

# Chapter 1

## Diversity, Plant Growth Promoting Attributes, and Agricultural Applications of Rhizospheric Microbes



**Gangavarapu Subrahmanyam, Amit Kumar, Sosanka Protim Sandilya, Mahananda Chutia and Ajar Nath Yadav**

**Abstract** Rhizosphere harbors potential microbiomes which play a pivotal role in nutrient cycling, enhancing soil fertility, maintaining plant health and productivity. Specific microbiomes that are assembled near roots are considered to be some of the most complex ecosystems on the Earth. Heterogeneous microbial communities of rhizospheric microbiomes considerably vary by soil type, land use pattern, plant species, and host genotype. It is demonstrated that root exudates act as substrates and signaling molecules which are required for establishing plant–rhizobacterial interactions. The present chapter focused on the rhizosphere microbiomes of different agricultural crops, their functions, and possible biotechnological applications for increasing crop production in a sustainable manner. Further, the plant growth-promoting mechanisms of rhizobacteria were highlighted. Although much work has been done on the biocontrol characteristics of rhizospheric bacteria, it has to be considered that soil type, plant species, and the pathogen affect altogether influence the biocontrol efficiency of strain applied against a soil-borne pathogen.

**Keywords** Bacterial community · Biotechnological application · Microbiome · Plant growth promotion · Rhizosphere

### 1.1 Introduction

Soil microorganisms play a pivotal role in nutrient cycling, regulating soil fertility, maintaining plant health, and productivity (Wagg et al. 2014). Soil microbial communities are exceedingly complex and consist of various organisms such as bacteria, archaea, fungi, algae, and viruses. Most of these microorganisms largely utilize plant root-derived nutrients such as root exudates and secondary metabolites (Huang et al.

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2014). Rhizosphere microorganisms are component of microbiomes that assemble near plant roots. Rhizospheric microbiomes are considered to be some of the most complex ecosystems on Earth. It is estimated that one gram of soil contains more than 50,000 different microbial species, but majority of them are uncultivable in nature (Roesch et al. 2007a, b). Beneficial free-living rhizospheric bacteria are generally referred to as plant growth-promoting rhizobacteria—“PGPR”. Conceptually, “PG-PR” represents beneficial portion of rhizospheric microbiome and can have positive effect on both growth and development of plants by direct or indirect mechanisms.

Chemical compounds that are released by roots apparently modify physical and chemical characteristics of the soil (Mukherjee et al. 2018) and subsequently regulates the diversity and composition of soil microbial community in the rhizosphere (Huang et al. 2014). Moreover, plants may also influence composition of rhizosphere microbial communities by selectively stimulating microorganisms with beneficial traits that are needed for both plant growth and health (Chaparro et al. 2014). For example, *Acidobacteria*, *Proteobacteria* (mainly *Alpha*, *Beta*, and *Deltaproteobacteria* classes), *Chloroflexi*, and *Actinobacteria* are enriched in the rhizosphere of *Oryza sativa*, whereas soybean selected a specific microbial community consists of *Bacteroidetes*, *Acidobacteria*, *Proteobacteria*, and *Actinobacteria* (Lu et al. 2018; Ding et al. 2019; Yadav et al. 2016b). These microbial populations are found to colonize in the root rhizosphere because of their functional traits and also beneficial to plant nutrient absorption, growth, and disease suppression. In turn, the plant provides root exudates to the microbes which are used as substrates and signaling molecules (Mendes et al. 2013).

Studies revealed that root microbiomes considerably vary by soil type, habitat, land use pattern, plant species, and host genotype (Bouffaud et al. 2014; Fitzpatrick et al. 2018; Lu et al. 2018; Ding et al. 2019; Yadav et al. 2019f). In recent, the relationship between rhizosphere microbial communities and plant genotypes is well studied and the results may lead to increased plant productivity (Bouffaud et al. 2014; Bulgarelli et al. 2015; Pérez-Jaramillo et al. 2017; Leff et al. 2017; Ding et al. 2019). In this chapter, we summarize recent progress made in rhizosphere microbiomes of agriculture crops. We also discuss the importance of rhizosphere microbial communities particularly PGPR and their immense biotechnological values for sustainable production and productivity of agriculture crops.

## 1.2 Rhizosphere and Root Exudates

The narrow zone of soil surrounding the plant roots and influenced by roots, root hair, and plant-produced exudates is referred to as rhizosphere (Dessaux et al. 2009). There are three distinct interacting systems which are reported in the plant rhizosphere, *viz.*, rhizoplane, rhizosphere, and the root itself. Rhizoplane is defined as the root surface including the strongly adhering soil particles. Group of bacteria which are inhabitants of rhizosphere and able to compete in colonizing the root system is known as “rhizobacteria” while the total microbial component (prokaryotes, eukaryotes, and

viruses) of rhizosphere is termed as rhizo-microbiome or rhizosphere microbiome. The “rhizobacteria” term was first time introduced by Kloepper and Schroth (1978) to refer the soil bacterial population that competitively colonize the roots and stimulate plant growth, thereby reducing the incidence of diseases in a sustainable manner.

Specific microbiomes that are assembled near roots are proposed to be some of the most complex ecosystems on the Earth (Raaijmakers et al. 2009). Most of these microorganisms utilize diverse array of compounds/nutrients which are derived from plant roots in the rhizosphere (Lu et al. 2018; Yadav et al. 2017b). The chemicals that are released by roots in the soil are known as “root exudates.” It was suggested that chemicals secreted by plant roots act as signaling molecules and recruit wide variety of heterogeneous and metabolically active soil microbial populations (Ahemad and Kibert 2014) (Table 1.1).

Most importantly, the exudation of chemical compounds by roots apparently modifies the physical and chemical characteristics of the soil and subsequently regulates the structure and composition of rhizosphere microbial community (Doornbos et al. 2012). Impact of root exudates on bacterial communities in the rhizosphere was extensively reviewed by Doornbos et al. (2012). Further, it is estimated that around five to twenty-one percent of carbon (photosynthetically fixed carbon) gets transported to the rhizosphere through the process of root exudation (Doornbos et al. 2012). Therefore, the rhizosphere is redefined by Dessaux et al. (2009) as “any volume of soil selectively influenced by plant roots, root hairs and plant-produced materials.”

**Table 1.1** Different kinds of compounds in root exudates of plants

Chemical nature	Compounds
Carbohydrates, amino acids, and derivatives	Chlorogenic acid, caffeic acid, cinnamic acid, canavanine, strigolactone 5-deoxystrigol, arabinogalactan proteins, arabinogalactan-like glycoprotein, glucose, fructose, galactose, ribose, xylose, rhamnose, arabinose, oligosaccharides, raffinose, maltose, $\alpha$ -Alanine, $\beta$ -alanine, asparagines, aspartate, cysteine, cystine, glutamate, glycine, isoleucine, leucine, lysine, methionine, serine, threonine, proline, valine, tryptophan, ornithine, histidine, arginine, homoserine, phenylalanine, $\gamma$ -Aminobutyric acid and $\alpha$ -Aminoadipic acid
Secondary metabolites and hormones	Benzoxazinoids, flavonoids, strigolactones, and related compounds that mimic quorum-sensing signals
Vitamins	Biotin, thiamine, pantothenate, riboflavin, and niacin
Enzymes	Protease, amylase, acid and alkaline-phosphatase and invertase
Organic acids	Malic acid, oxalic acid, fumaric acid, succinic acid, acetic acid, butyric acid, valeric acid, glycolic acid, erythronic acid, piscidic acid, citric acid, formic acid, aconitic acid, lactic acid, pyruvic acid, glutaric acid, malonic acid, tetric acid, and aldonic acid

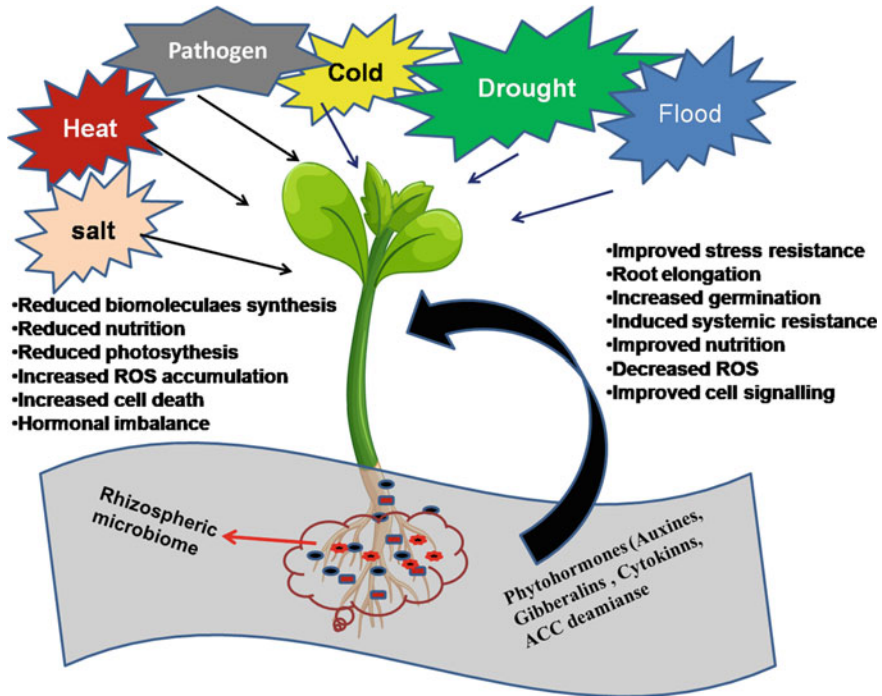
Source Huang et al. (2014), Ahemad and Kibert (2014)

The quality and quantity of the root exudates rely on type of plant species and distinct developmental/physiological status of plants (Kang et al. 2010). Furthermore, root exudates significantly enhance the plant-beneficial microbial–symbiotic interactions in the rhizosphere. These interactions, in turn, affect the rooting patterns, supply of available nutrients, thereby modifying the quantity and/or quality of root exudates. Microbial colonization in/on root tissues is known as root colonization, similarly microbial colonization of the adjoining volume of soil under the influence of the plant root system is defined as “rhizosphere colonization” (Ahemad and Kibert 2014). Compared with the bulk soil, microbial activity and biomass are relatively enhanced in the rhizosphere as a result of root exudation (Ahemad and Kibert 2014; Huang et al. 2014).

### 1.3 Rhizosphere Microbiome and Its Diversity

Most of the soils contain exceedingly high microbial diversity including bacteria, fungi, algae, viruses, and protozoa. It was reported that one gram of soil contains approximately  $9 \times 10^7$  bacteria,  $2 \times 10^5$  fungi,  $4 \times 10^6$  actinomycetes,  $5 \times 10^3$  protozoa, and  $3 \times 10^4$  algae. The rhizosphere which is under influence of root exudates can harbor up to  $10^{-11}$  microbial cells and around 30,000 different prokaryotic species per gram of root (Egamberdieva et al. 2008). Metagenomic analysis of tomato rhizosphere revealed that approximately 3,050 different bacterial species (OTUs at 3% distance cutoff) were associated in the rhizosphere (Tian et al. 2015). The rhizosphere microbiomes are very diverse and can actively interact with plants and mediate distinct agro-ecological process. The rhizosphere microbiome is considerably important in bridging the plant microbiomes and bulk soil and facilitates plant growth promotion by providing nutrition (Pathak et al. 2016). The rhizobacterial microbiota also improves host plant's health by protecting from phytopathogens and promotes plant growth and fitness in different physiochemical stresses by producing phytohormones (Fig. 1.1). It is imperative to elucidate the assembly, composition, and variation among the microbial communities present in the rhizosphere for understanding the diversity and metabolic functions of the rhizosphere microbiome. This information could be beneficial for sustainable management of plant health and the underlying mechanisms that drive microbiome assembly.

