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REVIEW

Rhizosphere interactions: root exudates, microbes, and microbial communities[1]

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Abstract: The study of the interactions between plants and their microbial communities in the rhizosphere is important for developing sustainable management practices and agricultural products such as biofertilizers and biopesticides. Plant roots release a broad variety of chemical compounds to attract and select microorganisms in the rhizosphere. In turn, these plant-associated microorganisms, via different mechanisms, influence plant health and growth. In this review, we summarize recent progress made in unraveling the interactions between plants and rhizosphere microbes through plant root exudates, focusing on how root exudate compounds mediate rhizospheric interactions both at the plant–microbe and plant–microbiome levels. We also discuss the potential of root exudates for harnessing rhizospheric interactions with microbes that could lead to sustainable agricultural practices.

Key words: rhizosphere, root exudates, microbial communities, plant–microbe interactions, plant–microbiome interactions.

Résumé : L'étude des interactions entre les plantes et leurs communautés microbiennes dans la rhizosphère est importante pour développer de pratiques de gestion durable et de produits agricoles comme les fertilisants et les pesticides biologiques. Les racines d'une plante libèrent une grande variété de composés chimiques afin d'attirer et sélectionner les microorganismes dans la rhizosphère. À leur tour, les microorganismes associés aux plantes, par l'intermédiaire de différents mécanismes, influencent la santé et la croissance de la plante. Dans cet article de revue, nous résumons les progrès réalisés récemment dans l'étude des interactions entre les plantes et les microbes de la rhizosphère à travers les exsudats des racines, en se concentrant sur la manière par laquelle les composés de l'exsudat agissent comme intermédiaires des interactions rhizosphériques à l'échelle plante–microbe et plante–microbiome. Nous discutons aussi du potentiel des exsudats de racines à maitriser les interactions rhizosphériques avec les microbes, ce qui pourrait conduire à des pratiques agricoles durables. [Traduit par la Rédaction]

Mots-clés : rhizosphère, exsudats de racines, communautés microbiennes, interactions plante–microbe, interactions plante–microbiome.

Introduction

The amount of microbial species in the rhizosphere may fluctuate from thousands to millions (Nihorimbere et al. 2011), and accordingly, the interactions between roots and soil microbes are often specialized and based on coevolutionary pressures (Dobbelaere et al. 2003; Duffy et al. 2004; Morgan et al. 2005; Morrissey et al. 2004). In the rhizosphere, plant–microbe interactions play important roles in a number of vital ecosystem processes, such as carbon sequestration and nutrient cycling (Singh et al. 2004). Positive plant–microbe interactions include plant–microbe symbioses, such as plant associations with plant-growth-promoting rhizobacteria (PGPR), epiphytes, and mycorrhizal fungi. These interactions have been shown to have many beneficial impacts on plants, including disease suppression (Haas and Défago 2005; Mendes et al. 2011; Weller et al. 2002), increased nutrient availability and uptake (Lugtenberg et al. 2002; Morrissey et al. 2004), and increased immunity to abiotic (Selvakumar et al. 2012; Zolla et al. 2013) and biotic stresses (Badri et al. 2013*b*; Zamioudis and Pieterse 2012), each of which leads to increases in plant productivity (Berg 2009). In turn, the plant provides the soil microbes with root exudates that are used as substrates and signaling molecules (Bais et al. 2006).

In this review, we summarize recent progress made in unraveling the interactions between plants and rhizosphere microbes through plant root exudates, focusing on how root exudate compounds mediate rhizospheric interactions (plant–microbe and microbe–microbe) and how root exudates affect the soil microbial community (plant–microbiome). We also discuss the importance of rhizosphere microbial communities and the immense benefits they provide to the plant. These interactions are depicted in Fig. 1.

Rhizosphere and root exudates

The term rhizosphere was first defined over a century ago by Lorentz Hiltner (Hartmann et al. 2008; Hiltner 1904) and redefined by Pinton as the zone that includes the soil influenced by the root along with the root tissues colonized by microorganisms (Morgan

