis et al. 2004).

3.4.4 Other Rhizosphere Inhabitants

Organisms whose populations tend not to react to influxes of readily decomposable organic matter are usually not affected by root growth. This grouping includes actinomycetes, protozoa, and algal populations.

The actinomycetes generally derive their energy supply from decomposition of less readily decomposable soil organic matter components, whereas algal population uses solar energy. Protozoan populations are limited by the distribution and density of prey required to support increases in protozoan cell numbers (Robert and Tate 1994).

3.5 Interactions Between Plants and Microbes in the Rhizosphere

The rhizosphere, a zone in the close vicinity of plant roots is a hot spot for potentially important microbes and copious organisms. Various unicellular and multicellular organisms such as bacteria, archaea, algae, fungi, protozoans, and arthropods together with plant roots form the most intricate ecosystem on earth (Raaijmakers et al. 2009). Plants release ample amount of nutrients in the form of rhizodeposits which determine the type and composition of rhizosphere microbiome. Various categories of compounds are exuded from plant roots including sugars, organic acids, nucleotides, peptides, enzymes, and other secondary metabolites which together regulate the microbial diversity and activity inside the rhizosphere. The plants may exert selective pressure by releasing unique rhizodeposits to stimulate the growth of beneficial microorganisms for their growth and development (Cook et al. 1995). Rhizospheric microorganisms thus impart ecological fitness to their host plant and vice versa. These plant-microbe interactions thus can be categorized as neutral, positive, and negative interactions, depending upon the type of microorganisms, host plants, as well as existing environmental conditions.

3.5.1 Negative Interactions in the Rhizosphere

Beneficial microorganisms colonize plant roots in response to root exudates, but they can attract pathogenic population as well. Plant diseases are directly involved in damaging crop plants and destructing agricultural economy. Soilborne pathogens cause significant damage to the crops, and among these fungi are the most devastating. Their damaging effects include mild as well as severe symptoms causing inconsiderate crop losses. Thus, they are the foremost chronic threat to food production and economic stability worldwide. The most common fungal pathogens include members of genus *Aspergillus*, *Fusarium*, *Pythium*, *Phytophthora*, *Mucor*, *Rhizopus*, and *Verticillium* (Tournas and Katsoudas 2005) and the common forest fungi, viz., *Armillaria* and *Poria* (Asiegbu et al. 2005). The common and most widely studied bacterial pathogens belong to the genus *Pseudomonas*, *Erwinia*, *Ralstonia*, and *Xanthomonas* (Tournas and Katsoudas 2005).

3.5.2 Positive Interactions in the Rhizosphere

In the rhizosphere, plant-microbe interactions are involved in imperative ecosystem functioning processes, such as nutrient mineralization and immobilization in biogeochemical cycles. Microorganisms form a number of symbiotic associations with plants such as colonization of rhizosphere by plant growth-promoting rhizobacteria (PGPR), mycorrhizae, and legume-rhizobium association. These interactions impart several benefits to plants and are of three types: First are the type of microorganisms that increase availability of the nutrients to plants and are referred as biofertilizers. They either directly interact with plants or are involved in soil biotic and abiotic processes of plant growth promotion. The second type are the group of microbes that increase the plant growth indirectly by protecting plants from pathogen attack. These are referred to as biocontrol agents. The third group includes microorganisms that stimulate the plant growth by secreting growth-promoting hormones and growth regulators such as auxins, cytokinins, gibberellins, etc. They are known as biostimulants. Literature has described the importance of rhizospheric microorganisms in stimulating plant growth and maintaining soil health (Welbaum et al. 2004), whereas plant roots exude various metabolites in rhizosphere that are used as nutrients and signaling molecules by the bacteria (Bais et al. 2004).

3.5.3 Root Exudates-Mediators of Plant-Microbe Interactions

The “rhizosphere,” a term coined by Hiltner (1904), was later redefined by Pinton as the zone in soil influenced by the plant roots along with the root tissues colonized by microorganisms (Pinton et al. 2001). Here, the soil plant-microbe interactions alter soil physical and chemical properties which further determine the soil microbial population (Nihorimbere et al. 2011). Approximately 5–20% of total photosynthetically fixed carbon is released in the form of root exudates by plants which are further used as nutrients by microbes in the rhizosphere (Chaparro et al. 2013). Furthermore, these rhizodeposits determine the plant-microbe interactions in the rhizosphere (Chaparro et al. 2013). An array of distinct signature compounds are released by plant roots which determine the microbial diversity in the rhizosphere, so if diverse is the plant community above ground, diverse will be the microbial population in the rhizosphere.