It has been revealed that the rhizosphere, rhizoplane (root surface), endosphere (root interior), and of host plants harbor a distinct microbiome (Edwards et al. 2015). Diversity, distribution, and the composition of the core rhizospheric microbiomes from several plant species such as *Arabidopsis* (Bulgarelli et al. 2012; Carvalhais et al. 2013; Chaparro et al. 2014), and economically important crops, viz., maize (Bouffaud et al. 2014), rice (Edwards et al. 2015; Malyan et al. 2016a, b; Lu et al. 2018; Moronta-Barrios et al. 2018; Ding et al. 2019), barley (Bulgarelli et al. 2015), citrus (Xu et al. 2018), sugar beet (Chapelle et al. 2016), sunflower (Leff et al. 2017), tomato (Tian et al. 2015), French bean (Pérez-Jaramillo et al. 2017), soybean (Mendes et al. 2011, 2014), wheat (Kour et al. 2019d; Verma et al. 2015a,

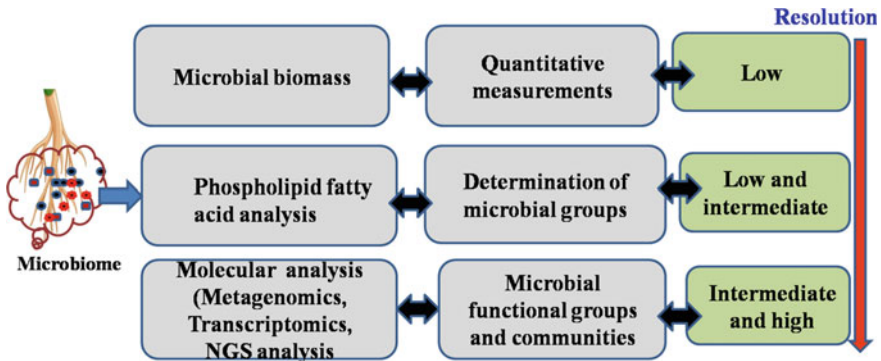


**Fig. 1.1** Amelioration of abiotic and biotic stresses in plants by phytohormones produced by rhizospheric microbiome

b, 2016a, b; Yadav 2017a, 2019), and other tropical crop plants (Yadav 2017a, b; Yadav et al. 2019a; Yadav and Yadav 2018) have been established. All these studies have utilized 16S rRNA gene-based high-throughput sequencing analysis for understanding the microbial community dynamics. Although different methodologies have been suggested to explore soil microbial diversity and functions, culture-independent molecular methods are appropriate choice for deciphering diversity of microbiomes in high resolution (Fig. 1.2). Dominant microbial communities and their functions in core rhizospheric microbiomes of different agricultural crops have been extensively summarized in Table 1.2.

### 1.3.1 Diversity of Rhizospheric Microbiome in Wild Plants

Microorganisms represent the richest gamut of molecular and chemical diversity in nature, as they comprise the simplest yet dynamic forms of life (Yadav et al. 2015). Interest in the exploration of microbial diversity has been spurred by the fact that microbes are essential for life as they perform numerous functions integral to the



**Fig. 1.2** Different methods for elucidation of rhizospheric microbiomes assembly and activity. Molecular methods are preferable choice to establish microbial communities with a higher resolution

sustenance of the biosphere, including nutrient cycling and environmental detoxification, which involve process such as augmentation, supplementation, and recycling of plant nutrients, so vital to sustainable agriculture (Kumar et al. 2019; Malyan et al. 2019; Rana et al. 2018; Yadav et al. 2017a, c, d). More recently, this largely unexplored reservoir of resources is the focus of investigations for innovative applications useful to mankind (Rastegari et al. 2019; Yadav et al. 2019c, d, e).

The distribution and diversity of bacterial community compositions in the rhizosphere microbiomes of six different wild plant species (*Bidens biternata* of the Asterales order, *Ageratum conyzoides*, *Artemisia argyi*, *Euphorbia hirta*, *Viola japonica* of the Malpighiales order, and *Erigeron annuus*) were evaluated by Lei et al. (2019). All the six different wild plant species were grown in the same experimental field. In this study, high-throughput sequencing of 16S rRNA gene targeting the hypervariable V3 and V4 regions was carried out with Illumina MiSeq platform. Comprehensive details for composition and distribution of rhizospheric microbiomes of wild plants have been shown in Fig. 1.2.

Approximately, 3000 OTUs for each rhizosphere sample were obtained. Rhizosphere microbiomes in the six wild plant species were dominated by bacterial phyla Proteobacteria (35%), Acidobacteria (12%), Actinobacteria (11%), Bacteroidetes (10%), Planctomycetes (8%), Chloroflexi (6%), and Verrucomicrobia (6%) and the details have been shown in Fig. 1.3a, b, c, d. *Rhizobiales* (8%) and *Sphingomonadales* (3.5%) orders of class Alphaproteobacteria (15%); *Nitrosomonadales* (4.28% ± 1.24%), and *Burkholderiales* (3%) orders of class Betaproteobacteria (9%); *Myxococcales* (5.5%) order of class Deltaproteobacteria (8%); and *Xanthomonadales* (4%) orders of class Gammaproteobacteria (7%) were found to be abundant in phylum Proteobacteria (Fig. 1.3a). Abundant members of phylum Actinobacteria were found to be Acidimicrobiales (4%). Similarly, Subgroup 4 (6%) and Subgroup 6 (4%) were abundant in Acidobacteria phylum.

The core rhizospheric microbiome of wild plant species showed a total of 1,109 operational taxonomic units (OTUs) affiliated to 113 bacterial genera accounting

**Table 1.2** Diversity and functions of rhizosphere microbiomes in different agricultural crops

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
<i>Phaseolus vulgaris</i>	Significant associations between rhizobacterial community composition, crop genotype, and specific root phenotypic traits were reported	<i>Bacteroidetes</i> and <i>Verrucomicrobia</i> in roots of wild beans; <i>Actinobacteria</i> and <i>Proteobacteria</i> were enriched on roots of modern bean accessions	Growth and health of common bean	Pérez-Jaramillo et al. (2017)
<i>Hordeum vulgare</i>	Host genotype has a significant effect on the diversity of root-associated bacterial communities	<i>Comamonadaceae</i> , <i>Flavobacteriaceae</i> , <i>Rhizobiaceae</i>	Traits related to pathogenesis, phage interactions, and nutrient mobilization are enriched in the barley root-associated microbiota	Bulgarelli et al. (2015)
<i>Arabidopsis thaliana</i>	Soil type defines the composition of root-inhabiting bacterial communities. Host genotype determines specific bacterial groups in microbiome of rhizosphere. Plant cell wall features serve as sufficient colonization (up to 40%) of root-associated microbiota	<i>Proteobacteria</i> , <i>Bacteroidetes</i> , <i>Actinobacteria</i> , <i>Acidobacteria</i> , <i>Planctomycetes</i>	Growth, health, and crop domestication	Bulgarelli et al. (2012)

(continued)

Table 1.2 (continued)

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
<i>Arabidopsis thaliana</i>	Jasmonic acid plant defence pathway may mediate plant–bacteria interactions in the soil and alters the composition of rhizosphere bacterial communities	<i>Bacillales</i> sp., <i>Bacillus</i> sp., <i>Planococcaceae</i> sp., <i>Lysinibacillus</i> sp., <i>Pseudomonas</i> sp.,	Induced systemic resistance (ISR)	Carvalhais et al. (2013)
<i>Beta vulgaris</i>	Invading pathogenic fungus and plant stress responses directly influence the shift in rhizobacterial community in microbiome composition	<i>Oxalobacteraceae</i> , <i>Burkholderiaceae</i> , <i>Sphingobacteriaceae</i> <i>Sphingomonadaceae</i>	Antagonistic traits that restrict pathogen colonization and infection	Chapelle et al. (2016)
<i>Helianthus annuus</i>	Plant-associated fungal communities are strongly influenced by host genetic factors than bacterial communities	<i>Nectriaceae</i> , <i>Olpidiaceae</i> <i>Mortierellaceae</i> , <i>unclassified Pleosporales</i> , <i>Preussia</i> spp., <i>unclassified Thelebolaceae</i> , <i>Fusarium</i> spp., <i>Conocybe</i> spp.	Native microflora may have symbiotic action	Leff et al. (2017)

(continued)



**Table 1.2** (continued)

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
<p><i>Poaceae</i> crops such as <i>Zea mays</i> L.; <i>Zea mays</i> ssp. <i>Parviglumis</i>; <i>Sorghum bicolor</i> cv. <i>Arprini</i>; (<i>Triticum aestivum</i> L. cv. <i>Fiorina</i>)</p>	<p>Bacterial community composition in the rhizosphere is different from that in bulk soil. Rhizobacterial community composition differed according to the <i>Poaceae</i> genotype. The extent of diversification of eukaryotic hosts can be a significant factor for selection of their associated bacterial compartment</p>	<p>Dominant members in the rhizospheric microbiome  <i>Rhodospirillales</i> such as <i>Azospirillum</i>, <i>Glucacetobacter</i>, <i>Rhodospirillum</i> <i>Sphingomonadaceae</i> (<i>Alphaproteobacteria</i>); <i>Burkholderiales</i> such as <i>Acidovorax</i>, <i>Alcaligenes</i>, <i>Burkholderia</i>, and <i>Hydrogenophaga</i> (<i>Betaproteobacteria</i>); <i>Francisella</i>, <i>Moraxella</i>, <i>Pantoea</i>, <i>Photobacterium</i>, <i>Pseudomonas</i>, and <i>Xanthomonas</i> (<i>Gammaproteobacteria</i>); <i>Myxococcales</i> such as <i>Anaeromyxobacter</i> (<i>Deltaproteobacteria</i>), (<i>v</i>) <i>Megasphaera</i>, <i>Mogibacterium</i>; <i>Bacillales</i> such as <i>Bacillus</i> and <i>Peanibacillus</i> (<i>Firmicutes</i>); <i>Collinsella</i>; and <i>Actinomycetales</i> such as <i>Actinomyces</i>, <i>Corynebacterium</i>, <i>Kocuria</i>, and <i>Propionibacterium</i> (<i>Actinobacteria</i>)</p>	<p>Normal growth and plant health</p>	<p>Bouffaud et al. (2014)</p>

(continued)

Table 1.2 (continued)

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
Citrus crop	Provided a comprehensive taxonomic and functional biogeographical analysis of the citrus rhizosphere microbiome	<i>Pseudomonas</i> , <i>Agrobacterium</i> , <i>Cupriavidus</i> , <i>Bradyrhizobium</i> , <i>Rhizobium</i> , <i>Mesorhizobium</i> , <i>Burkholderia</i> , <i>Cellvibrio</i> , <i>Sphingomonas</i> , <i>Variovorax</i> and <i>Paraburkholderia</i> , <i>Ascomycota</i> , <i>Fusarium</i> and <i>Hirsutella</i>	Nutrition acquisition and plant growth promotion	Xu et al. (2018)
<i>Amaranthus albus</i> , <i>Sonchus arvensis</i> , <i>Sisymbrium officinale</i> , <i>Medicago sativa</i> , <i>Solanum dulcamara</i> , and other 25 angiosperm plant species	Evolutionary divergence among host plant species affects the assembly of the endosphere and rhizosphere microbiome. This indicates that the potential role of host-associated microbial communities in mediating interactions between hosts and their biotic and abiotic environment	<i>Proteobacteria</i> , <i>Actinobacteria</i> , <i>Firmicutes</i> , <i>Verrucomicrobia</i> , <i>Bacteroidetes</i> , <i>Chloroflexi</i> , <i>Acidobacteria</i>	The root microbiome is associated with drought tolerance across host plant species	Fitzpatrick et al. (2018)
<i>Arabidopsis thaliana</i>	Different developmental stages of plant influence rhizosphere microbiome assemblage. Plant can select a subset of microbes at different stages of development, presumably for specific functions	<i>Acidobacteria</i> , <i>Actinobacteria</i> , <i>Bacteroidetes</i> , <i>Cyanobacteria</i>	Disease suppression	Chaparro et al. (2014)

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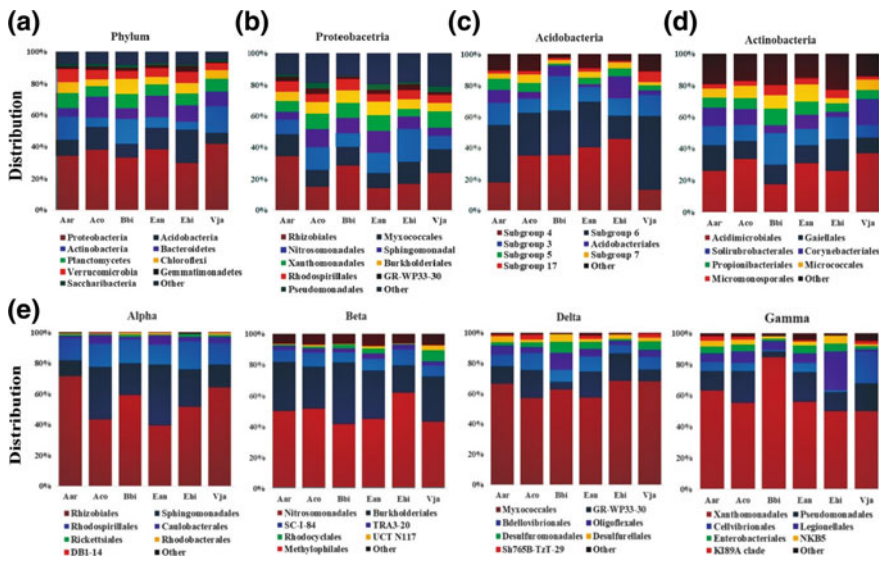
**Table 1.2** (continued)

