# Rhizosphere Interactions: Life Below Ground

## 1

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**Abstract**

The interface between roots and soil is a region with high interaction among a myriad of organisms that affect biogeochemical cycles, plant growth, and stress tolerance. Similarly chemical compounds secreted within the rhizosphere act as attractants to microorganisms. Due to its dynamic nature and complexity, understanding rhizospheric biology and activity is essential in ensuring improved plant function and productivity within an ecosystem. Sustainable agricultural practices are dependent on studies conducted with regards to plant–microbe interactions in the rhizosphere. This chapter is an exposition of rhizospheric interactions spanning the chemistry of exudates and signals that contribute towards the complexity of the rhizosphere. The information derived from recent studies and the utilization of current technological platforms will enable us to explore and gather more information at the plant and microbiome level.

## 1.1 Introduction

The rhizosphere was described by Lorenz Hiltner a century ago as a microbial hotspot that is dependent on plant roots (Hartmann et al. 2008). The interactions and activities within have been researched extensively due to the dynamic nature of this region (Bakker et al. 2013). Studies have shown that the microbial communities within the rhizosphere can affect the well-being of plants (Mendes et al. 2011) by either directly or indirectly affecting the biomass and composition within the plant's natural ecosystem (Schnitzer et al. 2011). The microbiota contributing towards

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these processes in the rhizosphere involve antagonists, mutualists, symbionts, and the rich plant root system (Kardol et al. 2007). The microbial activity is essential as they contribute towards physiological processes such as nutrient uptake and plant defense responses (Berendsen et al. 2012). Although much has been done to unravel the mysteries of these underground plant–microbe interactions, the complexity of these interactions leaves gaps in knowledge that requires further investigation (Urich et al. 2008; Jansson et al. 2011).

The variety of low molecular weight (LMW) exudates secreted into the plant's surrounding soil environment influences the complex interaction between the root and plant. These exudates when secreted into the environment contributed towards the highly interactive nature of this region. Though enormous strides have been made in understanding the interactions down under, much still remains elusive in our understanding with regard to the root–microbe–insect–nematode interactions within the rhizosphere (Weir et al. 2004; Walker et al. 2003). As plant roots remain hidden below ground, most of these interactions remain unnoticed especially the chemical components facilitating these belowground interactions (Bais et al. 2006).

Root chemicals result in varying consequences and responses in different plant systems. However to date, the mechanism underlying the chemical signal perception and response between the soil, roots, and invertebrates remains largely obscure. Ultimately the positive or negative way in which these chemicals are perceived will determine the plant and soil community's dynamics. We anticipate that deciphering the processes that direct the variety of activities within the rhizospheric microbiome will provide new avenues of crop manipulation for plant fitness and yield. Initial reports into these insights have been obtained through studies of *Arabidopsis thaliana* and *Medicago truncatula* plant systems. These studies have shown us how microbial ecosystems in the rhizosphere influence allocation, diversity, and belowground interactions (Berendsen et al. 2012; Bakker et al. 2012).

Here we have outlined current advances in deciphering the rhizospheric interactions, paying special emphasis on how these exudates mediate the various interactions below ground. In addition this chapter addresses how these beneficial interactions will influence plant growth, yield, and therefore contribute towards sustainable agriculture.

## 1.2 Rhizosphere and Root Exudates

The adaptability and survival of plants in any given environment is dependent on acquisition of resources from the soil environment (Badri et al. 2009b, 2013a; Chaparro et al. 2013a; Nihorimbere et al. 2011). The variation in amount of root exudates within the soil will determine the nutrient dynamics and hence affect the microbial population and diversity (Paterson et al. 2006). It has been reported that plants exude their photosynthetic components (5–21 %) such as sugars, proteins, and secondary metabolite into the root environment (Badri et al. 2013b; Badri and Vivanco 2009; Chaparro et al. 2013b). There are two groups of root exudates: (i) LMW exudates, e.g., amino acids, sugars, phenolics, secondary metabolites, and organic acids, and (ii) the HMW exudates, e.g., proteins and complex carbohydrates (Bais et al. 2006; Narasimhan et al. 2003). LMW and HMW compounds that are exuded into the soil environment are largely dependent on the plant cultivar and species, the developmental stages of the plant, soil chemistry, and microbial diversity (Badri and Vivanco 2009; Huang et al. 2015; Uren 2000). Recent reports have implicated root cells in the cap and root hairs as secretors of compounds from roots into the soil (Czarnota et al. 2003; Pineros et al. 2002; Nguyen 2003). In addition to secretion, root hairs are involved in anchoring and nutrient-water intake (Fan et al. 2001). The relationship between root exudates and microorganisms are chemotactically disposed, i.e., where plant roots secrete glucose, sugars, organic, and amino acids into the soil; microbes migrate chemotactically toward these exudates (Kumar et al. 2007).