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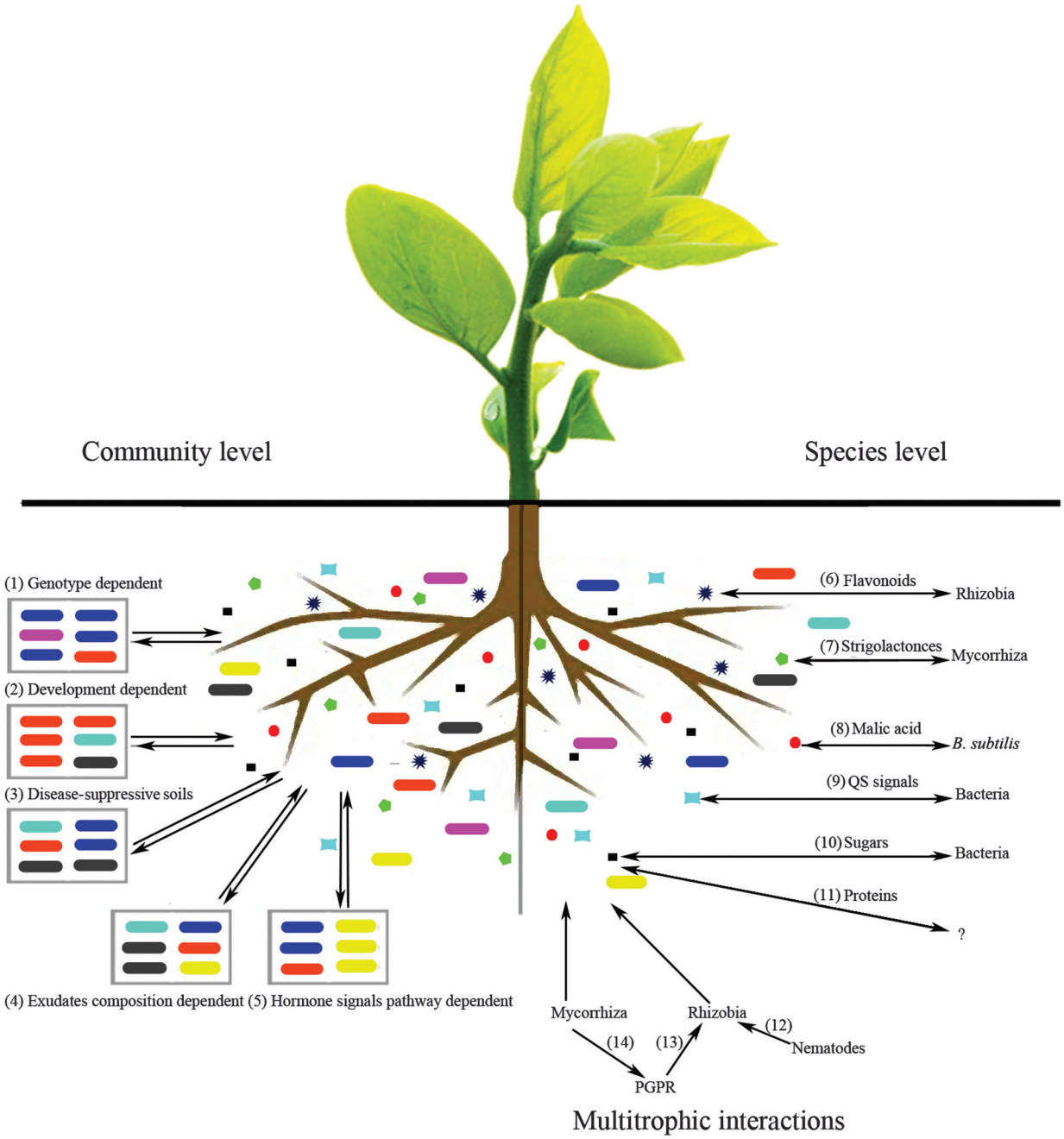
Fig. 1. Plant root exudates mediate a multitude of rhizospheric interactions: at the species level (right side), multitrophic interactions (bottom), and at the community level (left side). The rhizospheric microbial community structure changes depending upon (1) plant genotype (Broeckling et al. 2008; Bulgarelli et al. 2012; Lundberg et al. 2012; Micallef et al. 2009*a*, 2009*b*), (2) plant developmental stage (Chaparro et al. 2013*b*; İnceoğlu et al. 2011; Micallef et al. 2009*a*), (3) exposure to disease-suppressive soils (Mendes et al. 2011), (4) root exudate composition (Badri et al. 2009*a*, 2013*a*), and (5) plant hormone signaling (Carvalhais et al. 2013). Specific compounds released as root exudates mediate one-to-one, plant–microbe, or species-level interactions: (6) flavonoids act as signaling compounds to initiate symbiosis between legumes and rhizobia (Abdel-Lateif et al. 2012), (7) strigolactones stimulate mycorrhizal hyphal branching (Akiyama et al. 2005), (8) malic acid is involved in recruiting specific plant-growth-promoting (PGPR) (*Bacillus subtilis*) (Rudrappa et al. 2008), (9) disruption or initiation of quorum sensing (QS) in bacteria (Gao et al. 2003), and (10) sugars and amino acids act as chemoattractants for microbes (Somers et al. 2004). The roles of (11) proteins secreted by roots and their interaction with other organisms in the rhizosphere is very limited and needs further exploration to conclusively determine the mechanisms at play (De-la-Peña et al. 2008; Mathesius 2009). Other root exudates mediate multitrophic interactions: (12) plants attract nematodes, which act as carriers of rhizobia to the roots to increase nodulation (Horiuchi et al. 2005), (13) plant-growth-promoting rhizobacteria (PGPR) and rhizobia interaction result in the increase of nodulation efficiency (Guiñazú et al. 2010), and (14) PGPR interaction with mycorrhizae increase colonization efficiency (Hernandez and Chailloux 2004; Vosátka and Gryndler 1999). Different rods represent different microbial taxon. Each grey rectangle (left side) represents a distinct rhizosphere microbial community; different colored rods within each community represent the qualitative and quantitative distribution of microbes. Squares, pentagons, circles, stars, and rectangles represent different compounds released as root exudates. For the coloured version of the figure, see Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjb-2013-0225.