Plant root exudates can be subdivided into two main categories: molecules with low molecular weight, viz., sugars, phenolic compounds, other secondary metabolites, and hormones, and compounds with high molecular weight, viz., proteins and polysaccharides (Badri and Vivanco 2009). The amount and composition of rhizodeposits depend upon host plant, cultivar, growth stage, and a range of environmental factors, such as soil type, temperature, pH, microbial activities, and soil type (Uren 2000). These differences create the type of rhizobacterial communities that have a certain level of specificity for the host plant.

Certain compounds imitating bacterial quorum-sensing (QS) signals are also released by plant roots that either repress or stimulate QS responses of related bacterial species. In plants, root-microbe associations are governed by QS signals, whether they are beneficial, antagonistic, or symbiotic (Gao et al. 2003). Identifying these QS imitating compounds may lead to the development of a new antimicrobial compound or discovery of novel molecules. For example, different molecules that mimic the activity of *N*-acyl homoserine lactones and pose specific effects on bacterial quorum-sensing-mediated activities have been found in *Coronilla varia* L. (crown vetch), *Pisum sativum* L. (pea), *Oryza sativa* L. (rice), and *Solanum lycopersicum* (L.) Karst. (tomato) and also in *Chlamydomonas reinhardtii* (Teplitski et al. 2000, 2004; Daniels et al. 2002).

3.5.4 Impact of Root Exudates on Rhizospheric Microbiome

Plants roots pose selective pressure by releasing their unique signature molecules for attracting distinct microbial population, therefore, amend the diversity and composition of rhizospheric microbial communities. For example, root exudates from mutant *Arabidopsis* plant had more concentration of phenolic compounds than sugars when compared to its wild type, thus causing considerable changes in native microbial community structure (Badri et al. 2009). This change in the rhizodeposits composition can be further linked to the development of beneficial microbial population composed of PGPR, nitrogen fixers, and bioremediating bacterial population. Previous studies have also described that plants can develop a unique rhizobacterial community structure by releasing their unique root exudates profile (Berendsen et al. 2012; Bakker et al. 2012). For example, application of a root exudate compound, *p*-coumaric acid to cucumber seedlings, increased the native microbial population, thus alters the composition and organization of rhizobacterial communities, and increased the population of a soilborne fungal pathogen (*F. oxysporum* f.sp. *cucumerinum*) (Zhou and Wu 2012).

3.5.5 Rhizosphere Microbiome Influences Root Exudation Process

The rhizosphere colonizing microbes such as bacteria and fungi, also influence root exudation process (Matilla et al. 2010). Colonization of plant roots by arbuscular mycorrhizal (AM) fungi qualitatively changed the rhizodeposition, e.g., increasing the secretions of amino acids, gibberellins, and phenolics and decreasing the secretions of potassium, phosphorus, and sugars (Jones et al. 2004). Studies have described that various ectomycorrhizae have profound effects on composition as well as abundance of rhizodeposits on plants (Rosling et al. 2004). Moreover, certain compounds such as, oxalic acid and phytoalexins, are exuded by plant roots in response to pathogenic attack (Steinkellner et al. 2007). In addition to fungi, bacteria also influence root exudation profile. For example, an auxin secreting strain of *Bacillus amyloliquefaciens* FZB42 stimulates root exudation but reduce the uptake of phosphorus in *Triticum aestivum* (Talboys et al. 2014).

3.6 Rhizospheric Microbiome in Agriculture

Agricultural productivity lies on the foundation of microbial activities taking place in soil. The soil harbors an enormous microbial diversity, and existing extensive research has reinforced this fact (Roesch et al. 2007). The genetic potential and functional importance of the soil microbiome is gaining appreciation due to its direct role in plant productivity. Within a given soil type, native plants exert a selective pressure on this vast pool of biodiversity, thus restructuring and shaping rhizospheric microbial communities (Berg and Smalla 2009). At the same time, plants are also responsive to microbial activity, and may show either improved or reduced performance depending on the microbial activities in the rhizosphere. This active, two-way interaction between soil microbes and plants is significant in agricultural ecosystem, and enhancing our ability to redirect these interactions could offer progress toward agricultural sustainability through development of crop varieties that enhance beneficial functions within the rhizosphere microbiome.