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
<i>Oryza sativa</i>	Rhizosphere microbiome is shaped by soil- and plant-related conditions such as geographic location, soil type, rice genotype, oxic and anoxic interface, agricultural management and growth stages	<i>Proteobacteria</i> (mainly <i>Alpha-, Beta- and Deltaproteobacteria</i> classes), <i>Acidobacteria</i> , <i>Actinobacteria</i> and <i>Chloroflexi</i> phyla. <i>Archaeal</i> communities composed of <i>Crenarchaeota</i> , <i>Thaumarchaeota</i> and <i>Euryarchaeota</i> phyla	Growth promotion and disease inhibition	Ding et al. (2019), therein references
<i>Triticum aestivum</i> , <i>Hordeum vulgare</i> , <i>Oryza sativa</i> ( <i>indica and japonica</i> )	<i>Triticum aestivum</i> and <i>Hordeum vulgare</i> had shown much stronger selection effects than <i>Oryza sativa</i> for the rhizosphere microbial community	<i>Proteobacteria</i> , <i>Bacteroidetes</i> , <i>Acidobacteria</i> , <i>Planctomycetes</i> , <i>Nitrospirae</i> , <i>Actinobacteria</i> , <i>Verrucomicrobia</i> , <i>Firmicutes</i> , <i>Cyanobacteria</i> , <i>Chloroflexi</i> , <i>Gemmatimonadetes</i> , <i>Ascomycota</i> , <i>Basidiomycota</i> , <i>Zygomycota</i> , <i>Unidentified fungi</i>	Glycan, limonene, and pinene degradation; Nitrogen and sulfur metabolism; Plant growth promotion	Lu et al. (2018)

(continued)

Table 1.2 (continued)

Crop	Major findings on rhizospheric microbiome	Dominant members in the rhizospheric microbiome	Functions	References
<i>Solanum lycopersicum</i>	Nematode infections were associated with diversity and composition of rhizosphere bacterial populations in tomato plant roots. Root endophytes and rhizobacteria had significantly different community structures and species abundance	<i>Proteobacteria</i> , <i>Alphaproteobacteria</i> , <i>Sphingomonadales</i> , <i>Rhizobiales</i>	Degradation of plant polysaccharides; Carbohydrate and protein metabolism and biological nitrogen fixation	Tian et al. (2015)
<i>Glycine max</i> (L.)	Selection of the microbial community in the rhizosphere is based on niche-based processes as a result of the selection power of the plant and other environmental factors	phyla <i>Actinobacteria</i> , <i>Acidobacteria</i> , <i>Chloroflexi</i> , <i>Cyanobacteria</i> , <i>Chlamydiae</i> , <i>Tenericutes</i> , <i>Deferribacteres</i> , <i>Chlorobi</i> , <i>Verrucomicrobia</i> , and <i>Aquificae</i>	Growth promotion and nutrition	Mendes et al. (2014)



**Fig. 1.3** The composition and relative abundance of major bacterial taxa in a typical rhizosphere of six different wild plant species Adapted with permission from Lie et al. (2019)

for more than 70% of the total sequencing data analyzed. The predominant bacterial genera of core OTUs are *Variovorax*, *Acidibacter*, *Ferruginibacter*, *Bradyrhizobium*, *Blastocatella*, *Variibacter*, *Sphingomonas*, and unclassified bacteria (Fig. 1.3e). The predominant bacterial orders were found to be composed of *Xanthomonadales*, *Rhodospirillales*, *Rhizobiales*, *Burkholderiales*, *Sphingomonadales*, *Myxococcales*, *Nitrosomonadales* of Proteobacteria; *Acidimicrobiales* of Actinobacteria; *Subgroup 4* and *Subgroup 6* of Acidobacteria.

Variations in microbial community compositions at the order level in the rhizosphere of six different plant species were also demonstrated (Lei et al. 2019). Predominant bacterial group in *E. hirta* rhizosphere is Proteobacteria, while the same group is least represent in *V. japonica* microbiome. Highly enriched *Rhizobiales* order of Proteobacteria was found in *V. japonica* and *A. argyi*. Predominant members of *Myxococcales* were noticed in *V. japonica* rhizosphere. Abundant members of *Nitrosomonadales* were observed in *E. hirta*. Similarly, higher abundance of *Burkholderiales* and *Sphingomonadales* was noticed in *E. annuus*. Members of *Xanthomonadales* were dominated in *V. japonica* rhizosphere.

### 1.3.2 Diversity of Rhizospheric Microbiome in Agriculture Crops

#### 1.3.2.1 Rhizospheric Microbiome of Rice

The structure of microbial communities present in the rice rhizosphere is very complex, dynamic, and diverse (Edwards et al. 2015; Lu et al. 2018; Moronta-Barrios et al. 2018; Ding et al. 2019). Recently, microbiome inhabiting rice roots and rhizosphere is extensively reviewed by Ding et al. (2019). A study taken by Edwards et al. (2015) revealed that endosphere (inside the root compartment), rhizoplane (surface of the root), and rhizosphere of rice had distinct microbiomes. Microbial communities from the rice rhizosphere are established by amplification of the 16S rRNA gene (variable regions V4-V5) followed by high-throughput sequencing using the Illumina MiSeq platform (Edwards et al. 2015). Results indicate that rice endosphere microbial communities had the lowest  $\alpha$ -diversity, whereas rice rhizosphere had higher  $\alpha$ -diversity. Furthermore, the mean  $\alpha$ -diversity was found to be relatively high in the rhizosphere than in the bulk soil (Edwards et al. 2015).

The most dominant bacterial genera of rice rhizosphere is summarized in Fig. 1.4. Bacterial community profiles and their relative abundance are shown in Fig. 1.5 (Lu

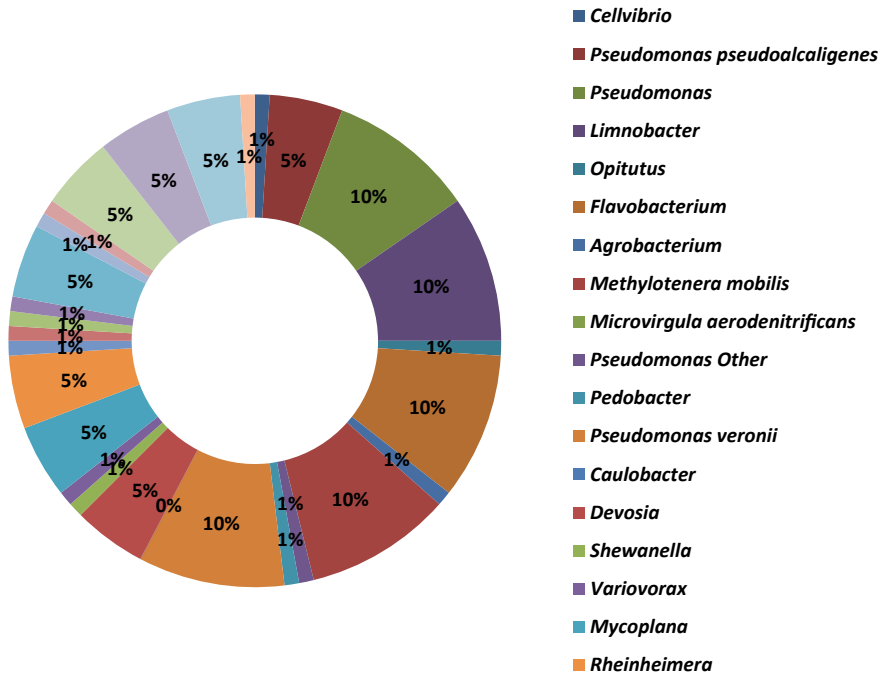
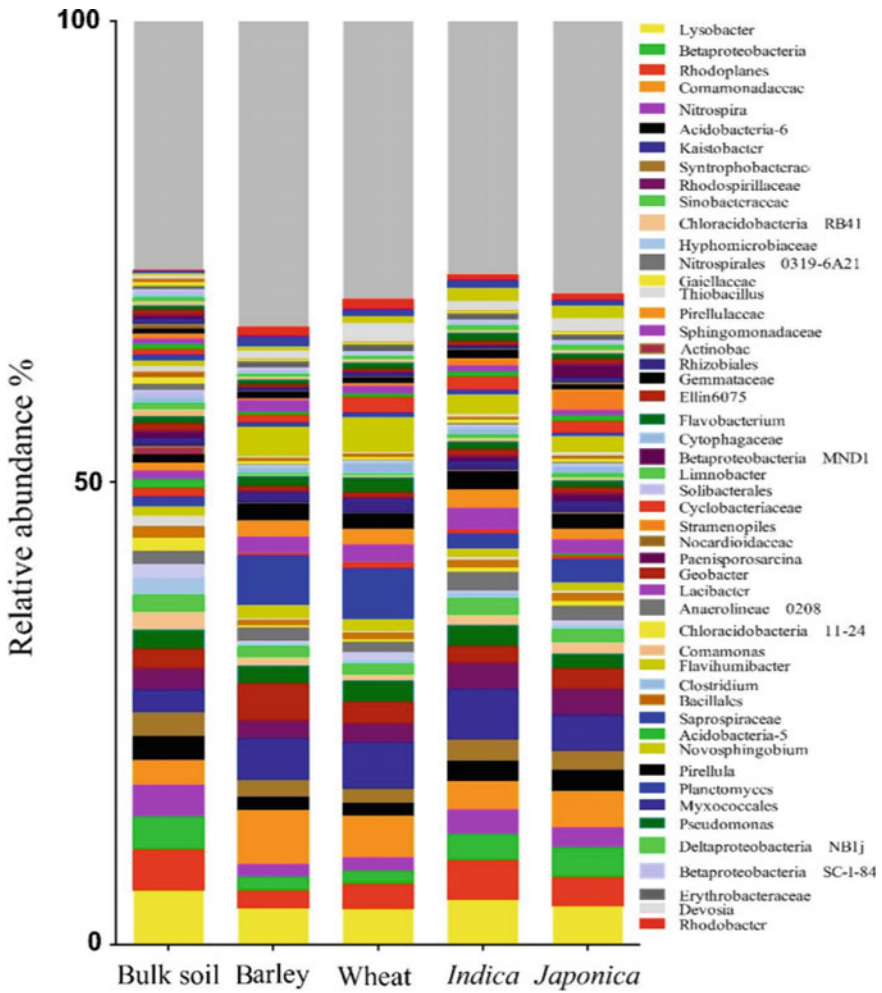


Fig. 1.4 Dominant bacterial genera in the rhizosphere microbiome of rice Adapted from Moronta-Barrios et al. (2018)



**Fig. 1.5** Bacterial community profiling in the rhizospheric microbiomes of *Hordeum vulgare* (Barley), *Triticum aestivum* (Wheat), *Oryza sativa* Indica and Japonica (Rice) Adapted with permission from Lu et al. (2018)

et al. 2018). Bacterial, archaeal, and fungal communities and their relative abundance in the rice rhizosphere have been studied (Ding et al. 2019). Bacterial populations were found to be abundant in the rice rhizosphere (Edwards et al. 2015). The abundance of rhizosphere microbial populations such as bacterial, fungal, and archaeal was twice those that of the bulk soil which is an indication of rhizospheric effect (Ding et al. 2019).

Proteobacteria dominated the microbiome of rice rhizosphere accounting more than 71%. Among Proteobacteria, the most abundant class was Gammaproteobacteria followed by Betaproteobacteria, Alphaproteobacteria, Deltaproteobacteria, and

*Epsilonproteobacteria* (Moronta-Barrios et al. 2018). Representatives of *Epsilonproteobacteria* and *Deltaproteobacteria* classes were not detected in the rice endorhizosphere. Phyla *Verrucomicrobia* and *Bacteroidetes* were abundant across the samples. Representative members of *Nitrospirae* and *Acidobacteria* were found only in rice-rhizospheric samples (Moronta-Barrios et al. 2018). Bacterial phyla *Proteobacteria*, *Firmicutes*, *Chloroflexi*, *Nitrospirae*, *Spirochaetes*, *Fibrobacteres*, *Planctomycetes*, *Bacteroidetes*, *Proteobacteria*, *Actinobacteria*, *Verrucomicrobia*, *Cyanobacteria*, and *Acidobacteria* are the most commonly found bacterial members of the rice rhizosphere (Edwards et al. 2015; Lu et al. 2018; Moronta-Barrios et al. 2018; Ding et al. 2019). Similarly, the most common bacterial genera of rice rhizosphere are as follows: *Pseudomonas* sp., *Limnobacter*, *Devosia*, *Opitutus*, *Flavobacterium*, *Shewanella*, *Caulobacter*, *Agrobacterium*, *Pseudomonas veronii*, *Methylothena mobilis*, *Microvirgula aerodenitrificans*, *Pedobacter*, *Rhodofera*, *Variovorax*, *Mycoplana*, *Rheinheimera*, *Flavisolibacter*, *Fluviicola*, *Chryseobacterium*, *Asticcacaulis*, *Halothiobacillus*, *Pleomorphomonas*, *Sphingobium*, *Thiobacillus*, *Bacillus* sp., *Flavobacterium gelidilacus*, *Methylophaga*, and *Acidovorax* (Moronta-Barrios et al. 2018). Further details on dominant microbial communities and their functions in rice-rhizospheric microbiomes have been summarized in Table 1.2.