et al. 2005; Pinton et al. 2001). There are three distinct zones in the rhizosphere: the endorhizosphere, the rhizoplane, and the ectorhizosphere (Lynch 1987). In this environment, the interactions between plant roots, soil, and microbes significantly alter soil physical and chemical properties, which in turn alter the microbial population in the rhizosphere (Nihorimbere et al. 2011). Additionally, plant root exudates mediate the interactions between plant roots and the microbial communities in the rhizosphere (Badri et al. 2009*b*, 2013*a*; Chaparro et al. 2013*a*). Plant roots release 5%–21% of their photosynthetically fixed carbon as soluble sugars, amino acids, or secondary metabolites (Badri and Vivanco 2009; Badri et al. 2013*b*; Chaparro et al. 2013*a*), and these are used by the microbial communities in the rhizosphere.

Root exudates have been grouped into two classes: low molecular weight compounds, such as amino acids, organic acids, sugars, phenolic compounds, and other secondary metabolites, and high molecular weight compounds, such as polysaccharides and proteins (Bais et al. 2006; Badri and Vivanco 2009; Narasimhan et al. 2003). The qualitative and quantitative composition of root exudates is determined by cultivar, plant species, plant developmental stage, and various environmental factors, including soil type, pH, temperature, and the presence of microorganisms (Badri and Vivanco 2009; Uren 2000). These differences generate microbial communities in the rhizosphere that have a certain degree of specificity for each plant species.

Mechanism of root exudation

Plants use a variety of transport mechanisms to export and secrete compounds into the rhizosphere (Badri and Vivanco 2009; Weston et al. 2012). Generally, root exudates can be released by plant roots via either passive (diffusates) or active (secretions) mechanisms. The majority of low molecular weight organic compounds are released from plants through a passive process. Small polar and uncharged molecules are transported by direct passive diffusion, a process that depends on membrane permeability, the polarity of the exuded compounds, and cytosolic pH (Badri and Vivanco 2009). Plant root cells secrete other compounds, such as secondary metabolites, polysaccharides, and proteins, with the aid of different membrane-bound proteins (Weston et al. 2012). These transporter proteins include the ATP-binding cassette (ABC) transporters (Badri et al. 2008, 2009*a*; Loyola-Vargas et al. 2007; Sugiyama et al. 2008), the multidrug and toxic compound extrusion (MATE) family (Yazaki 2005), the major facilitator superfamily (Reddy et al. 2012), and the aluminum-activated malate transporter family (Weston et al. 2012). Although the details of these membrane-bound transport protein functions are not well understood, they have been associated with the transport of a wide range of compounds into the rhizosphere. Badri et al. (2008, 2009*a*) found that 25 ABC transporter genes were significantly overexpressed in the *Arabidopsis thaliana* (L.) Heynh. roots and played important roles in these secretion processes. In addition to ABC transporters, MATEs are active transporters that export a broad range of substrates across membranes by using the electrochemical gradient of other ions (Weston et al. 2012). Many MATE genes that play a role in exporting different compounds, such as plant-derived alkaloids, toxic compounds, antibiotics, citrate anions, and phenolic compounds, from the root cells have been identified and characterized in *Arabidopsis* (Diener et al. 2001; Li et al. 2002; Liu et al. 2009), sorghum (Magalhaes et al. 2007), barley (Furukawa et al. 2007), and rice (Ishimaru et al. 2011).