There are many mechanisms by which rhizosphere microorganisms may positively impact plant performance. Whenever host plants can capture services provided by the soil microbiome, agricultural productivity may be enhanced by fully exploiting beneficial microbial activities. Beneficial microbial activities in the rhizosphere microbiome include:

- Production of phytohormones
- Provision of nutrients
- Rhizoremediation
- Improvement of plant resistance to pathogen infection

3.6.1 Production of Phytohormones (Phytostimulation)

Rhizobacteria are known to produce various phytohormones such as auxins, cytokinins, and gibberellins which are involved in plant growth promotion process. These growth regulators are either synthesized by plant itself or they can be released by various rhizobacterial species such as *Bacillus* and *Pseudomonas* (Steenhoudt and Vanderleyden 2000). Rhizobacteria belonging to genus *Bacillus* and *Pseudomonas* are known to produce different growth regulators that make plants to develop a number of fine roots, thus increasing the total surface area for nutrient and water absorption. Various growth hormones released are auxins, mainly indole-3-acetic acid, cytokinins, gibberellins, and ethylene inhibitors. Indole-3-acetic acid is known to stimulate root initiation, cell division, and elongation and is known to be produced by 70% of the rhizobacterial species (Barazani and Friedman 2001).

Generally indole-3-acetic acid increases root extension, cell division process, germination of seeds and tubers, flow rate of water and nutrients through vascular tissues, and secondary root development, mediates of geotropic and phototropic response, and provides resistance to plant stress. In addition to this, bacterial IAA alters the root exudation profile by loosening the plant cell wall, thus enhancing the amount of rhizodeposits and providing more nutrients to enhance rhizobacterial growth (Glick 2012). Due to this, rhizobacterial IAA plays an important role in phytostimulation as well as in pathogenesis and is regarded as a central molecule in plant-microbe interactions (Spaepen et al. 2007). Production of other hormones by rhizobacteria such as cytokinins and gibberellins is also known to be responsible for plant growth and development (Ullah et al. 2014).

In addition, rhizobacteria can also manipulate hormonal balance in plants. For example, ethylene is regarded as a senescence hormone which is known to inhibit plant growth in normal conditions, but at low concentration, it stimulates growth in many plants including *Arabidopsis thaliana*.

3.6.2 Provision of Nutrients (Biofertilization)

A number of plant growth-promoting rhizobacteria have been commercialized already which are known to promote plant growth through a variety of mechanisms including repression of plant diseases (bioprotectants), growth hormone production (biostimulants), and increased nutrient availability (biofertilizers). Biofertilization is one of the most extensively studied mechanisms which involve increasing the availability of plant deficient nutrients, viz., nitrogen, phosphorus, and iron. In India, most of the cultivable land lack satisfactory amount of one or more of these nutrients which resulted in suboptimal plant growth. To preclude this nutrient deficiency and to get high plant yield, farmers are depending upon more and more chemical fertilizers which, besides being pricey, has resulted in depletion of nonrenewable sources of energy, used for their synthesis. Chemical fertilizers are also known to adversely affect the human health and environment; therefore, it would be advantageous to fulfill nutrient demand of crop plants by certain biological means that could replace a part if not the full demand of these chemical fertilizers (Glick 2012).

3.6.2.1 Nitrogen Fixation

About 65% of the total nitrogen demand of crop plants is fulfilled by biological nitrogen fixation (BNF) (Bloemberg and Lugtenberg 2001). Nitrogen (N) is the most crucial primary mineral element required for plant growth and development. Although nitrogen is abundant (78%) in the atmosphere, it remains in the fixed form which cannot be utilized by the plants. The atmospheric nitrogen is converted to plant-usable forms through the process of BNF which involves conversion of nitrogen to ammonia by a complex enzyme system called nitrogenase present in nitrogen-fixing microorganisms (Kim and Rees 1994). About 2/3rd of the total nitrogen fixed is through BNF, whereas rest of the nitrogen is industrially synthesized by Haber and Bosch process (Rubio and Ludden 2008). The BNF constitutes a cost-effective and environment-friendly substitute for chemical fertilizers (Ladha et al. 1997).

Nitrogen fixers can be categorized as (1) symbiotic nitrogen fixers including bacteria belonging to family *Rhizobiaceae* (e.g., *Rhizobium*) that form symbiosis with legume plants and actinomycetes *Frankia* which form symbiotic association with non-legume trees such as *Alnus* and *Casuarina* and (2) free-living (*Azotobacter*, *Derxia*) or associative (*Azospirillum*) non-symbiotic nitrogen-fixing bacteria or cyanobacteria such as *Anabaena* and *Nostoc* (Bhattacharyya and Jha 2012). Free-living nitrogen-fixing plant growth-promoting rhizobacteria are also known as diazotrophs and form a nonobligatory association with the host plant (Glick et al. 1999). A few examples of nitrogen-fixing rhizobacterial species along with their host plants have been illustrated in Table 3.1.

