Rhizospheric Microbial Communities: Occurrence, Distribution, and Functions

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Abstract

Plant–microbe interactions are crucial for many ecological processes. These interactions majorly take place in the rhizosphere and are mediated by the secretion of organic compounds by plant roots. These compounds act as signalling molecules and also as carbon sources for microbes. Microbial community in the rhizosphere is very diverse and consists of bacteria, archaebacteria, viruses, fungi, actinomycetes, protozoans, arthropods, algae, and nematodes. The rhizospheric microbes promote plant growth by different mechanisms such as biocontrol activity, phytohormone secretion, siderophore production, mineral solubilization, nitrogen fixation, and enzyme production. Since, a large proportion of microbial diversity is still not cultured, the detection and phylogenetic characterization of such un-/non-cultured microorganisms require advanced molecular techniques viz. metagenomics, metabolomics, metatranscriptomics, and metaproteomics. Several factors affect the rhizosphere microbial population, including root exudates, type and age of the plant, status of plant health, and application of fertilizers, pesticides, and amendments. Plant growth-promoting microbes of the rhizosphere can be used as biofertilizers and biocontrol agents and rhizosphere competence is an important factor that determines their success. This chapter discusses all these aspects of rhizospheric microbial communities, especially their occurrence, distribution, and functions.

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12.1 Introduction

The interplay between plants and microorganisms play a crucial role in ecosystem processes, such as nutrient cycling. These interactions benefit both plants and microbes. The beneficial impact of these interactions on plant includes increased nutrient availability, protection against diseases, and increased tolerance to biotic and abiotic stresses. The plant secretes different root exudates which act as signalling molecules and also as substrates for many microbes. The rhizosphere is the zone where all these interactions take place. About 10–60% of the carbon which is fixed by the process of photosynthesis is released as root exudates from the plant as soluble sugars, amino acids, or products of plant secondary metabolism for the benefit of microbes (Prashar et al. 2014).

The rhizospheric microorganisms interact with the roots of the plants, soil, and other microbes in many ways and are crucial for the growth and development of plants. Plants can shape the microflora according to their needs by changing the composition of the exudates secreted by their roots (Meena et al. 2017). The rhizospheric microbial community is very diverse and the various groups present in the rhizosphere include fungi, virus, bacteria, nematodes, etc. Various microbes from the rhizosphere show beneficial activities in terms of the promotion of growth and development of plants. Therefore, the use of these beneficial rhizospheric microbes as biofertilizers can be a very important environment-friendly alternative for sustainable crop production (Dubey et al. 2016).

Rhizospheric microbial communities are very complex and affect plant health, and hence it is very important to study their interactions and exact role in the rhizosphere. Many advanced molecular techniques including metagenomics, metabolomics, metatranscriptomics, and metaproteomics are now employed routinely to gain information about the rhizospheric microbes interacting with the plants.

12.2 The Rhizosphere: History and Scope

The term "rhizosphere" (meaning "root and environment of influence") was first defined by Hiltner (1904), as "the compartment of soil which is influenced by plant roots" and is the site of interaction of roots, soil microbiota, and soil.

There are three separate zones in the rhizosphere: the endo- and ecto-rhizosphere and the rhizoplane (Fig. 12.1). The ecto-rhizosphere consists of soil in close contact with the roots of the plant, whereas the endorhizospheric zone majorly includes the inner tissue as well as the endodermis and cortical layers of the root. The

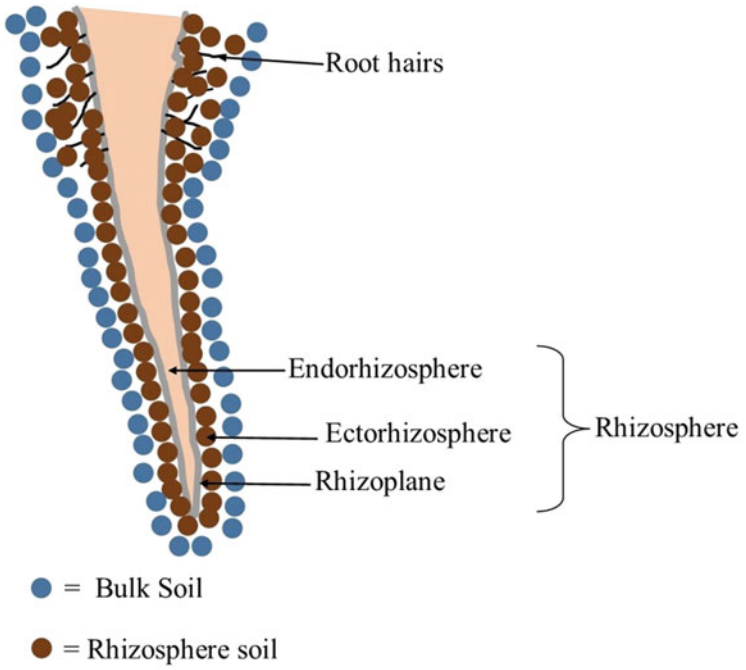

Fig. 12.1 The diagrammatic representation of the three separate zones in the rhizosphere

intermediate zone, i.e. the rhizoplane, includes the root surface and harbors most of the microorganisms and includes the mucilage and epidermal layers as well as the cortex. The physico-chemical soil characteristics are directly or indirectly affected by the interaction between root, soil, and rhizospheric microbes which ultimately change the rhizospheric microbial population (Huang et al. 2014; Shaikh et al. 2018).

The quantity of the microorganisms present in the rhizosphere is far greater than that in the non-rhizospheric soil since different carbon sources as well as other nutrients are present in higher quantities in the rhizosphere and the inhabiting microbes utilize these as energy sources. These organic compounds are deposited in the rhizosphere by plant roots. The rhizosphere is also the location of the interaction of soil-borne pathogens and plant roots. These pathogens compete with rhizospheric microbes for space and nutrients to cause infection the plants. In disease suppressive soil, the growth of the pathogens is suppressed by the rhizosphere microbes. Thus, the interaction between pathogens, rhizosphere microbes, and plant roots are key elements in shaping plant protective microbiome (Chapelle et al. 2016).

12.3 Structure and Abundance of Microbial Groups in the Rhizosphere

Rhizosphere harbors all types of microorganisms—bacteria, archaebacteria, viruses, fungi, actinomycetes, protozoans, arthropods, algae, and nematodes. All types of microbe–microbe and plant–microbe interactions occur in the rhizosphere. Rhizospheric soil contains up to 10^{11} microbial cells/gram of root (White et al. 2017). The approximate number of bacteria in the rhizosphere is 1.2×10^8 per gram of dry soil which is very high as compared to other groups of microbes. The number (Ahmad and Baker 1988) of fungi, algae, and actinomycetes is 12×10^5, 5×10^5, and 4.6×10^7, respectively (Shaikh et al. 2018). A summary of the most abundant members of different groups of microorganisms is provided in Table 12.1.

12.3.1 Bacteria

Different bacterial species are found in the rhizosphere depending on the root zone, plant health, and growth phase of the plant. *Proteobacteria*, *Firmicutes*, *Actinobacteria*, *Acidobacteria*, and *Bacteroidetes* dominate in the rhizospheric zones of different field crops, horticultural crops, and conifer plantations. *Proteobacteria* constitute the most abundant group followed by *Acidobacteria* (Lagos et al. 2015).

The high nutrient availability in the rhizosphere generally promotes bacterial species, like *Pseudomonas* sp., which are a fast-growing and opportunistic species. However, few studies have also shown that the *Actinobacteria* and *Coryneform* and not the Pseudomonads are the dominating bacteria in the rhizosphere of different plants belonging to family Gramineae (Miller et al. 1989, 1990).

