Rhizosphere as Hotspot for Plant-Soil-Microbe Interaction

Shamina Imran Pathan, Maria Teresa Ceccherini, Francesco Sunseri, and Antonio Lupini

Abstract In the last decades, many studies were addressed to focus the interplay between plant and microbial community into the soil and especially in the small soil zone in contact to plant root, called rhizosphere, which can be considered as a hotspot for interactions and therefore is a major target for improving nutrient use efficiency in crops. In this regard, unraveling the microbial activities that can be used to improve nutrient use efficiency may be the major challenge considering a sustainable agricultural contest. However, although using different approaches (metabolomics and transcriptomic) it has made it possible to characterize many interaction mechanisms, more remains largely unknown. Here, we summarize and discuss the abiotic and biotic factors that may manage plant-microbe interactions in the rhizosphere as well as in those parts of the soil furthest from the root, focusing on root architecture and nitrate as well.

Keywords Metabolomics · Transcriptomic · Rhizosphere · Plant-microbe interaction

Abbreviations

AM	Arbuscular mycorrhizal
ECM	Ectomycorrhizae

S. I. Pathan
Department of Agrifood Production and Environmental Sciences, University of Florence, Florence, Italy
e-mail: shamina.pathan@unifi.it

M. T. Ceccherini
DAGRI – Department of Agriculture, Food, Environment and Forestry, University of Florence, Florence, Italy
e-mail: mariateresa.ceccherini@unifi.it

F. Sunseri · A. Lupini (✉)
Department of AGRARIA, Mediterranean University of Reggio Calabria, Reggio Calabria, Italy
e-mail: francesco.sunseri@unifi.it; antonio.lupini@unirc.it

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GS	Glutamine synthetase
HMW	High molecular weight
JA	Jasmonic acid
LMW	Low molecular weight
N	Nitrogen
NiR	Nitrite reductase
NR	Nitrate reductase
NUE	Nutrient use efficiency
P	Phosphorus
PGPR	Plant growth-promoting rhizobacteria
PLFA	Phospholipid fatty acid analysis
SOM	Soil organic matter
T-DNA	Transmission of DNA
UpE	Uptake efficiency
UtE	Utilization efficiency

1 Introduction

To meet the food needs of the population, an agricultural model based on the overuse of fertilizers has been adopted in recent decades. This model has created severe problems for both environmental quality and human health (Good et al. 2004). In addition, this approach has involuntarily led to the selection of genotypes with a low nutrient use efficiency. Given forecasts that the world population is increasing, around 9.2 billion on 2050 (FAO 2009), more crop production is needed using alternative strategies reducing the input of chemicals and improving food quality without negatively affecting the environment (Xu et al. 2012).

The rhizosphere is often defined as the area of soil around a root where the population of microorganisms depends on inputs from the plant. The rhizosphere is a soil microenvironment where plants and microorganisms can coexist in positive, negative, or neutral interactions (Lynch and Whipps 1990; Kardol et al. 2007) (Fig. 1). It is populated with numerous organisms, including fungi, bacteria, etc. and possibly exhibiting one of the highest levels of biological biodiversity of any environment in the world (Bender et al. 2016) (Fig. 1). Given the strong interaction between plants and microbes in the rhizosphere, it can be considered an extension of the plant's genome (Berendsen et al. 2012; Verma et al. 2015). As crop yield is strongly dependent on water and nutrient uptake from the soil, the rhizosphere can be considered as a *hotspot* for interactions and therefore is a major target for improving nutrient use efficiency in crops.

Rhizosphere microbes may improve plant growth not only by making nutrients more available for uptake by the root (e.g., phosphate-solubilizing bacteria) but also through the production of phytohormones that can improve plant resistance to biotic and abiotic stresses (Berendsen et al. 2012). Plant roots secrete exudates derived from photosynthesis providing an important carbon supply for the growth of microorganisms (Brimecombe et al. 2007).

