Soil Microbe Diversity and Root Exudates as Important Aspects of Rhizosphere Ecosystem

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Abstract The rhizosphere is an area of soil surrounding plant roots in which soil's most reactions take place. The term "rhizosphere" was coined by Lorenz Hiltner, and it is 1–2 mm wide. The rhizosphere is divided into three zones: endorhizosphere, rhizoplane, and ectorhizosphere. The two dynamic properties of soil rhizosphere are root exudates and soil microbes. Root exudates are the chemical compounds that are secreted by roots and act as a source of food for soil microbes and play a pivotal role in soil microbe and plant interaction. These are low- and high-molecular-weight compounds. The root exudates are important for root-microbe and root-root communication. The other important aspect of rhizosphere is soil microbes. The soil microbes include bacteria, fungi, and actinomycetes. These organisms are important for both soil and fungi. The main aspect of this chapter is to give brief information about the underground world, and its future perspective is to understand soil microbe and plant interaction for enhancing sustainable agriculture. Studies on gene expression in the

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rhizosphere and the use of other molecular techniques like m-RNA, proteomics, labeled root compounds, stable isotope probes, and reporter technology will help in exploring underground undiscovered world.

Keywords Rhizosphere • Roots • Exudates • Soil microbes • Allelochemicals • Ecosystem

1 Introduction

The rhizosphere is the area of soil roots where most of the reactions are affected by plant roots. The rhizosphere is about 1–2 mm wide with no distinct boundaries (Brimecombe et al. 2007). Lorenz Hiltner is a German scientist who coined the term "rhizosphere" to explain plant root association. At Munich in 2004, a meeting was organized in his memory. The term rhizosphere is from the Greek words "*rhiza*" which means root and "*sphere*" which means field or area of influence (Hartmann et al. 2008). The rhizosphere is broadly classified into the following three zones, viz., endorhizosphere, rhizoplane, ectorhizosphere (Clark 1949; Lynch 1987; Pinton et al. 2001a). The endorhizosphere consists of root tissues including cortical cells and the endodermis. Rhizoplane is the area of root surface where soil microbes and soil particles interact. It comprises of the cortex, epidermis, and mucilage. The third zone is ectorhizosphere which is formed from soil particles adjacent to roots. In addition to these three fundamental zones, few other layers are also found which include the mycorrhizosphere, rhizosheath, and bulk soil (Linderman 1988; Curl and Truelove 1986; Gobat et al. 2004). Mycorrhizosphere is the mycorrhizal association of plants. Rhizosheath is the strongly adhering dense layer and consists of root hairs, mucoid layer, soil particles, and soil microbes. Bulk soil is the portion of soil which is not the component of rhizosphere (Brundrett 2009; Lambers et al. 2008) (Figs. 1 and 2).

The rhizosphere is called the hot spot of soil microbes (Brimecombe et al. 2007). In Kashmiri Language, we may call rhizosphere as Wazwan point for soil microbes. The rhizosphere is also called as human gut microbiome for plants (Mendes et al. 2011). Rhizosphere is considered as the spot where soil genesis actually starts (Pate et al. 2001). To soil microorganisms, rhizosphere is the lush oasis in the desert. Because it is underground, rhizosphere is considered as the last frontier in agriculture. Soil microbial community also has greater reservoir of biological diversity in the world (Curtis et al. 2002; Chaparro et al. 2013; Philippot et al. 2013; Buée et al. 2009). The rhizosphere soil contains up to 10^{11} microbial cells/g (Egamberdiyeva et al. 2008) and over 30,000 prokaryotic species. The combined genome of the rhizosphere is greater than that of plant and thus is called plants' second genome (Bron et al. 2012). The eelworms are being used to quantify the extent of rhizosphere because they are highly in peculiar in reacting to chemicals exudated by plant roots (Bolton et al. 1992) (Table 1).