Lee et al. (2015) determined the distribution of bacteria in general as well as some specific bacteria, such as archaebacteria, methanotrophic-, and methanogenic bacteria using pyrosequencing of 16S rRNA, in both the rhizospheric as well as bulk soil

Table 12.1 List of most abundant members of different groups of microorganisms in the rhizosphere

S. No.	Groups	Most abundant Genus/class/phylum
1.	Bacteria	*Pseudomonas* sp., *Bacillus* sp., *Arthrobacter* sp., *Rhizobia* sp., *Agrobacterium* sp., *Alcaligenes* sp., *Azotobacter* sp., *Mycobacterium* sp., *Flavobacter* sp., *Cellulomonas* sp. and *Micrococcus* sp.
2.	Actinobacteria	*Streptomyces* sp., *Micromonospora* sp., and *Nocardia* sp.
3.	Fungi	Ascomycota and Basidiomycota
4.	Arbuscular mycorrhizal fungi	*Glomus* sp., *Acaulospora* sp., *Gigaspora* sp.
5.	Virus	Myoviridae, Podoviridae, and Siphoviridae
6.	Archaebacteria	Crenarchaeota, Euryarchaeota, Thaumarchaeota

of paddy fields flooded with water. In the case of bacteria, major phyla at all depths in both the soils included, *Proteobacteria*, *Cyanobacteria*, *Chloroflexi*, *Bacteroidetes*, *Acidobacteria*, *Actinobacteria*, and *Firmicutes*. With the depth gradient of both the soils, the relative abundance of *Chloroflexi*, *Acidobacteria*, and *Actinobacteria* increased and that of *Cyanobacteria* and *Bacteroides* decreased. Archaebacteria belonging to phylum *Euryarchaeota* were found predominantly in both the soils at all depths.

Bacteria belonging to groups like *Actinobacteria*, *Firmicutes*, *Acidobacteria*, *Verrumicrobiaceae*, and *Chloroflexi* were isolated from *Jatropha curcas* rhizosphere (Dubey et al. 2016). The analysis of the bacterial population of the rhizosphere of the wild and domesticated barley using 16S rRNA pyrosequencing proved *Actinobacteria*, *Bacteroidetes*, and *Proteobacteria* to be the dominating ones (Bulgarelli et al. 2015). The rhizosphere and the non-rhizospheric soils of *Morus alba* commonly had the species of *Arthrobacter*, *Bacillus*, *Pseudomonas*, *Ensifer*, *Flavobacterium*, and *Brevibacillus* (Zhang et al. 2016). However, some bacteria were specific to the rhizosphere soil of *Morus alba*. These bacteria include the species of *Stenotrophomonas*, *Burkholderia*, *Acinetobacter*, *Sphingobium*, and *Variovorax*. Bacteria such as *Cupriavidus*, *Microbacterium*, *Sinomonas*, and *Agrobacterium* were only found in bulk soils.

Gaya Karunasinghe et al. (2020) isolated salt-tolerant *Serratia marcescens*, *Pseudomonas aeruginosa*, and *Alcaligenes faecalis* from the rhizosphere soil of tomato and checked their antagonism against *Pythium aphanidermatum.* Among these isolates, *Serratia marcescens* showed the highest activity and suppressed the disease by 68%.

Besides supporting the growth and development of associated plants, the rhizospheric microorganisms also enhance the rate of phytoremediation of heavy metals in the rhizospheric region by both direct and indirect pathways. Phytoremediation through direct processes involves phytostabilization or phytoextraction and through indirect promotion involves plant metal tolerance conferred by microbes. Wang et al. (2020) have found that rhizosphere bacteria in mining areas assist indigenous weeds as these can accumulate or exclude the heavy metals. Among all the weeds (*Cyperus difformis*, *C. iria*, *Digitaria sanguinalis*, *Echinochloa crusgalli*, *Fimbristylis miliacea,* and *Ludwigia prostrata*), the highest accumulation of copper, lead, and zinc occurred in the leaves and stems of *L. prostrata*. However, cadmium accumulation in the roots of *Ludwigia prostrata* was found lower than that in *D. sanguinalis* and *F. miliacea*. Highest Cd accumulation was recorded in *D. sanguinalis*. The bacterial diversity in the rhizosphere followed the order *C. difformis* (highest diversity) > *E. crusgalli* > *D. sanguinalis* > *L. prostrata* > *C. iria* > *F. miliacea*.

Cordero et al. (2019) isolated microbes from the rhizoplane and the rhizosphere of lentil, wheat, field pea, and canola and reported that the rhizosphere bacterial communities varied depending on the crops and sampling site location whereas root interior bacterial communities varied with plant species only. *Acidobacteria*, *Firmicutes*, and *Gemmatimonadetes* dominated the rhizosphere soil. The root interior of all crops was dominated by *Acinetobacter* sp., *Arthrobacter* sp., *Rhizobium*

sp., *Streptomyces* sp., *Variovorax* sp., and *Xanthomonas* sp. *Pseudomonas* sp., and *Stenotrophomonas* sp. were present in both the rhizosphere and interior of the root. In another study, 15 rhizospheric bacteria from tomato were found to possess at least one of the tested plant growth-promoting (PGP) activities, such as antibiotic resistance, P-solubilization, amylase activity, IAA production, etc. (Sunera et al. 2020). Two selected bacteria, *Klebsiella variicola* and *Bacillus cereus* increased the mineral (K, Fe, Cu, Zn, etc.,) uptake after their application on tomato and mung bean plants. Imriz et al. (2020) investigated the rhizosphere bacteria of wheat and barley for their biocontrol activity against fungal pathogen *Fusarium culmorum* using dual culture technique. From 463 isolates, only 31 showed the biocontrol activity against *F. culmorum*. In another study, Rana et al. (2011) isolated 100 bacteria from the rhizosphere of wheat and based on screening for different PGP attributes found that the species of *Bacillus*, *Providencia*, and *Brevundimonas* were most efficient in improving wheat growth under controlled conditions. Further, Rana et al. (2012) also demonstrated that the use of *Providencia* sp. and *Anabaena* sp. could help save half of the N-fertilizer and at the same time improving the protein content of wheat by 18.6%.

12.3.2 Fungi

Diverse kinds of fungi, both beneficial and harmful, are present in the rhizosphere. The diversity of the rhizospheric fungi depends on the type of plant, its health status, the characteristics of root exudates, as well as the presence of antagonists. Mahamuni et al. (2012) isolated *Aspergillus niger*, *Aspergillus awamori*, *Aspergillus fumigatus*, *Alternaria alternata*, *Curvularia pallescens*, *Penicillium oxalicum*, *Penicillium rubrum,* and *Trichoderma viride* from the rhizosphere of sugarcane and sugar beet, which were capable of solubilizing phosphate from soil. Different fungi belonging to Ascomycota and Basidiomycota were isolated from the rhizosphere of soybean in a continuous cropping system (Bai et al. 2015). Sugiyama et al. (2014) analyzed rhizospheric soil of soybean using pyrosequencing and reported that the rhizospheric microflora changes with the growth stage of the plant. Ascomycota group of fungi were dominant in all types of soil (Moshiri et al. 2019) followed by Basidiomycota.

Gqozo et al. (2020) investigated the fungal diversity in the bulk and rhizosphere soil of wheat using next-generation sequencing and found Ascomycota to be the dominating phylum in the rhizosphere soil followed by Basidiomycota. Among Ascomycota, members of classes Sordariomycetes, Dothideomycetes, Eurotiomycetes, and Orbiliomycetes were found to be the dominating. The prevalent genera were *Fusarium*, *Aureobasidium*, and *Colletotrichum*. Agaricomycetes and Tremellomycetes belonging to class Basidiomycota.

Manici and Caputo (2020) investigated the effect of binucleate *Rhizoctonia* sp., which is the anamorphic stage of *Ceratobasidium* sp., on the growth of apple plants. Binucleate *Rhizoctonia* after colonizing the rhizosphere increased the fresh and dry shoot biomass and also helped the plant to mitigate water stress. Temperature or the

season also influenced the fungal population. Ascomycota was found to dominate during summer and Basidiomycota during winter in the rhizosphere soil of *Coptis chinensis* fields which were not cropped for more than 3 years (Alami et al. 2020).

Gao et al. (2019) investigated how the continuous cropping of sweet potato affected its rhizosphere fungal community and found a significant increase in the diversity and richness of the fungi. Ascomycota dominated the rhizosphere soil which decreased after continuous cropping. The number of pathogenic fungi belonging to *Verticillium*, *Colletotrichum*, *Fusarium,* etc. increased whereas that of beneficial fungi such as *Chaetomium* sp. decreased. The increased number of pathogenic fungi led to decreased yield and quality of sweet potato.

Salinity also affects rhizospheric fungal communities. The effect of salinity was investigated on the rhizospheric fungal population of the halophytic black mangrove, *Avicennia germinans,* from a semi-arid mangrove. Samples were taken from three different sites having different salinity (23.2%, 14.61%, and 2.8%). *Aspergillus* sp., *Saitozyma* sp., *Trichoderma* sp., *Podosphaera* sp., and *Cystofilobasidium* sp. were dominant in samples from high salt containing location (23.2%) while *Penicillium*, *Trichoderma*, *Cystobasidium*, and *Aspergillus* dominated the samples taken from lowest salinity conditions (2.8%). Genus *Amorosia*, *Phaeoacremonium*, *Aspergillus*, *Talaromyces*, and *Trichoderma* were prevalent in the samples having 14.61% salinity. *Aspergillus* sp. was found to be present in all three levels of salinity (Vanegas et al. 2019).