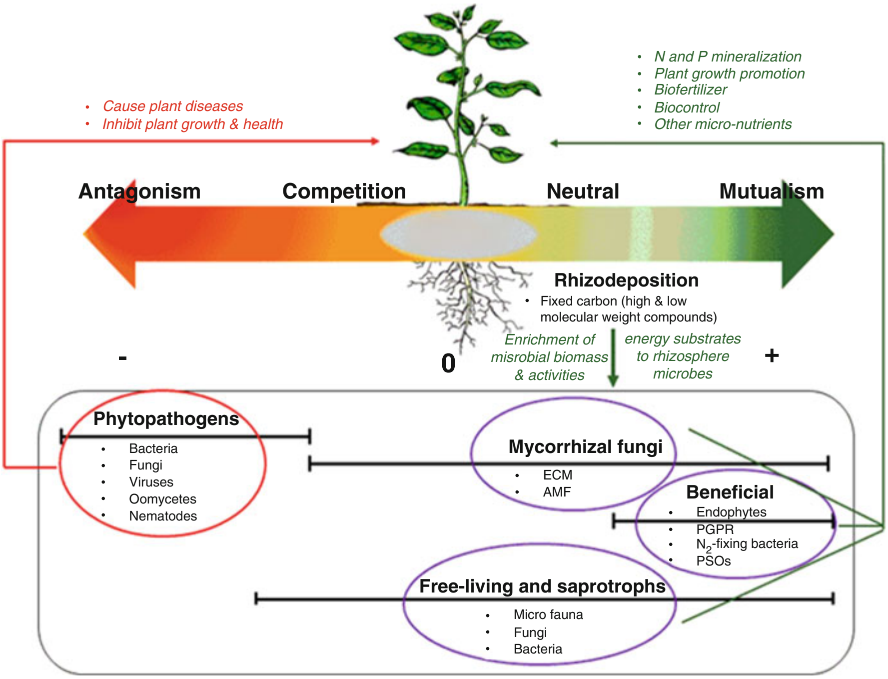

Fig. 1 Representative overview of different plant-rhizosphere microbe interactions and their activities (The figure has been adapted from Quiza et al. 2015 and modified)

Therefore, engineering the rhizosphere may be a useful target for developing more sustainable agriculture (Zhang et al. 2017). Despite the importance of the rhizosphere and the innumerable publications in this field by using new technologies related to DNA sequencing and metabolomics, to date much remains to be discovered. More information is needed to understand the mechanisms involved in rhizosphere interactions and particularly how plants control their microbiome and vice versa how microorganisms influence crops.

The present review focuses on the recent knowledge of the rhizosphere, emphasizing particularly microbe and root interactions in relation to nitrogen supply.

Finally, this chapter reports some examples of how these interactions can be used to improve crops in a background scenario of more sustainable agriculture in the context of climate change.

2 Rhizosphere as an Active Network

The “rhizosphere” term was first conceived by Hiltner (1904) to delineate the plant root-soil interface. The rhizosphere was defined as the soil microenvironment where chemical, physical, and biological properties are affected by plant roots and their metabolic activities. Thus, the rhizosphere is one of the most dynamic networks of the terrestrial ecosystem, where direct plant-soil-microbe interaction takes place. Plant roots release up to 40% of photosynthetically fixed carbon directly into soil (Bais et al. 2006) mainly in the form of high and low molecular weight compounds (Newman 1985; McNear 2013). These compounds especially low molecular weight molecules such as amino and organic acids, phenolic compounds, sugar, etc. can be used by rhizosphere microbes as energy sources, which cause enrichment of the microbial biomass and activity (Doornbos et al. 2012). Moreover, exudation significantly influences soil physical and chemical properties (Nardi et al. 2000) such as soil pH (Javed et al. 2012), soil aggregation and erosion prevention (Naveed et al. 2017; Wang et al. 2017; Meena and Meena 2017), and water holding capacity (Young 1995). On the other side, root exudation helps the plants to gain essential nutrients from the soil through acidification and oxidation/reduction processes in the rhizosphere (McNear 2013). Nitrogen (N) and phosphorus (P) are key plant growth-limiting nutrients, and rhizosphere microbes play a key role through degradation and mineralization processes to deliver these essential nutrients to the plant. Much of the soil N and P are stored in complex organic forms that plants cannot easily access often requiring breakdown and solubilization by microbes before uptake by roots can occur. Thus, the rhizosphere is the apropos niche for plant and soil microbes, where key plant-soil-microbe interactions take place giving benefits to both organisms for plant mineral nutrient acquisition and substrate for microbial energy requirements. These interactions can either be beneficial (symbiotic) for the crop, for example, plant interactions with epiphytes, such as plant growth-promoting rhizobacteria (PGPR), nitrogen-fixing bacteria, and mycorrhiza fungi, or can be negative (parasitic) with plant pathogenic microorganisms (Singh et al. 2004; Raaijmakers et al. 2009; Walkers et al. 2003; Dadhich and Meena 2014). Hence, the rhizosphere is the hotspot where the plant and soil microbial community communicate with each other through the plant roots and mediated by root exudations.