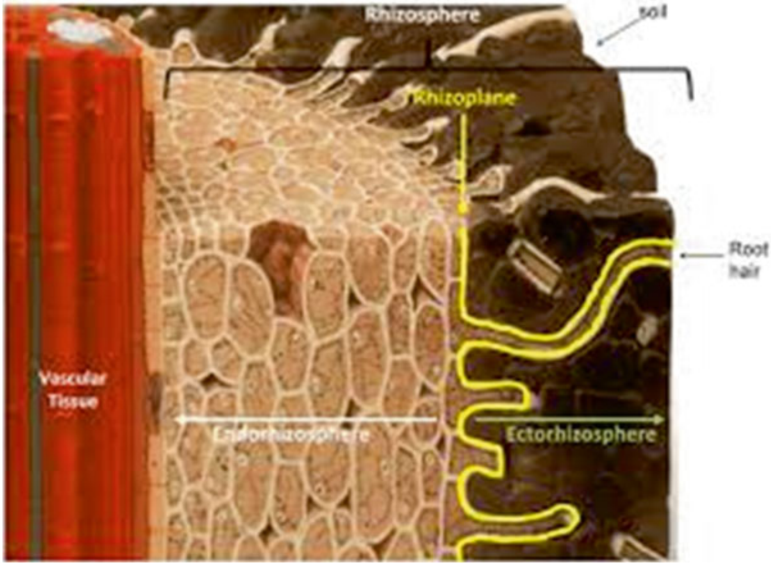

Fig. 1 Ectorhizosphere of the soil root ecosystem

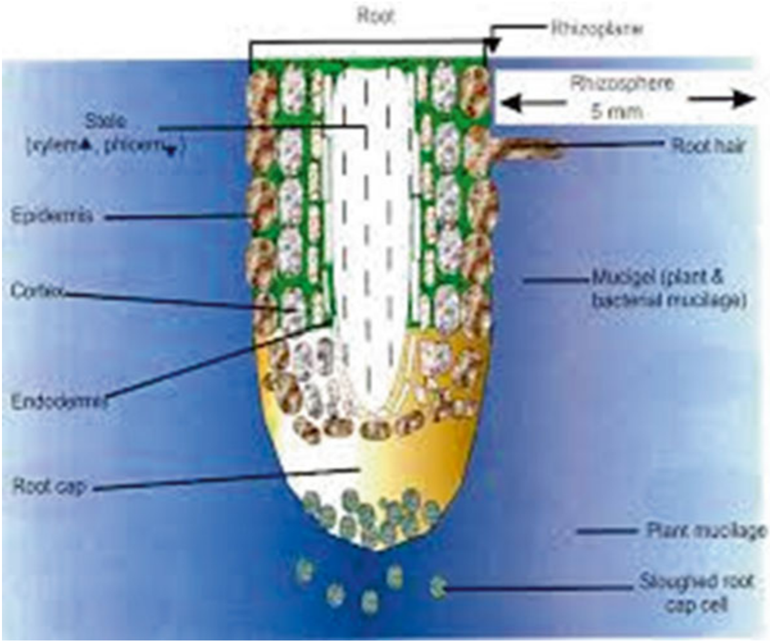

Fig. 2 The endorhizosphere and its different components

Table 1 Similarity between the human gut and rhizosphere

Characters	Human gut	Rhizosphere	References
Important for nutrient uptake	Microbes help in the breakdown of food and generate essential nutrients, such as vitamins B and D. In reward, microbes of the human gut get the carbon source from mucin	Soil bacteria, fungi, and actinomycetes assist plants to the uptake of nitrogen, phosphorus, potassium, and other important nutrients for their growth. The microbes also help in genesis and formation of minerals and degradation of organic matter. The root exudates and other rhizodeposits provide the energy source of soil microbes	Bais et al. (2006), VanDer et al. (2008), Derrien et al. (2010), Fagundes et al. (2012)
Restricts colonization of pathogens	Certain interactions of beneficial microorganisms include nutrient competition, inhibitory protein production, alteration of receptor sites, and modification of toxins	Certain soil beneficial microorganisms suppress plant pathogens by certain interactions like nutrient competition, antibiotic and lytic enzyme production, and consumption of pathogen stimulatory compounds	Lugtenberg and Kamilova (2009), Doornbos et al. (2012), Fagundes et al. (2012)
Modulate host immunity	The microbes stimulate host innate immunity system that not only affect intestinal mucosa but also produce immune responses in the respiratory tract. Also the development of microflora in the gut of humans during first year of life is very important for the development of the immune system	The rhizobacteria suppress diseases and systemically boost defense system of plants. The rhizobacteria trigger plant resistance to the pathogens. Most important chemicals are jasmonates	Bron et al. (2012), Ent et al. (2009), Fagundes et al. (2012), Ichinohe et al. (2011)