In another study, Kazerooni et al. (2017) compared the diversity of tomato rhizosphere fungi under the conventional as well as desert farming systems. They used two different techniques, pyrosequencing and culture-based technique for this purpose. Culture-based techniques revealed that in both conventional and desert farming systems, Ascomycota was found to be the most abundant phylum. Zygomycota and Oomycota were found only in desert farming and conventional farming, respectively. *Aspergillus* was the most abundant genera in both farming systems. Pyrosequencing methods indicated that Microsporidia was the most abundant taxa in the conventional farming system followed by Ascomycota, Chytridiomycota, Basidiomycota, and Zygomycota. In the desert farming system, Ascomycota was found to be the most abundant taxa. Zygomycota and Chytridiomycota were absent in the desert farming system.

12.3.3 Arbuscular Mycorrhizal Fungi (AMF)

AMFs are present as symbionts of most of the higher plant roots, except the members of Cruciferae, Chenopodiaceae, and Caryophyllaceae families, and cover nearly about 80% of plant's root. Plant roots provide photosynthetically fixed carbon to AMF and obtain mineral nutrients in return. AMFs are divided into two major groups: (a) ectomycorrhiza and (b) endomycorrhiza. Ectomycorrhiza have dense mycelial sheath invading the root cortex and are limited to most temperate forest trees; while endomycorrhiza form external hyphal networks in the soil and grow extensively within the cells of the root cortex of most of the field crops. In addition to

improving plant nutrition, AMF provides resistance to plant against soil-borne pathogenic microorganisms and insects feeding on areal parts, drought, salinity, and heavy metals as well as in improving soil aggregate stability (Tripaldi et al. 2017).

Various species of AMF have been reported from different plants with *Glomus*, *Acaulospora*, *Gigaspora* being the most common one. Jefwa et al. (2012) isolated 22 AMFs from the rhizospheric zone of banana and plantain. These fungi belonged to *Acaulospora* sp., *Archaeospora* sp., *Glomus* sp., *Scutellospora* sp., and *Gigaspora* sp., and the highest abundance in the banana rhizosphere was of *Acaulospora scrobiculata*. Whereas, the most abundant species of AMF in the rhizosphere of soybean were *Glomus fasciculatum* and *Glomus mosseae* (Danesh et al. 2006). In a study, Kumalawati et al. (2014) isolated different AMF from the rhizospheric region of sugarcane belonging to the genus, *Glomus*, *Acaulospora*, *Gigaspora,* and *Sclerocystis*. They also found that two genera, *Glomus* and *Gigaspora,* have similar abundance and spore characteristics indicating their widespread capability to associate with sugarcane.

AMF increases the plant efficiency for the absorption of phosphate from the soil solution and also increase the growth of plants under salt stress. Phosphate solubilizing rhizobacteria solubilize phosphate which is absorbed and transferred by mycelium of external arbuscular mycorrhiza. In a study, seeds of *Kosteletzkya virginica* were inoculated with *Glomus mosseae* and *Glomus aggregatum*, both from saline soil and *Mortierella* sp. which was first grown on solid Martin culture media. Co-inoculation of AMF and *Mortierella* sp. enhanced the root colonizing efficiency under saline conditions (Zhang et al. 2011).

Hyphae and spores of AMF secrete glomalin protein in the soil from which it can be estimated quantitatively as "glomalin-related soil protein (Wu et al. 2015a)." It plays an important role in carbon storage, soil aggregation, carbon storage, and stress tolerance. AMF is also a source of different soil enzymes (Wu et al. 2015a). Root exudates and mycorrhiza act as sources of energy to the rhizosphere microbiota, which secrete extracellular enzymes for degrading soil organic matter (Shahzad et al. 2015). Synergism of AMF and *Bradyrhizobium* with beneficial rhizospheric microbes has also been found to increase nitrogen and phosphorous acquisition in soybean and improve the rhizospheric environment (Meena et al. 2018).

The diversity of AMF is correlated with plant diversity rather than bacterial diversity in soil. Bi et al. (2020) isolated AMF from the rhizosphere of *Leymus chinensis*, *Calamagrostis rigidula*, *Lespedeza hedysaroides*, *Vicia amoena*, *Carex* sp., and *Artemisia* sp. to check the specificity and diversity of AMF in the Sonnen grassland of China. A total of 24 species belonging to six different genera (*Acaulospora* sp., *Glomus* sp., *Gigaspora* sp., *Pacispora* sp., *Racocetra* sp., and *Rhizophagus* sp.) were isolated, among which *Glomus* sp. and *Acaulospora* sp. dominated. *Glomus* sp. also dominated in the rhizosphere of all plants except *Artemisia lavandulaefolia,* in which *Acaulospora laevis* was the most dominating species.

In an interesting experiment of tomato-potato onion intercropping, Gao et al. (2020) found that the AMF abundance in the rhizosphere of tomato was increased by

intercropping, whereas that in case of potato onion declined (*Allium cepa* var. aggregatum). Phosphorus fertilization moderated these effects and was found to be the key factor in driving the AMF communities. When phosphorous fertilizers are applied in a higher amount, the AMF root colonization was negatively affected but the moderate application of phosphorous stimulated the AMF root colonization. AMF species namely *Diversispora*, *Archaeospora*, and *Paraglomus* were found in soil where no phosphorous fertilization was done, while phosphorous fertilized soil was dominated by *Glomus*.

AMF is also crucial for the nitrogen cycle as AMF competes with ammonia oxidizers for ammonium ion (NH_4^+). Wattenburger et al. (2020) examined the abundance of ammonia-oxidizing bacteria and archaebacteria in the rhizosphere and bulk soil of corn under conventional cultivation and diversified cultivation systems and found it to be significantly affected by the cropping system and rhizosphere, but not by AMF in nitrogen-enriched soil.

Jamiołkowska et al. (2019) concluded that when AMF *Claroideoglomus etunicatum* was inoculated on tomato plants, it directly affected the rhizosphere population of fungi and increased the number of saprotrophs. A total of 3086 fungal colonies were isolated from the tomato rhizosphere during a 3-year mycological analysis using Warcup's method. These fungi belonged to 42 different genera mainly dominated by *Fusarium*, *Mucor*, *Penicillium*, and *Trichoderma.*

Plant hormones strigolactones are released from roots which induce branching in AMF. In a study, Carvalhais et al. (2019) reported that the fungal rhizosphere community was affected by the release of strigolactones from the roots of *Arabidopsis thaliana*. However, no effect on the bacterial rhizosphere community was observed. Fungi attracted to the roots due to the release of strigolactones comprise mainly, *Epicoccum* sp., *Penicillium* sp., *Fibulochlamys* sp., *Herpotrichiellaceae* sp., *Mycosphaerella* sp., and *Mycosphaerellaceae* sp.

12.3.4 Viruses

Viruses present in soil are of great ecological importance. Viruses can transfer genes from host to host and potentially cause microbial mortality, which affects microbial evolution in the rhizosphere. Rhizosphere has a high population of various kinds of microorganisms is high compared to bulk soil which can be linked to high viral diversity and abundance in the rhizosphere. The viral abundance of different soils can be enumerated using plaque assay, epifluorescence microscopy (EFM), and transmission electron microscopy (TEM) and it is reported that around 10^8 virus particles are present per gram dry weight of soil (Williamson et al. 2003). The viral particles are most abundant in forests and wetlands followed by cold deserts, fields, and agricultural soils. The lowest abundance of viral particles is found in hot deserts. In the soil systems, tailed phages belonging to Myoviridae, Podoviridae, and Siphoviridae (Pratama et al. 2020) are more abundant. Swanson et al. (2009) took different samples from the rhizosphere of *Triticum aestivum* and analyzed the presence of different virus particles in the samples. The majority of tailed phages

isolated belonged to family *Podoviridae,* whereas members of family *Myoviridae* and *Siphoviridae* were almost equal in numbers. Different spherical viruses, filamentous particles, rod-shaped type viruses, and bacilliform particles were also found in the rhizospheric samples.