3 Root Exudates Regulating Factors

Plant roots discharge immense amounts and ranges of organic compounds into the rhizosphere soil, known as root exudates or rhizodeposition, and through these exudates, plants can directly communicate with rhizosphere microbiota. Root exudates are an important nutrient for the microbial community in rhizosphere soil and therefore encourage root-microbe colonization (Bacilio et al. 2002). Plant roots can exude many different compounds such as acids, oxygen, and ions, but most are organic molecules (Uren 2000; Bais et al. 2006). These organic-based exudates can be categorized into high and low molecular weight (HMW and LMW, respectively) compounds. The majority of exudates are LMW, including amino and organic acids, sugars, phenolic compounds, and many other secondary metabolites, while considered HMW exudates are more complicated compounds such as mucilage and cellulose (Huang et al. 2014; Rovira 1969). Although root exudates are a key driver of plant-microbe communication in rhizosphere soils, less attention has been given to the mechanisms and regulatory processes that control root exudation. Plant age and genotype, as well as other external biotic such as nutrient availability and root architecture and abiotic factors like soil properties, temperature, stress, or toxic conditions, are known to regulate the quantity and quality of root exudates (Badri and Vivanco 2009; Varma et al. 2017).

3.1 Abiotic Factors

3.1.1 Soil Properties

Soil physical and chemical properties such as pH, texture, moisture, etc. significantly regulate the root exudation process; mainly soil moisture content is one of the key drivers of the root exudation, as high soil moisture leads to hypoxia condition due to the inadequate accessibility of O_2 in the soil. Root mucilage exudation can improve the physical pathway for water and nutrient delivery to roots, and this is particularly important as soil dries (Carminati et al. 2016). Low soil moisture can cause temporary plant wilting which caused an increase in the release of amino acids from plant roots (Katznelson et al. 1954). Some bi-cropping studies suggested that high moisture content could help in the rapid transfer of maize root exudates to adjacent bean plants (Ivano 1962). Water stress, including both drought and flood conditions, can significantly impact on the quantity and quality of wheatgrass root exudates as the stress-induced exudation of organic acids such as malic, fumaric, malonic, succinic, and oxalic acids (Henry et al. 2007). Similarly, Song et al. (2012) also reported that exudation of various organic acids such as malic, lactic, acetic, succinic, citric, and maleic acid concentration was increased by osmotic stress in drought-tolerant and non-drought-tolerant maize in hydroponics. Furthermore, soil pH can have a significant effect on root exudation resulting in acidification and alkalinization. Stoltz and Greger (2002) found that the increased soil pH produced by *Eriophorum angustifolium* and *E. scheuchzeri* roots could decrease the leaching of toxic elements such as Cd, Cu, Pb, and Zn, while Wang et al. (2006) reported that a lower pH could lead to higher soil leaching of toxic elements such as Cd and Zn. Recent studies on *E. angustifolium* roots showed that changes in the rhizosphere to a more alkaline pH significantly influenced the exudation of organic acids (oxalic, succinic, and formic acids) in root mucilage under moderately toxic soil conditions (Javed et al. 2012). There are very few studies focused on how soil texture can influence the root exudation process. Soils with different textures have different chemical and physical properties which can cause direct or indirect induction or inhibition of LMW and HMW compound secretion by plant roots. Sandy substrates can induce root exudation as high secretion rates of amino acids were reported when plants were grown in quartz sand (Boulter et al. 1966). Since soil characteristics significantly affect root exudation, little attention has been given to these types of studies, which may be due to the plasticity and variability of root exudates. The study of root exudates is hindered by difficulties in the collection of representative samples, especially in the soil and under field conditions. Plant root exudates may be dissimilar in soil and hydroponics. However, recent molecular techniques combining with stable isotope probing could shed more light on the effect of soil physical characteristics on root exudation.

3.1.2 Temperature

Temperature can have major effects on root exudation. Rovira (1956) reported that higher temperature could cause the increase in the exudation of different amino acids, especially asparagine from *Solanum lycopersicum* (tomato) and *Trifolium subterraneum* (subterranean clover). Other studies showed that exudation of tannins and phenolic compounds was markedly inhibited at low temperature (4 °C) compared to the amount at 30 °C in fava beans (*Vicia faba*) (Bekkara et al. 1998). Contrariwise, Husain and Mckeen (1963) found that strawberry roots secrete higher amount of organic acids at low temperature (5–10 °C) than at higher temperature (20–30 °C), which also leads to root colonization with the pathogenic fungus *Rhizoctonia fragariae* (Husain and Mckeen 1963; Hale and Moore 1979). A generalized plant exudation response to temperature may not be found; it seems more likely that each species responds differently to temperature extremes.