## 1.3 System of Root Emission

Despite the huge strides made by scientists in investigating exudates within the rhizospheric domain, the mechanisms involved in root secretions are poorly understood. The synthesis and release of root-derived components are generally constitutive, while the secretion mechanisms of these exudates are thought to be passive involving three separate pathways such as dissemination, vesicle transport, and particle channels (Dennis et al. 2010).

### 1.3.1 Diffusion

Membrane permeability and the cytosolic pH largely influences the passive diffusion of small polar and uncharged molecules produced by plants across the cell's lipid membranes (Marschner 1995; Sanders and Bethke 2000). This is the simplest form of mobilizing molecules across the membrane.

### 1.3.2 Vesicular Transport

High molecular weight root exudates are secreted through different mechanisms such as vesicular transport (Battey and Blackbourn 1993). Field et al. (2006) reviewed vesicle-mediated trafficking of proteins, but this review however did not involve the mechanism of transport for phytochemicals (Grotewold 2004). While there are extensive reports on the phytochemical exudates in leaf tissue, little has been reported with regards to phytochemical exudates from roots. Vesicular secretion has been implicated in the transportation of antimicrobial products at the location of bacterial or fungal infections. One such example is the pigmented 3-deoxyanthocyanidins, an antimicrobial flavonoid observed in fungal infection sites of sorghum leaves (Snyder et al. 1991). Roots of knapweed plants have been reported to secrete cytotoxic and antimicrobial catechin flavonoids (Bais et al. 2002).

Although certain researchers have implicated the cytoplasmic surface of the endoplasmic reticulum (ER) as the site of synthesis for certain root exudates from the phenylpropanoids and flavonoids families (Winkel-Shirley 2001), the mechanism of transport from the ER to the membrane is unknown. However there is a possibility that these compounds are transported through ER-originating vesicles that secrete their contents once bound to the cell's membrane.

### 1.3.3 Transporter Proteins

Transporter proteins are responsible for the transportation or passage of amino acids, sugars, and carboxylate anions from root cell cytoplasm to soil (Colangelo and Guerinot 2006; Hirner et al. 2006; Lee et al. 2007; Svennerstam et al. 2007). ABC transporter proteins are implicated in various cellular processes, spanning the discharge of harmful compounds, translocation of lipids, disease resistance, salt stress, nutrient transport, and substantial metal resilience (Stein et al. 2006; Kobae et al. 2006). The utilization of *Arabidopsis* ABC transporter knockout mutants proved that these transporters were involved in root secretions. What's more, the ABC transporters are confined to the plasma membrane (Sidler et al. 1998) and are involved in auxin pumping and secretion of resistance metabolites (Badri et al. 2009a).

Another transporting system, MATE, is involved in the discharge of phytochemicals. MATEs, through electrochemical gradient of other ions, are effectively able to transport substrates across cell membranes. Numerous MATE genes involved in transporting compounds such as toxic materials, plant-inferred alkaloids, antimicrobials, phenolics, and anions have been identified and characterized in the root cells of sorghum, *Arabidopsis*, rice, and grain (Furukawa et al. 2007; Ishimaru et al. 2011; Liu et al. 2009; Magalhaes et al. 2007; Weston et al. 2012).

Further, MFS transporter proteins assist with the release of secondary metabolites such as phytosiderophores from root cells (Kim and Guerinot 2007). These proteins can work as uniporters, co-transporters, or antiporters. In rice for instance, deoxymugineic and avenic acids are aided by *TOM1* (transporter of mugineic corrosive family phytosiderophores1) (Nozoye et al. 2011) in translocation of proteins. Through transgenic studies it was proven that the expression of *TOM1* is induced in the state of limited iron supply where overexpressing *TOM1* showed improved deoxymugineic acid release and enhanced resilience to a limited iron supply. ALMT transporter proteins belongs to the *ALMT* gene family that enables malate efflux from plants. *ALMT* genes encode the pore-forming anion channels within the membranes that facilitate the passive transport of substances across the membranes (down their electrochemical slopes) (Ryan et al. 2011; Weston et al. 2012). Other than the above transporters, monosaccharide transporters have been associated with hexose, pentose, ribose, and polyols transport (Klepek et al. 2005; Buttner 2007), while silicon efflux transporters have been associated with the excretion of silicon from rice root cells to soil (Ma and Yamaji 2008).

## 1.4 Rhizospheric Plant–Microbe Interactions

Root-secreted phytochemicals can result in beneficial, deleterious, or neutral interactions (Raaijmakers et al. 2009; Mercado-Blanco and Bakker 2007). Likewise, microbes are also able to transition from pathogenic to symbiotic in response to differing environments (Newton et al. 2010). Hence we can anticipate that the chemical diversity exhibited by root exudates will be an excellent source to look for novel, biologically active compounds, including antimicrobials (Huang et al. 2014). Previous reports have highlighted that the association of plants and the microbial community in the soil is important for plant health. These communities are dependent on the root exudates that positively or negatively affect the microorganisms within the soil. In the following sections, the integral role played by the exudates in plant–microbe and microbe–plant interactions will be expounded. Figure 1.1 presents the various underground processes that occur within the rhizosphere (Huang et al. 2014; Zhuang et al. 2013).