Similarly, Cubo Sánchez et al. (2020) studied the virulent phage diversity of the *Medicago marina* rhizosphere, using seven different strains of bacteria *Sinorhizobium meliloti* as a host for viruses. Eight new sinorhizobiophage lytic phages were isolated from the rhizosphere. These viruses belonged to family Myoviridae, Syphoviridae, Podoviridae, and Inoviridae. Berrios and Ely (2019) isolated the Kronos virus from the rhizosphere of the dichotomous plant by using *Caulobacter* wild type strain. Hence, the phage numbers and diversity depend on the type of bacterial/fungal species present in the rhizosphere.

12.3.5 Archaebacteria

The diversity of archaebacteria in the rhizosphere is less known when compared to bacteria due to a limited number of such studies. Archaebacteria can be crucial for plant survival by transforming soil mercury by reduction, methylation, and demethylation (Ma et al. 2019). In the recent past, many studies have explored the archaeal diversity of rhizosphere of many crops, such as *Jatropha curcas* (Dubey et al. 2016), rice fields (Srivastva et al. 2018; Ma et al. 2019), rhizosphere of *Suaeda nudiflora* and Banni grass (Yadav et al. 2019), and tomato rhizosphere (Taffner et al. 2020), etc.

The rhizosphere bacterial and archaebacterial diversity associated with *J. curcas* was explored by employing terminal restriction fragment length (T-RFLP) and targeted the 16S rDNA region. Bacterial indicative terminal restriction fragments were *Actinobacteria*, *Firmicutes*, *Acidobacteria*, *Verrumicrobiaceae*, and *Chloroflexi* while the archaeal terminal restriction fragments were majorly crenarchaeota and euryarchaeota (Dubey et al. 2016). Ma et al. (2019) isolated archaebacteria from the rhizosphere of the rice fields containing mercury gradient and reported that Thaumarchaeota was prevalent in the rhizosphere as well as non-rhizospheric soil of rice fields, followed by Crenarchaeota and Euryarchaeota. *Methanolobus tindarius*, *Methanomethylovorans hollandica*, *Methanospirillum hungatei*, *Methanomassiliicoccus luminyensis*, *Methanocorpusculum bavaricum*, *Methanofollis liminatans*, *Methanosphaerula palustris*, and *Methanocella paludicola* are the well-known archaebacteria which methylate mercury. These are all known to possess the *hgcAB* gene cluster which is linked to mercury methylation. In another study, archaebacterial diversity and abundance of nitrogen fertilized rice fields were studied and it was reported that the *Methanocellales*, *Methanomicrobiaceae*, *Methanobacteriaceae*, *Methanisarcinaceae*, and *Methanosaetaceae* were found in all types of soils but their abundance varied with the type of soil (Srivastva et al. 2018). Yadav et al. (2019) isolated archaebacteria from different plant rhizospheres in Rann of Kutch and reported that the culturable archaebacterial diversity associated with the rhizospheres of *Suaeda nudiflora* and

Banni grass were maximum and minimum, respectively, with a seasonal fluctuation in their number and genera. The amplification and sequencing of the16s rDNA region showed that 16 different genera, majorly of halophilic archaea were found during all the seasons. Taffner et al. (2020) isolated archaea from the tomato rhizosphere and found Thaumarchaeota and Euryarchaeota as dominated rhizospheric archaebacterial groups.

12.4 Plant Growth-Promoting (PGP) Rhizobacteria and the Rhizosphere

Microbes that are present in the rhizosphere soil can secrete phytohormones (indole acetic acid, gibberellins, siderophores), enzymes, and antibiotics, and solubilize minerals, thereby, improving the growth and developments of plants. Different plant beneficial rhizobacteria like *Pseudomonas* sp., *Azospirillum* sp., *Azotobacter* sp., *Bacillus* sp., *Burkholderia* sp., *Enterobacter* sp., *Rhizobium* sp., *Erwinia* sp., *Mycobacterium* sp., *Mesorhizobium* sp., *Flavobacterium* sp., etc., have been reported from the rhizosphere of different crop and wild plants (Table 12.2).

12.4.1 Antagonistic Plant Growth-Promoting (PGP) Rhizobacteria

Different mechanisms are employed by rhizospheric microbes to control the phytopathogens including the production of antibiotic, bacteriocin, siderophore, volatile and low molecular weight organic compounds, hydrolytic enzymes (e.g., chitinases and glucanases, etc.), phytoalexins (Sindhu et al. 2016) as well as induction of systemic response. Therefore, many microbes in the rhizosphere act as antagonists of the pathogenic macro- and microorganisms and enhance crop productivity.

Research by Zhao et al. (2018) showed that five bacterial strains, namely *Bacillus cereus*, *B. subtilis*, *Pseudomonas putida*, *P. fluorescens*, and *Serratia proteamaculans,* isolated from fields of cucumber, tomatoes, and other crops, showed antagonistic activity against root-knot disease-causing nematode. *Serratia proteamaculans* was the superior bacteria, causing more than 99% and 61% mortality in *Meloidogyne incognita* juveniles and eggs, respectively, resulting in the highest root and shoot growth during pot experiment.

Biocontrol activity of bacteria *Bacillus amyloliquefaciens* Ba13 against yellow leaf curl virus disease in tomato was reported by Guo et al. (2019). It was mediated by the induction of systemic response against virus and also influenced the rhizospheric microbial community, by decreasing the number of pathogenic *Fusarium solani,* and *F. oxysporium*. Actinomycete *Streptomyces pactum* was also reported for its biocontrol activity against the leaf curl virus by Li et al. (2019). Figueroa-López et al. (2016) isolated bacteria viz. *Bacillus*, *Pseudomonas*, *Enterobacter*, and *Lysinibacillus* from maize rhizosphere which exhibited biocontrol activity against *Fusarium verticillioides,* the causative agent of rot in maize. Etesami

Table 12.2 Different PGPR isolated from different crops and their PGP attributes

S. No.	Crop	PGPR	PGPR attribute	Reference
1.	Tomato	*Bacillus* sp., *Pseudomonas* sp.,	Biocontrol	Zhao et al. (2018)
2.	Wheat	*Lysinibacillus* sp.	Salt tolerance, IAA production	Damodaran et al. (2019)
3.	*Salicornia* sp.	*Staphylococcus* sp.	Salt tolerance, IAA, and ACC-deaminase production, phosphate solubilization	Razzaghi Komaresofla et al. (2019)
4.	Wheat	*Pseudomonas* sp.	IAA production, P-solubilization	Emami et al. (2019)
5.	Rice	*Brevibacterium sediminis*	Biocontrol, IAA and HCN production, P-solubilization, ammonia generation, chitinase synthesis	Chopra et al. (2020)
6.	Maize	*Enterobacter cloacae*	IAA, and ACC deaminase, and Siderophore production, P-solubilization	Abedinzadeh et al. (2019)
7.	Wheat	*Pseudomonas* sp.	P-solubilization, auxin production, HCN production, siderophore production	Karimzadeh et al. (2020)
8.	*Salicornia bigelovii*	*Streptomyces* sp.	IAA synthesis, generation of ACC deaminase	Mathew et al. (2020)
9.	Wheat	*B. pumilus*, *Pseudomonas putida*, *Stenotrophomonas maltophilia*	P-solubilization, HCN production, Ammonia production, Siderophore production	Kumar et al. (2019)
10.	Maize	*Bacillus* sp.	Salt stress, ethylene metabolism, IAA production	Misra and Chauhan (2020)
11.	Tomato	*Bacillus* sp.	Biocontrol, ammonia production, IAA production, P-solubilization	Pathania et al. (2020)
12.	Soybean	*Streptomyces* sp.	IAA production, P-solubilization	Wahyudi et al. (2019)
13.	Rice	*B. subtilis* *P. fluorescens*	Biocontrol siderophore production, Chitinase production	Karnwal and Mannan (2018)
14.	Chilli	*Bacillus amyloliquefaciens*	Biocontrol, IAA synthesis, Siderophore and ammonia generation, Cellulose production, P-solubilization	Passari et al. (2018)

and Alikhani (2018) tested the antagonism of rhizospheric and endorhizospheric bacteria (majorly *Bacillus* sp.) of rice, clover, and rapeseed, grown under rotation, against five different fungal pathogens belonging to *Magnaporthe* sp., and *Fusarium* sp. The biocontrol activity of microbial agents, thus, depends upon the rhizospheric microbial community also. In a similar study, Gómez-Lama Cabanás et al. (2018)

have reported the biocontrol efficacy of olive rhizosphere inhabiting *Pseudomonas* sp. against *Verticillium* wilt causing pathogen.