3.1.3 Light Intensity

A few studies have shown that the composition and quantity of root exudates were affected by light intensity, as it is directly linked to photosynthetic C fixation, the main C source for root exudates. For example, Rovira (1956) reported that trefoils grown under full daylight released higher amounts of serine, glutamic acid, and alanine but shadow inhibited the exudation of aspartic and glutamic acid, phenylalanine, and leucine in grown plants. Many authors reported the quantity of root exudates was significantly increased by the high light intensity and prolongation of the photoperiod, for example, phosphatidylserine in Zn-deficient wheat (Cakmak et al. 1998), catechin in spotted knapweed (Tharayil and Triebwasser 2010; Yadav et al. 2018), and citrate in white tulips (Cheng et al. 2014). Although fluctuations in light intensity combined with the altered photosynthetic spectrum (longer wavelengths) affected the synthesis of secondary metabolites in the leaves of birch and woody plants, the root exudates were not measured (Lavola et al. 1998). However, Yang (2016) reported that light intensity not only influences the quantity but also significantly impacts on the composition of root exudates in sugar beet. Recently Martin et al. (2018a, b) reported that fluctuations in light exposure increased the exudation of dissolved organic carbon and protein-like and humic-like dissolved organic matter, whereas constant low and continuous light significantly inhibit the exudation of total dissolved nitrogen. These findings suggest that light intensity and exposure time are two of the key factors that regulate synthesis and secretion of root exudates, and these should get more attention for future studies on root exudates and their regulating factors.

3.1.4 Nutrient Availability in the Rhizosphere: Nitrogen as Nutrient and Sensor

Although the rhizosphere is confined in a small area (about 2 mm) between root and soil, it is an important zone affecting nutrient dynamics influenced by a plethora of microbial activities useful for improving crop uptake efficiency (Dakora and Phillips 2002). Different factors combine to determine the availability of nutrients in this zone, such as soil chemistry, plant genotype, and nutrient supply (Jones et al. 2004). The availability of nutrients depends on the activity of microorganisms, which in turn are regulated by quantity and quality of the root exudates, thus creating different local micro-ecosystem compared to the bulk soil (Neumann et al. 2009; Meena et al. 2018). Various plant mechanisms have been developed to cope nutrient-limited conditions, but the exudation of organic acids and enzymes into the soil by roots can enhance soil organic matter (SOM) decomposition thus releasing nutrients making them available for plant uptake (Charholm et al. 2015). Some plant species exhibit specific rhizosphere effects on the availability of nutrients, such as the Solanaceae influencing phosphorus mobility in the soil (Safari and Rashidi 2012). Grasses can produce phytosiderophores to increase iron availability by chelation of the metal ion, particularly under Fe-limiting conditions (Ueno et al. (2007). From the bulk soil to the root surface, the microorganism populations increase in quantity but decrease in species diversity, thereby influencing the availability of nutrients. In the rhizosphere, there is an equilibrium between the plant, soil, and microorganisms which is usually characterized by low nutrient concentrations, where a constant turnover can ensure a steady supply for roots (Shen et al. 2013). Considering phosphorus, for example, it can be present in large amounts in the soil, but it is totally unavailable for the plant as both organic and inorganic forms are insoluble (Bhattacharyya and Jha 2012; Igual et al. 2001; Gyaneshwar et al. 2002). Applications of P fertilizers may not combat this limiting condition due to the phenomena of precipitation occurring in the soil (Mckenzie and Roberts 1990). However, in the rhizosphere, some microorganisms are defined as P-solubilizing, such as *Azotobacter*, *Burkholderia*, *Erwinia*, *Flavobacterium*, and *Serratia* (Bhattacharyya and Jha 2012), and these have the ability to make this element soluble by synthesizing the low molecular weight organic acids which dissolved the inorganic phosphorus converting it to soluble forms (Zaidi et al. 2009) and therefore available for plant uptake (Mehnaz and Lazarovits 2006).

N_2 fixation is another important example of a microbe-plant interaction (discussed in Sect. 5.1), and its significance is dictated by the role that this element (N) has in plant physiology and is often limiting crop productivity. Among nutrients affecting plant growth and development, N plays a pivotal role, and nitrate, which is the main N-form in aerobic soils, can also be considered as a “signaling molecule.”