### 1.4.1 Positive Plant–Microbe Interactions

(a) *Nitrogen fixation*

The nitrogen levels within the rhizosphere will determine the diversity of nitrogen (N)-fixing bacteria within the soil (Zahran 1999). In nitrogen-limiting conditions, the nodule containing nitrogen-fixing bacteria produces flavonols and flavones that attract and initiate legume–rhizobia symbiosis (Zhang et al. 2009; Coronado et al. 1995). The flavones and flavonols induced bacterial nod gene expression, which lead to the initiation of root nodulation. The aerobic $N_2$-fixing bacterium also exhibited $N_2$ase activity when inoculated into the rhizosphere of rice, wheat, and oat seedlings. Further, microscopic observations of this $N_2$-fixing bacterium in barley roots suggest that this organism is an endophyte that associates with root tissue to form vesicle-like structures (Santi et al. 2013). The aggregation of rhizobia to legume root tissues is dependent on the association to specific sugar-binding sites. During nitrogen fixation, lectins (functions as binding protein) bind polysaccharides to stimulate aggregation. Lectins sustain increased nod factor concentrations and mitotic activity necessary for nodulation (Mathesius and Watt 2010). In general mixed cultures have been shown to increase nitrogen-fixing capacity as observed in the association between *Staphylococcus* sp. and diazotrophic bacteria that increased the nitrogen-fixing capacity of *L. anguillarum* by 17 %. Another example is the production of nodulating compounds such as exopolysaccharides (EPS and EPS II) by a mixed culture of *Rhizobium* sp. and *Sinorhizobium* sp. Exopolysaccharide-deficient mutants were incapable of invading legumes and establishing symbiotic relations (Jones et al. 2008). Legume-secreted isoflavonoids such as daidzein and genistein have been reported to effectively induce *Bradyrhizobium japonicum* nod genes, while nod genes in *Sinorhizobium meliloti* were induced by luteolin (Juan et al. 2007). The level of specificity exhibited enables the rhizobial community to identify their specific host accurately (Bais et al. 2006) (Table 1.1).

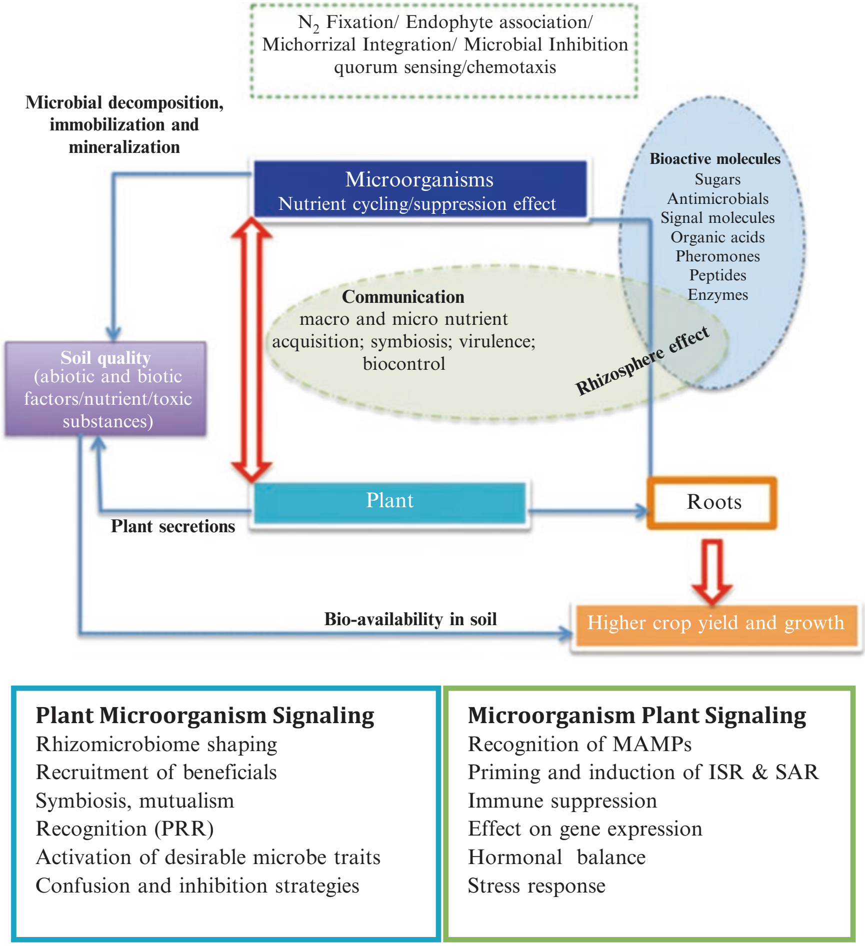

**Fig. 1.1** Plant-microbe interactions and their role in belowground ecosystem and sustainable agriculture (Modified from Zhuang et al. 2013)