3.6.2.2 Phosphorus Solubilization

Phosphorus (P), is the second most crucial mineral element required by plants, and is found in abundance in soil in both organic as well as inorganic forms. Despite of its abundance in soil, the majority of P is present in fixed insoluble forms which are unavailable to plants. The plants take up P in only two soluble forms, the monobasic ($H_2PO_4^-$) and the diabasic (HPO_4^{2-}) forms (Bhattacharyya and Jha 2012). The insoluble forms of soil phosphorus include inorganic mineral phosphates such as apatite or organic forms such as phosphomonesters, phosphotriesters, and inositol phosphate (soil phytate) (Glick 2012). To conquer phosphorus deficiency, farmers are frequently applying phosphatic chemical fertilizers in fields of which plants absorb a relatively small amount and the rest is quickly converted into insoluble forms of mineral phosphates in the soil. The regular application of phosphatic fertilizers is expensive as well as damaging to the environment. So this has led to the search for an environment-friendly and economic method to improving crop yield in P-deficient soil. In this context, the phosphate-solubilizing microorganisms (PSMs) may make available the unavailable forms of phosphorus to the plants and may act as a good replacement to chemical phosphatic fertilizers (Khan et al. 2006).

Table 3.1 Rhizobacterial species and their ability to fix atmospheric N_2 in certain plants

Rhizobacteria	Host crops	References
Burkholderia sp.	Rice	Baldani and Dobereiner (2000)
Azotobacter sp.	Wheat	Mrkovacki and Milic (2001)
Gluconacetobacter sp.	Sugarcane	Boddey et al. (2001)
Herbaspirillum sp.	Rice	James et al. (2002)
Pseudomonas stutzeri	Green pepper	Yan et al. (2008)
Bacillus subtilis	Tomato	Walia et al. (2014)
Bacillus methylotrophicus	Apple	Mehta et al. (2014)
Bacillus subtilis	Tomato	Sharma et al. (2015)

Among a variety of PSMs found in the rhizosphere, phosphate-solubilizing bacteria (PSB) are most widely recognized biofertilizers that supply plants with P from insoluble or unavailable sources of phosphorus. Bacteria belonging to genus *Bacillus*, *Pseudomonas*, *Rhizobium*, *Enterobacter*, *Erwinia*, *Azotobacter*, *Thiobacillus*, and *Serratia* are the most widely recognized phosphate-solubilizing bacteria (Bhattacharyya and Jha 2012).

Mechanism Involved in Phosphate Solubilization

Phosphorus exists in two forms in soil: first as inorganic phosphorus which includes insoluble mineral compounds which are mostly formed after application of chemical fertilizers and second type as organic phosphate compounds which form major pool of bound P constituting 20–80% of total P in soil (Richardson 1994).

(a) Mineral phosphate solubilization

Mineral phosphate solubilization involves action of various organic acids secreted by soil microorganisms. The organic acids acidify the surrounding medium resulting in low pH, as a result, phosphorus may be released from mineral phosphates by proton substitution for Ca^{2+} (Goldstein et al. 1993). Various organic acids are known to be produced by various phosphate-solubilizing microorganisms, and among them, gluconic acid has been documented to be the most significant agent of mineral phosphate solubilization (Rodriguez and Fraga 1999). Another organic acid identified in PSB strains is 2-ketogluconic acid, found in *Rhizobium leguminosarum*, *Rhizobium meliloti*, and *Bacillus firmus* (Banik and Dey 1982; Halder et al. 1990; Halder and Chakrabartty 1993). Various other organic acids, such as citric, glycolic, oxalic, and succinic acid, have also been identified in phosphate-solubilizing *Bacillus* strains (Mehta et al. 2014). Other mechanisms have also been considered, such as inorganic acid production, like sulphydric, carbonic, and nitric acid, and synthesis of various phosphorus chelating agents by rhizobacteria (Rodriguez and Fraga 1999).

(b) Organic phosphate solubilization

The mechanism of mineralization of organic phosphorus involves action of various phosphatases or phosphohydrolases. Soil organic matter is decomposed by saprophytic microorganisms, and the saprobes containing various phosphatases cause the release of radical orthophosphate from carbon skeleton of organic molecule in a hydrolysis reaction. The release of phosphorus involves breaking down of phosphoester bonds. Phosphatases are of two types depending upon their pH requirement for optimum catalytic activity: alkaline phosphatases work in an alkaline environment and acid phosphatases show optimum catalysis at acidic pH. This organic phosphate solubilization by microbes is greatly influenced by different environmental factors; more particularly, slightly alkaline conditions favor the solubilization of organic phosphorus (Paul and Clark 1988).