Nitrate can act as a signal to regulate plant gene expression, metabolism, physiology, growth, and development (Krouk et al. 2011; Vidal and Gutiérrez 2008). Although the capacity of the plant to assimilate N depends from on carbon turnover, an increase in biomass is principally limited by nitrogen uptake from the rhizosphere. In plants grown using nitrate-free conditions, the presence of nitrate leads to the modulation of enzymes responsible for assimilation, such as nitrate reductase (NR), nitrite reductase (NiR), and glutamine synthetase (GS), which play fundamental roles in crop production (Crawford 1995; Stitt 1999). In the last decades, genomics, bioinformatics, and systematic have described a complex regulatory network at transcriptional and posttranscriptional levels for the plant's responses to nitrate (Krouk et al. 2010). In *Arabidopsis*, nitrate and N metabolites regulate the expression of numerous genes involving a wide range of processes. Studies of the effect of nitrate supply on the quality and quantity of root exudates are missing, especially in space and time. According to Scheible et al. (2004), who provided an illustration of the signaling action of N in *Arabidopsis* grown in an N-free solution, nitrate supply determines a massive reprograming of genome expression. Within 30 min, the re-addition of nitrate induces gene expression involved in uptake, reduction of nitrate, and organic acid skeleton production. On the other hand, after longer times (about 3 h), the nitrate supply induces specific genes belonging to trehalose and hormone metabolism, protein kinases and phosphatases, receptor kinases, and transcription factors (Scheible et al. 2004), and some of these processes may be important in root-rhizosphere interactions, thereby increasing or reducing the crop nitrate uptake efficiency. As affirmed by Krouk et al. (2010), up to 10% of the transcriptome is responsive to nitrate, and many genes are considered as signals, as these genes are still nitrate-regulated in *Arabidopsis* NR-deficient mutants, where the first enzyme of the nitrate assimilation pathway is missing (Wang et al. 2004; Kumar et al. 2018).

Finally, the global nitrate signaling pathways show complex regulation either into the plants by transcriptions factor or external to the plants by nitrate availability, which in turn is strongly dependent on the rhizosphere activities. Thus, the rhizosphere is the *hotspot* where both the concentration of microorganisms is very high compared to bulk soil and the concomitant activity of roots and microorganisms allows the creation of a microenvironment favoring mineralization (Parkin et al. 2002) and denitrification (Qian et al. 1997). Finally, little is known about the mechanisms that microorganisms have on local nitrate signals in the rhizosphere.

3.2 Biotic Factors

3.2.1 Plant/Rhizosphere and Nutrient Use Efficiency

The current requirement in most agriculture is to reduce the inputs of fertilizers in formulating management practices for more sustainable production. New strategies for plant nutrition will require adequate consideration of rhizosphere processes for improving crop productivity (Shen et al. 2013; Zhang et al. 2017). Starting from a general point of view and focusing on specific topics, strategies to maximize the efficiency of rhizosphere processes related to plant nutrition can be assessed by manipulating root growth patterns and targeted fertilizer applications (Zhang et al. 2010; Chen et al. 2011).

Nutrient use efficiency (NUE) is determined by two components: uptake efficiency (UpE), or the root's ability to take up nutrients from the soil, and utilization efficiency (UtE), as the plant capacity to assimilate or utilize the nutrients (Good et al. 2004; Xu et al. 2012; Lupini et al. 2017; Dadhich et al. 2015). In this context, as rhizosphere is strictly in contact with the roots, UpE is the component most influenced by the rhizosphere processes and on which it is possible to identify strategies for improving NUE.

In legume species *Rhizobium* spp. accommodated in specialized nodule structures can fix a considerable amount of N to supply the plant. Other microorganisms increase in the availability of nutrients in nonlegumes (Boddey et al. 2003). There are some microorganisms, such as *Azospirillum* spp., which can supply N to plants (Assmus et al. 1995) increasing the NUE more specifically the UpE. Relationships between the roots and microorganisms in the rhizosphere favor nutrient uptake: on the one hand, there are the root exudates that provide organic compounds to microorganisms (Parkin et al. 2002), and on the other side, they provide inorganic compounds more easily taken up by the plant (Marschner 1995). Some types of bacteria form a biofilm on the roots, thereby ensuring an improvement in nutrient uptake (Beauregard et al. 2013) by providing a robust water contact between soil particles and the root. Using PCR coupled with denaturing gradient gel electrophoresis and fluorescence approaches, Briones et al. (2003) demonstrated a strong correlation among ammonia-oxidizing bacteria and NUE of some rice cultivars also underlining that the presence of these bacteria improved nitrate uptake. Therefore, nutrient uptake may be improved through the selective production of root exudates, which favor the association with specific bacteria and decreasing the abundance of others. Nutrient availability in the rhizosphere is strongly regulated by exudation, but the manipulation of high-affinity nutrient transport systems at plasma membrane level is poorly studied, and increased chelating creates nutrient-limited zones around the roots (George et al. 2005; Liu et al. 2005). Furthermore, the selectivity of root exudates could be achieved through the molecular manipulation of the transporters to improve both the mineralization processes and the numbers of beneficial microorganisms in the rhizosphere. To date, few transporters involved in plant/microbe rhizosphere cross talk were completely functionally characterized (Kretzschmar et al. 2012; Rudrappa et al. 2008), and further studies are needed in crop species. Some authors have demonstrated that plant roots secrete organic compounds to inhibit nitrification (Subbarao et al. 2013) and denitrification (Cordero and Datta 2016), which may be used in agriculture to improve NUE. Manipulating these microbial processes in the rhizosphere can be used to develop crops with higher NUE by decreasing N leaching losses.