A mixed inoculation of *Rhizobium* sp. and *Azotobacter* sp. resulted in *Azotobacter* sp. significantly increasing *Rhizobium* nodulation. Both microorganisms enhanced growth and yield in various soil and mineral compositions. These findings suggest that there exist a mutualistic relationship between *Azotobacter*, *Azospirillum*, and *Rhizobium*, which results in improved yields in crops (Parmar 1995; Parmar and Dadarwal 1997). Researchers have reported that *Azotobacter* and *Azospirillum* contribute towards a plethora of positive responses in plants that include good root development, increase in nutrient and water uptake, inhibition of pathogenic and non-beneficial interactions, and a small contribution towards nitrogen fixation (Okon and Itzigsohn 1995; Steenhoudt and Vanderleyden 2000).

**Table 1.1** Biomolecules involved in direct and indirect microbe and root-based activity

| Activity | Biomolecules | Function |
|---|---|---|
| *Direct microorganism-based activity* | | |
| Nitrogen fixation | EPS, EPS II, lipochitooligosaccharides, flavanols, flavanones, nodulating factors | Division of root cortical cells and nodule morphogenesis |
| Mycorrhizal association | Sesquiterpene, Myc factor | Fungal factors that trigger mycorrhization |
| Metal uptake | Glutathione, metallothioneins, and acid such as ferulic, chorismic, mugineic, caffeic, p-coumaric, oxalic | Metallic bioavailability |
| Virulence factors | Extracellular polysaccharide, phytotoxins, effector proteins | Crucial for virulence and suppression of resistance reactions |
| PGPR | LPS, EPS, antimicrobials, siderophores, lipopeptides, cell wall-degrading enzyme (CWDE) | Protection of plants against pathogens<br>Improved nutrient uptake and growth |
| *Direct root-based activity* | | |
| Bacterial and fungal symbionts | Flavonoids (glyceollin, coumestrol, daidzein, glyceollin, coumestrol, genistein), strigolactones, jasmonates, auxins, abscisic acid, ethylene, gibberellin | Stimulating pre-symbiotic processes and enhanced Arbuscular mycorrhiza fungi (AMF) colonization of roots |
| Carbon uptake | Arabinose, fructose, ribose, hexose | Carbon utilization and metabolism |
| Pathogenicity factors and defense response | Phytoalexins, naphthoquinones, indole, saponins, benzoxazinone, flavonoid, terpenoid, rosmarinic acid, glucosinolates | Protection against pathogenic microorganisms |
| *Indirect microorganism-based activity* | | |
| Quorum sensing | Peptide molecules, N-acyl homoserine lactones (AHLs), quinolone, p-coumarate | Cellular communication, swarming, biofilm, and antibiotic production |
| *Indirect root-based activity* | | |
| Defense | Phospholipases, phosphatases, MAP kinases: Lipoxygenase, linolenic acid, jasmonate, methyl jasmonate | Activation of other defense reactions |

### (b) *Mycorrhizal interactions*

The “fair-trade” between plant and mycorrhiza involves the provision of N by mycorrhiza and carbon by the plant (Fellbaum et al. 2012). A quantitative and qualitative change in the chemical content of soil and plant observed during AMF establishment includes the transient rise in phytoalexin levels during colonization (Leyval and Berthelin 1993). The beneficial fungal isolates or plant cultivars involved in AMF symbiosis can influence the concentration and types of flavonoids produced. The type of flavonoids produced influences the mycorrhizal spore germination, hyphal growth and root colonization. For example, strigolactone, a sesquiterpene lactone, is essential in inducing AMF hyphal branching (Akiyama et al. 2005; Siegrid et al. 2007). Morandi et al. (1984) reported that flavonoids such as glyceollin, coumestrol, and daidzein stimulates AMF colonization in soybean and thus implicates flavonoids as signaling compounds involved in AMF root colonization. In contrast there are chemicals that inhibit hyphal growth of mycorrhiza such as observed within a non-nodule-forming legumes (Oba et al. 2002). Further, it has also been reported that sugars, carbohydrates, and strigolactone 5-deoxygol facilitate the symbiotic associations between the mycorrhiza and non-legume crops (Yoneyama et al. 2008; Fang and St. Leger 2010; Kiers et al. 2011).