Rhizospheric interactions

Root exudates are involved in plant–microbe interactions

In the last decade, the means by which root exudates mediate rhizospheric interactions have been extensively studied (Fig. 1) (Badri et al. 2013*a*; Broeckling et al. 2008; Chaparro et al. 2013*a*, 2013*b*; Doornbos et al. 2012; Micallef et al. 2009*a*, 2009*b*). Plant root-secreted phytochemicals can mediate a number of interactions, such as plant–plant, plant–microbe, and plant–faunal. These interactions can vary from neutral to beneficial or deleterious (Mercado-Blanco and Bakker 2007; Raaijmakers et al. 2009). In some cases, microbes can transition from pathogenic to symbiotic depending upon the environmental conditions (Newton et al. 2010). For example, rhizobia, symbiotic nitrogen (N)-fixing bacteria, range from a symbiotic to a neutral interaction with plants depending on soil N levels (Davidson and Robson 1986; Zahran 1999). Furthermore, under N-limiting conditions, legumes secrete more flavones and flavonols to attract and initiate legume–rhizobia symbiosis (Coronado et al. 1995; Zhang et al. 2009). Similarly, mycorrhiza symbiotic relationships are governed by an equal exchange of nutrients and benefits for each member (Kiers et al. 2011). For example, it was observed in experiments with *Medicago truncatula* Gaertn. that as more carbon was given to the mycorrhizal partner, the mycorrhiza in turn provided the plant with more phosphorous (Kiers et al. 2011). This "fair-trade" between plant and mycorrhiza also occurs with respect to N, as the mycorrhiza only provides the plant with N when it receives plant carbon (Fellbaum et al. 2012). In other words both members of the relationship need to benefit.

Carbohydrates and amino acids

Several studies have shown that plant root-secreted phytochemicals mediate plant–microbe interactions in the soil. For example, the increased secretion of chlorogenic acid and caffeic acid and the decreased secretion of cinnamic acid by grafted-root watermelon improved its resistance to *Fusarium oxysporum* f.sp. *niveum* (Ling et al. 2013). Canavanine, secreted from the seed coat or roots of leguminous plants, acts as an antimicrobial for many rhizosphere bacteria but not rhizobia, suggesting that the host plant secretes this compound for selection of the beneficial microbes (Cai et al. 2009). However, additional studies are needed to identify the specific factors that determine these host–rhizobium interactions. Similarly, symbiotic associations between non-legumes and mycorrhizal fungi are mediated by root-secreted compounds, such as strigolactone 5-deoxystrigol (Yoneyama et al. 2008), sugars (Fang and St. Leger 2010), and carbohydrates (Kiers et al. 2011).

In addition to these symbiotic interactions, root exudates are involved in the initiation of plant–PGPR interactions. PGPR are able to help plants through a variety of direct and indirect mechanisms. Plant roots are likely to attract PGPR through the release of cues (root exudates) in which carbohydrates and amino acids predominantly act as chemoattractants. Recent studies have shown that arabinogalactan proteins (AGPs), which belong to the hydroxyproline-rich glycoprotein superfamily of plant cell wall proteins, play key roles in various interactions between plant roots and rhizospheric microbes in the rhizosphere (Nguema-Ona et al. 2013). Plant root tips release living root border cells, border-like cells, and mucilage into the rhizosphere, which contains large amounts of AGPs (Cannesan et al. 2012; Hawes et al. 1998; Vicré et al. 2005). Although plant roots secrete AGPs abundantly into the rhizosphere, the role of AGPs in rhizospheric interactions has not been well studied. Recent studies have shown that AGPs are essential for plant–microbe interactions in the rhizosphere. For instance, AGPs are able to attract beneficial microbes (bacteria and fungi) and repel plant root pathogens (Cannesan et al. 2012; Gaspar et al. 2004; Vicré et al. 2005; Xie et al. 2012). AGPs secreted by *Arabidopsis* root cap cells and border-like cells affect the colonization of *Rhizobium* sp., suggesting AGPs play important roles in recognition and attachment of rhizobia to the plant root surface (Vicré et al. 2005). In a recent study, a plant arabinogalactan-like glycoprotein was found to be essential for the growth of bacteria on the roots of both legumes and non-legumes and was shown to promote the polar surface attachment by *Rhizobium leguminosarum* (Xie et al. 2012). The mechanisms by which AGPs influence the establishment and colonization of beneficial microbes to plant

roots, how they shape the configuration of the microbial community, and other important functions of AGPs in the rhizosphere remain elusive.

Secondary metabolites and hormones

In addition to carbohydrates and amino acids, plants produce and release numerous secondary metabolites and hormones into the rhizosphere, many of which play a role in plant–microbe interactions. Plants use these compounds to attract beneficial soil microorganisms and defend themselves against pathogens (Neal et al. 2012). For instance, benzoxazinoids, found in the root exudates of maize, attract plant-beneficial rhizobacteria (Neal et al. 2012). Similarly, flavonoids act as chemoattractants to draw rhizobia to the root surface by regulating expression of the *nod* gene, which is responsible for the synthesis of Nod factors (lipochitooligosaccharides) that play important roles in nodulation establishment (Abdel-Lateif et al. 2012). Rudrappa et al. (2008) demonstrated that malic acid released in the root exudates recruits the PGPR *Bacillus subtilis* to the rhizosphere upon infection with *A. thaliana* foliar pathogens. Further studies showed that the presence of *B. subtilis* invokes abscisic acid and salicylic acid signaling pathways in *A. thaliana*, resulting in the closure of stomata and the restriction of pathogen entry (Kumar et al. 2012).