3.2.2 Plant Root as Main Trait to Improve NUE

The major limiting factors for the twenty-first-century crop production are the scarcity of water and nutrients in the soil. The plant root system is fundamental for acquiring nutrients and water which are primarily taken up from the soil. In this context, different approaches may be used to improve NUE: (i) changing root architecture to enhance nutrient acquisition especially in nutrient-limiting conditions and (ii) managing the rhizosphere processes starting from root modifications. In fact, it is now well established that root architecture plays a fundamental role in nutrient use efficiency (Lynch 2011) and influencing microorganisms in the soil too (Wang et al. 2011; Wu et al. 2012). Improving the capacity of the root to explore the soil by modifying root architecture is a pivotal task. Thus, understanding internal and/or external factors tuning the growth and development of this organ is an important target to improve water and nutrient use efficiency. Among macroelements, N (mostly nitrate) and phosphorus are the main limiting factors for plant growth and development (Gojon et al. 2009), and plants have adopted strategies to improve nutrient uptake efficiency by modifying root morphology and architecture. Nutrient dynamics in the rhizosphere can lead to substantial and specific changes in roots. Using varying N levels, it was possible to identify specific root adaptations regulated by local or systemic signaling (Bellegarde et al. 2017; Yadav et al. 2017). At the molecular level, genes, transcription factors, proteins, and miRNAs have all been identified to have their role in root architecture and nutrient use efficiency. Mlodzínga et al. (2015) showed the role of a gene (*AHA2*), a plasma membrane H^+-ATPase in root morphology and architecture of rice under N-limiting conditions. Other molecular evidence was established in P-limiting conditions, as *OsPHR2* gene and the*OsMYB2P-1* transcription factor influenced root hair development and root architecture in rice (Wu and Wang 2008; Dai et al. 2012). QTLs were also associated with root architecture in maize (Li et al. 2015), rice (Li et al. 2009), and bean (Cichy et al. 2009). Of course, these results will be useful to use as molecular markers in breeding programs to improve root architecture and consequently nutrient use efficiency.

Root morphology is also a genetic factor modifying the rhizobiome. Diverse root types can contribute differently to microorganism selection in the rhizosphere. Recent publications point out how the microbe-community can change along roots and among root types. Edwards et al. (2015) showed how the dynamics of the root-associated microbes was strongly dependent on root niche in rice plants, whereas other authors have underlined the bacterial variation among plants, depending on age and genotypes (Lundberg et al. 2012) or different genotypes changing their *ribotype* profile (16S rRNA gene sequence) depending on host cells (Bulgarelli et al. 2012). Among different root zones, the highest number of bacteria is localized at the root tip, which may be able to select for specific microbes. In wheat seedlings, De Angelis et al. (2008), using high-density 16S rRNA microarray (PhyloChip), showed a differing number of microorganisms with the following hierarchy, bulk soil < mature root < root tips = root hairs, whereas specific colonization by *Bacillus subtilis* was observed in the root elongation zone of *Arabidopsis*, suggesting a possible protection mechanism against root pathogens (Massalha et al. 2017). The mature root zone included decomposers which may be associated with the degradation of cells from older root parts (Jones et al. 2009). Distinct communities were also confirmed in lateral roots as compared to tips and basal regions. In this respect, *Brachypodium distachyon* was employed as a monocotyledon model, and the communities assayed were dependent on root type (nodal or seminal) and root axis (Kawasaki et al. 2016a, b). Thus, as the plant genotype and root system regulates rhizosphere microbiota, more work in this field may be interesting for improving crop productivity. There is an emerging need to evaluate the differences among plant populations within the same species. Comparing wild and modern bean accessions, Pérez-Jaramillo et al. (2017) showed a difference in bacterial numbers that was highly correlated with root morphology. In conclusion, some authors affirm that root phenotype influences rhizosphere colonization by differences in cell wall structure, surface area, and exudate metabolic profiles (Pérez-Jaramillo et al. 2017; Saleem et al. 2016). Thus, it may be important to consider factors modifying root morphology such as nutrient and stresses to drive agronomic practices that optimize rhizosphere interactions.