12.4.2 Mineral Solubilizers

Rhizospheric microbial population supports the growth and development of plants by solubilizing different minerals in the rhizosphere. Different mineral-solubilizing rhizospheric microbes help in increasing the solubility of macro- and micro-nutrients, such as phosphate, potassium, zinc, silicon, aluminum, iron, etc. (Zhang et al. 2016; Dhaked et al. 2017). Zhang et al. (2016) reported the presence of highly efficient bacteria, capable of solubilizing zinc, silicon, aluminum, and iron, in the rhizosphere soils of *Morus alba*. These bacteria were dominated by *Arthrobacter* sp., *Bacillus* sp., and *Stenotrophomonas* sp., in contrast to *Arthrobacter* sp. and *Pseudomonas* sp. dominating in the bulk soil. Furthermore, *Bacillus licheniformis* isolated from the rhizosphere of different crops showed the highest efficiency for solubilizing phosphate and potassium from tri-calcium phosphate and waste muscovite, respectively (Bahadur et al. 2017). Different fungi namely, *Aspergillus* sp., *Trichoderma* sp., and *Penicillium* sp. have also been reported for their phosphate solubilizing activity (Mahamuni et al. 2012).

Verma and Kaur (2015) isolated bacteria from the rhizosphere of apple, which was found to solubilize the mineral phosphate. *Pseudomonas* sp. was the most potential solubilizer with other plant growth supporting activities, such as the production of HCN, IAA, siderophore, and ammonia apart from acting as a biological control agent against pathogenic fungi, *Dematophora nectarix,* and *Phytophthora cactorum*.

The mechanism of phosphate solubilization by these bacteria includes the production of organic acids which convert the complex insoluble forms of phosphate into soluble forms by chelating the cations bound to phosphorous (Zheng et al. 2018). Many different organic acids are produced by bacteria which include oxalic, fumaric, malic, 2-ketoglutaric acid, malate, gluconate, citric, tartaric acid, etc. (Babana et al. 2013; Illmer and Schinner 1992).

12.4.3 Nitrogen Fixation and Phytohormone Production

Many bacteria in the crop rhizosphere can fix atmospheric nitrogen (N). Some of the predominating nitrogen-fixing bacteria are *Azotobacter* sp., *Azospirillum* sp., *Herbaspirillum* sp., *Burkholderia* sp., and *Pseudomonas* sp.

Li et al. (2017) isolated *Pseudomonas* from the sugarcane rhizosphere which showed the ability to fix nitrogen as well as the production of IAA, ACC deaminase, and antibiotics. Tam and Diep (2015) reported the presence of N-fixing *Bacillus*, *Proteobacteria*, *Acidobacteria*, and *Bacteroides,* in the sugarcane rhizosphere. All these have shown the ability to solubilize phosphate and IAA production. Similar research by Majeed et al. (2015) reported seven out of nine isolates bacterial isolates

for PGP activities, such as N-fixation, as well as abilities to produce IAA and solubilize inorganic phosphate.

Phytohormones (IAA, auxin, etc.,) are secreted by the rhizospheric microbial population which directly affects the growth and development of plants. For example, Bahadur et al. (2017) isolated mineral solubilizers from the rhizosphere of different crops grown in the Gangetic planes, exhibiting PGP activities through the synthesis of IAA, ammonia, HCN, etc. The highest amount of IAA production was shown by *Brevibacillus formosus* followed by *Bacillus subtilis*.

12.5 Advanced Techniques for Studying Rhizospheric Microbial Communities

The major proportion of microbes, nearly 99% present in the rhizosphere are un-culturable. These microbes cannot be isolated using simple techniques; therefore, advanced biochemical and molecular techniques are used for their isolation and studies. Various techniques, traditional as well as modern molecular techniques, used to study the rhizospheric microbes have been discussed in detail in various reviews (Nannipieri et al. 2017; Vitorino and Bessa 2018; Salmonová and Bunešová 2017; van Elsas and Boersma 2011). These different techniques with their advantages and disadvantages are summarized in Table 12.3 and an overview of some important advanced techniques is presented in the following discussion.

12.5.1 Fingerprinting Techniques

For the study of rhizosphere, microbiome fingerprinting techniques, T-RFLP, denaturing gradient gel electrophoresis (DGGE), and single-strand conformation polymorphism (SSCP) are generally used. Yang et al. (2001) employed a PCR-DGGE 16S rDNA fingerprinting technique to study the difference in the healthy and *Phytophthora* infected avocado root rhizosphere population. They found different microbial communities dominated the healthy and infected plant rhizosphere. However, the rhizospheric population of trees treated with antagonist *Pseudomonas fluorescens* and nontreated healthy trees indicated the role of Pseudomonas in restoring the rhizospheric microbes in diseased plants. Kawasaki et al. (2016) analyzed the rhizosphere microbiome of *Brachypodium distachyon* using the T-RFLP technique (by targeting the 16S rDNA and ITS region of bacteria and fungi, respectively, and root exudates using HPLC analysis. They reported the similarity between the rhizosphere microbial communities and root exudates of *Brachypodium distachyon* and wheat, in contrast to differences between those from *B. distachyon* and *Arabidopsis* rhizosphere.

Zachow et al. (2014) carried out SSCP analysis to check the difference between the rhizospheric microbiome of modern sugar beet and *Beta vulgaris* ssp. *maritima*. They reported that *Beta vulgaris* spp. *Maritima*, which is an ancestor of all beet crops

Table 12.3 Techniques commonly used for the study of rhizospheric microorganisms

S.No.	Technique	Description	Advantages	Disadvantages
A. Culture-based techniques				
1.	Direct plating	Microbes are cultures on solid growth medium	Simple and sensitive, Isolates can be utilized for various purposes	Only 0.5–1.0% of total microbes are culturable due to different growth requirements of microbes
2.	Community-level physiological profiles (CLPP)	Heterotrophic microbial communities are classified and characterized based on carbon source utilization patterns	Simple and high throughput, requires less time	Sample preparation and inoculation needs accuracy, data analysis and interpretation is difficult
3.	Most probable number	Used for enumeration of low abundance specific groups of microorganisms	Useful for enumeration of low abundance microorganisms	Labor intensive, only specific groups can be enumerated
B. Culture-independent techniques				
1.	Phospholipid fatty acid (PLFA) analysis/fatty acid methyl ester analysis (FAME)	Fatty acid acids are extracted and unique fatty acids for each group of microorganisms is quantified to estimate the microbial activity	Culturing of microorganisms is not required, information on all organisms is acquired simultaneously	The sample has to be processed immediately after sampling, biased towards the more abundant group of microorganisms, not a high throughput method
2.	Fluorescent in situ hybridization (FISH)	16S or 23S rDNA region is hybridized with fluorescent dye-tagged taxon-specific oligonucleotide probes after fixing the whole cell and then visualized under scanning confocal laser microscopy	Microbial detection across various phylogenetic levels, more sensitive than immunofluorescence due to non-specific bonding with the particles of the soil	Not as sensitive as nucleic acid hybridization using environmental samples, absence of low copy number sequences are difficult to detect
3.	DNA microarray	A very small array of complementary DNA probes which are between 5×10^2 to 5×10^3 bases, or oligonucleotides having between 15–17 base pairs, linked directly to a solid matrix, Allows concomitant hybridization of many probe sets complementary to target DNA/RNA	Analysis of genes of the magnitude of 10^3, highly specific detection	Species having high abundance are detected, only culturable, low microbial diversity can be analyzed, non-specific hybridization may produce misleading signals, lack of specificity, sensitivity, and quantification

(continued)

Table 12.3 (continued)