3.6.2.3 Sequestering Iron by Rhizobacteria

Iron is one more essential nutrient for plants besides nitrogen and phosphorus. It serves as a cofactor in enzymes involved in various physiological processes such as nitrogen fixation, respiration, and photosynthesis. Iron is taken up by plants as ferric iron (Fe^{+3}), which readily reacts to form various oxides and hydroxides that cannot be utilized by the plants. Plants absorb iron for soil in two ways:

- Release low molecular weight organic compounds called siderophores which can chelate iron, and make it available to the plants.
- Plants absorb the complex formed between organic compound and ferric iron, where the iron is reduced and easily absorbed by the plants.

Iron can bind reversibly to various functional groups present in the siderophores. These iron transport siderophores are normally either hydroxamates or phenolates-catecholates. In these types of siderophores, the distance between various functional groups is optimal to bind iron. *Bacillus* and *Pseudomonads* are widely known to produce the siderophores, and among these pyoverdine and pyochelin are the most commonly produced siderophores by *Pseudomonads*. Besides iron nutrition, siderophores also provide protection from fungal pathogens (Glick 1995). They hamper the growth of fungal pathogens by limiting the iron availability to pathogen (generally fungi), since bacterial siderophores have more affinity to chelate iron than fungal siderophores.

3.6.3 Rhizobacteria as Rhizoremediators

Rhizobacterial communities are sensitive and can sequester heavy metals due to presence of various functional groups; therefore, they can be used in bioremediation of soil (Umrania 2006). Various communities of microbes have been known to treat metal-polluted soil, but the composition of microbes inhabiting these heavy metal-polluted soil is exactly not known. The rhizosphere, with high concentration of root exudates, is known to attract more bacterial genera compared to the bulk soil (Penrose and Glick 2001). The root exudates as well as metal pollutants in the rhizosphere are utilized as nutrients by rhizoremediating bacteria and in reverse, they facilitate the plant growth by various mechanisms. The bioremediating PGPRs treating various heavy metals are given in Table 3.2.

Table 3.2 Bioremediation of heavy metals by PGPR

Bacteria	Plant	Heavy metal	Function	References
Kluyvera ascorbata	Indian mustard, tomato, canola	Lead, nickel, zinc	Decreased plant growth inhibition by heavy metals	Burd et al. (2000)
Azotobacter chroococcum	*Brassica juncea*	Lead, zinc	Stimulated plant growth and protected from metal toxicity	Wu et al. (2006)
Bacillus subtilis	*Brassica juncea*	Nickel	Facilitated nickel accumulation	Zaidi et al. (2006)
Aeromonas aquarium, *Pseudomonas composti*, and *Bacillus* sp.	*Spartina densiflora*	Different heavy metals	High PGP activities and resistance to heavy metals	Moreno et al. (2014)

The main problem associated with bacterial soil bioremediation system is that the process is effective under in situ conditions, but fails under ex situ remediation of the bulk soil, where their mechanism of action involves metabolism of soil pollutants. The other bottleneck of this technology is that the microorganisms starve very soon, and thus they are inept for bioremediation in the long run (Bottiglieri and Keel 2006). This can be overcome by separating the energy required in microbial metabolism from that required to remediate the pollutants. For this, a method has been developed in which rhizobacteria involved in rhizoremediation utilize the root exudates as primary source of nutrients. One of these methods includes the use of *P. putida* PCL1444 in rhizoremediation by Kuiper et al. (2001). The strain depends upon root exudates as primary source of nutrients and simultaneously degrades naphthalene in the rhizosphere.

3.6.4 Improvement of Plant Resistance to Pathogen Infection

Improvement of plant resistance to pathogens through one or more mechanisms of biocontrol is one of the aspects of indirect plant growth promotion by rhizobacteria. The use of microorganisms as biocontrol agents is an environment-friendly approach.

3.6.4.1 Mechanisms of Biocontrol

PGPR provide resistance to plant diseases through various mechanisms (Fig. 3.2), such as production of different antibiotics, viz., pyocyanin, phenazine, 2,4-diacetylphloroglucinol, iturin, surfactin, and fengycins; production of siderophores, HCN, and hydrolytic enzymes; and competition for nutrients and space (Elad and Chet 1987; Defago et al. 1990; Pierson and Thomashow 1992; Velazhahan et al. 1999). The brief accounts of important mechanisms involved in biocontrol are given in Table 3.3.