Distinguish friend from foe	Pathogens and symbionts have similar molecular patterns which are perceived by immune system, but the mechanism of immune system response is still unknown. Many mechanisms are present to prevent stimulation of immune system like physical barrier of mucous and reduced pathogen receptors in epithelial cells. Regulatory T cells suppress immune response of commensal gut microbes	Pathogens and symbionts have similar molecular patterns but are recognized by the immune system which is still unknown and thus differentiates friend from foe. Both pathogens and beneficial soil microorganisms suppress plant immune system and promote their own colonization through secretion of effector molecules	Chinen and Rudensky (2012), Lathrop et al. (2011), Zamioudis and Pieterse (2012)
Microbiome density and diversity	Microbial diversity is very high in the human gut ranging from 10^{11} to 10^{12} cells per ml of intestinal fluid, but its phylogenetic diversity is very low having only 7 of 55 described bacterial phyla which mostly include firmicutes and bacteroides. It is seen that more than 500–1000 sp. of bacteria exist in the human gut. There occurs stratified type of microbial variation and certain category of another community known as enterotypes	The rhizosphere microbial density is higher than bulk soil, and it ranges from 10^8 to 10^9 cells/g. These microbial communities are considered most diverse communities in the world with 10^4 bacterial sps./g of soil. Rhizosphere microbes vary between plant species if grown in same soil	Weinert et al. (2011), Arumugam et al. (2011), Roesch et al. (2007), Weller et al. (2002)

2 The Dynamic Properties of Rhizosphere Are Root Exudates and Soil Microbes

2.1 Root Exudates

The knowledge of roots and its biology, biochemistry, and genetic evolution has considerably increased during the last few years, but the certain processes occurring in the rhizosphere by the roots such as root exudates and root border cells are still unknown (Benfey and Scheres 2000; Hawes et al. 2000). The plant roots provide mechanical anchorage to the plants and assist in water and mineral nutrient uptake. Some special functions including synthesizes, secretion, and accumulation of diverse group of chemical compounds are also performed by the plant roots (Flores et al. 1999). These compounds exudated by the plant roots play a pivotal function as chemical attractants in the soil root ecosystem (Estabrook and Yoder 1998; Bais et al. 2001). These chemical compounds are referred as root exudates. A diverse group of these chemical compounds have been found exudating from intact and healthy roots. These compounds include sugars, amino acids, peptides, vitamins, nucleotides, organic acids, enzymes, fungal stimulants, and inhabitants and also some other compounds which help in plant water uptake, plant defense, and stimulation (Pate et al. 2001; Pate and Verboom 2009; Taylor et al. 2009). Sugars, organic acids, coumarins, lipids, flavonoids, enzymes, amino acids, proteins, aliphatics, and aromatics are examples of primary substance found within the roots (Shukla et al. 2011). Among these, the organic acids are of considerable importance because of its role in providing substrate for microorganisms and also acting as intermediate in biological and chemical reactions in the soil (Philippe 2006; Wutzler and Reichstein 2013). The ability of plant roots to produce a wide range of chemical compounds is the most striking feature of plant roots with nearly 5–21 % of all photosynthetically fixed carbon being transferred to rhizosphere through root exudation (Marschner 1995). These root exudates are being classified as low-molecular-weight compounds and high-molecular-weight compounds. Sugars, amino acids, phenols, organic acids, and various other secondary metabolites are included in low-molecular-weight compounds, whereas mucilage and proteins are included in high-molecular-weight compounds (walker et al. 2003). These root exudates are relatively important in mediating the communication of plants with soil microbes (Bais et al. 2004; 2006; Weir et al. 2004; Broeckling et al. 2008). Root exudation is an important element of rhizodeposition and is a primary source of soil organic carbon released by the roots (Hutsch et al. 2000; Nguyen 2003). Whipps and Lynch (1985) first coined the term rhizodeposition as materials lost from roots, which include lysates, insoluble exudates, soluble material, and certain gases like carbon dioxide and ethylene.

2.1.1 Interaction Studies of Root Exudates

Another important function of root exudates is that it acts as a messenger that initiates and intimates physical and biological communication between the soil microbes and plant roots. Root-mediated rhizospheric communication is grouped into two categories: negative and positive interactions (Weller et al. 2002; Mendes et al. 2011; Elsas et al. 2012). Positive interactions involve communication of plant roots with certain plant growth-promoting rhizobacteria (PGPR). These plant roots produce certain chemicals that act as signals and attract certain microbes and stimulate chemotaxis (Thimmaraju et al. 2008). Positive interactions of root exudates also include growth enhancers that enhance growth of neighboring plants and help in cross-species signaling. The negative interaction of root exudates includes secretion of insecticidal and nematicidal compounds, phytotoxins, and secretion of antibiotics (Bais et al. 2006).