S.No.	Technique	Description	Advantages	Disadvantages
4.	Single-strand conformation polymorphism (SSCP)	Distinct ssDNA is resolved through gel electrophoresis on the basis of differences in the nucleotide sequences leading to hetero duplexes formation and changes in movement of DNA through gel	Simultaneous and multiple-sample analysis with high speed, reliability and reproducibility	Sometimes PCR-induced sequence artifacts or bias occurs
5.	Restriction fragment length polymorphism (RFLP)	Based upon polymorphisms of the DNA, run on electrophoresis followed by restriction digestion, blotting on suitable membranes, and hybridization with suitable probes (made by cloning)	Detection of the structure related differences in the population of microorganisms	Sometimes PCR-induced sequence artifacts or bias occurs
6.	Terminal restriction fragment length polymorphism (T-RFLP)	An extension of the RFLP/ ARDRA analysis, Different from RFLP in that one primer is fluorescently tagged with either 4, 7, 2′, 7′-tetrachloro-6-carboxyfluorescein or 6-phosphoramidite fluorochrome-5-carboxyfluorescein	Pattern of bands is not complicated as in RFLP, automation is possible, numerous sample analysis is possible with better reproducibility when comparing different populations of microorganisms	Sometimes PCR-induced sequence artifacts or bias occurs, extraction and lysis need to be efficient, Taq polymerase dependent variation can occur, restriction enzyme needs to be well chosen for analysis
7.	Ribosomal intergenic spacer analysis Swanson et al. (2009)/automated ribosomal intergenic spacer analysis (ARISA)/ amplified ribosomal DNA restriction analysis (ARDRA)	IGS region of 16S and 23S rDNA is subjected to amplification, denaturation, and separation on denaturing-PAGE	Highly reproducible community profiles of different bacterial strains or the closely related species	Requires large quantities of DNA Swanson et al. (2009) PCR biases
8.	Denaturing and temperature gradient gel electrophoresis (DGGE and TGGE)	Separation of DNA segments having with only single nucleotide differences is possible, due to distinct T_m and resolution	Simultaneous and multiple-sample analysis with high speed, reliability and reproducibility	Sometimes PCR-induced sequence artifacts or bias occurs, extraction, lysis, storage need to be efficient, multiple-species can be migrated in one band, detection of dominating species

harbored a distinctive set of rhizospheric microflora than modern domesticated sugar beet.

12.5.2 Quantitative PCR and Gene Expression

The quantitative PCR technique detects and quantifies specific genes and their expression. Dudenhöffer et al. (2016) quantified the total and specific disease suppressive bacteria using quantitative real-time PCR. Growth of disease suppressive bacteria especially fluorescent pseudomonads was selectively enhanced by the barley plant for biocontrol of pathogenic fungi, *Fusarium graminearum*.

Shrestha et al. (2010) used PCR for amplification of the *pmoA* gene and quantitative RT-PCR to determine the copy number of *pmoA* gene to check the efficacy of nitrogen fertilizers on the metabolism, microbial diversity, and gene expression in methanotrophic bacteria present in the rhizosphere of rice. It was found that type-I methanotrophic bacteria dominated during the whole season whether nitrogen fertilizer was applied or not, while the population of type-II methanotrophic bacteria increased only under the more conducive conditions, like ammonium sulfate fertilizer application. Studies have also employed quantitative PCR analysis (Marques et al. 2014) to determine the effect of resistance breeding on the microbial communities of the common bean rhizosphere, by analyzing the bacterial gene expression in rhizospheric and non-rhizospheric soil (Mendes et al. 2018). It was found that the pseudomonads, bacilli, and members of solibacteraceae and cytophagaceae dominated in the rhizospheric soil of the *Fusarium oxysporium* (Mendes et al. 2018) resistant varieties than in susceptible ones. Microarrays and real-time quantitative PCR are used for rhizospheric studies of microbial communities. Despite being powerful techniques, these are not without limitations. Using quantitative PCR only a few genes can be analyzed at once and for microarrays analysis, previous knowledge about targeted sequences is generally required (Carvalhais et al. 2013).

12.5.3 Meta-Omics Techniques

Apart from the techniques for studying the diversity and characteristics of the culturable microorganisms, many methods have also been developed for studying the microbial diversity and community structure of rhizospheric and non-rhizoshperic soils, namely, metagenomics, metatranscriptomics, metaproteomics, and metabolomics. These recent techniques based on the principles and tools of molecular biology have shown that the abundance of microbes in the rhizosphere and bulk soil is far more than predicted earlier (Lagos et al. 2015) using culturable methods. Basic principles and applications of these techniques concerning rhizosphere microbial diversity are discussed below.

The relative abundance and microbial types can be easily predicted using metagenomics, as it focuses on the DNA (Carvalhais et al. 2013). Mukhtar et al.

(2016) estimated the microbial diversity of the rhizosphere and rhizoplane, as well as that of histoplane of para grass cultivated in the saline environment. Culturable microbes were estimated and characterized by amplification and sequencing of 16S rDNA region, and biochemical analysis. While non-culturable microbes were characterized using 16S rRNA gene amplification from the metagenome. The most probable numbers of microbes from the studied regions of para grass were 150×10^7, 47×10^7, and 130×10^7, respectively. Using 16S rRNA gene sequencing analysis, a total of 26 operational taxonomic units (OTUs) were obtained from the rhizosphere. While for non-culturable microbes, a total of 48 16S rRNA clones, grouped into 25 OTUs, were obtained from the rhizosphere.

In contrast to metagenomics, metatranscriptomics focuses on RNA and involves the characterization of mRNA produced in the cells. This technique provides information about genes that are transcribed by the microbes and thus, helps in understanding the metabolism of the microbial population (Carvalhais et al. 2013; Lagos et al. 2015; Verma et al. 2018). Bacterial metabolism and gene expression in the rhizosphere before and after treatment with glyphosate has been analyzed using a metatranscriptomic approach (Newman et al. 2016b). The rhizospheric bacteria were reported to invest most of their energy in carbohydrate metabolism and transcription. After treatment with glyphosate, expression of genes encoding ATP-synthase and cytochrome c-553 increased significantly, denoting increased respiration after glyphosate treatment.

Metaproteomics provides information about the role of soil microbiota in different biogeochemical processes, degradation, or bioremediation processes by measuring the proteins present in the rhizospheric samples (Verma et al. 2018; Abiraami et al. 2020). Bona et al. (2018) characterized the rhizosphere of the *Vitis vinifera* using metaproteomics. They isolated protein from the soil, digested it with trypsin, and analyzed using mass spectroscopy. More than 570 proteins from over a hundred of bacterial genera were identified from bulk and rhizospheric soil, out of which 20 proteins were under constitutive expression due to their involvement in nutrient transport. It was analyzed that 56 proteins were expressed by bulk soil specific bacteria, 54 proteins were expressed by rhizosphere specific bacterial genera. Furthermore, a total of 59 bacterial genera were common in both the soil types.

For root exudate analysis, different metabolomics techniques can be used. Metabolomics can be used to analyze multiple compounds in one go. Metabolomic techniques may be used to identify compounds present in root exudate depends on the class of the compound. For example, in the case of volatile root exudates, GC-MS can be used, while for analysis of phenolics, flavonoids, or other water-soluble root exudates, liquid chromatography or nuclear magnetic resonance techniques can be used. A combination of different techniques can be used when there is insufficient knowledge about the types of molecules present in root exudates that are needed to be analyzed. Metabolomics also provides information about signalling networks present in the rhizosphere (van Dam and Bouwmeester 2016).

12.6 Factors Affecting Rhizospheric Microbial Population

Various factors influence the rhizospheric microbial population qualitatively as well as quantitatively (Fig. 12.2). The higher number of microbes in rhizospheric soil than bulk soil is due to the rhizospheric effect. The rhizospheric effect is measured by calculating R:S ratio (root:soil ratio) which is the proportion of the quantity of microbes present in the rhizosphere and bulk soil (Hiltner 1904). Both biotic and abiotic factors, directly as well indirectly affect the colonization of the microbial population in the rhizosphere. Such factors include pH of the soil, temperature, root exudates, competition, and inorganic nutrients, etc. and are summarized in Table 12.4 and discussed below.

12.6.1 Root Exudates

Microbes present in soil compete for available nutrients and other resources, which affect the growth of these microbes. Roots of plants influence the activity of these microbes by secreting root exudates, which are the compounds that are released from roots into the soil. The plant secretes these root exudates that promote specific microbes for colonization in the rhizosphere (Doornbos et al. 2012). These compounds include primary as well as secondary metabolites.