There are several reports on the involvement of rhizosphere PGPR (*Pseudomonas*, *Burkholderia*, *Bacillus*, *Trichoderma*, and *Gliocladium*) in improving plant growth and health (Compant et al. 2010; Lugtenberg and Kamilova 2009; Saharan and Nehra 2011). However, further studies are needed to identify the function of specific root-released chemical signals in recruiting specific PGPR to the roots. For example, de Weert et al. (2002) observed that flagella-driven chemotaxis toward root exudate compounds is necessary for the colonization of the tomato rhizosphere by a pseudomonad PGPR. In addition, *Pseudomonas* species contain chemotaxis sensory proteins for amino acids that aid in their colonization of tomato roots (Oku et al. 2012).

Plant roots also secrete compounds that mimic quorum-sensing (QS) signals of bacteria to stimulate or repress QS-regulated responses of associated bacteria (Gao et al. 2003). In plants, QS plays important roles in establishing root–microbe associations, whether they are symbiotic, pathogenic, or beneficial. Identification of these QS-mimicking or -quenching compounds may lead to the discovery of new molecules and the development of new antimicrobial compounds. At least 15 compounds in the young seedlings and seedling exudates of *M. truncatula* were found to be able to stimulate or inhibit responses in QS bacteria (Gao et al. 2003). Similarly, compounds that imitate the activity of *N*-acyl homoserine lactones and have specific effects on QS-regulated behavior in bacteria have been found in the plants *Pisum sativum* L. (pea), *Coronilla varia* L. (crown vetch), *M. truncatula*, *Oryza sativa* L. (rice), *Glycine max* (L.) Merr. (soybean), and *Lycopersicon lycopersicum* (L.) Karst. (tomato), and in the green alga *Chlamydomonas reinhardtii* (Daniels et al. 2002; Teplitski et al. 2000, 2004). More recently, strigolactones produced by the moss *Physcomitrella patens* were found to act as signaling factors controlling developmental processes and the output of QS-like signals (Proust et al. 2011).

Proteins

Along with primary and secondary metabolites, plants also secrete proteins as root exudates (Basu et al. 1994, 1999; Charmont et al. 2005), but the knowledge on how these secreted proteins influence the rhizosphere microbial interactions remains limited. A few studies have demonstrated the importance of root-secreted proteins during the recognition of pathogenic and nonpathogenic bacteria (De-la-Peña et al. 2008; Wen et al. 2007). Among the most studied proteins in this context are lectins, which function as defense and recognition factors in symbiotic interactions (De Hoff et al. 2009). Furthermore, proteomic analysis of the *A. thaliana* root exudates through plant age showed that plant roots secreted more proteins involved in defense, such as chitinases, glucanases, and myrosinases, during flowering time (De-la-Peña et al. 2010). Additionally, De-la-Peña et al. (2008) determined that the patterns of proteins released as root exudates are dependent on the identity of the microbes that are exposed to *Arabidopsis* roots. For instance, *Pseudomonas syringae* pv. tomato DC3000, a pathogen of *A. thaliana*, highly induced the secretion by *Arabidopsis* plants of plant proteins related to defense, such as peroxidases, glycosyl hydrolase family 17, chitinase, and glycosyl hydrolase family 18. However, the interaction between *A. thaliana* and *Sinorhizobium meliloti* Rm1021, a symbiont of *Medicago sativa* L., did not induce the secretion of these proteins. Our knowledge of plant rhizosphere–microbe interactions will not be complete without elucidating the role of root-secreted proteins in these associations. A combined approach of transcriptomic and proteomic tools would help us reveal the role of proteins in rhizosphere–microbe interactions.

Root exudates mediate multitrophic interactions

While one-to-one interactions are the most studied (see above), several investigations of multipartite interactions have also shed light on the complexity of the rhizosphere. For example, haricot bean and switchgrass were observed to form endophytic associations with the soil-dwelling, insect-pathogenic fungus *Metarhizium robertsii*, and this association provided the plants with insect-derived N (Behie et al. 2012). Furthermore, sucrose and raffinose, which comprise the root exudates, allow for the attraction and colonization of *M. robertsii* to the roots and enable this tripartite interaction to occur (Fang and St. Leger 2010). In addition, it was observed that plant-derived volatile compounds from the legume *M. truncatula* are able to attract the nematode *Caenorhabditis elegans*, which transports *S. meliloti* to the plants roots for the purpose of initiating symbiosis (Horiuchi et al. 2005). Interestingly, the associations between PGPR and mycorrhizae increase the colonization efficiency of mycorrhizae (Hernandez and Chailloux 2004; Vosátka and Gryndler 1999), and the interactions between PGPR and rhizobia increase the nodulation efficiency of the latter (Guiñazú et al. 2010). Further, plants under a symbiotic relationship with leaf endophytes were shown to enhance arbuscular mycorrhizal fungal associations through root exudation (Novas et al. 2011). The signaling components involved in these tripartite interactions (plants–mycorrhizae–bacteria) still need to be elucidated. Further investigations are needed to understand the mechanisms of action and to determine what role root exudation may play in contributing to these beneficial multipartite interactions.