Root Rhizosphere Communication

Performance of plant species depends upon its ability to recognize and receive changes in environment and to respond to these changes for acclimatization. These changes are very important for growth and development of plants and microbes (Chaparro et al. 2014). Root exudate is a major food source of soil microbes that communicate with the plants and is considered most diverse ecosystem on earth (Vogel et al. 2009). These interactions of soil microorganisms and plant roots are categorized into root-root communication and root-microbe communication.

Root-Root Communication

When roots communicate with neighboring roots of other plant species, they prevent their invadence by release of certain chemical messengers (Ahmed et al. 2007). Allelopathy is the phenomena which involve beneficial, harmful, direct, and indirect effect on plants through secretion of secondary metabolites (Li et al. 2010). Allelopathy is known for more than 2000 years with respect to plant interference (Callaway and Aschehoug 2000; Ridenour and Callaway 2001; Weston and Duke 2003). Allelopathy also has importance in agriculture, because the allelochemicals produced by the plants control weed population (Haribal and Enwick 1998). The most important allelochemicals in the plant ecosystem include phenolic compounds. Phenols are the chemical compounds having a hydroxyl group (−OH) attached to an aromatic hydrocarbon group (Zeng et al. 2008). Phenolic compounds which play an important role in allelopathy are produced from pentose phosphate pathway. 4-Phosphate erythrose and phosphoenolpyruvic acid undergo certain condensation reaction with sedoheptulose 7-phosphate and generate phenolic compounds. There occurs a series of reactions in shikimic and acetic acid metabolic pathway. The phenolic allelochemicals have adverse impact on the photosynthesis and respiration of other plant species by weakening their oxygen absorption capacity and by reducing their photosynthetic rate by reducing chlorophyll content. Patterson (1981) reported that 10–30 μmol/l caffeic acid, ferulic acid, vanillic acid, coumaric acid, and cinnamic acid could considerably reduce growth of soybean. Bais et al. (2002) reported (+) catechin and (−) catechin as root phytotoxin. + catechin was produced invasive behavior of knapwood and (−) catechin was inhibitory to the soilborne bacteria. It has also been seen that certain allelochemicals released by the host roots stimulate haustoria formation (Estabrook and Yoder 1998; Yoder 2001). Allelochemicals produced by the black walnut causes growth inhibition and is one of the earliest classical examples of allelopathy (Bais et al. 2006). The naphthoquinone, juglone (5-hydroxy-1, 4- naphthoquinone), is responsible for the walnut toxicity. Juglone is generally found in nontoxic form, but when exposed to air it becomes oxidized and thus becomes toxic. Juglone is extracted from fresh bark of stripped roots or from fresh fruit hulls (Kocacali et al. 2009). Many other close relative species of black walnut like butternut or white walnut (*Juglans cinerea*) also produce juglone, but in limited quantities. Wheat is also known to produce root exudates with allelopathic activity. Due to simple phenolic compounds like p-coumaric, p-hydroxybenzoic, ferulic acid, vanillic acid, and syringic acid, the presence of hydroxamic acids is responsible for wheat allelopathy (Yongqing 2006). Sorghum roots also secrete a mixture of hydrophobic substances which are biologically active and include sorgoleone, characterized as (2-hydroxy-5-methoxy-3-pentadecatriene)-p-benzoquinone. Sorgoleone is used as an important bioherbicide which is used for broadleaf and grass weeds at concentrations below 10 μM in hydroponic bioassays (Xiaohan et al. 2004). Some plants also secrete secondary metabolites that suppress growth of specific plants (autotoxicity). Autotoxicity is a phenomenon mostly applicable in agricultural crops and weeds, as well as in some plants that inhabit natural systems. Phytotoxic root exudates play an important role in mediating autoinhibition in some species like *Cucumis sativus* (garden cucumber), *Centaurea maculosa* (spotted knapweed) (Perry et al. 2005), and *Asparagus officinalis* (garden asparagus) (Yu et al. 2003).