Various plant-related and external factors determine the quantitative as well as qualitative characteristics of the root exudates. In soil, the roots are exposed to different microbes which can be beneficial or pathogenic. Plants attract only specific microbes and can alter the diversity and composition of the rhizospheric microbial

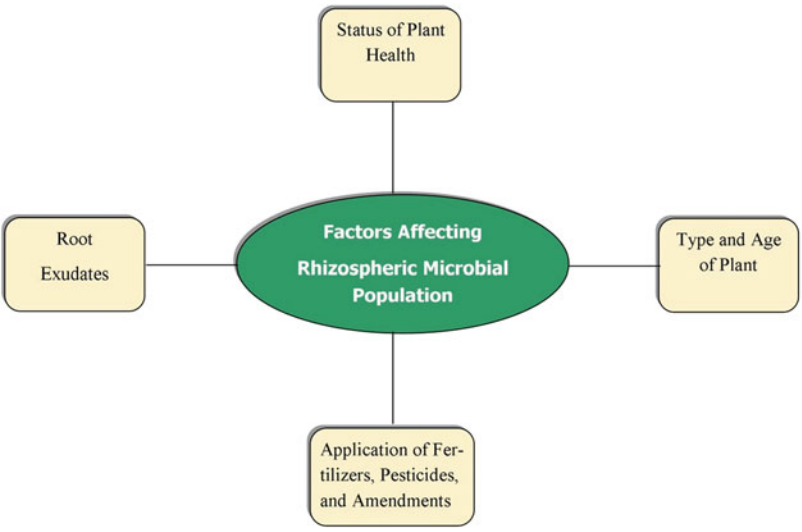

Fig. 12.2 Various factors influencing the rhizospheric microbial population

Table 12.4 Factors affecting the rhizospheric population

S. No.	Factor	Impact on microbial community	Reference
1.	Root exudates	Specific microbes are attracted to colonization and affect the rhizosphere microbial population both qualitatively and quantitatively	Doornbos et al. (2012) and van Loon et al. (1998)
2.	Type of plant	Rhizosphere microbial population varies with plant genotype and cultivar	Pérez-Jaramillo et al. (2016) and Weinert et al. (2011)
3.	Age of plant	Rhizosphere microbial community composition depends upon plant growth stage	Marques et al. (2014) and Sinegani and Sharifi (2007)
4.	Plant health status	Rhizospheric microbial population dynamics of healthy plant differs with that of diseased plant. Both rhizospheric bacteria and fungi are abundant in healthy plant than diseased plant	Wu et al. (2015b)
5.	Application of fertilizers	After N-fertilizers application number of *Azospirillum lipoferum* and *Gluconacetobacter diazotrophicus* in rhizosphere is negatively affected, Bacillales, Nitrosomonadales, and Rhodocyclales become more dominating, while Chloroflexales, Gemmatimonadetes, and Phycisphaerae become less abundant	Zhu et al. (2016)
6.	Application of pesticides	Glyphosate application increased the number of pathogenic fungi (*Fusarium*) in the rhizosphere and negatively affected the fluorescent *Pseudomonads.* The number of Acidobacteria decreased after treatment with glyphosate and that of proteobacteria increased	Newman et al. (2016a) and Zobiole et al. (2011)
7.	Application of biofertilizers and compost	The number of beneficial microbial populations increased and the number of fungi decreased in the rhizosphere	Fu et al. (2017) and Mickan et al. (2018)
8.	Application of vermicompost	The activity of pathogens, *Pythium aphanidermatum*, *Pythium ultimum*, and *Rhizoctonia solani* was suppressed, the relative abundance of Ascomycota and Chytridiomycota increased and that of Glomeromycota and Zygomycota decreased	You et al. (2019)

population. Plant roots release different compounds in the form of organic-, fatty- or amino acids, simple carbohydrates, sterols, growth factors, etc. The process of release of these compounds is also known as rhizodeposition. These secreted compounds from roots are grouped into two classes: (1) low molecular weight

compounds, like phenolics, sugars, amino acids, organic acids, etc. and (2) higher molecular weight compounds viz., polysaccharides and proteins (Huang et al. 2014; Prashar et al. 2014). Root exudates are also classified as active and passive, depending upon the role and mode of secretion from roots. Active exudates have a specific function and are released via open pores of the cell membrane while passive exudates have an unknown function and constitute approximately 3–5% of total photosynthetically fixed carbon. Passive root exudates are released from the roots via diffusion. Further, exudates can be classified, based on their biological activity, as signal molecules, phytoalexins, phytohormones, enzymes, or allelochemicals (Prashar et al. 2014).

Limited plant nutrients also affect the root exudates and rhizospheric microbiome. In a study, it was shown that limiting the amount of nitrogen negatively influenced amino acid secretion in maize rhizosphere, which further suppressed the transcription of genes affecting translation in the bacterium *B. amyloliquefaciens* (Carvalhais et al. 2011).

12.6.2 Type and Age of the Plant

Rhizospheric microbial population is influenced by the plant characteristics (Pérez-Jaramillo et al. 2016; Sinegani and Sharifi 2007). Each plant recruits a particular set of the rhizospheric microbiome and rhizospheric microbial composition of plant species also varies with the phylogenetic distance (Pérez-Jaramillo et al. 2016). Rhizospheric microbial composition also varies with the genotypes of the same species. In a study, the relation between rhizospheric microbial composition and the growth of three cultivars of potato was analyzed using PhyloChips, which detected 2432 operational taxonomic units. Further, the rhizospheric microbial composition varied with cultivar, and varying microbial populations belonged mainly to the *Pseudomonadales*, *Actinomycetales,* and *Enterobacteriales* (Weinert et al. 2011). Marques et al. (2014) reported that age as well as the genotype significantly affected the rhizospheric population of sweet potato.

In a study, Sinegani and Sharifi (2007) investigated the number of AMF spores in 14 rhizospheric soils of different crops. They found the abundance of AMF varied based on the type of crop and vegetative stage of the crop. The rhizospheric AMF spore counts were the highest for *Zea mays* and the lowest for *Raphanus sativa,* during the mid-vegetative growth. After the vegetative growth culminated, the AMF spore counts were the highest in the *Allium cepa* rhizosphere and lowest in *Raphanus sativa*. During termination of the vegetative phase of development, the rhizosphere of *Triticum aestivum*, *Zea mays*, *Trifolium repens*, *Solanum tuberosum*, *Satureja hortensis*, and *Allium cepa* had the elevated counts of AMF spores.

12.6.3 Status of Plant Health

The rhizospheric microbial communities associated with the diseased plants differ significantly from the healthy plants of the same species. Wu et al. (2015b) demonstrated this in their experiment on rhizosphere soils from roots of diseased (root-rot disease) and healthy plants of *Panax notoginseng*. Microbial community of rhizosphere soil of both diseased and healthy plants was analyzed using throughput sequencing of the amplified bacterial 16S or fungal 18S rDNA region and higher abundance of both bacteria and fungi in the rhizosphere of the healthy plants were found. Many bacteria were found dominant in the rhizosphere of both healthy and diseased plants, while some were specific to the rhizosphere of either healthy or diseased plants. Comparative analysis using Paired-T tests showed that Proteobacteria were more abundant while Acidobacteria, Cyanobacteria, Firmicutes, Verrucomicrobia were low in abundance in the rhizosphere of diseased plants. The rhizospheric fungi belonging to Ascomycota were more abundant while those belonging to Glomeromycota were less abundant in diseased plants. Basidiomycota and Zygomycota were the major phyla that were equally abundant in the rhizosphere of both the plants.

12.6.4 Application of Fertilizers, Pesticides, and Amendments

Rhizospheric microbial communities are very important for plant growth. The application of different amendments alters the rhizospheric microbial populations. In different studies, the effect of pesticide application on the quantity and quality of rhizospheric microbes has been established.

For example, glyphosate amendment the quantity of *Fusarium* in the rhizosphere, simultaneously affecting the population of fluorescent *Pseudomonads* as well as indole acetic acid-producing bacteria, and Mn-reducing bacteria (Zobiole et al. 2011). In another similar study, the initial rhizosphere population of soybean and corn was dominated by *Proteobacteria*, *Acidobacteria*, and *Actinobacteria* but after treatment with glyphosate, the number of *Acidobacteria* decreased in the rhizosphere of both soybean and corn. These bacteria were primarily involved in the cellulose biodegradation. The relative abundance of *Proteobacteria* increased after treatment with glyphosate (Newman et al. 2016a).

Application of N-fertilizers in high amounts also negatively affects the number of many bacteria, such as *Azospirillum lipoferum*, *Gluconacetobacter diazotrophicus,* etc. in the rhizosphere. Zhu et al. (2016) concluded after GC-MS analysis of the rhizospheric region that when N-fertilizers were amended, the amount of root exudates also increased. They also analyzed the effect of increasing N-rates on rhizospheric microbial population and found that Bacillales, Nitrosomonadales, and Rhodocyclales capable of ammonia oxidation, were significantly abundant relative to other groups of bacteria. Conversely, Chloroflexales, Gemmatimonadetes, and Phycisphaerae got significantly reduced.