Impacts of root exudates on soil microbial communities

A large body of literature exists regarding one-to-one interactions (plant–microbe), but plants are exposed to numerous microbes in the soil, both beneficial and pathogenic. Therefore, it is important to understand these rhizospheric interactions at the microbial community level instead of simply at the species level. Previous studies suggested that plants select and attract specific microbes and, therefore, alter the composition and diversity of microbial communities in the rhizosphere in a plant-specific manner (Broeckling et al. 2008; Houlden et al. 2008). For example, an *Arabidopsis* ABC transporter mutant that secreted more phenolics than sugars compared with the wild type caused significant changes to the natural microbial community (Badri et al. 2009*a*). These changes in root exudate composition were associated with beneficial bacterial communities enriched with PGPR, N_2-fixing bacteria, and metal remediation bacteria. Micallef et al. (2009*b*) showed not only that different *Arabidopsis* ecotypes exuded unique suites of compounds but also that these differences in root exudation supported distinct rhizosphere bacterial communities. Similarly, Badri et al. (2013*b*) observed that the addition of distinct blends of natural chemicals derived from *Arabidopsis* root exudates added to the soil produced distinct rhizosphere microbial

communities that appeared to have the ability to degrade atrazine or contained more symbiotic bacteria.

Numerous studies have demonstrated that plants can drive and shape the selection of microbes by secreting specific root exudate compounds that shape the rhizosphere microbial community (Bakker et al. 2012; Berendsen et al. 2012; Chaparro et al. 2012). For example, application of *p*-coumaric acid (a known root exudate component) to cucumber seedlings grown in soil increased bacterial and fungal community abundances, changed the organization and composition of rhizosphere bacterial and fungal communities, and increased the density of a soil-borne pathogen of cucumber (*F. oxysporum* f.sp. *cucumerinum* Owen) (Zhou and Wu 2012). The abundances of the bacterial taxa *Firmicutes*, *Betaproteobacteria*, and *Gammaproteobacteria* and of the fungal taxa *Sordariomycete* and *Zygomycota* also increased in the cucumber rhizosphere, indicating that these bacterial and fungal groups may be involved in the degradation of *p*-coumaric acid. Another study showed that vanillic acid (a cucumber root exudate compound) shifted the soil microbial communities of cucumber (Zhou and Wu 2013). Similarly, it was shown that activation of a plant's induced systemic resistance via the induction of the jasmonic acid defense pathway significantly altered the rhizosphere microbial community (Carvalhais et al. 2013). These changes in the microbial community resulted in the enrichment of microbes, including *Bacillus*, *Bacillales*, *Paenibacillus amylolyticus*, and *Lysinibacillus*, that are reported to be involved in plant defense.

Phenolic compounds in plant root exudates influence microbial communities in the rhizosphere. A recent study showed that in the absence of the plant (*A. thaliana*), natural blends of phytochemicals present in the root exudates can modulate the soil microbiome and that these different groups of compounds impact the soil microbiome composition at various levels (Badri et al. 2013*a*). A positive correlation was found with phenolic compounds and a higher number of unique operational taxonomic units compared with other groups of compounds, such as sugars, sugar alcohols, and amino acids, which implies that phenolic compounds act as specific substrates or signaling molecules for a large group of microbial species in the soil. Other studies also found that phenolic compounds play important roles in shaping the rhizosphere microbial community (Fang et al. 2013; Michalet et al. 2013). Inhibition of phenylalanine ammonia-lyase gene expression in rice reduced the abundance of phenolics in rice plants (Fang et al. 2013). This reduction of phenolic exudates in transgenic rice seemed to shape the rhizospheric microbial community, with eight phyla decreasing in abundance in transgenic plants when compared with the wild-type control (Fang et al. 2013). Phytochemical analysis of *Eperua falcata* tree root exudates showed that *E. falcata* influences very specific interactions with soil microbes via its root exudate compounds, and its root exudation patterns are related to distinct root morphologies, which are associated with shifts in root flavonoid content (Michalet et al. 2013).