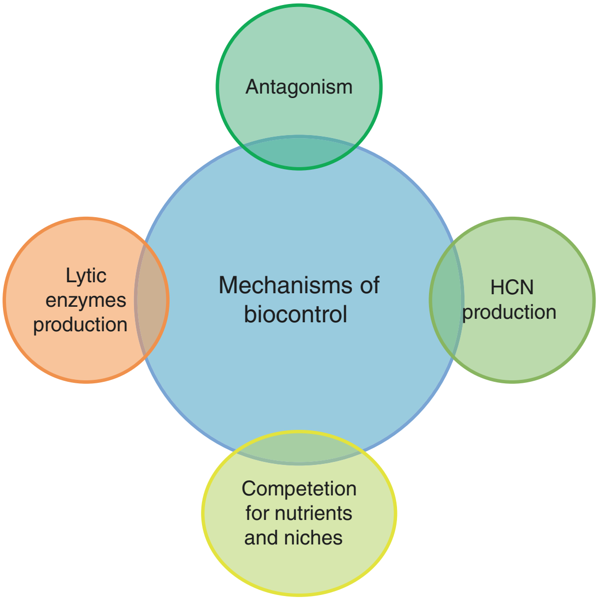

Fig. 3.2 Mechanisms of biocontrol by rhizobacteria

Table 3.3 Mechanisms involved in biocontrol of plant diseases

Method	Mechanism	Examples
Antagonism by rhizobacteria	The rhizobacteria produce various antibiotics which can kill pathogens. Some of these either act upon cell membrane or interfere with metabolic processes. To be a suitable biocontrol agent, the bacteria must release the antibiotics, in the right place around the root surface at the right time	Phenazines, 2,4-diacetylphloroglucinol, and pyoluteorin by *Pseudomonas* spp. (Mavrodi et al. 2006; Thomashow and Weller 1996; Nowak-Thompson et al. 1999); zwittermycin A by *Bacillus* (Emmert et al. 2004); fengycin, iturin, and surfactins by *Bacillus subtilis* (Kim et al. 2010)
HCN production	It is a secondary metabolite produced by the rhizobacteria and negatively influences the plant growth and root development. HCN acts as an inhibitor of electron transport chain at cytochrome oxidase complex and acts as an environment-friendly mechanism of biocontrol of weeds. Besides this, HCN is synthesized by various organisms such as bacteria, fungi, algae, insects, and plants as a mean to avoid predation	HCN production by *Pseudomonas fluorescens* resulted in inhibition of fungal pathogens such as *Pythium ultimum* and *Rhizoctonia solani* in sugar beet rhizosphere (Nelson et al. 2002); HCN-producing *Pseudomonas fluorescens* strain resulted in reduced root and shoot growth of weeds in rye, barley, and wheat rhizosphere (Ramette et al. 2003)
Lytic enzyme production	Enzymes are the biocatalysts produced generally by microorganisms, differing from other catalysts, and comprise the tools which determine the course of the multitude of life processes. Various hydrolytic enzymes are produced by rhizospheric microorganisms such as chitinases, proteases, cellulases, and β-1,3-glucanases that lyse various components of fungal cell wall which contributed to the antagonistic behavior of these microbes	A strain of *Pseudomonas* produced chitinase against pathogenic *Rhizoctonia solani* which hydrolyze the cell wall and reduced the disease development (Radjacommare et al. 2004); *Paenibacillus* strains releasing cell wall-degrading enzymes such as chitinases, cellulases, and β-1,3-glucanases were found to inhibit various bacterial and fungal pathogens (Von der Weid et al. 2000)
Competition for nutrient and space	Competition of beneficial rhizobacterial strains with phytopathogens for nutrition and space in the rhizosphere has been accounted as a biocontrol mechanism, and these competitively advanced strains can be effectively utilized to combat the pathogens	A mixture of competitive root-colonizing strains was applied to the seedlings and showed better growth in response to aggressive root colonization as compared to moderate colonizer *P. fluorescens* WCS365 (Spaink et al. 1998)

3.7 Manipulation of Rhizosphere Microbiome

Microbes form the most important module in the rhizosphere, and the composition of rhizobacterial communities greatly influences the plant-soil environment. The rhizobacterial community structure and its distribution greatly affect the plant growth. Hence, in order to enhance the population of helpful native or foreign soil microbes that enhance plant growth directly or indirectly, there is a need to develop efficient methods to alter the rhizosphere. Since the rhizosphere is a complex habitat, so efforts can be made to generate suitable environment for maximum plant growth by soil amendments, engineering improved plants and redirecting plant-microbe interactions. Rhizosphere microbiome is greatly affected by soil type and plant genotype, and plants are known to employ their unique members in rhizosphere microbiome. For example, malic acid release in root exudates stimulates the growth of beneficial *Bacillus subtilis* in plant rhizosphere (Rudrappa et al. 2008). Nonetheless, several metabolites acting as chemoattractants for useful microbes can also stimulate seed germination and growth of phytopathogens. For example, isoflavones exuded from soybean roots not only attract the symbiotic bacterium *Bradyrhizobium japonicum* but also stimulate the growth of phytopathogen *Phytophthora sojae* (Morris et al. 1998).