Root Microbiome Communication

In the unseen underground ecosystem, some complex communication occurs which includes root- root and root-microbe interaction which has both beneficial and harmful outcomes (Bais et al. 2006). The sophisticated processes include root-microbe interaction which includes both mutualistic and pathogenic relationship, metabolic processes including parasitic plants and root secretion, energy transfer which comprises electric potential, and resource distribution and information transfer which include quorum sensing. These processes play a critical role in terrestrial ecosystem (Bouwmeester et al. 2007; Gewin 2010). Some microbial bioactive compounds which function within the belowground ecosystem play a dynamic role in plant life. Roots of the plants continuously secrete organic compounds which help in harnessing beneficial microbes and suppressing plant pathogens (Berg and Smalla

2009; Marschner and Timonen 2005). Thus, these roots have stimulatory or inhibitory influence on soil microbes which help in their community structure development as they increase their competition for nutrients and other resources (Cesco et al. 2010, 2012).

There occurs a dynamic interaction between soil microbes and plants in nature which is based on coevolutionary pressures (Klironomos 2002; Dobbelaere et al. 2003; Duffy et al. 2004; Morrissey et al. 2004; Morgan et al. 2005; Reinhart and Callaway 2006). Consequently, the microbial communities in the rhizosphere vary due to certain factors like different species of plant (Batten et al. 2006; Innes et al. 2004), their genotypes (Kowalchuk et al. 2006), and their different developmental stages (Mougel et al. 2006; Wei et al. 2007). Microbial community in soil is closely related to highly diverse plant communities, but their connecting link is still unclear and it is believed that their close relationship occurs due to widely occurring habitat heterogeneity or enhanced plant biomass. It may be also due to different carbon substrates which act as signaling compounds as they are secreted by the plant roots. These compounds belong to a class called flavonoids which are responsible for specific microbe-host interactions. These flavonoids act as signaling molecules and are highly present in symbiotic and pathogenic microbes; there occur a large number of flavonoids in the plants and a greater number of flavonoids are identified in legumes. More than 4000 different flavonoids occur which mediate host specificity (Perret et al. 2000). In several *Fusarium* plant interactions, flavonoids help in micro- and macroconidia germination but have no effect on hyphal growth during infection. Certain isoflavonoid compounds are also present in legume crops. Soya bean (*Glycine max*) produces genistein, daidzein, and, isoflavonoids which effectively stimulate *Bradyrhizobiumjaponicum* nod genes but have negative effect on the *Sinorhizobium meliloti* nod gene expression. *S. meliloti* nod gene expression gets stimulated by luteolin (Juan et al. 2007). This phenomenon helps rhizobia to differentiate between hosts and other legumes. The specific flavonoid produced by the legumes not only stimulates nod gene expression but also has its effect on rhizobial chemotaxis (Bais et al. 2006). Strigolactones recently have been identified as important signaling molecules in the AMF-plant interaction and thus are "hot issues" in the mycorrhizal study. Ectomycorrhizal fungi are also stimulated by Brassicaceae (Zeng et al. 2003). There occurs a specific interaction between rhizobia and legume allowing only few rhizobial strains to nodulate with specific host legumes. *Medicago*, *Melilotus*, and *Trigonella* genera are nodulated with *S. meliloti*, whereas *Rhizobium leguminosarum* bv. viciae stimulates nodulation in *Pisum*, *Vicia*, *Lens*, and *Lathyrus* genera (Bais et al. 2006). Scientists demonstrated that plant roots secrete L-MA (malic acid) which acts as effective signaling molecule to establish beneficial rhizobial communities (Thimmaraju et al. 2008). *Arabidopsis thaliana* and *Medicago truncatula* are the two model plant species which are unable to maintain nonresident soil fungal populations, but maintain resident soil fungal populations. These phenomena occur largely due to root exudates. In vitro-generated root exudates applied to the soil fungi show similar results to that of plants growing in same soil (Yanhong et al. 2009).

2.2 Rhizosphere Soil Microbes

Someone has rightly said that rhizosphere microorganisms have two faces like Janus, the Roman god of doors and gates who symbolizes changes and transitions from one condition to another (one part of the face looks at the plant roots and the other at the soil; the ears and nose sense other gods, and the mouth is wide open for swallowing). It is also well established that soil is a good medium for plants and microbes, but the plants and their associated microbes help in genesis and weathering of soil (Pate et al. 2001; Pate and Verboom 2009; Taylor et al. 2009; Pausch et al. 2013). Soil formation occurs due to weathering process which primarily occurs due to soil microbes (Raven and Edwards 2001; Beerling and Berner 2005; Taylor et al. 2009). The soil microflora includes bacteria, fungi, actinomycetes, protozoa, and algae (Raaijmakers and Weller 2001; Singh et al. 2007; Grayston et al. 1998; Broeckling et al. 2008). Recently the nucleic acid analysis revealed enormous diversity in the soil (Nannipieri et al. 2003a, b; Suzuki et al. 2006).