4 Microbial Selection by Plants

The rhizosphere is where the plant and soil microbe communities are directly linked to each other based on their nutrient requirements. It is well documented that plants can shape their rhizobiome (rhizosphere microbial community), as plant genotype, growth stage, and soil type significantly affect the abundance, composition, and diversity of the rhizobiome (Berg and Smalla 2009; Philippot et al. 2013; Bulgarelli et al. 2013a, b). Selection of the rhizobiome is directly related to the plant root exudation pattern and other abiotic factors such as soil temperature, moisture, chemistry, and physical structure (Pugnaire et al. 2004; Hartmann et al. 2009; Bargett and van der Putten 2014). Recently, Burns et al. (2015) studied different predictors which can affect the rhizosphere microbial community using statistical methods, and they pointed out that plant species is the main determinant of the rhizosphere microbiome, which suggests there is an active microbial selection by plants. Plant-soil feedback strongly relies on plant species and rhizosphere microbe association (Kulmatiskietal. 2008) which implicates plant-microbe coexistence and community assembly (Bever et al. 2010). Furthermore, Burns et al. (2015) also reported that spatial location is also a key predictor which shapes the microbial community, and they also suggested that everything is not everywhere with localized hotspots on the root surface for specific populations.

Since Smalla et al. (2001) first studied the rhizosphere bacterial community using culture-independent techniques and suggested that each plant was colonized by their own bacterial community, numerous studies have focused on how different plant genotypes, plant growth period, and nutrient use efficiency have shaped or influenced abundance, composition, diversity, and functions of rhizosphere microbial communities. Due to recent advances in sequencing technology, there is a long list of studies on this topic, but here we will mainly focus on agriculturally important plants such as wheat, rice, and maize and how these plants and their genetic variation can influence the rhizosphere biome. Donn et al. (2014) studied the rhizobiome of two different wheat lines and suggested that the plant growth stage and level of adhesion of soil microbes to the root were main drivers of the bacterial community. The authors found a tenfold enrichment in the abundance of *Pseudomonas*, *Actinobacteria*, *copiotrophs*, and *oligotrophs* in the loosely bound rhizosphere soil during vegetative growth. Furthermore, *Pseudomonas* was highly abundant in the Janz wheat line, whereas *copiotrophs* were more abundant in the H45 line (Donn et al. 2014). Similar findings were observed by Kawasaki et al. (2016a, b) who showed that the binding of soil microbes to a root and root structure have a profound impact on the rhizobiome of *Brachypodium distachyon* (model plant for wheat) and its rhizosphere community was enriched by *Burkholderiales*. One recent study showed the intense effect of plant domestication and breeding on exudation which has directly influenced rhizosphere metabolites in wheat lines (Lannuci et al. 2017). Likewise, Liu et al. (2016) studied the effect of Jasmonic acid (JA) signaling on the wheat rhizosphere microbiome and showed plant organ-specific effects as JA signaling only had a significant impact on diversity and composition of root endophytes but not shoot endophytes or the rhizosphere community.

Lu et al. (2014) studied the rice rhizosphere microbiota using PLFA-based stable isotope labeling and found the rice plant had significantly influenced the microbial community through photosynthetic rhizodeposition. Breidenbach et al. (2016) studied the abundance and composition of the microbial community in the rice rhizosphere soil and showed that the abundance of archaea and bacteria was significantly higher (twofold) in the rhizosphere when compared with the bulk soil. Furthermore, these authors found profound fluctuations in *Proteobacteria*, *Gemmatimonadetes*, and *Verrucomicrobia* communities and showed their effect on functional groups such as iron reducers and fermenters. One recent study showed the autonomous behavior of rice plant in relation to the microbial community, as plants were grown in different types of soil, had the same effect on the composition of rhizosphere microbial community (Li et al. 2014). Similarly, the study of rice plants has showed that plant domestication and genotype play key roles in shaping the rhizosphere community (Lannuci et al. 2017; Shenton et al. 2016; Meena et al. 2015). Moreover, the enrichment of different bacterial phyla *Anaerolineae* and *Methanotrophs* in the wild and bred rice cultivars, respectively, were identified (Shenton et al. 2016).