Soil is a multifaceted and diverse environment, which regulates physiology and metabolism in plants, accumulation of rhizodeposits, and community structure of rhizosphere microbiome in tandem. Various techniques have been advised to manipulate the rhizobacterial community structure and redirecting their metabolic activities in soil.

3.7.1 Manipulation by Introducing or Stimulating Microorganisms

The most direct methods to manipulate the rhizosphere microbiome include (1) introduction of one or more useful microbes in soil, on seeds or plant materials, and (2) stimulating indigenous beneficial rhizospheric population by soil and plant management practices. In spite of the fact that root colonization by beneficial microbes is still poorly understood, soil microbiologists and agronomists have been trying to alter the rhizosphere microflora by introducing selected beneficial microbial strains, either by coating seeds with inoculum or by placing the inoculum into the soil in close proximity to the seeds and seedlings. Numerous plant growth-promoting rhizobacterial strains have been inoculated into bulk soil to boost up the growth of crop plants (Bhattacharyya and Jha 2012). Introduction of other beneficial strains in order to protect the host plant from various phytopathogens can also result in alteration of rhizospheric microbiome. Small-scale inoculation of a biocontrol agent for short time interval is not sufficient to completely remove the pathogen as if the treatment is stopped very early, the pathogen can recover and reestablish again in the environment. Hence, the inoculated strain should multiply and aggressively colonize the rhizosphere to achieve a cell density above than the threshold value in a particular time to give maximum benefits to the host plant. Instead of single-strain inoculum, the use of multi-strain consortia with synergistic plant growth-promoting potential may prove more beneficial to overall plant growth and disease resistance (Bakker et al. 2012).

3.7.2 Soil Sterilization and Application of Specific Compounds

In soil sterilization, heating, drying, and irradiation are used. Sterilization is also achieved by fumigation using certain chemicals like chloroform, chloropicrin, methyl bromide, or carbon sulfide. These treatments resulted in improved plant growth even in the absence of phytopathogens (Rovira 1976). These beneficial effects can be attributed to chemical modifications like increase in ammonia content; organic matter decomposition, including dead microorganisms; recolonization of soil by non-pathogenic microbes, especially *Bacillus* and *Pseudomonas* which are known to stimulate plant growth (Ridge 1976); and elimination of nitrifying bacteria, which are particularly susceptible to soil fumigation (Jenkinson and Powlson 1976).

Among the different types of inhibitors that have been known, nitrification inhibitors are considered most important due to their possible use in the field. Inhibitors such as 2-chloro-6-(trichloromethyl)-pyridine have been successfully used to inhibit nitrification, thereby increasing the use efficiency of nitrogen fertilizers by reducing denitrification and leaching loss of nitrate ion. Unfortunately, in tropical areas, the inhibitors are readily decomposed by the soil microbes so that nitrification occurs even before plant requirements for nitrogen are at their peak. Another reason for the limited use of nitrification inhibitors is their high price. Although some low-cost substitutes have been proposed, such as neem cake, but these are not much effective as 2-chloro-6-(trichloromethyl)-pyridine (Prasad and De Datta 1978). The stimulation of a particular component of the microflora can also be achieved by adding their specific substrate to the soil. A classic example is that of the selective multiplication of amylase-producing bacteria in a soil amended by starch (Madhav et al. 2011).

3.7.3 Soil Management and Fertilization

Inoculation of soil even with specific microorganisms, like *Rhizobium*, is unsuccessful when one or more limiting environmental factors are still operating in the soil microenvironment. Therefore, improving environmental conditions is a prerequisite that can be successfully achieved by various soil management techniques, such as applying of organic inputs, irrigation, liming, or slow release from mineral fertilizers.

The whole rhizospheric environment is a function of various interactions as well as competing processes that are defined by soil type, moisture level, and metabolic and physiological activities of root-associated microorganisms and host plant.