2.2.1 Microorganisms and Their Mode of Action

The soil microbes can generally be divided into beneficial, harmful, and neutral microbes. The beneficial soil microbes can further be divided into three categories. The first category helps in nutrient supply (Ma et al. 2003; Robin et al. 2008; Michaud et al. 2008). The second group includes those that stimulate plant growth by suppressing activity of phytopathogens. The third group of microbes directly promotes growth of plants by secreting phytohormones (Welbaum et al. 2004; Brimecombe et al. 2007) (Fig. 3).

2.2.2 Nutrient Availability and Plant Growth Promotion

The most population in the rhizosphere is occupied by the bacteria. Those rhizosphere bacteria which enhance plant growth are called plant growth-promoting rhizobacteria (PGPR) (Kloepper JW Schroth 1978; Lucy et al. 2004). The most dynamic function of PGPR is secretion of phytohormones. A diverse group of PGPR are inoculated on the crops which include *Azospirillum* (Cassan and Garcia 2008), *Bacillus* (Jacobsen et al. 2004), *Pseudomonas* (Loper and Gross 2007), *Rhizobium* (Long 2001), *Serretia* (De Vleeschauwer and Hofte 2007), *Stenotrophomonas* (Ryan et al. 2009), and *Streptomyces* (Schrey and Tarkka 2008). Some fungi belonging to genera *Ampelomyces*, *Coniothyrium*, and *Trichoderma* have also beneficial effects (Harman et al. 2004). The mode of action of PGPR involves complex mechanism which promotes plant growth, development, and protection. The most versatile functions of PGPR are biofertilization, phytostimulation, and biocontrol (Morgan et al. 2005; Muller et al. 2009; Chet and Chernin 2002). The success of plant-microbe interaction depends on colonization (Lugtenberg et al. 2002;

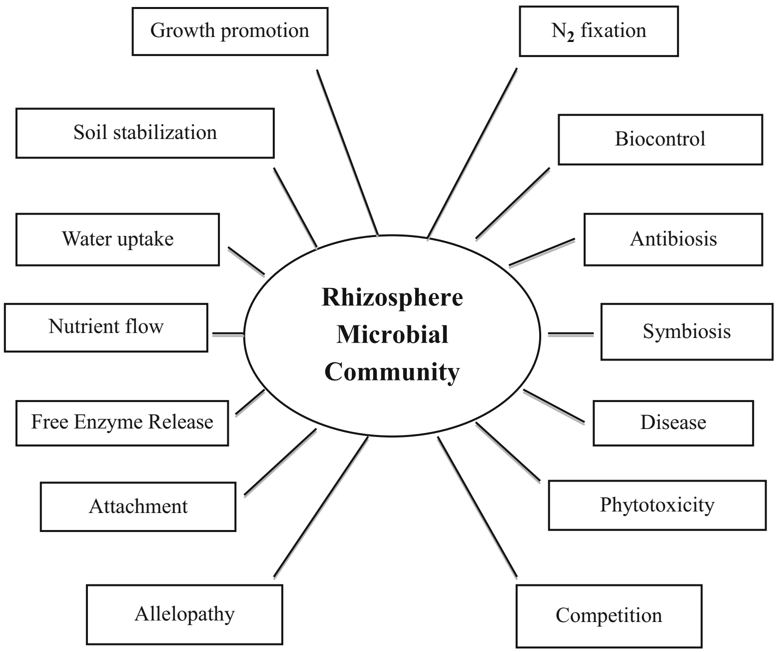

Fig. 3 Shows role of rhizosphere microbial community and its harmful and beneficial effects

Kamilova et al. 2005). The steps of colonization include attraction, recognition, adherence, invasion, colonization, and growth (Pinton et al. 2007; Berg 2009).