Vesicular-arbuscular mycorrhizae (VAM) on the other hand are a group of fungi that are involved in the mobilization of phosphorus from soil with low levels of available phosphorous. The associative relationship of these fungi with legumes influences the root and shoot development as well as the phosphorous uptake that eventually results in enhanced nodulation and nitrogen fixation. Combinatorial inoculation of soil systems with *Rhizobium* and VAM has unequivocally contributed towards plant growth enhancement, nodulation, and $N_2$ fixation. The effectiveness of *Rhizobacterium* sp. as nodulating and $N_2$-fixing fungi in the mycotrophic legume, *Anthyllis cytisoides*, further substantiates AM's function in supplying P to root nodules (Requena et al. 2001). Research shows that other root–microbe symbionts share the same symbiotic genetic pathway as the $N_2$-fixing rhizobia. "Myc" triggers gene activation in roots through a diffusible signaling factor that is required for mycorrhization. This signaling factor results in elevated calcium levels which inevitably caused calcium fluctuations required for epidermal root cell priming for fungal colonization (Meier et al. 2013; Zhuang et al. 2013). These specific interactions have provided insights into functional compatibility between AMF and PGPR as plant growth promoters.

### (c) *Endophytic associations*

Plants have supported endophytes that are either nonpathogenic bacterial or fungal species with no detrimental effects to the host. Although this is a long-standing interaction, but it has not been well studied and documented. Hosts that harbor these endophytes have shown increased resistance to plant stresses. The presence of these endophytes can result in the alteration of root exudates causing a change in the secretion of phenolics and hence altering the pH within the rhizosphere and elevating tolerance toward mineral deficiencies. While endophytic relationships are largely beneficial, there are however some opportunistic associations. The altered exudates from endophytic plants may affect the microbial community within the soil and influence the biology and ecology of the system (Malinowski and Belesky 2000). Plants involved in symbiotic relations with endophytes have also been reported to enhance AMF interactions through root exudates (Novas et al. 2011).

### (d) *PGPR*

PGPRs have been characterized as organisms that colonize and suppress plant pathogens. This group of organisms has been exploited extensively for economic gains due to its inhibitory potential (Parmar 1995). Through a plethora of direct and indirect mechanisms, the PGPR is found to positively influence plants. It is believed that soil microorganisms involved in this interaction are recruited by cues exuded by the host roots hence establishing the PGPRs population and activities. PGPRs on the other hand are reported to produce chemicals that affect plant growth and resistance indicating a two-way relationship between plants and PGPR for improved plant health (Ryu et al. 2004). The involvement of rhizospheric PGPRs in triggering the host immune response through various pathways such as jasmonate and salicylic acid has been previously reported and associated with plant fitness (Compant et al. 2010; Saharan and Nehra 2011). Chemical agents such as amino acids and carbohydrates were reported to be the signals involved in the mobilization of PGPRs to specific roots (de Weert et al. 2002).

Plant growth has been enhanced by bacterial communities that include *Azotobacter*, *Bacillus*, *Azospirillum*, *Enterobacter*, *Serratia*, *Klebsiella*, and *Pseudomonas*. Compared to single inoculums, dual inoculations significantly improved plant weight, dry mass, protein content, and grain yield. Yadegari et al. (2008) reported that combined inoculation of PGPRs increased growth, development, nodulation, and nitrogenase activity. The cumulative effects of growth-promoting substances exuded by organisms such as *Pseudomonas* sp. CRP55b, *Rhizobium* Ca181, *Pseudomonas* sp. CRP55b, *Azospirillum* spp., and *Pseudomonas fluorescens* P21 resulted in an increase of apical and root growth, plant biomass, and crop yield (Rokhzadi et al. 2008). The mechanisms contributing toward the increase in yield and growth are multitudinous, where substances or processes such as phytohormones, plant growth-regulating substances (PGRs), mineralization, cyanogens, siderophores, and phytoalexins/flavonoids collectively resulted in enhanced agricultural output (Mukerji et al. 2006; Nadarajah 2016).

Rhizobacteria produce phytostimulators in the absence of pathogens. These compounds include hormone analogues such as gibberellic acid, indole acetic acid (IAA), ethylene, and cytokinins (Lambrecht et al. 2000). The production of IAA is a plant growth-promoting trait among PGPRs. Tryptophan-dependent and tryptophan-independent pathways have been identified as contributing toward IAA biosynthesis in rhizobacteria (Steenhoudt and Vanderleyden 2000). Shoot development is stimulated in response to the action by cytokinins and gibberellins. Additionally cytokinins are also involved in cell division, primary root development, nodulation, and branching (Murray et al. 2007; Tirichine et al. 2007; Ortiz-Castro et al. 2009). N-Acyl-L-homoserine lactones, another class of phytostimulants, are associated with cellular communication and modulation of gene expression in plants (Choi et al. 2008; Ortiz-Castro et al. 2009).