Methanogenic archaea, viz., *Methanobacterium*, *Methanosarcina*, *Methanocella*, and *Methanosaeta* were also reported in the rice rhizosphere (Malyan et al. 2016a; Edwards et al. 2015). *Firmicutes*, *Bacteroidetes*, *Betaproteobacteria*, and *Chloroflexi* were found to be differentially enriched in rice rhizosphere. The *Betaproteobacterial* OTUs that are enriched in rice rhizosphere belong to mainly *Comamonadaceae* and *Rhodocyclaceae* families (Edwards et al. 2015). Total bacterial count of rice rhizosphere is approximately  $5 \times 10^9$  cells g dw<sup>-1</sup> soil, whereas as archeal members are found to be  $2.5 \times 10^8$  cell g dwt<sup>-1</sup> soil.

### 1.3.2.2 Rhizospheric Microbiome of Wheat and Barley

Rhizosphere community of wheat was analyzed by comparative metatranscriptomics approach (Hayden et al. 2018). The rhizosphere community of wheat was predominately bacteria. Classes *Gammaproteobacteria*, *Alphaproteobacteria*, and *Actinobacteria* were dominant in the rhizosphere of wheat and barley. Bacterial families such as *Micrococcaceae*, *Enterobacteriaceae*, and *Pseudomonadaceae* were abundant in the rhizosphere microbiomes (Hayden et al. 2018). Predominant archaeal members in the rhizosphere are affiliated to family *Nitrososphaeraceae* under phylum Thaumarchaeota. *Ascomycota* is the dominant fungal phylum found in the rhizosphere representing more than 72% of total fungal transcripts. Other fungal phyla in the rhizosphere of wheat and barley were affiliated to Basidiomycota (>10%), which includes the genus *Rhizoctonia*, and Glomeromycota (4%) form arbuscular mycorrhizae. Interestingly, fungal families represent a smaller proportion of the total microbial transcripts analyzed in the rhizosphere (Hayden et al. 2018). Rhizosphere



community of barley was reported by Lu et al. (2018). Bacterial phyla *Proteobacteria*, *Bacteroidetes*, *Acidobacteria*, *Planctomycetes*, *Nitrospirae*, *Actinobacteria*, *Verrucomicrobia*, *Firmicutes*, *Cyanobacteria*, *Chloroflexi*, and *Gemmatimonadetes* were associated with barley rhizosphere. Further, fungi *Ascomycota*, *Basidiomycota*, *Zygomycota*, and Unidentified fungi were distributed in the barley rhizosphere (Hayden et al. 2018).

### 1.3.2.3 Rhizospheric Microbiome of Soybean

Shotgun metagenomics approach was used to study functional and taxonomic diversities of microbial communities in the rhizosphere of soybean, *Glycine max* (L.) (Mendes et al. 2014). Metagenomic libraries were dominated by bacteria (>95%) followed by eukaryotes (3%) and archaea and virus (1%). *Proteobacteria* was found to be the most abundant phylum in soybean rhizosphere and represented around 47% distribution. Other dominant bacterial phyla in the rhizosphere of soybean were found to be *Actinobacteria* (23%), *Acidobacteria* (5%), and *Firmicutes* (6%) (Mendes et al. 2014). In general, 28% of total sequences found in the soybean rhizosphere were novel and were not affiliated to known bacterial taxa. Results indicate clear differences in microbial community structure among rhizosphere and bulk soil. Overrepresentation of the phyla *Acidobacteria*, *Actinobacteria*, *Chloroflexi*, *Chlamydiae*, *Cyanobacteria*, *Deferribacteres*, *Tenericutes*, *Chlorobi*, *Aquificae*, and *Verrucomicrobia* was found in rhizosphere and the results were significant at  $P < 0.01$  (Mendes et al. 2014). Similarly, abundance of class *Mollicutes*, *Bacilli*, *Clostridia*, *Epsilonproteobacteria*, *Gammaproteobacteria*, *Thermomicrobia*, and *Chlamydiae* was found in the rhizosphere of *Glycine max* (L.).

### 1.3.2.4 Rhizospheric Microbiome of French Bean

Microbiome of French bean was elucidated by amplification of 16S rRNA (V3–V4 region) followed by high-throughput sequencing performed at Illumina MiSeq platform (Pérez-Jaramillo et al. 2017). Phylum *Proteobacteria* was the dominant member, whereas lower abundance of *Acidobacteria* was noticed in wild bean rhizosphere. The phyla *Verrucomicrobia* and *Bacteroidetes* were predominant in the wild bean rhizosphere. Phylum *Actinobacteria* was found to be more abundant in the modern bean rhizosphere and these results were statistically significant.

Significant increase in the relative abundance of bacterial families *Sphingomonadaceae* and *Rhizobiaceae* was observed in the rhizosphere as compared to the bulk soil. Furthermore, it was noticed that there is a gradual decrease in the relative abundance of the *Chitinophagaceae* and *Cytophagaceae* of the *Bacteroidetes* phylum in the French bean rhizosphere. Gradual increases in relative abundance of families *Streptomycetae* and *Nocardiodaceae* of *Actinobacteria* and *Rhizobiaceae* of *Proteobacteria*.

### 1.3.2.5 Microbiome of Maize and Other Members of Poaceae Crops

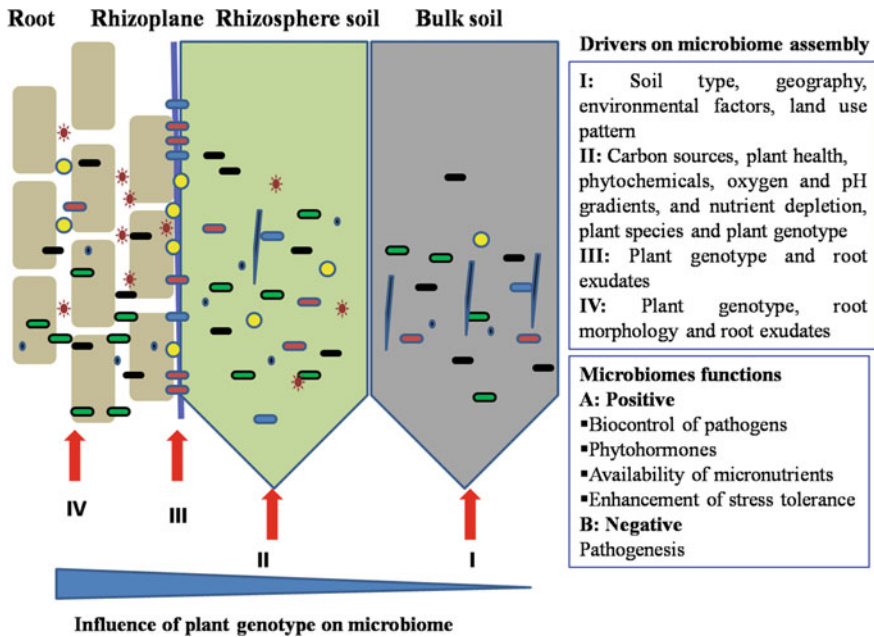
Rhizospheric microbiome of Poaceae crops such as *Zea mays* L.; *Zea mays* ssp. *Parviglumis*; *Sorghum bicolor* cv. *Arprim*; *Triticum aestivum* L. cv. *Fiorina* was established by Bouffaud et al. (2014). The dominant bacterial members of *Microbiome of Poaceae crops* were found to be *Rhodospirillales* such as *Gluconacetobacter*, *Rhodospirillum*, *Azospirillum*, and *Sphingomonadaceae* of class *Burkholderiales*; *Actinomycetales* such as *Corynebacterium*, *Actinomyces*, *Propionibacterium*, and *Kocuria*; *Acidovorax* of *Alphaproteobacteria*; *Xanthomonas*, *Francisella*, *Pantoea*, *Moraxella*, *Pseudomonas*, and *Photorhabdus* of class *Gammaproteobacteria*; *Burkholderia*, *Hydrogenophaga*, and *Alcaligenes* of class *Betaproteobacteria*; *Myxococcales* such as *Anaeromyxobacter* of class *Deltaproteobacteria*; *Mogibacterium*, *Bacillales* (*Firmicutes*) such as *Bacillus* and *Paenibacillus*; *Megasphaera* and *Collinsella* (Bouffaud et al. 2014).

## 1.4 Factors Influencing Rhizospheric Microbiome in Agriculture Crops

The rhizosphere microbiomes participate in very important functions suitable for plant growth promotion. The key functions mediated by rhizosphere microbiome include abiotic stress tolerance, nutrient acquisition, and protection against plant pathogen infection. Therefore, understanding the assembly of rhizosphere microbiome and their molecular mechanisms will provide us basic information. This information will be useful to develop soil management practices, designing of healthy rhizosphere microbiome, and introduction of biofertilizers and biological control agents to develop sustainable agricultural strategies. Different factors that are influencing structure, assembly, and function of rhizospheric microbiomes are depicted in Fig. 1.6.

Rhizobacterial community composition in *Phaseolus vulgaris* was influenced by specific root morphological traits and host plant genotype (Pérez-Jaramillo et al. 2017). Impact of host plant genotype on rhizosphere microbial community was mediated by qualitative and quantitative composition of root exudates (Huang et al. 2014; Ahemad and Kibert 2014). Host genotype had a tremendous effect on the composition of root-associated microbial communities in *Hordeum vulgare* (Bulgarelli et al. 2015). Bulgarelli et al. (2012) reported that host genotype and soil type define the diversity of root-inhabiting bacterial communities in *Arabidopsis thaliana*. Plant cell wall properties confer sufficient colonization (40%) of root-associated microbiota in *Arabidopsis thaliana* (Bulgarelli et al. 2012).

Invading fungal pathogens and plant stress response induces a shift in microbiome composition of sugar beet (Chapelle et al. 2016). Rhizosphere microbial community structure varied according to the Poaceae genotype (Bouffaud et al. 2014). Evolutionary divergence among host plants and type of plant species affects the assembly



**Fig. 1.6** Factors influencing assembly of microbiomes in agriculture crops. Microbial community structures in the four different compartments (I–IV) such as bulk soil, rhizosphere, rhizoplane, and root systems are distinct in nature

of the rhizosphere and endosphere and microbiome (Fitzpatrick et al. 2018). The root microbiome is also associated with drought tolerance of host plants (Fitzpatrick et al. 2018, Kour et al. 2019). Different developmental stages of plant also influence rhizosphere microbiome assemblages (Chaparro et al. 2014). Rhizosphere microbiome of *Oryza sativa* is shaped by plant and soil-related conditions such as soil type, geographic location, rice genotype, oxic–anoxic interface, agricultural management, and growth stages (Ding et al. 2019). Selection of the microbial community in the wheat rhizosphere depends on niche-based processes as a result of environmental factors and the selection power of the plant (Mendes et al. 2014). Further, agricultural management practices and growth stages of host plants exerted much influence on the rice rhizosphere microbiome (Edwards et al. 2015).

### 1.5 Plant Growth-Promoting Mechanisms of Rhizospheric Microbiome

Rhizobacteria plays a crucial role in growth promotion and immunity of the agricultural crops. These plant growth promoters follow certain mechanisms during the entire sequential process for nutrient mobilization, phytohormones for the growth

and development, and chemical agents for defense-related issues of the crops (Suman et al. 2016; Verma et al. 2017; Yadav et al. 2018a, b). According to Mahanty et al. (2016), similar mechanisms are adopted by all bacterial genera during promotion of plant growth, although they are phylogenetically of different origins. The mechanisms behind the scene could mainly be divided into two types, direct mechanisms and indirect mechanisms. Comprehensive details of plant growth-promoting mechanisms of rhizobacteria in different agricultural crops have been summarized in Table 1.3.

### **1.5.1 Direct Mechanism**

The direct mechanisms mainly involve the bacterial activities like phosphate solubilization, nitrogen fixation, secretion of plant hormones, ACC deaminase activities, and siderophore production.

#### **1.5.1.1 Phosphate Solubilization**

In spite of the large reservoir of phosphorus in soil, a very low amount of it is available to the plants (Ahemad and Kibret 2014). This is because plants utilize them in only two forms: (a) monobasic and (b) dibasic ions (Bhattacharyya and Jha 2012). It has also been reported that due to rapid conversion of phosphorus into insoluble complexes of different metal oxides most of the cultivable soils are deficit of available phosphate (Sandilya et al. 2016). Phosphate fertilizers are mostly applied to the agricultural soils in order to overcome the overall loss. But, continuous use of these chemical fertilizers is harmful to the soil and the environment in vivo. Hence, the importance of biofertilizers having plant growth-promoting traits was raised worldwide.