Plant growth in the agriculture is enhanced by certain abiotic and biotic factors. The abiotic factors comprise light, temperature, water, and air. The biotic factors include PGPR which help in plant growth by secreting enzymes (Lynch 1990; Marilley and Aragno 1999; Garcia et al. 2001). Interestingly the inoculation of PGPR increases the crop yield and plant growth (Farzana et al. 2009). Some plant growth-promoting rhizobacteria have more than one trait (Joseph et al. 2007; Yasmin et al. 2007; Egamberdiyeva 2007). These PGPR release volatile compounds like 2,3-butanediol and acetoin that help in growth and development of Arabidopsis thaliana (Ryu et al. 2003). There have also been reports that diazotrophical bacterial application in the soil increases crop yield, plant height, and microbial population in the soil (Anjum et al. 2007). Due to certain combination of PGPR, carbohydrates, and IBA (double and triple combinations), there occurs increased rooting capacity of apple (Karakurt et al. 2009). PGPR are the most effective model organism that can replace pesticides and other harmful supplements which cause soil and environmental pollutions. These PGPR also act as biofertilizers and bioenhancers and reduce use of chemical fertilizers (Ashrafuzzaman et al. 2009). Utilization of PGPR with alternative use of chemical fertilizers reduces pollution, preserves environment, and increases agricultural productivity (Ştefa et al. 2008). Combination of PGPR and arbuscular mycorrhizal fungi enhances nutrient use efficiency of plants and allows low rate of application of fertilizers (Adesemoye et al. 2009; Tanvir et al. 2015). The bacteria and archaea are responsible for biological nitrogen fixation. These include symbiotic nitrogen fixers like rhizobium, which are obligate symbionts in legume plants and *Frankia* in nonleguminous plants and certain free-living forms like cyanobacteria, azospirillum, azotobacter, and diazotroph.

2.2.3 Pathogen Inhibition

Soil microbes live around plant roots and feed on root secretions and dead root cells. Root colonization not only results in high plant growth-promoting rhizobacterial population densities but also functions as antagonistic metabolites (Shoda 2000; Raaijmakers et al. 2002). The different mechanisms involved are antibiosis, parasitism, and induced systemic resistance. Antibiosis is the phenomenon where microbial growth gets inhibited by different compounds like antibiotics, toxins, biosurfactants, and volatile organic compounds. Parasitism is the phenomenon where cell wall-degrading enzymes such as chitinase and β-1,3-glucanase are secreted which degrade cell wall (Compant et al. 2005; Haas and Defago 2005). A wide range of antifungal metabolites such as zwittermicin-A, kanosamine, and lipopeptides are secreted by *Bacillus subtilis.* These antifungal metabolites include surfactin, iturin, and fengycin families (Emmert and Handelsman 1999; Ongena and Thonart 2006). Competition for the carbon source of energy is responsible for fungi inhibition by reducing fungal spore germination (Chin et al. 2003; Alabouvette et al. 2006). Another mechanism of pathogen inhibition is induced resistance. The induced resistance involves the use of beneficial bacteria that not only reduces the activity of pathogenic microorganisms through antagonism but also stimulates plant defense mechanism (Shoda 2000; VanLoon 2007). In some instances, the mechanism of induced systemic resistance coincides with systemic acquired resistance. Both induced systemic resistance and systemic acquired resistance enhance the resistance of plant which depends on signaling compounds like ethylene, jasmonic acid, and salicylic acid (VanLoon 2007).

2.2.4 Rhizosphere Effect

The rhizosphere effect is determined by dividing the number of microorganisms per gram of rhizosphere soil by the number of microorganisms in a gram of control soil (Wasaki et al. 2005; Herman et al. 2006). The rhizosphere effect greatly reduces as we move away from roots. For bacteria and fungi, R:S value ranges from 5 to 20. Actinomycetes is a less effected group of soil microorganisms having R:S effect of 2–12 (Curl and Truelove 1986; Foster 1986; Lynch 1990; Rovira 1991; Pinton et al. 2001a, b; Whipps 2001).