A multitude of plant responses including stress is regulated by ethylene. Various factors such as temperature, nutrition, gravity, and plant hormone levels influence ethylene production (Glick 2005). In incidences of high ethylene levels, the plant undergoes stress and exhibits impaired root growth (Argueso et al. 2007). However the modulation of ethylene via ACC-deaminase is crucial in the degradation of 1-aminocyclopropane-1-carboxylic acid (ACC ethylene precursor). Various microbes have been reported to cleave ACC to ketobutyrate and ammonia as a means of improving plant stress response to ethylene production (Glick 2005; Stearns et al. 2012). Further, ACC-deaminase activity in *Achromobacter piechaudii* ARV8 improved seedling biomass in tomato and pepper (Mayak et al. 2004). Similarly a study of ACC-deaminase in *Brassica napus* revealed a downregulation of ethylene stress response while recording upregulated gene expression of auxin production genes (Stearns et al. 2012). Arshad et al. (2008) and Mayak et al. (2004) in their reports indicated a role for ACC-deaminase in reducing ethylene levels and thus contributing toward management of drought, salinity, and generally various other abiotic stresses. This therefore clearly indicates that microorganisms with ACC-deaminase activity benefits the overall well-being of plants. Understanding the overall contribution of microbial communities in reducing and mediating ethylene stress in plants may be utilized to generate technologies for plant abiotic stress management.

### (e) *Enzymes and proteins*

While it has been reported that plants secrete enzymes and proteins in addition to primary and secondary metabolites into the rhizosphere (Charmont et al. 2005), information is lacking on how these substances influence the rhizosphere (De Hoff et al. 2009; De-la-Peña et al. 2008). A proteomic analysis on *A. thaliana* root exudates indicates that there is a difference in the secreted proteins according to developmental stages. During the flowering stage, defense-related proteins such as glucanases, chitinases, and myrosinases were produced (De-la-Peña et al. 2010). Higher levels of defense-related proteins such as peroxidases, hydrolase, and chitinase have been reported as secretomes into the plant root systems of *A. thaliana* in response to an infection by pathogenic *Pseudomonas syringae* pv. tomato DC3000. However when inoculated with a nonpathogenic isolate, *S. meliloti* Rm1021, no defense response proteins were secreted into the rhizosphere.

Arabinogalactan protein (AGP) is a hydroxyproline-rich glycoprotein superfamily that is found in plant cell wall proteins. AGPs play a vital role in root and rhizospheric microbe interaction (Nguema-Ona et al. 2013). Cannesan et al. (2012) and Vicré et al. (2005) reported that root tip cells and AGP containing mucilage was observed in the rhizosphere. This glycoprotein acts as an attractant to root pathogen inhibiting microbes and is implicated in the colonization by *Rhizobium* sp. through recognition and attachment to root surfaces (Vicré et al. 2005; Cannesan et al. 2012; Xie et al. 2012). Xie et al. (2012) reported on a similar glycoprotein, which promotes surface attachment of *Rhizobium leguminosarum* to roots of legumes and non-legumes. *P. fluorescens* strain WCS365 colonization of tomato roots involves a plethora of amino acids which includes aspartic acid, glutamic acid, leucine, lysine, and isoleucine (Simons et al. 1997). In another study, the exposure of plants to *Rhizobium* sp. (Sb16) and *Cyanobacterium* sp. (Sb26) (Naher et al. 2008) resulted in higher levels of amino acid exudates in rice. This may perhaps be a consequence to secretion of microbial products that result in amino acid exudates (Chaparro et al. 2013a, b; Phillips et al. 2004). However, the influence of these enzymes and proteins in the establishment, colonization, and configuration of microbial communities remains elusive.

(f) *Sugars*

Chaparro et al. (2013a) reported that the rate of sugars exuded decreased with the plant's development. This could possibly be the consequence of pathways and cycles utilizing sugars being synergistically regulated by sugars and amino acids (Poysti et al. 2007). Considering the large number of genes (27) identified and correlated to carbohydrate metabolism in microbes, sugars are probably actively utilized by these organisms. Metabolic priming of soil microbes enhanced degradation and mineralization of soil organic matter in the presence of fructose and alanine (Hamer and Marschner 2005). The observed priming effect is due to the ability of these substrates to trigger metabolism and enzyme production (Kuzyakov 2002). The priming of enzyme activities results in increased metabolic capabilities of the soil microbiome, which improves the plant acquisition of various limiting nutrients.

### 1.4.2 Antagonistic Plant–Microbe Interactions

(a) *Quorum sensing (QS)*

QS involves cell-to-cell communication between microorganisms in an environment. It has been implied that the plant's root systems have developed the mechanism to exude chemical signals (mimics, blockers, and or degrading enzymes) that have the ability to affect microbial QS (Gao et al. 2003). Diffusion of these small signal molecules (autoinducers), which are present in both Gram-negative and Gram-positive bacteria, is known to mediate QS. QS is essential in the development of plant–microbe interactions regardless if it's beneficial or non-beneficial. These QS-mimicking or quenching signals are potential targets for the discovery and development of new antimicrobial molecules.