The microbial community in the rhizosphere is influenced by plant species and developmental stage (Bulgarelli et al. 2012; Chaparro et al. 2013*b*; Lundberg et al. 2012; Turner et al. 2013). A metatranscriptomics study on the microbial communities in the rhizosphere of wheat, oat, and pea showed that the microbiomes in the rhizosphere not only differed from bulk soil but also between plant species and that these changes were evident at the kingdom level (Turner et al. 2013). In addition to those species, a recent report described the impact of genetic variation on the rhizosphere microbiome within a single plant species. Here, significant variation of the bacterial community (the relative abundance, richness, and diversity) was observed in the rhizosphere of 27 maize inbred lines and could thus be attributed to host genetics (Peiffer et al. 2013).

Recently, Lundberg et al. (2012) and Bulgarelli et al. (2012) analyzed the endophytic and rhizospheric communities of *Arabidopsis* plants by performing in-depth pyrosequencing of *Arabidopsis* rhizosphere and its endophytic compartment at distinct stages in plant development. They found that the endophytic compartment was enriched with bacteria classified as *Actinobacteria*, *Proteobacteria*, and *Firmicutes*, while being depleted of *Acidobacteria*, *Gemmatimonadetes*, and *Verrucomicrobia*. Bulgarelli et al. (2012) also determined that while some bacteria, mainly *Betaproteobacteria*, that inhabit the *Arabidopsis* rhizosphere are attracted to the rhizosphere by plant-cell-wall features, bacteria belonging to *Actinobacteria* seem to require metabolically active root cells to colonize the rhizosphere. Interestingly, these results were corroborated by a recent study that determined that microbes belonging to phyla *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Cyanobacteria* not only changed as the *Arabidopsis* plant aged but also correlated with root exudate compounds, as identified through gas chromatography – mass spectrometry (Chaparro et al. 2013*b*). Chaparro et al. (2013*b*) also observed that the plant seemed to select these particular microbes at specific stages of plant development. For example, *Actinobacteria* were selected early in plant development to potentially help the plant in defense, as young plants are more susceptible to disease. On the other hand, *Cyanobacteria*, which have been shown to provide the plant with vital inorganic N, were more abundant in late plant development when the plant requires more N. The plant seems to not only select microbes at the taxonomic level but also to select particular microbial functions that are necessary for plant health, and these functions correlate with the release of root exudate compounds.

Additionally, the impacts of soil type, plant genotype, and growth stage on bacterial communities were also investigated in the rhizosphere of soybeans. It was found that bacterial communities changed with plant growth stage, and that bacteria belonging to the phyla *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, *Nitrospirae*, *Firmicutes*, *Verrucomicrobia*, and *Acidobacteria* commonly inhabit the soybean rhizosphere (Xu et al. 2009). The organization of bacterial communities in a field planted with six potato cultivars at three growth stages (young, flowering, and senescent) were examined by DNA-based pyrosequencing (İnceoğlu et al. 2011, 2012). The young plants revealed bacterial community structures that were more readily influenced by cultivar. Furthermore, members of *Pseudomonas*, *Beta-*, *Alpha-*, and *Delta-proteobacteria* were more abundant under different ecological conditions than were members of the *Acidobacteria*.

The soil fungal community is also affected by plant species and development stage (Hannula et al. 2010; Turner et al. 2013; Wang et al. 2009); however, more studies on the effect of specific root exudate compounds on the fungal community in the rhizosphere are needed. A metatranscriptomics comparison of the microbial communities in wheat, oat, and pea revealed that fungi were highly enriched in the pea rhizosphere compared with that of other crops (Turner et al. 2013). A study of the dynamics of rhizosphere microbial community structure and function in the rhizosphere showed that rice-planted soil had significantly different bacterial and fungal communities than those of unplanted soil (Hussain et al. 2012). Furthermore, it was found that the dynamics and function of the microbial community in the rhizosphere showed significant correlation with plant growth stages (Hussain et al. 2012). In contrast, the fungal communities in the soybean rhizosphere collected from reproductive growth stages showed changes mainly regulated by soil type (Wang et al. 2009). Moreover, Hannula et al. (2010) showed that *Basidiomycetes* were the most abundant in the bulk soil and the rhizosphere of young potato plants while *Ascomycetes* were more abundant at later growth stages. While root exudation changes with plant type it is unclear what role root exudation has on shaping the fungal community in the rhizosphere.