3 Quorum Sensing: The Bacterial Communication

"Quorum sensing" (QS) is the communication of bacteria which includes cell density. It is cell-to-cell communication. The bacterial quorum sensing occurs by the binding of signals with their receptor proteins. When binding occurs, it regulates gene expression in response to cell density (Gonzalez and Marketon 2003; Hong et al. 2012). The signaling molecules involved in quorum sensing are called autoinducers. These autoinducers are synthesized at particular stage of life cycle or may be synthesized for stimulating response, once the signaling molecule has reached at a particular concentration (Gonzalez and Marketon 2003). The quorum sensing is a cell density level: once a particular cell density is achieved, the concentration of quorum-sensing signals becomes enough to induce gene expression, either directly through transcriptional regulator or indirectly by signaling cascade activation (Fuqua et al. 2001). *N*-acyl homoserine lactone (AHL) is the most studied quorum-sensing signal molecule (Williams et al. 2007). AHL signals are highly preserved in nature having same homoserine lactone moiety, but differ in length and structure of acyl side chain. The *N*-acylated side chains have fatty acids. These chains have varying degrees of saturation, different chain lengths (4–18 carbons), and presence of different groups (hydroxy, oxo-, or no substituent at the C3 position) (Swift et al. 1997; Schuster et al. 2013). LuxI synthase gene using intermediate of fatty acid biosynthesis and *S*-adenosyl methionine synthesizes AHL molecules. The AHL molecules will incorporate LuxR protein and regulate downstream gene expression. Each LuxR protein is specific for its AHL signal molecules (Parsek and Greenberg 2000). AHL regulates many target genes, but basic mechanism of gene regulation and AHL biosynthesis seem to be specific in quorum-sensing bacterial species (Dong et al. 2002). QS mechanism with LuxI/LuxR signal molecules in *Agrobacterium tumefaciens* causes crown gall disease of plants. *Agrobacterium tumefaciens* with tumor-derived opines and transcriptional factor OccR or AccR regulate gene expression of LuxR homologue TraR (Oger et al. 1998; Zhu and Winans 1988). *Pseudomonas aeruginosa* uses LasI/R and RhlI/R to promote regulation and expression of virulence factors and biofilm formation (Glessner et al. 1999). Another class of homoserine lactone known as *p*-coumaroyl-homoserine lactone (pC-HSL) has been discovered to be produced by the bacteria *Rhodopseudomonas palustris*. The intracellular fatty acid is not used as precursor in the synthesis of pC-HSL molecules, and synthesis occurs due to RpaI and LuxI by using environmental *p*-coumaric acid (Schaefer et al. 2008). Many bacteria use QS to gain maximal competition advantages, and to measure the advantages of QS some organisms use quorum quenching (QQ) (Lin et al. 2003; Rodolfo et al. 2015). This QS widely occurs in prokaryotes and eukaryotes and plays an important role in pathogen-host and microbial interactions (Dong et al. 2002).

4 Conclusion

In this chapter, we discussed an overview of ecology of various organisms and the root exudates. Various microorganisms are present in the rhizosphere, and they form a complex community which is connected with each other and with the external environment. The genetic and functional diversity of soil microbes is very important for both plant and soil health. The major challenge ahead of rhizosphere is the discovery of new signaling molecules that occur between different organisms; these discoveries are very important to enhance our knowledge to deal with the new pest and disease problems in the sustainable manner. There also occurs challenges to adopt new crops and cropping systems which absorb most of the nutrients from soil particularly nitrogen and phosphorus because our phosphorus sources are getting diminished. Today rhizosphere is considered a new research field with many exciting challenges. These challenges can be both fundamental and applied. There are some major developments in biogeochemistry and ecology of rhizosphere which need a global consideration. In symbiotic association, a great achievement has been made, but there still occurs a great lacuna of knowledge in other biological interactions. Rhizodeposition is considered the central concept in rhizosphere ecosystem and beyond rhizosphere ecology. Rhizodeposition is very important for terrestrial ecosystem biodiversity and functioning. In rhizosphere studying of gene expression is used for understanding certain processes like inducing microbial activity, biological control, nutrient competition, and certain molecular interactions between roots and roots and roots and microorganisms. Some techniques have been developed to characterize m-RNA (Nannipieri et al. 2003a, b), but soil proteomics is still not so developed (Nannipieri 2006; Ogunseitan 2006). Stable isotope probe (SIP) has also been used in understanding functional activity and community structure in soil (Radajewski et al. 2000; Manefield et al. 2006). Labeled root exudate compounds and monitoring microorganisms of rhizosphere also involve the use of stable isotope compounds (Manefield et al. 2006). At single cell level, reporter technology is to be used to assess functions of rhizosphere soil including gene expression (Sorensen and Nybroe 2006). The increasing knowledge of the promoter, regulator, and reporter gene insertion techniques shall allow use of reporter gene technology for regulation, expression, and induction of any gene in rhizosphere. The methodological improvement of new technology will allow designing of new reporter bacteria to respond to specific root exudates.

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