Native rhizobacteria pays an immense attribute to solubilize the inorganic phosphate so as to make it available for the utilization of various crops or plants (Widawati 2011). Certain bacterial genera, viz., *Bacillus*, *Pseudomonas*, *Azospirillum*, *Achromobacter*, *Acetobacter*, *Acinetobacter*, *Enterobacter*, *Klebsiella*, and *Serratia* are able to solubilize the inorganic form of phosphate to the available form (Kumar et al. 2012; Rana et al. 2019a, b). Besides, the role of bacterial organic acids for cation uptake by the plants is also worth mentioning (Sandilya et al. 2016). Researchers further stated that the bacterial genera belonging to the Proteobacteria and some of the *Firmicutes* and *Actinobacteria* are the most capable of the abovementioned conversion process.

**Table 1.3** Plant growth-promoting mechanisms of plant microbiomes

Rhizobacteria	PGP traits	Crops/Plant rhizosphere	References
<i>Bacillus</i> sp. <i>Burkholderia</i> sp.	Phosphate solubilizer	<i>Zea mays</i>	Oliveira et al. (2009)
<i>Pseudomonas aeruginosa</i> strain MAJ PIA 03 <i>Bacillus firmus</i> strain MAJ PSB12	IAA, GA <sub>3</sub> , ACC deaminase activity, HCN production, NH <sub>3</sub> production, Siderophore production, antagonist, and phosphate solubilizer	<i>Ricinus communis</i>	Sandilya et al. (2016, 2017)
<i>Rhodococcus</i> sp. EC35, <i>Pseudomonas</i> sp. EAV, and <i>Arthrobacter nicotinovorans</i> EAPAA	Phosphate solubilizer	<i>Zea mays</i>	Sofia et al. (2014)
<i>Azospirillum brasilense</i> Az39, <i>Bradyrhizobium japonicum</i> E109	Phyostimulation	<i>Glycine max</i>	Cassan et al. (2009)
<i>P. fluorescens</i> Aur6, <i>Chryseobacterium balustinum</i> Aur9	Biocontrol agents	<i>Oryza sativa</i>	Lucas et al. (2009)
<i>Bacillus</i> , <i>Azotobacter</i> , <i>Pseudomonas</i> , and <i>Acinetobacter</i>	IAA, NH <sub>3</sub> , HCN, Siderophore, phosphate solubilizer, antagonistic activity, nitrate reducer	<i>Momordica charantia</i>	Singh et al. (2017)
<i>Pseudomonas putida</i> , <i>Gluconacetobacter azotocaptans</i> , <i>Azospirillum lipoferum</i>	Phosphate solubilizer, plant hormones, siderophore	<i>Zea mays</i>	Mehnaz and Lazarovits (2006)
<i>Sphingobacterium canadense</i>	Phosphate solubilizer, plant hormones, siderophore	<i>Zea mays</i>	Mehnaz et al. (2007)
<i>Chryseobacterium palustre</i> , <i>Chryseobacterium humi</i> , <i>Sphingobacterium</i> , <i>Bacillus</i> , <i>Achromobacter</i>	IAA, HCN, NH <sub>3</sub> , siderophore, ACC deaminase	<i>Zea mays</i>	Marques et al. (2010)
<i>Pseudomonas fluorescens</i> strain Psd	Zinc solubilizer, nitrate reducer	<i>Triticum aestivum</i>	Sirohi et al. (2015)
<i>Bacillus</i> sp. strain WG4	Antifungal metabolite pyrrolo [1, 2-a] pyrazine-1, 4-dione, hexahydro-3-(phenylmethyl)	<i>Zingiber officinale</i>	Jimtha et al. (2016)
<i>Bacillus</i> sp. PSB10	IAA, siderophores, HCN, ammonia	<i>Cicer arietinum</i>	Wani and Khan (2010)

(continued)

**Table 1.3** (continued)

Rhizobacteria	PGP traits	Crops/Plant rhizosphere	References
<i>Bradyrhizobium</i> sp. 750, <i>Pseudomonas</i> sp., <i>Ochrobactrum cytisi</i>	Heavy metal mobilization	<i>Lupinus luteus</i>	Mehnaz et al. (2010)
<i>Mesorhizobium</i> sp. strain MRC4	IAA, siderophores, HCN, ammonia, exo-polysaccharides	<i>Cicer arietinum</i>	Ahemad and Khan (2009, 2010a, b)

### 1.5.1.2 Nitrogen Fixation

Nitrogen being the most important limiting factors, its fixation in nature is an interesting phenomena led by the plant growth-promoting rhizobacteria both in the symbiotic and non-symbiotic or free-living forms (Fagodiya et al. 2017a, b). It has been believed that the free-living nitrogen fixers provide a very lower amount of available nitrogen to the plants in comparison to the symbiotic nitrogen fixers since time immemorial (James and Olivares 1997). The *nif* genes found in the nitrogen-fixing rhizobacteria complete the nitrogenase enzyme by the means of its structural and regulatory proteins responsible for activation of the Fe protein, iron molybdenum, cofactor biosynthesis, and electron donation in case of the former and synthesis and function of the enzyme in the later (Glick 2012). Numerous PGPR genera capable of converting nitrate into nitrite by the catalysis of the nitrate reductase enzyme have also been reported. The most common among them are *Azospirillum*, *Azotobacter*, *Achromobacter*, *Bradyrhizobium*, *Beijerinckia*, and *Rhizobium* (Kour et al. 2019b, c; Yadav et al. 2019b).

### 1.5.1.3 Phytohormones and ACC Deaminase Enzyme Activity

Major plant hormones such as IAA and GA<sub>3</sub> (Marques et al. 2010; Ahmed and Hasnain 2010 and Khan et al. 2014) along with cytokinin secretion (Liu et al. 2013) by the PGPR's have often being reported by various authors. The IAA secreted by the bacterial population associated with the roots of the agricultural crops could augment the root surface area and length that could pave an easier route for absorption of the soil nutrients by the plants (Ahemad and Khan 2012). Amino acid tryptophan being a major precursor of IAA boosts the level of IAA biosynthesis. Almost five different types of IAA pathways have been reported by Spaepen and Vanderleyden (2011).

The role of GA<sub>3</sub> has also been explained by some authors in the context of plant growth-promoting rhizobacteria. The most important among them are the induction of seed germination and emergence and development of stem, leaf, flower, and fruits (Bottoni et al. 2004). The most common bacterial strains *Bacillus cereus*, *Sphingomonas* sp. LK11 were reported by them to enhance the growth and production

of red pepper and tomato. Similarly, some other mechanisms of a plant body, viz., cytokinesis, sensitivity of vascular cambium, and their differentiation and root apical dominance are being conducted by the hormone cytokinin. Root-associated bacteria such as *Azotobacter chroococcum*, *Bacillus megaterium*, and *B. subtilis* were accounted to produce cytokinin thereby enhancing plant growth. On the other hand, synthesis of ethylene by the plant growth-promoting rhizobacteria induces ripening of fruits, opening of flowers, and leaf abscission.

Plants growing under stress are able to withstand the adverse effects of the environment with the due help of these phytohormones (de Garcia et al. 2006). Ethylenes produced in such conditions are called as “stress ethylene” that adds to the existing production of ethylene. However, excessive production of ethylene is a harmful phenomena for the longer development of the roots and in order to check such level of production, PGPR’s with the help of 1-aminocyclopropane-1-carboxylate (ACC) deaminase plays a vital role in the early stages of growth which modulates the level of ethylene by hydrolyzing ACC, a precursor of ethylene, in ammonia and a-ketobutyrate (Glick et al. 1998; Marques et al. 2010). Bacteria synthesizing IAA along with endogenous plant IAA could stimulate plant growth or accelerate the amalgamation of the enzyme ACC synthase translating the compound S-adenosyl methionine to ACC being the immediate precursor of ethylene in higher plants (Glick 2012). Different kinds of phytohormones and their plant growth-promoting activity in agriculture crops have been summarized in Table 1.4.

#### 1.5.1.4 Siderophore Production

Iron being one of the most important nutrients for all forms of life is found to occur as  $Fe^{3+}$  that could most likely form insoluble hydroxides and oxyhydroxides making it nearly impossible for plants and microflora for easy access (Rajkumar et al. 2010). In order to overcome such situations, bacteria secretes siderophores which are iron chelating agents with low molecular mass. According to Glick (2012), siderophores are mostly water soluble and could be divided into extracellular and intracellular siderophores. Siderophore forming  $Fe^{3+}$ -siderophore complex on the bacterial membranes gets reduced to  $Fe^{2+}$ . These ionic forms of iron are released into the cell from the complex via another mechanism linking both the membrane systems (inner and outer) which may finally lead to the destruction or recycling of the left out siderophore (Rajkumar et al. 2010). Thus, the siderophores prove to be excellent iron solubilizing agents from minerals and other inorganic sources. Pseudomonads, the bacterial genera, are the best-known secretors of siderophores playing an important role in the overall plant growth promotion activities (Sandilya et al. 2017).

**Table 1.4** Phytohormones produced by microbiomes

Phytohormone produced	Plant growth-promoting rhizobacteria	Agriculture crop	References
Indole-3-acetic acid (IAA)	<i>Aeromonas veronii</i>	<i>Oryza sativa</i>	Mehnaz et al. (2001)
	<i>Azospirillum brasilense</i>	<i>Triticum aestivum</i> L.	Kaushik et al. (2000)
	<i>Enterobacter</i> sp.	<i>Saccharum officinarum</i>	Mirza et al. (2001)
	<i>Enterobacter cloacae</i>	<i>Oryza sativa</i>	Mehnaz et al. (2001)
	<i>Pseudomonas</i> sp. RJ10	<i>Brassica napus</i>	Sheng and Xia (2006)
	<i>Bacillus</i> sp. RJ16	<i>Brassica napus</i>	Sheng and Xia (2006)
	<i>Enterobacter</i> sp.	<i>Cicer arietinum</i> L.	Fierro-Coronado et al. (2014)
	<i>Pseudomonas</i> sp, <i>Bacillus</i> sp.	<i>Sulla carnosa</i>	Hidri et al. (2016)
	<i>Bacillus licheniformis</i>	<i>Triticum aestivum</i> L.	Singh and Jha (2016)
	<i>Bacillus subtilis</i>	<i>Acacia gerrardii</i> Benth	Hashem et al. (2016)
	<i>Pseudomonas</i> sp.	<i>Zea mays</i>	Mishra et al. (2017)
	<i>Enterobacter</i> sp. CID	<i>Vigna radiata</i> L.	Subrahmanyam and Archana (2011)
	<i>Proteus vulgaris</i> JBSL202	<i>Arabidopsis thaliana</i>	Bhattacharyya et al. (2015)
Cytokinin	<i>Pseudomonas fluorescens</i>	<i>Glycine max</i> L.	De Salamone et al. (2001)
	<i>Pseudomonas fluorescens</i>	<i>Pinus</i> sp.	Bent et al. (2001)
	<i>Paenibacillus polymyxa</i>	<i>Triticum aestivum</i> L.	Timmusk et al. (1999)
	<i>Micrococcus luteus</i>	<i>Zea mays</i>	Raza and Faisal (2013)
	<i>Bacillus subtilis</i>	<i>Platycladus orientalis</i>	Liu et al. (2013)
	<i>Arthrobacter</i> sp., <i>Bacillus</i> sp., <i>Azospirillum</i> sp.	<i>Glycine max</i> L.	Naz et al. (2009)
	<i>Proteus vulgaris</i> JBSL202	<i>Arabidopsis thaliana</i>	Bhattacharyya et al. (2015)
Gibberellin	<i>Bacillus</i> sp.	<i>Alnus</i> sp.	Gutierrez-Manero et al. (2001)

(continued)



**Table 1.4** (continued)

Phytohormone produced	Plant growth-promoting rhizobacteria	Agriculture crop	References
	<i>Aspergillus fumigatus</i>	<i>Glycine max</i> L.	Khan et al. (2011)
	<i>Azospirillum lipoferum</i>	<i>Triticum aestivum</i> L.	Creus et al. (2004)
	<i>Phoma glomerata</i> , <i>Penicillium</i> sp.	<i>Cucumis sativus</i>	Waqas et al. (2012)
	<i>Proteus vulgaris</i> JBLS202	<i>Arabidopsis thaliana</i>	Bhattacharyya et al. (2015)
ACC deaminase	<i>Enterobacter cloacae</i>	<i>Brassica napus</i>	Saleh and Glick (2001)
	<i>Pseudomonas putida</i>	<i>Vigna radiata</i> L.	Mayak et al. (1999)
	<i>Pseudomonas</i> sp.	<i>Zea mays</i> L.	Shaharoona et al. (2006)
	<i>Methylobacterium fujisawaense</i>	<i>Brassica</i> sp.	Madhaiyan et al. (2006)
	<i>Rhizobium leguminosarum</i>	<i>Pisum sativum</i>	Ma et al. (2003)
	<i>Achromobacter xylooxidans</i> , <i>Acidovorax facilis</i>	<i>Brassica juncea</i> L. Czern	Belimov et al. (2005)
	<i>Bacillus</i> , <i>Microbacterium</i> , <i>Methylophaga</i> , <i>Agromyces</i>	<i>Oryza sativa</i>	Bal et al. (2013)
	<i>Enterobacter sakazakii</i> 8MR5, <i>Pseudomonas</i> sp. 4MKS8, <i>Klebsiella oxytoca</i> 10MKR7	<i>Zea mays</i> L.	Babalola et al. (2003)
	<i>Methylobacterium fujisawaense</i>	<i>Brassica campestris</i>	Madhaiyan et al. (2006)
	<i>Enterobacter</i> sp. C1D	<i>Vigna radiata</i> L.	Subrahmanyam et al. (2018)