Rhizosphere microbes influence plant root exudation

The microbes colonized in the rhizosphere, including fungi and bacteria, also influence plant root exudation (Jones et al. 2004; Leyval and Berthelin 1993; Matilla et al. 2010). Many studies have shown that the colonization of arbuscular mycorrhizal fungi change plant root exudation qualitatively, e.g., increasing secretions of N, phenolics, and gibberellins and reducing secretions of total sugars, potassium ions, and phosphorus (Jones et al. 2004). Previous studies have shown that different ectomycorrhizal fungal taxa have distinct effects on the abundance and composition of plant root exudates (Fransson and Johansson 2010; Rosling et al. 2004). The inoculation with ectomycorrhizal fungus and (or) rhizobacteria can alter root exudation quantitatively and qualitatively (Leyval and Berthelin 1993). A more recent study has shown that both the abundance and identity of root-associated fungi influence plant root exudation rates (Meier et al. 2013). Furthermore, in response to pathogen attack, plants release compounds as root exudates, such as oxalic acids, phytoalexins, proteins, and other unknown substances (Nelson 1990; Steinkellner et al. 2007). In addition to fungi, bacteria influence plant root exudation too. For instance, *A. thaliana* was found to produce distinct root exudation profiles when cultured with *Pseudomonas putida* KT2440 compared with the plant without *P. putida*, suggesting that bacteria are also modulating plant root exudation (Matilla et al. 2010).

In addition to plant root exudation, the soil microbiome may also influence the plant metabolome (Badri et al. 2013*b*). Distinct soil microbiomes were applied to *A. thaliana* and this not only affected plant growth but also influenced the leaf metabolome, which in turn influenced the feeding behavior of the larvae of the herbivore *Trichopulsia ni* (Badri et al. 2013*b*). Similarly, inoculation of *Arabidopsis* plants under drought stress with distinct microbial communities originating from pine, corn, and *Arabidopsis* soils demonstrated that a sympatric microbiome, with a history of *Arabidopsis* growth, was able to alter the plant's ability to detect drought stress and increased its biomass production compared with the pine and corn microbial communities (Zolla et al. 2013). This may be due to the ability of soil microbes to modulate ethylene levels by degrading the ethylene precursor 1-aminocyclopropane-1-carboxylic-acid (ACC) using the enzyme ACC deaminase (Glick 2005). The plant hormone ethylene is involved in a multitude of plant responses particularly related to plant stress, and its production is regulated by light, temperature, nutrition gravity, and even the status and levels of other plant hormones (Glick 2005). High levels of ethylene exacerbate stress responses and even cause root growth impairment (Argueso et al. 2007). A multitude of soil microbes are able to alleviate plant stress responses to ethylene production by catalyzing the cleavage of ACC, the direct precursor to ethylene, to α-ketobutyrate and ammonia (Glick 2005; Stearns et al. 2012). Thus, lowering plant ethylene levels increases the plants' ability to resist a variety of abiotic and biotic stresses. ACC deaminase activity has been shown to help in ameliorating drought stress (Arshad et al. 2008), water stress, salinity stress (Mayak et al. 2004), overall abiotic stress, and to also help in plant growth promotion (Glick et al. 2007; Yang et al. 2009). For example, the soil bacterium *Achromobacter piechaudi* ARV8 that has ACC deaminase activity was able to increase tomato and pepper seedling biomass (Mayak et al. 2004). Recently, Stearns et al. (2012) studied the response of *Brassica napus* to ACC deaminase bacteria and revealed that genes involved in auxin production were upregulated in the plant while genes involved in ethylene stress response were downregulated. This provides a clear indication to the benefits ACC-deaminase-containing bacteria have on the plant. Determining how the overall bacterial community is involved in mediating and reducing ethylene-mediated stress could create technologies to help the plant deal with abiotic stress.

Concluding remarks and future perspectives

The majority of the above-mentioned studies were conducted to identify the composition and diversity of the microbes present in different environments and are summarized in Fig. 1. However, rather than identifying which microbes are present, identifying what they are doing would provide more insights into these complex interactions. For example, experiments to understand the mechanism of disease-suppressive soils revealed that bacteria consistently associated with disease suppression belonged to phyla *Proteobacteria*, *Firmicutes*, and *Actinobacteria* and that the disease suppression of the members of *Gammaproteobacteria* was governed by nonribosomal peptide synthetase, which protects plants from fungal infection (Mendes et al. 2011). In addition, identification of the compounds present in the root exudates that influence the soil microbial community structure and function would help build novel strategies for improving plant performance and for increasing crop yield and sustainability.

Plants have complex interactions with microbes in the rhizosphere (Berendsen et al. 2012). There is an enormous body of literature demonstrating that rhizospheric interactions at the one-to-one (plant–microbe) level are mediated directly or indirectly by root exudates. However, recent developments in next-generation sequencing technology have allowed researchers to study these interactions at the community level. These studies have focused mainly on identifying what types of microbes are present in the different environments. Furthermore, studies are warranted to analyze these interactions at the functional level to identify the signals involved in interspecies interactions. The majority of studies analyze how plant root exudates attract and regulate these microbial interactions, but knowledge is lacking on how specific microbes modulate these interactions especially at the community level and how root-associated microbial communities influence plant root exudation. Further research is needed to identify the microbial factors influencing the host root exudation process. This will help develop strategies to engineer microbes to manipulate plant root exudation and in turn the microbial communities in the rhizosphere.

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