Farmers manipulate physical and chemical environment around the roots of their crop plants during the irrigation or at the time of application of organic and chemical fertilizers. Nitrate-based fertilizers increase the alkalinity in rhizosphere, whereas ammonium-based fertilizers tend to acidify the rhizosphere. These changes in the soil pH alter the soil chemical environment which affect the plant growth and can alter soil chemistry around plant roots and influence the growth as well as composition of rhizosphere microbiome.

3.7.4 Manipulating the Rhizosphere Microbiome Using Biotechnological Approaches of Plant Breeding and Genetic Engineering

Numerous approaches have been developed to manipulate and redirect the composition and activities of rhizospheric microorganisms. Various root exudates are involved in attracting phytopathogens and activation of their virulence factors. Therefore, it is important to alter the quality as well as quantity of root exudates via genetic engineering which alters the structure of rhizosphere microbiome. More long-standing alterations in the rhizosphere that carry along the plant growth cycle can be generated using biotechnological approaches. In this type of approach, the plants with superior rhizospheric traits are selected, and these traits are further included into the breeding line that resulted in significant alterations in the rhizosphere. The identification of useful, heritable, and easily detectable traits is a prerequisite for successful breeding program to alter the rhizosphere. Although our knowledge about rhizospheric interactions and communications is increasing day by day, studies regarding engineering of rhizosphere through breeding program for improvement of rhizosphere-associated characters are still lacking (Wissuwa et al. 2009). At present, no breeding plan is available for evaluation of multidimensional interactions between plant and rhizosphere microbiome (Bakker et al. 2012). Gene loci linked to the resistance against *Pythium torulosum* were identified among various phenotypic variants of recombinant inbred lines of tomato (Smith et al. 1999). The study revealed that genetic variations within host plants can be utilized for the improvement of positive interactions between rhizosphere, microorganisms, and plants.

Genetic engineering is a more efficient process to manipulate the rhizosphere compared to conventional breeding programs. Previously, the process of genetic engineering has been employed to alter various rhizospheric factors such as pH and organic and inorganic ion effluxes (Gevaudant et al. 2007; Li et al. 2005). Besides this, plants are engineered to secrete specific signal compounds that attract a unique group of microbes, thus revealing that plants communicate with rhizosphere microbiome. For example, potato plant engineered to show high expression of lactonase gene interferes with bacterial quorum-sensing signal and showed increased resistance to pathogenic bacteria *Pectobacterium carotovorum*. Genetically engineered potato plants showing higher production of 5-*O*-glucosyltransferase and pectate lyase also showed increased resistance toward *Pectobacterium carotovorum* (Dong et al. 2001; Wegener 2001; Lorenc-Kukula et al. 2005).

3.8 Conclusion and Future Perspectives

The role of rhizosphere microbiome to execute and maintain the plant ecosystem is well established, but the conventional techniques used to understand their function in the rhizosphere are still not sufficient. Furthermore, for the enormous majority of microorganisms in the rhizosphere, no knowledge exists. Therefore, combining conventional methods with highly advanced next-generation sequencing techniques will strengthen our understanding about microbial community structure and function in the rhizosphere environment. Unraveling new plant signal molecules and root exudates in the root environment will make available biochemical as well as microbial markers to reveal that how beneficial microbes are being recruited and stimulated by the plants in rhizosphere. Exploring the rhizosphere microbiome also holds great potential to discover plentiful but previously unidentified soil microbes, their functioning, and mining of genes for various applications.

Various effective strategies should be designed to alter the rhizosphere microbiome in a way to favor the growth of antagonistic microorganisms that prevent the growth of devastating phytopathogens in soil. Among few possible approaches are plant breeding and genetic engineering programs; those are directed to investigate the molecular mechanism involved in plant-microbe interactions in the rhizosphere. Breeding of tomato using QTL mapping to incorporate characters supporting growth of favorable microbes in soil (Smith et al. 1999) and genetic modification of potato for expression of lactonase gene product interfering with bacterial quorum-sensing phenomenon and showing increased resistance toward *Pectobacterium carotovorum* (Dong et al. 2001) have given a remarkable success in this.

A lot of work is still required to be done in the future, to completely understand the structure and function of rhizosphere microbiome. Less than 5% of total soil bacterial and fungal population is culturable, and the rest of the vast population is still not culturable. Therefore, it is challenging to understand the functioning of noncultivable microbial population in rhizosphere. Their function to alter the rhizosphere and response to external environment is poorly understood. Moreover, there are many unexplored species of rhizospheric bacteria and fungi having explicit role in biofertilization, biostimulation, and phytoprotection, but they until now are still unidentified. Lastly, global climate change has also an impact on structure and function of microbial species in rhizosphere microbiome. To decipher the extent of climate change on rhizosphere microbiome is still to be explored.

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