### 1.5.2 Indirect Mechanisms

Plant growth-promoting rhizobacteria has been implemented in various crop fields for their promising capability to work both as biocontrol agents and growth promoters since last two decades. Bacteria secretes various metabolites and chemical agents that makes them wonderful candidates for controlling different crop diseases

most of them being originated from fungal sources. According to Bhattacharyya and Jha (2012), PGPRs are able to synthesize different antifungal secondary metabolites such as phenazines, HCN, pyrrolnitrin, 2, 4-diacetylphloroglucinol, viscosinamide, tensin, and pyoluteorin. Availability of bacterial antagonist in the rhizosphere soil may even adapt the plant for developing induced systemic resistance against broad-spectrum bacterial, fungal, and viral pathogens (Lugtenberg and Kamilova 2009). Cyanide is the most dangerous chemical known for its high toxic properties which can well inhibit the pathogens sensitizing agricultural crops. HCN being the secondary metabolite secreted by the PGPRs does not have any pessimistic effect on the host plants, and hence they are frequently used for controlling weeds (Zeller et al. 2007). According to various reports, HCN-producing PGPRs are very helpful in controlling dreaded phytopathogens such as *Pythium ultimum*, *Fusarium oxysporum*, and pathogenic *Agrobacterium*. The mode of action mechanisms involves lysis of fungal cell walls (Maksimov et al. 2011), root colonization (Kamilova et al. 2005), reduction of stress ethylene level (Van Loon 2007), siderophore and antibiotic production (Beneduzi et al. 2012).

Certain genera like *Bacillus* have been best studied for their ability to secrete antimicrobial traits with higher rate of agricultural applicability (Compant et al. 2005). The members of this group of bacteria hold a key role in biocontrol aspects as they could reluctantly replicate at a very faster rate and are mostly resistant to environmental stress (Shafi et al. 2017). They secrete bacillomycins, iturins, and mycosubtilin very much effective against fungal pathogens, particularly *Aspergillus flavus* (Gong et al. 2015). Similarly, Lee et al. (2015) reported almost 99.1% of the antagonistic success in crops fields inoculated with *Bacillus amyloliquefaciens* strain HK34 against *Phytophthora cactorum* in *Lycopersicon esculentum*, *Sclerotium rolfsii*, *Capsicum annuum* var. *acuminatum*, *Colletotrichum gloeosporioides*, and *Cucumis sativus*.

Apart from that, other bacterial genera like *Pseudomonas* and *Paenibacillus* have also been reported by various authors having antimicrobial properties in both in vitro and in vivo conditions. Although laboratory results may not always be relied under field conditions, PGPR has been reported to be effective in both the conditions in different agricultural cropping systems. That is why they may be termed as multifunctional agents by controlling a wide spectrum range of phytopathogens and a spectacular replacement for chemical fertilizers by enhancing plant growth and overall yield per hectares of cultivated soil further playing a vital role in maintaining ecological balance across the globe (Ahemad and Kibret 2014).

Although much work has been done on the biocontrol characteristics of rhizospheric bacteria, it has to be considered that soil type, plant species, and pathogen affect in rhizosphere competence and/or biocontrol efficiency of applied biocontrol strain against a soil-borne pathogen.

## 1.6 Biotechnological Applications of Rhizosphere Microbiomes

In the recent past, sustainable technologies have gained lot of momentum to improve quality and yield of agricultural crop production. Nevertheless, still there is uncertainty about success of chemical-based formulations in plant protection management. In general, pests and diseases are mainly controlled by chemical-based pesticides which pose major health risks as well as adverse negative impacts in the ecosystem and environment. In addition to this, indiscriminate use of chemical fertilizers resulted in negative impacts on biodiversity and function of biogeochemical cycles. Most importantly, agricultural practices require novel products according to the demand of farmers and consumers. Therefore, alternative management tools have to be developed on the basis of biological solutions.

The plant rhizosphere hosts a considerable amount of microbiome. Plant growth-promoting rhizobacteria (PGPR) is an integral component of rhizosphere microbiome and is competent to promote plant growth by direct and indirect mechanisms. PGPR also promotes defense against diseases causing organisms using diverse plant-beneficial functions. Therefore, it is anticipated that crop inoculation with suitable PGPR could reduce the use of pesticides and fertilizers in agrosystems. Biotechnological applications of various PGPR inoculants for enhancing crop production were summarized in Table 1.5. Since most of the research information on PGPR comes from rhizosphere microbiome, one can further explore and exploit biotechnical prospects of rhizosphere microbiomes for sustainable agricultural production. We have specially highlighted the production of extracellular lytic enzymes, bioactive metabolites, and volatile organic compounds (VOCs) of rhizosphere bacteria in this section and the details are given extensively in Table 1.6.

### 1.6.1 Production of Lytic Enzymes by Rhizospheric Bacteria

Rhizosphere bacteria can benefit plant growth indirectly through biocontrol mechanisms which can inhibit the growth and colonization of phytopathogens. This potential antagonism character of biocontrol agent might occur through different mechanisms which include production of extracellular lytic enzymes, secondary metabolites, siderophores, antibiotics, and induction of systemic responses (Saraf et al. 2014, Jadhav and Sayyed 2016; Kour et al. 2019a; Yadav et al. 2016a, 2019f). One of the important mechanisms for biocontrol agent is the production of lytic enzymes which are able to degrade the membrane constituents of phytopathogens, such as proteases (Felestrino et al. 2018), acylases, and lactonases (Combes-Meynet et al. 2011). These hydrolytic enzymes degrade the structural integrity of the pathogen cell wall. Their ability to inhibit phytopathogens makes them to be the preferable choice in biological control process. The application of

**Table 1.5** Biotechnological applications of bio-inoculants for sustainable agriculture

SN	Crop	Organism/Biofertilizers	Mode of action	References
1	Canola and lettuce	<i>Rhizobium leguminosarum</i>	Early development, Growth promotion	Sneha et al. (2018), Abd El-Lattief (2016)
2	Wheat, oat, barley mustard, seasum, rice, linseeds, sunflower, castor, maize, sorghum, cotton, jute, sugar beets, tobacco, tea, coffee, rubber, and coconuts	<i>A. chroococcum</i> , <i>A. vinelandii</i> , <i>A. beijerinckii</i> , <i>A. nigricans</i> , <i>A. armeniacus</i> , and <i>A. paspali</i> .	Nitrogen fixation, produce thiamine and riboflavin, indole acetic acid (IAA), gibberellins (GA) and cytokinins (CK), improves the plant growth by enhancing seed germination and advancing the root architecture, inhibiting pathogenic microorganisms around the root systems of crop plants	Revillas et al. (2000), Abd El-Fattah et al. (2013), Gholami et al. (2009), Mali and Bodhankar (2009), Wani et al. (2013), Bhardwaj et al. (2014)
3	Chickpea lentil, pea, alfalfa and sugar beet rhizosphere, berseem, ground nut and soybean <i>Cicerarietinum</i> and <i>Tigonella foenum-gracecum</i>	<i>Rhizobium</i> inoculants	Increase the grain yields	Patil and Medhane, (1974), Rashid et al. (2012), Ramachandran et al. (2011), Hussain et al. (2002), Grossman et al. (2011), Sharma et al. (2011, 2012a, b), Kumar et al. (2013)
4	Tomato	<i>Pseudomonas putida</i>	Early developments, Growth stimulation	Sneha et al. (2018), Abd El-Lattief (2016)
5	Wheat and maize	<i>Azospirillumbrasileense</i> and <i>A. irakense</i>	Growth of wheat and maize plants by secrete gibberellins, ethylene, and auxins	Abd El-Lattief (2016); Perrig et al. (2007), Bhardwaj et al. (2014), Sneha et al. (2018)

(continued)

**Table 1.5** (continued)

SN	Crop	Organism/Biofertilizers	Mode of action	References
6	Banana Pearl millet	<i>P. flourescens</i>	Enhance growth, leaf nutrient contents, and yield	Sneha et al. (2018), Abd El-Lattief (2016)
7	Rice	<i>Cylindrospermum musicola</i>	Nitrogen fixation, liberation of growth-promoting substances and vitamins; increase the root growth	Venkataraman and Neelakantan (1967)
8	Canola	<i>Azotobacter</i> and <i>Azospirillum</i> spp.	Growth and productivity	Sneha et al. (2018), Abd El-Lattief (2016)
9	Maize crop.	<i>P. alcaligenes</i> , <i>Bacillus polymyxa</i> , and <i>Mycobacterium phlei</i>	Improves the uptake of N, P, and K	Sneha et al. (2018), Abd El-Lattief (2016)
10	Chick pea.	<i>Pseudomonas</i> , <i>Azotobacter</i> , and <i>Azospirillum</i> spp.	Stimulates growth and increases the yield	Sneha et al. (2018), Abd El-Lattief (2016)
11	Wheat	<i>R. leguminismarum</i> and <i>Pseudomonas</i> spp.	Enhances the yield and phosphorus uptake	Sneha et al. (2018) Abd El-Lattief (2016)
12	Maize.	<i>P. putida</i> , <i>P. fluorescens</i> , <i>A. brasilense</i> , and <i>A. lipoferum</i>	Enhances seed germination, seedling growth, and yield	Sneha et al. (2018), Abd El-Lattief (2016)
13	Wheat, maize, and rice	<i>Azotobacter</i> , <i>Azotobacter</i> , <i>Alcaligenes</i> , <i>Azospirillum</i> , <i>Bacillus</i> , <i>Enterobacter</i> , <i>Herbaspirillum</i> , <i>Klebsiella</i> , <i>Pseudomonas</i> , and <i>Rhizobium</i>	Improves growth and grain yield	Sridhar (2012), James (2000)
14	Wheat maize, and rice	<i>Azospirillum</i>	Synthesis of phytohormones (indole-3-acetic acid, IAA), and regulation of plant hormonal balance by deamination of the ethylene precursor	Abd El-Lattief (2016)

(continued)

**Table 1.5** (continued)

SN	Crop	Organism/Biofertilizers	Mode of action	References
15	Rice	<i>Alcaligenes</i> , <i>Azospirillum</i> , <i>Bacillus</i> , <i>Herba spirillum</i> , <i>Klebsiella</i> , <i>Pseudomonas</i> , and <i>Rhizobium</i>	N-fixation	Sneha et al. (2018)
16	Chickpea	Co-inoculation ( <i>Pseudomonas</i> + <i>Bacillus</i> strains + effective <i>Rhizobium</i> spp.)	Stimulate chickpea growth, nodulation, and nitrogen fixation	Sneha et al. (2018)
17	Chickpea	Co-inoculation (PSB + <i>Rhizobium</i> + <i>Trichoderma</i> )	Increase sugar, protein, starch contents, nodule weight and seed nitrogen, potassium, phosphorus	Mohammadi (2010, 2011)
18	Rice	Green manure and biofertilizer	Stimulated the growth of plants with more number of tillers and broader leaves, increased leaf area	Shanmugam and Veeraputhran (2000)

these hydrolytic enzymes from rhizospheric origin is a viable solution as they are totally natural and are eco-friendly in nature (Mishra et al. 2019).

Lytic enzymes produced by various microorganisms can hydrolyze polymeric compounds like cellulose, hemicellulose, chitin, and protein of phytopathogens. Extracellular hydrolytic enzymes like chitinases, lipases, proteases, and glucanases are involved in the lysis of fungal cell wall (Neeraja et al. 2010). These enzymes either disintegrate or digest the molecular components of cell wall of fungal phytopathogens. Therefore, this process would be considered as eco-friendly control of soil-borne pathogens in agriculture crops. These enzymes further involve in nutrient cycling by decomposition of organic matter and plant residues in the rhizosphere. It is demonstrated that extracellular lytic enzymes produced by *Myxobacteria* sp. have the ability to suppress fungal plant pathogens (Bull et al. 2002). In another study, glucanase-producing antagonistic bacteria *Lysobacter* sp. is capable of controlling diseases of *Pythium* sp. and *Bipolaris* sp. (Palumbo 2005). These hydrolytic enzymes rescue plants from biotic stresses and directly contribute in the parasitization of phytopathogens.