Molecules that imitate acylated homo-Ser lactones (AHLs) with specific effects on QS-controlled behavior have been reported in *Oryza sativa* L. (rice), *Pisum sativum* L. (pea), and *Glycine max* (L.) Merr. (soybean). The lasIR system of QS sensing in *P. aeruginosa* regulates virulence factors such as toxins and extracellular enzymes. A second system, rhlIR, also modulates expression of virulence factors. In PUPa3, both systems form useful associations with plants. AHL signaling in *Chromobacterium violaceum* was inhibited by an arginine analog, L-canavanine, that did not interfere with its growth in alfalfa or other legumes. L-Canavanine also regulates QS ability in *S. meliloti* and is also responsible for the control of EPS II biosynthesis in this organism (Daniels et al. 2002; Teplitski et al. 2000; 2004; Zhuang et al. 2013).

The pcoIR system in *P. fluorescens* is connected to the biosynthesis of antimicrobial compounds, e.g., pyrrolnitrin, phenazines, hydrogen cyanide, and pyoluteorin. Similarly the pcoIR system in *P. fluorescens* 2P24 indirectly regulates the production of metabolites, including siderophores, 2,4-diacetylphloroglucinol, and hydrogen cyanide. Tyrosol, farnesol, trisporic acid, and dimethoxycinnamate are some of the signal molecules produced by *Uromyces phaseoli*, *Candida albicans*, and zygomycetes in their host–microbe interactions. 3-oxo-C12-HSL from *P. aeruginosa* inhibits structural changes from yeast-like to filamentous in *C. albicans* (required for virulence). In turn, AHL synthesis in *P. aeruginosa* is strongly suppressed by farnesol. However, the pathways and specific mechanisms involved in fungal QS remain obscure (Hogan 2006; Sanchez-Contreras et al. 2007; Wu et al. 2010; Zhuang et al. 2013).

GABA is another component involved in cellular communication. GABA quenches QS and reduces the virulence of *A. tumefaciens* (Chevrot et al. 2006) while utilizing GABA as sole nutrient source in *P. putida* (Ramos-González et al. 2005). Proline however reverses GABA's ability to quench QS (Haudecoeur et al. 2009). These opposing signals require further investigation to understand the interplay involved in the complex rhizospheric interaction.

(b) *Antimicrobial*

Plant secondary metabolites are compounds that attract beneficial microbes and defend plants against negative interactions. Plants synthesize secondary metabolites such as phenols or their oxygen-substituted derivatives in a limitless manner (Badri et al. 2008; Neal et al. 2012). One such example is rosmarinic acid (RA) (Bais et al. 2002). Basil roots, for instance, have been reported to exude RA when induced or challenged by fungi. RA demonstrates powerful antimicrobial activity against a vast selection of soil microbes, including *P. aeruginosa* (Bais et al. 2002). Fungal (*Phytophthora cinnamomi* and *Pythium ultimum*) elicitation of basil roots produced naphthoquinones and RA that are strong inhibitors of pathogenic and opportunistic microorganisms in the soil including the opportunist plant pathogen *P. aeruginosa*. In addition, grafted watermelon roots with high levels of chlorogenic and caffeic acid exudates and low levels of cinnamic acid (Ling et al. 2013) were resistant towards *Fusarium oxysporum* f.sp. *niveum* infections. Cai et al. (2009) reported that the antimicrobial agent canavanine obtained from leguminous plants inhibits rhizospheric bacteria excluding rhizobia. This suggests canavanine's involvement in the selection of beneficial microbes.

Most antimicrobial products are broad spectrum, and their specificity is determined by the existence of enzymatic machinery to detoxify any of the host products. Antimicrobial compounds are induced through the activation of linked signal transduction pathways as a consequence of pathogen perception by host resistance gene-encoded receptors. However, most studies have not looked into the mechanism of accumulation of these secondary metabolites within the plants and its excretion into the soil environment. In a study conducted on root exudates from *Gladiolus* spp. L., the resistant varieties produced root exudates that had antimicrobial effects against *Fusarium oxysporum* sp. *gladioli*, while the susceptible lines showed no reduction on conidial germination (Taddei et al. 2002). The inhibition of conidial germination of *F. oxysporum gladioli* by resistant cultivars is mainly regulated by the presence of aromatic-phenolic compounds.