In a study on banana rhizosphere, *Bacillus amyloliquefaciens* NJN-6, and compost-based biofertilizer were found to enhance beneficial microbes and simultaneously decreased wilt causing *Fusarium* sp. in the rhizosphere (Fu et al. 2017). Nevita et al. (2018) inoculated chopped rice straw residue with indigenously isolated *B. cereus*, *Stenotrophomonas maltophilia*, and *K. pneumonia* (10^9 CFU/kg) individually for its application as bacterial probiotic compost to enhance the growth of rice. The microbial communities and their numbers were significantly altered after the application of probiotic compost. In the rhizosphere treated with *B. cereus* probiotic bacterial compost, the relative abundance of Proteobacteria decreased while that of Acidobacteria, Actinobacteria, and Firmicutes increased as compared to control rhizosphere. In the case of *S. maltophilia* probiotic bacterial compost application, the relative abundance of both Proteobacteria and Actinobacteria decreased and that of Acidobacteria, Firmicutes, and Bacteroidetes increased in contrast to untreated control. When treated with *K. pneumonia* probiotic bacterial compost Bacteroidetes and Firmicutes increased, while Proteobacteria decreased. Mickan et al. (2018) determined the correlation between the application of clay and compost and the rhizosphere population of *Trifolium subterraneum* under water stress conditions. Compost application decreased AMF colonization by 29.8%.

Underwater stress conditions, AMF colonization in unamended soil decreased in contrast that in clay supplemented soil. Different treatments (clay, compost, and clay +compost) had a large positive impact on microbial populations. Gram-negative phyla Bacteroidetes, Gemmatimonadetes, and Proteobacteria dominated in clay amended soil, Chloroflexi and Proteobacteria dominated in compost amended soil, and Chloroflexi, Bacteroidetes, and Proteobacteria showed dominance in clay+compost amended soil (Mickan et al. 2018). However, Acidobacteria, Planctomycetes, Firmicutes, Actinobacteria, and Verrucomicrobia had decreased abundance when the soil was supplemented with clay. In compost amended soil, Verrucomicrobia, Acidobacteria, Planctomycetes, and Firmicutes had decreased abundance, while in clay+compost amended soil, Acidobacteria, Verrucomicrobia, Planctomycetes, Firmicutes, and Actinobacteria had a low abundance. Underwater stress conditions, the relative abundance of Actinobacteria decreased in compost amended soil and increased in all other treatments (clay, clay+compost, and unamended). The relative abundance of Proteobacteria decreased in clay+compost amended soil when there was water scarcity.

You et al. (2019) reported that while applying vermicompost-bamboo powder suppression of damping-off disease in cucumber occurred. The activity of pathogens, *Pythium aphanidermatum*, *Pythium ultimum*, and *Rhizoctonia solani* was suppressed by the use of vermicompost-bamboo powder. Zhao et al. (2017) reported that Ascomycota and Chytridiomycota had elevated, while Glomeromycota and Zygomycota had decreased abundance in cucumber rhizosphere after the treatment of soil with vermicompost and inorganic fertilizer mixture as compared to unamended soil. When treated with the mixture of both fertilizers (Zheng et al. 2018), Glomeromycota and Zygomycota decreased. However, an increase in abundance of Chytridiomycota and a decrease in that of Glomeromycota and Zygomycota occurred when the treatment of soil with inorganic fertilizer was

done. In all the three treatments (vermicompost and inorganic fertilizer mixture, inorganic and organic fertilizer mixture, and inorganic fertilizer), the relative abundance of Basidiomycota decreased.

12.7 Rhizosphere Competence and PGPR Development

The microbes applied as PGPR first need to multiply and colonize in the rhizosphere in the presence of other microbial populations. Rhizosphere competence defines the growth and functional capacity of the microbes in the plant rhizosphere by competing with other resident microbes present there for nutrition and space on the root surface of plants (Monfil and Casas-Flores 2014). The multiplication and colonization of PGPR inoculants are affected by different factors including soil type, presence of grazers, moisture content of the soil, edaphic factors like soil pH, competition from native microbes, availability of nutrients, and suitable host plant root. Several rhizosphere competence traits help in colonization and multiplication of applied inoculants. These traits include the formation of biofilm, the production of siderophores, motility, antagonistic activity, protease activity, and the ability to utilize root exudates (Kaur et al. 2017).

Microbes present in the rhizosphere interact with plant roots, soil, and other microbes in several distinct ways. These interactions in the rhizosphere can be beneficial, harmful, or neutral. Beneficial interactions that promote plant growth and improve soil quality include biocontrol, bioremediation, phytostimulation, and bio fertilization (de Weert and Bloemberg 2006).

Bach et al. (2016) studied the rhizospheric competence and biological control activity of three biocontrol bacteria *Bacillus mycoides*, *Burkholderia cepacia*, and *Paenibacillus riograndensis* and reported that these bacteria enhance their growth and survive under high competition in the rhizosphere. These bacteria have shown the proteolytic activity, production of hydrolytic enzymes, and catalase activity. Antagonistic activity of these bacteria was checked against filamentous fungi and all of them inhibited the growth of filamentous fungi.

The efficacy of PGPR generally decreases when used at the field scale. For a successful biocontrol activity, the biocontrol agent must have high rhizosphere competence so that it can easily compete with the rhizospheric population for nutrition and space, and can perform its function (Schreiter et al. 2018). Similarly, *Pseudomonas* sp. has been found to grow in potato and lettuce rhizosphere grown under three types of soils (Schreiter et al. 2018) was investigated to observe the biocontrol ability against fungal pathogen *Rhizoctonia solani* and rhizospheric competence. The population of *Pseudomonas* remained unaffected in both the rhizospheres under each soil type and the presence of *Rhizoctonia solani* (Schreiter et al. 2018).

12.8 Rhizosphere Engineering for Better Plant and Soil Health

Plant health and productivity can be improved by manipulating the rhizosphere by various methods. To alleviate the different environmental stresses, plants use different strategies to modify the rhizosphere. Rhizosphere engineering can enhance plant stress tolerance ability under several harsh environments. Rhizosphere engineering can be done for improving the overall plant health and growth. It is generally carried out by amending the soil, plant engineering, engineering the microbial partners, and engineering the plant–microbe interactions (Dessaux et al. 2016). It can also be done in several other ways, including transcriptome engineering which can be used to overexpress genes encoding enzymes related to the accumulation of osmolytes and proteins. These osmolytes and proteins improve abiotic stress tolerance ability by ion transporting ions and scavenging the reactive oxygen species. Another strategy is the isolation and identification of stress-tolerant microbes from the rhizosphere of different plants and inoculating them in the rhizosphere of different plants to reduce abiotic stress (Ahkami et al. 2017).

12.9 Conclusions

The rhizosphere of the plants constitutes an interesting environment, where several types of interactions interplay between plant, soil, and microorganisms. Many plant beneficial microorganisms are found in this region, which is in the vicinity of the plant roots. These microorganisms include bacteria, archaebacteria, viruses, fungi, actinomycetes, protozoans, arthropods, algae, and nematodes. The bacteria generally outnumber other microbes in the rhizosphere. All types of microbe–microbe and plant–microbe interactions occur in the rhizosphere, which may be positive or negative, and beneficial or detrimental to plant growth and crop productivity. Many different methods and techniques are applied to study the rhizospheric microbial communities. Both culturable and non-culturable microorganisms and their influence can be studied and predicted in the plant rhizosphere. The modern techniques include fingerprinting techniques such as terminal restriction fragment length polymorphism, denaturing gradient gel electrophoresis, and single-strand conformation polymorphism quantitative PCR based gene expression analysis and meta-omics-based techniques (namely, metagenomics, metatranscriptomics, metaproteomics, and metabolomics). These recent techniques based on the principles and tools of molecular biology have shown great capabilities in studying the details of the rhizospheric microbial populations in lesser time.

Many different plant-associated, as well as external environment associated factors, affect the population of rhizospheric microorganisms. Further, the dominant rhizospheric microbes are found to possess rhizospheric competence, i.e. their ability to survive the close competition with other microorganisms for nutrition and space. The rhizospheric microbial communities are not constant and can dynamically change, depending upon the different amendments, such as organic or inorganic fertilizers, biofertilizers, pesticides, compost, biocontrol agents, etc. All the

principles of rhizosphere–microbe interactions can be made use of, in enhancing the overall crop productivity and disease management by engineering the rhizosphere. It is generally carried out by amending the soil, plant engineering, engineering the microbial partners, and engineering the plant–microbe interactions. It can also be done in several other ways, including transcriptome engineering or bioprospecting followed by the application of stress-tolerant microbes. In conclusion, rhizosphere engineering is one of the practical solutions to achieve the goals of enhanced productivity and lead to sustainable agriculture.

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