Hydrolytic enzymes of rhizospheric microbes were reviewed extensively by Jadhav and Sayyed 2016. Many rhizobacterial microbial species are capable of producing extracellular enzymes and effectively hydrolyze wide variety of polymeric substances like cellulose, hemicellulose, proteins, and chitin of phytopathogens (Jadhav and Sayyed 2016). Microbial strains like *B. subtilis* strains PCL1608 PCL1612, *Streptomyces cyaneofuscatus* B-49, *Serratia marcescens* strain ETR17,

**Table 1.6** Biotechnological prospects of different rhizobacteria suitable for enhanced production of agricultural crops

Biotechnological prospects	Rhizospheric organism	Crop	Growth parameter	References
<b>Hydrolytic enzymes</b>				
$\beta$ -1,3-glucanase and $\beta$ -1,4-glucanase activities, Chitinase, oxalate oxidase	<i>Bacillus</i> sp.	Bean	Biocontrol	Kumar et al. (2012)
Glucanases, protease	<i>B. subtilis</i> strains, PCL1608 and PCL1612	Avocado	Biocontrol	Cazorla et al. (2007)
Chitinase	<i>Bacillus subtilis</i> BP 9	Cotton	Biocontrol	Gajbhiye et al. (2010)
Chitinase, $\beta$ -1,3-glucosidase, cellulose., Protease	<i>Streptomyces cyaneofuscatus</i> B-49, <i>Streptomyces kanamyceticu</i> X-4, <i>Streptomyces rochei</i> Z-13, <i>Streptomyces flavotricin</i>	Cotton, chili pepper, canola	Biocontrol	Xue et al. (2013)
Glucanases, proteases or chitinases,	<i>B. megaterium</i> B5, <i>B. cereus</i> sensulato B25, and <i>Bacillus</i> sp. B35	Maize	Biocontrol	Ramírez et al. (2016)
$\beta$ -1,3-, $\beta$ -1,4-, and $\beta$ -1,6-glucanases	<i>Actinoplanes philippinensis</i> , <i>Microbispora rosea</i> , <i>Micromonospora chalcea</i> , and <i>Streptomyces griseoalbus</i>	Cucumber	Biocontrol	El-Tarabily (2006)
Chitinase, $\beta$ -1,3 glucanase (laminarinase) and $\beta$ -1,4 glucanase (cellulase)	<i>Pseudomonas fluorescens</i> and <i>Bacillus subtilis</i>	Tomato	Biocontrol	El-Gamal et al. (2016)

(continued)

Table 1.6 (continued)

Biotechnological prospects	Rhizospheric organism	Crop	Growth parameter	References
chitinase, protease, lipase, cellulase	<i>Serratia marcescens</i> strain ETR17	Tea	Biocontrol	Purkayastha et al. (2018)
Extracellular proteases and lipases	<i>Lysobacter enzymogenes</i>	Cucumber	Biocontrol	Folman et al. (2003)
<b>Antibiotics/secondary metabolites</b>				
DAPG and HCN	<i>P. fluorescens</i> strains CHA0, Pf-5, Q2-87,	Tobacco	Biocontrol	Weller (2007)
DAPG and HCN	<i>P. fluorescens</i> Pf-5	Cotton	Biocontrol	Nowak-Thompson et al. (1994)
DAPG and HCN	<i>P. fluorescens</i>	Rice	Biocontrol	Reddy et al. (2007)
DAPG and HCN	<i>P. fluorescens</i> Q2-87	Wheat	Biocontrol	Harrison et al. (1993)
HCN	<i>Bacillus</i> sp. BPR7	Bean	Biocontrol	Kumar et al. (2012)
HCN	<i>Bacillus subtilis</i> BP-9	Cotton	Biocontrol	Gajbhiye et al. (2010)
Bacilysin and iturin	<i>Bacillus subtilis</i> ME488	Cucumber and pepper	Biocontrol	Chung et al. (2008)
Pyrolnitrin and prodigiosin	<i>Serratia marcescens</i> strain ETR17	Tea	Biocontrol	Purkayastha et al. (2018)
Lipopeptides surfactin, fengycin, and/or iturin A	<i>B. subtilis</i> strains, PCL1608 and PCL1612	Avocado	Biocontrol	Cazorla et al. (2007)
Viscosinamide, cyclic lipopeptides	<i>P. fluorescens</i> DR54	Cotton	Biocontrol	Nielsen et al. (1999)
Antifungal protein	<i>Bacillus</i> sp. KM 5	Rice	Biocontrol	Majumdar et al. (2011)
polymyxin B I	<i>Paenibacillus</i> sp. strain B2	sorghum	Biocontrol	Selim et al. (2005)

(continued)



Table 1.6 (continued)

Biotechnological prospects	Rhizospheric organism	Crop	Growth parameter	References
Eicosane (C <sub>20</sub> H <sub>42</sub> ) and dibutyl phthalate (C <sub>16</sub> H <sub>22</sub> O <sub>4</sub> ), cyclononasiloxane, octadecamethyl-(C <sub>18</sub> H <sub>54</sub> O <sub>9</sub> Si <sub>9</sub> ) and benzoic acid, 2,5-bis(trimethylsiloxy) (C <sub>16</sub> H <sub>30</sub> O <sub>4</sub> Si <sub>3</sub> )	<i>Streptomyces</i> strain KX852460	Tobacco	Biocontrol	Ashan et al. (2017)
Fungichromin	<i>Streptomyces padanus</i> strain PMS-702 i	Cabbage	Biocontrol	Shih et al. (2003)
Pyrrrolinitrin	<i>P. fluorescens</i> BL915	Wheat	Biocontrol	Chin-A-Woeng et al. (2003)
Oomycin A	<i>P. fluorescens</i>	Cotton	Biocontrol	Howie and Suslow (1991)
Phenazine-1-carboxylic acid	<i>P. fluorescens</i>	Wheat		Pierson and Pierson (1996)
<b>Volatile organic compounds (VOCs)</b>				
VOCs	<i>Bacillus subtilis</i> GB03	Arabidopsis	Vegetative growth promotion, elevated photosynthetic capacity, and iron accumulation	Xie et al. (2009)
VOCs	<i>Bacillus subtilis</i> GB03	Arabidopsis	Vegetative growth promotion, plant acquisition of iron, and increased photosynthetic capacity	Zhnag et al. (2009)
2-pentylfuran, aldehydes, alkanes, ketones, and aroma components	<i>Bacillus megaterium</i>	Arabidopsis	Fresh weight	Zou et al. (2010)

(continued)

Table 1.6 (continued)

Biotechnological prospects	Rhizospheric organism	Crop	Growth parameter	References
4-nitroguaiacol and quinoline	<i>Pseudomonas simiae</i>	Soybean	Salt tolerance, increased shoot and root length, fresh weight and leaf surface area	Vaishnav et al. (2016)
13-Tetradecadien-1-ol, 2-butanone and 2-Methyl-n-1-tridecene	<i>Pseudomonas fluorescens</i> SS10	Tobacco	Fresh weight, dry weight	Park et al. (2015)
Dimethylhexadecylamine	<i>Arthrobacter agilis</i> UMCV2	<i>Sorghum</i>	Fresh weight, shoot length, chlorophyll concentration, and lateral root number	Castulo-Rubio et al. (2015)
Brassinosteroid	<i>Proteus vulgaris</i> JBLS202	Arabidopsis	Fresh weight	Bhattacharyya et al. (2015)
Long-chain VOC signaling molecules, acetoin 2,3-butanediol, ethanethiol, isoprene, and acetic acid-butyl ester, tridecane, a C13 hydrocarbon compound	<i>Pseudomonas fluorescens</i> 89B-61, <i>Bacillus amyloliquefaciens</i> IN937a, <i>Bacillus subtilis</i> GB03, and <i>Paenibacillus polymyxa</i> E681	<i>Arabidopsis</i>	Induced systemic resistance	Lee et al. (2012a)
$\beta$ -Caryophyllene	<i>Fusarium oxysporum</i> MSA 35	Lettuce	Root length, fresh weight, chlorophyll content	Minerdi et al. (2011)
Sesquiterpenes	<i>Laccaria bicolor</i>	<i>Arabidopsis</i> and <i>Populus</i>	Lateral root development	Ditengou et al. (2015)
$\alpha$ -pinene, (-)-trans-caryophyllene, tetrahydro-2,2,5,5-tetramethylfuran, dehydroaromadendrene, and (+)-sativene	<i>Cladosporium cladosporioides</i> CL-1	Tobacco	Fresh weight	Paul and Park (2013)
2,3-butanediol	<i>Bacillus subtilis</i>	Pepper	Plant defences/resistance	Yi et al. (2016)

**Table 1.7** Mode of action of different lytic enzymes produced by rhizobacteria

S.No	Extracellular lytic enzyme	Mode of action
1	Chitinase	Degradation of chitin involves breakdown of chitin polymer into monomer, random cleavage at internal sites of chitin micro-fibril or progressive release of diacetylchitobiose in a stepwise manner without releasing monosaccharide or oligosaccharides
2	Glucanase	Glucanase can hydrolyze the substrate by sequentially cleaving glucose residues from non-reducing end. The enzyme can also initiate cleaving linkages at random sites along the polysaccharide chain, releasing smaller oligosaccharides
3	Protease	Protease can hydrolyze major proteins of phytopathogenes into small peptide chains, subsequently release their constituent amino acids and thereby destroy capacity of phytopathogen's protein to act on plant cells. Some of the proteases are capable of inactivating extracellular enzymes produced by phytopathogenic fungi
4	Cellulase	Cellulases hydrolyze the $\beta$ -(1,4) glucosidic linkages in cellulose polymer and play a significant role in recycling this polysaccharide in the rhizosphere. Cellulose chains are composed of complex, rigid, insoluble, crystalline microfibrils. Therefore, complete degradation of cellulose involves a complex interaction between different cellulolytic enzymes such as cellulose/endoglucanases, exo-cellobiohydrolase/exo-glucanases, and $\beta$ -glucosidases act synergistically to convert cellulose into glucose molecules

*Pseudomonas fluorescens*, *Serratia marcescens* strain ETR17, and many other antagonistic microbes have a potential to synthesize hydrolytic enzymes for the biocontrol of fungal phytopathogens like *P. ultimum*, *F. oxysporum*, *R. solani*, and *S. rolfii*, (Cazorla et al. 2007; Kumar et al. 2012a, b; Purkayastha et al. 2018, El-Gamal et al. 2016). The mode of actions of extracellular enzymes is given in Table 1.7.

Chitinolytic microorganisms are heavily colonized in plant rhizosphere among which actinobacteria are the most abundant members (Yadav et al. 2018c). Actinobacteria such as *Streptomyces flavotricini*, *Streptomyces kanamyceticu*, *Streptomyces cyaneofuscatus*, and *Streptomyces rochei* produce chitinases and inhibit the growth of phytopathogen, viz, *Verticillium dahlia* in cotton rhizosphere (Xue et al. 2013). Chitinase-producing *Bacillus thuringiensis* spp. *colmeri* can inhibit the growth of plant pathogenic fungi, including *Rhizoctonia solani*, *Penicillium chrysogenum*, and *Physalospora piricola* (Liu et al. 2010). Biocontrol agent *Bacillus subtilis* inhibits the growth of pathogenic fungi *Fusarium oxysporum* through production of extracellular chitinase (Gajbhiye et al. 2010). Chitinases produced by *Brevibacillus laterosporus* effectively inhibit the growth of phytopathogenic fungi *Fusarium equiseti* (Prasanna et al. 2013). *Lysobacter enzymogenes* showed to inhibit *Pythium aphanidermatum* by producing extracellular protease and lipases (Folman et al. 2003)

Minimal use of chitinase-based fungicides in agriculture crops was associated with the perception that their efficacy will be slowly reduced in the soil environment. Nevertheless, Dahiya et al. (2006) extensively reviewed biotechnological prospects

of chitinolytic enzymes and suggested that chitinases can be used as supplementary inputs along with other chemical-based fungicides to enhance their effectiveness against phytopathogenic fungi and reduce the required amount of chemical fungicides. In addition to this, it was shown that the application of mixed consortia containing two different chitinolytic bacteria is more effective in controlling the pathogen. Application of chitinase-producing *Streptomyces* sp. 385, *Paenibacillus* sp. 300, and both together is more effective in controlling cucumber wilt caused by *F. oxysporum* than individual strains applied (Singh et al. 1999). Similar kind of observation was reported by El-Tarabily et al. (2000) wherein growth of fungal pathogen *Sclerotinia* responsible for vegetable rot was effectively controlled by combination of *S. marcescens*, *Streptomyces viridodiasticus*, and *Micromonospora carbonacea* strains. In recent, chitinase, protease, lipase, and cellulose-producing *Serratia marcescens* strain ETR17 showed in vitro antagonism toward nine different root and foliar pathogens of tea (Purkayastha et al. 2018).