Fungal communities in the rhizosphere produced abundant antimicrobial substances (Hoffmeister and Keller 2007; Brakhage and Schroeckh 2011). For example, *Trichoderma* species have been reported to produce a large array of antimicrobials (Elad et al. 2008) among other bioactive compounds. Fungal and bacterial biocontrol strains produced several antimicrobial compounds with similar or varying degree of activity. Bacteriocin such as agrocin 84 (Kim et al. 2006) exhibits narrow-spectrum antimicrobial activity against closely related genera, while polyketides and peptides exhibit broad-spectrum activity (Raaijmakers et al. 2010). The effectiveness of these compounds varies from microbe to microbe. The antimicrobial compounds found within the root cells differ in composition to the antimicrobials found in root exudates (Bednarek and Osbourn 2009).

## 1.5 Multitrophic Interactions in the Rhizosphere

From the one-to-one interactions observed in the rhizosphere, here we look into the multipartite interactions that present the complexity within the rhizosphere. In the root soil environment of plants such as switch grass, endophytic associations of microbe–insect–plant enhanced N availability for the plant (Behie et al. 2012). The presence of raffinose and sucrose in root exudates of switch grass attracted *Metarhizium robertsii* and enabled the tripartite interaction. In addition, plant volatiles from the legume *M. truncatula* attracted *Caenorhabditis elegans*, a nematode that transported *S. meliloti* to the plant's roots to initiate symbiosis (Fang and St. Leger 2010; Horiuchi et al. 2005). Similarly the tripartite relations between PGPR–mycorrhizae and PGPR–rhizobia resulted in the efficient colonization of mycorrhizae and nodulation of rhizobia, respectively (Guiñazú et al. 2010). Due to the complexity of the multipartite interactions, very little is known of the mechanisms involved, and hence more studies are needed to elucidate these mechanisms, colonization, establishment, and benefits of the interaction.

## 1.6 Concluding Remarks

The above segments have dealt with the various ways in which the plant–microbe interaction in the rhizosphere affects both the plant and the soil microbial community. These interactions have been known to effect soil fertility, thus affecting plant health, overall yield, and growth. Hence, it is evident that microorganisms are key players in plant productivity and should be given due attention in the interest of advancing our knowledge in rhizosphere biology. As we transition from conventional agriculture to sustainable agriculture, it is important to understand the differences and the benefits of this transition.

Conventional agriculture practices selection of high yielding genotypes coupled with high fertilizers inputs and pesticides to reduce losses from biotic infestations while enhancing growth and yield. Rhizospheric microorganisms play a minor role

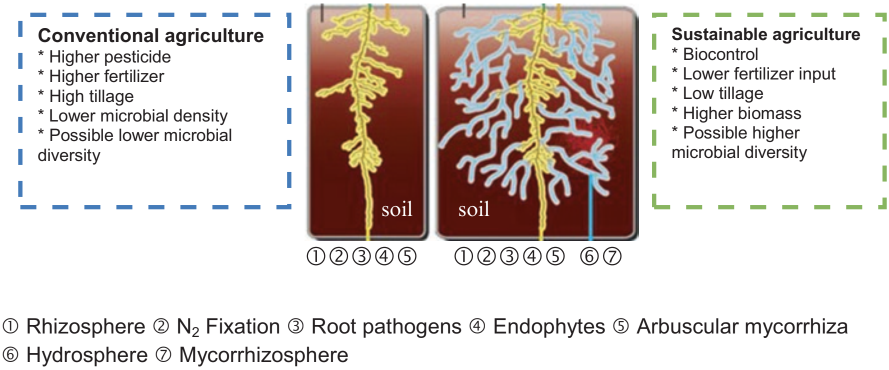

**Fig. 1.2** Conventional vs. sustainable agriculture. The above diagram differentiates between conventional and sustainable agriculture, highlighting the contribution of microbes in sustainable agriculture (① rhizosphere ② $N_2$ fixation ③ root pathogens ④ endophytes ⑤ arbuscular mycorrhiza ⑥ hydrosphere ⑦ mycorrhizosphere)

in conventional agriculture unless they are pathogens. By excluding the microorganisms from the equation, agriculture has been dependent on plant genotypes which may not be as well adapted to adverse conditions. However, in sustainable agriculture, the microorganisms within the rhizosphere are important in crop production (Fig. 1.2). Hence through sustainable agriculture, one could select for plant genotypes that are able to mobilize nutrients from their environments directly or indirectly through interactions with rhizospheric organisms. The results from sustainable agriculture can be further enhanced through the application of good management practices, inclusive of crop rotation, mulching, and utilization of PGPRs.

In this chapter we have provided a comprehensive outline of the major interactions within the rhizosphere and how these interactions affect the plant and the microbial population. Understanding the microbial community and the potential that it carries in enhancing plant processes that leads to enhanced yield and growth would be beneficial to end users, i.e., the farmers. Enhanced yield may be attained through exploiting soil biological fertility, where lesser pesticides and fertilizers are required for improved yield and growth. Therefore through the utilization of existing knowledge and modern technologies, it is expected that valuable insight may be garnered to fill in the gaps in knowledge and information required to provide new opportunities and practices that increase crop production.

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