Actinomycetes were considered to be strong biocontrol agents against fungal pathogens. This is mainly due to production of different types of antifungal compounds such as antibiotics and extracellular hydrolytic enzymes which includes chitinases and glucanases (Xue et al. 2013; Yadav et al. 2018c). *Streptomyces halstedii*, *Streptomyces cavourensis* SY224, and *Streptomyces griseus* are known to produce potential antifungal extracellular chitinases, which makes them to be used as biocontrol agents in crop protection strategies (Ki et al. 2012; Gherbawy et al. 2012). *Lysobacter* spp. was reported to be an effective biocontrol agent against soil-borne pathogens through production of extracellular enzymes and other metabolites (Folman et al. 2003). *Lysobacter* spp. was abundant in the soil which is suppressive to root pathogen, viz., *Rhizoctonia solani*. Certain antagonistic strains showed in vitro biocontrol activity against *Xanthomonas campestris*, *R. solani*, and other important phytopathogens such as *Aspergillus niger*, *Fusarium oxysporum*, and *Pythium ultimum*.

These natural microbial biofungicides will be used as integrated pest management supplement for reduction of negative impact of chemical pesticides on the environment and maintain the sustainable production of agriculture.

### 1.6.2 Production of Antibiotics

Rhizospheric bacteria produce distinct antimicrobial products to inhibit the growth and colonization of plant pathogens to compete the nutrients present in the rhizosphere. This has become a beneficial trait to the host plant as disease development is significantly reduced by PGPR. Rhizosphere harbors diverse actinomycetes species which have been further exploited for secondary metabolites (Yadav et al. 2018b; Geetanjali and Jain 2016). Actinobacteria is known to produce wide variety of natural antimicrobial products (approximately 10,000 secondary metabolites) (Passari et al. 2015, 2017; Yadav et al. 2018a, b). Production of antibiotics by Actinobacteria was

extensively reviewed by Yadav et al. (2018b, c). Application of secondary metabolites producing rhizobacterial isolates against phytopathogens is increasing over the past decade (Yilmaz et al. 2008). A variety of antimicrobial agents such as 2,4-diacetylphloroglucinol (DAPG), pyoluteorin (PRN), phenazine, cyclic lipopeptides, tensin, and pyrrolnitrin (PLT) have been screened and identified from *Pseudomonas* sp., *Arthrobacter* sp., and *Streptomyces* sp., (Weller 2007; Gupta et al. 2015). Details of antibiotics/secondary metabolites producing organisms and their application in different crops have been summarized in Table 1.6.

Rhizospheric soil isolates *Bacillus* sp. S2 and *Pseudomonas fluorescens* S5 were found to exert good antimicrobial activity against multi-drug-resistant clinical pathogens such as *Pseudomonas aeruginosa*, *Klebsiella pneumonia*, *Escherichia coli*, and *Staphylococcus aureus* obtained from different samples (Dhore et al. 2014). Thirty *Pseudomonas fluorescens* strains isolated from rice rhizosphere against pathogenic fungi *Sarocladium oryzae*, *Dreschelaria oryzae*, *Magnaporthe grisea*, and *Rhizoctonia solani*. Among these, *P. fluorescens* Pf 003 effectively inhibited (62–85%) the mycelial growth in all the pathogenic fungi in dual culture. The antifungal compounds extracted with ethyl acetate from *P. fluorescens* at 5% completely inhibited the pathogens (Reddy et al. 2007). Walia et al. (2013) isolated the bacteria from the tomato rhizosphere for having broad-spectrum antifungal activity against *Sclerotinia sclerotiorum*, *Rhizoctonia solani*, and *Fusarium oxysporum*.

DAPG, phenazines, PLT, and PRN are considered to be potent antibiotics synthesized by *Pseudomonas* biocontrol agents affiliated to gammaproteobacteria (Table 1.6). In recent, antibiotics-producing *Pseudomonas* spp. has got much attention in biocontrol research, and corresponding genes involved in the expression and regulation of these metabolites are now fully understood (Weller 2007 and there in references). For the last 30 years, developments on biocontrol applications of *Pseudomonas* sp. against soil-borne pathogens have been summarized by Weller (2007). *P. fluorescens* strain CHA0 was isolated from tobacco rhizosphere which is naturally suppressive to black root rot of tobacco caused by *Thielaviopsis basicola* (Stutz et al. 1986). *P. fluorescens* CHA0 produces siderophore (pseudobactin), PLT, DAPG, PRN, HCN, salicylic acid, pyoverdine, indoleacetic acid, pyochelin, and other secondary metabolites (Voisard et al. 1994). Antagonistic bacterium *P. fluorescens* F113 isolated from sugar beet was applied in the field for suppression of damping-off of sugar beet infection caused by a pathogen *Pythium ultimum* (Cronin et al. 1997a, b).

Antibiotics such as bacilysin- and iturin-producing *Bacillus subtilis* ME488 suppressed soil-borne pathogens in pepper and cucumber crops (Chung et al. 2008). Secondary metabolites, viz., Pyrrolnitrin and prodigiosin-producing *Serratia marcescens* strain ETR17 *Serratia marcescens* strain ETR17 showed significant level of in vitro antagonistic property against different root and foliar pathogens of tea (Purkayastha et al. 2018). Antifungal lipopeptides such as surfactin-, fengycin-, and iturin-producing *B. subtilis* strains PCL1608 and PCL1612 have shown biocontrol mechanism toward soil-borne pathogen *Fusarium oxysporum* (Cazorla et al. 2007). *Paenibacillus* sp. strain B2 isolated sorghum mycorrhizosphere showed production of antibiotic polymyxin B1 and significantly inhibited the growth of fungal pathogens (Selim et al. 2005). Antifungal peptides-producing *Bacillus* sp. KM 5 isolated from

rice rhizosphere showed antagonist activity toward pathogenic fungi *Gibberella fujikuroi*, *Sclerotium rolfsii* Saccardo, *Fusarium udum*, *Helminthosporium oryzae*, and *Rhizoctonia solani* Nees (Majumdar et al. 2011).

### 1.6.3 Production of Volatile Organic Compounds (VOCs)

Volatile organic compounds are lipophilic low molecular weight (<300 g mol<sup>-1</sup>) compounds emitted from microbial metabolic pathways with high vapor pressure and low boiling point. VOCs can act as signal molecules in rhizosphere over short and long distances (Fincheira and Quiroz 2018). It is evidenced that VOCs released from diverse rhizospheric microorganisms, e.g., *Arthrobacter* sp., *Proteus* sp., *Bacillus* sp., *Fusarium* sp., *Pseudomonas* sp., *Alternaria* sp. and *Laccaria* sp., can promote plant growth on a specific “target”. Detailed description about chemical nature of VOCs and their functions have been summarized in Table 1.6. Ryu et al. (2003) reported for the first time about the mechanism mediated by volatile organic compounds released by *Bacillus subtilis* GB03 which induced growth on *Arabidopsis thaliana*. This study evidenced that VOCs can modulate stress, growth, nutrition, and health processes in host plants. Some identified VOCs compounds, such as acetoin,  $\beta$ -Caryophyllene 2,3-butanediol, Sesquiterpenes, 2-pentylfuran, and dimethylhexadecylamine, have shown their ability to elicit plant growth at above and below ground biomass (Fincheira and Quiroz 2018; Chung et al. 2016) (Table 1.6).

Few studies indicate that VOCs act as signals and chemical messengers to regulate phytohormone synthesis, metabolic pathways, and nutrition levels. Effects of VOCs for induction of resistance and tolerance in plants are documented, wherein compounds such as 3-pentanol, dimethyl disulfide, 6-pentyl- $\alpha$ -pyrone, and acetoin were reported. VOCs derived by rhizospheric bacteria showed antagonistic activity toward plant pathogen *Rhizoctonia solani* and inhibit mycelial growth (Kai et al. 2007). Certain plant volatiles are proven to induce plant growth promotion through biochemical signals, eliciting local defence reactions known as induced systemic resistance (Chung et al. 2016; Kai et al. 2007). Long-chain VOCs signaling molecules, acetoin 2,3-butanediol, ethanethiol, isoprene, and acetic acid-butyl ester, and tridecane are found to be involved in induced resistance in *Arabidopsis* (Lee et al. 2012a, b). Yi et al. (2016) reported that 2,3-butanediol is produced by a *Bacillus subtilis* isolate involved in plant defense mechanisms. Root exudates of pepper inoculated with the *B. subtilis* were used to challenge various phytopathogens. For example, growth of *Trichoderma* sp (saprophytic fungus) and *Ralstonia solanacearum* (soil-borne pathogen) was inhibited by VOCs. This indicates that VOCs triggered the secretion of root exudates and subsequently acted as a plant defence inducer toward soil-borne fungal and bacterial pathogens.

Volatile organic compounds such as dehydroaromadendrene,  $\alpha$ -pinene, tetrahydro-2,2,5,5-tetramethylfuran, (-)-trans-caryophyllene, and (+)-sativene-producing *Cladosporium cladosporioides* strain CL-1 showed increased growth parameters in Tobacco crop (Paul and Park 2013). In another study, rhizospheric

isolates such as *Bacillus subtilis* GB03, *Bacillus amyloliquefaciens* IN937, *Pseudomonas fluorescens* 89B-61, and *Paenibacillus polymyxa* E681 produced Brassinosteroid a long-chain VOC and signaling molecules such as acetoin 2,3-butanediol, ethanethiol, acetic acid-butyl ester, and isoprene. These VOCs are involved in induced systemic resistance in *Arabidopsis* (Lee et al. 2012a, b). Fresh weight, shoot length, chlorophyll concentration, and lateral root numbers of *Sorghum* were significantly increased by dimethylhexadecylamine produced by *Arthrobacter agilis* UMCV2. Salt tolerance, increased shoot and root length, fresh weight, and leaf surface area were increased in soybean by VOCs, 4-nitroguaiacol, and quinoline produced by Vaishnav et al. (2016). VOCs of fungal origin also showed increased growth parameters in host plants like lettuce, *Arabidopsis*, and tobacco. *Fusarium oxysporum* MSA 35 showed production of  $\beta$ -Caryophyllene and increased fresh weight of tobacco in field experiment (Minerdi et al. 2011). Sesquiterpenes synthesized by ectomycorrhizal fungi *Laccaria bicolor* increased the lateral root of *Arabidopsis* (Ditengou et al. 2015). In the same study, it was demonstrated that other ectomycorrhizal ascomycote, *Cenococcum geophilum*, which cannot synthesize Sesquiterpenes does not promote lateral root of *Arabidopsis*. These studies indicate that volatile organic compounds emitted by microorganisms in the rhizosphere are cheaper, effective, efficient, and eco-friendly alternatives for controlling phytopathogens.

Environmentally friendly biotechnological approaches offer the development of PGPR inoculants and their potential application in metal-contaminated systems. Plant growth promotion by PGPR is a result from improved nutrient acquisition or phytohormonal stimulation (Table 1.3). Different mechanisms involved in plant growth promotion were shown in Fig. 1.6. PGPR inoculants were widely used in agriculture, forestry, horticulture, and in environmental restoration/phytoremediation sectors.

## 1.7 Conclusion and Future Prospects

Although studies have focused on plant microbiome structure and its function under natural and agricultural environments, there have been no significant coordinated efforts to combine and translate research results into practical solutions for farmers. According to Busby et al. (2017), integration of beneficial plant microbiome into agricultural production is one of the ways to assist in achieving these goals. However, this requires large-scale efforts from academic and industry researchers, farmers, and policy-makers to understand and manage complex plant–microbiome interactions under current challenges of the agriculture production.

For achieving this goal, five key research priorities have been identified by Busby et al. (2017). Few research priorities include development of host–microbiome model systems with associated microbial culture collections and reference genomes; characterization and refinement of a model “plant genotype–environment stress–microbiome–management interactions”; elucidation of the role core microbiome and determine functional mechanisms of plant–microbiome interactions. These research priorities may enable us to manipulate agricultural microbiomes and thereby to



develop management strategies for increased production and productivity of global agriculture in a sustainable manner. One of the challenges for future research work includes protection and conservation of rhizosphere biodiversity and their potential application in agricultural soils. Sustainable agriculture production may not be possible unless integration of plant germplasm and beneficial microbial species in the current agricultural practices globally.

Exploitation and production of natural drug formulations from microbial species have gained a significant leap during last three decades. Therapeutic applications of anticancerous compounds extracted from actinobacteria have been well addressed (Busi and Pattnaik 2018). The research priority is now shifted toward rhizosphere microbial communities for developing new drugs through high-throughput screening and fermentation techniques. Exploitation of bioprospecting potential of rhizosphere microbiomes is an upcoming new avenue.

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