Compared to other crops, there have been large numbers of studies on the maize rhizobiome. This may be due to its unique phenotypic and molecular diversity; we have discussed the more recent studies done on the maize rhizobiome. Cavaglieri et al. (2009) studied maize rhizobiome using microbial culturing-dependent techniques, and they reported that the plant growth stage has a significant influence on the rhizoplane and endo-rhizosphere community with noteworthy enrichment in some bacterial species such as *Bacillus*, *Arthrobacter*, *Azotobacter*, and *Listeria* and fungi such as *Aspergillus* and *Fusarium*. García-Salamanca et al. (2013) studied the bacterial community of the maize rhizosphere in carbonate-rich soil and reported a substantial enrichment of *Gammaproteobacteria* in rhizosphere soil which could be due to the high availability of carbonate. The rhizosphere bacterial diversity of 27 different maize inbred lines which were grown in field condition showed a remarkable influence of plant heredity on diversity and composition of rhizosphere bacterial community (Pieffer et al. 2013). Li et al. (2014) also studied the maize rhizobiome using a pyrosequencing approach, and they reported the preferential colonization of some bacterial groups such as *Proteobacteria*, *Bacteroidetes*, and *Actinobacteria* in rhizosphere. These authors also showed that the plant growth stage had a profound effect on the bacterial community composition in rhizosphere soil; fluctuations were mainly observed at the family, genus, and OTU level. Recently, few studies have focused on how maize plant N use efficiency (NUE) could shape the totals and functional diversity of rhizosphere soil microbes (Pathan et al. 2015a, b; Baraniya et al. 2016). These authors showed that the Lo5 maize line with higher NUE had stronger influence on the microbial community composition (bacteria and fungi). Both the composition and diversity of bacterial β-glucosidase and protease genes in rhizosphere soils were compared between Lo5 and T250 maize, a low NUE line. All these findings suggest the plant and its different characteristics such as plant heredity, growth stages, physiological traits, and plant nutrient requirements are key factors which drive the formation and structure of the rhizosphere microbial community. It should be noted that many of these studies have only been focused on bacteria and very few of them have focused on the fungal or archaeal communities, which suggests that future research should consider these other rhizosphere organisms in different plants.

5 Plant-Microbe Interaction

5.1 N_2-Fixing Bacteria

Nitrogen is a key nutrient for plant development, and it is usually a plant growth-limiting factor. Although more than two thirds of the global atmosphere comprise N_2, plants are incapable of using this elemental form of N. On the other side, some soil prokaryotes known as diazotrophs have a dinitrogenase enzyme which enables these prokaryotes to convert N_2 into ammonia followed by nitrite (ammonia oxidizers) and nitrate (nitrite reductase), N forms used by plants (Lam et al. 1996; Franche et al. 2009). Due to the plant's large requirement for N, some have formed beneficial symbiotic associations with these diazotrophs (N_2-fixing bacteria). This symbiotic association between plants and N_2-fixing bacteria is a kind of mutualistic symbiosis where the host plant directly consumes inorganic N such as ammonia or nitrate from the soil which is fixed by the N_2-fixing bacteria. In return the plant provides sheltered environment and fixed carbon and other nutrients to the diazotrophic prokaryotes. Legumes (Fabaceae family) are the foremost symbiotic plants that associate with *rhizobia* (gram-negative), a member of

Alphaproteobacteria (Oldroyd and Downie 2008). Legume-rhizobia interaction instigates root nodule formation, which begins with the release of flavonoids by the plant under N starvation conditions (Oldroyd et al. 2011; Mcnear 2013). Flavonoid signals are responsible for activating *nod* genes in rhizobia which encoded lipochitooligosaccharides, known as nod factors (Mcnear 2013; Mus et al. 2016). Nod factors are pivotal symbiotic signals as they induce invasion of bacteria into the host plant and nodule formation where the bacteria ultimately are housed (Mcnear 2013; Mus et al. 2016). The structure of the nod factors such as the length of backbone, size, and saturation of fatty acyl chain depend on the rhizobia species (Mcnear 2013; Mus et al. 2016) which leads to host specificity during formation of the plant-rhizobia association (Oldroyd and Downie 2008). Even though two different species of rhizobium, *etli* and *lati*, carry identical nod factors, both species have distinct host specificity (*Phaseolus* spp. and *Lotus* spp., respectively) (Cárdenas et al. 1995). Host plant selection specificity is astounding as out of millions of microbes; only a tiny number are able to create efficacious symbiosis with host plants (Mcnear 2013). Only one nonlegume plant, called *Parasponia* species (Cannabaceae family), is capable to form a symbiotic association with rhizobia (Sytsma et al. 2002). Invasion of rhizobia occurs through crack entry into the host plant *Parasponia* (Lancelle and Torrey 1985), which is different from legume plants, where the rhizobia enter through root hair curling. Furthermore, the proliferation of rhizobia and N fixation takes place after the formation of fixation threads, and these threads branch all over the nodule cells; however, they still stay in contact with the apoplast (Behm et al. 2014; Mus et al. 2016; Ashoka et al. 2017). Somehow, development of the *Parasponia-rhizobia* association is quite young and is a primitive form of nodulation. Behm et al. (2014) suggested that the *Parasponia-rhizobia* symbiosis can be used as a model system to understand the control mechanisms which emerge during the early stages of N_2-fixing mutualism evolution.

Apart from rhizobia, members of the *Actinobacteria* phylum, *Frankia* sp. (gram-positive), have been shown to nodulate (actinorhizas) with broad spectrum of woody plants, called actinorhizal plants. Actinorhizal plants are distributed in 8 different families, containing 17 genera and 150 species. Actinorhizal development processes are very similar to legume nodules, but they are much larger in size and longer lived compared to legume nodules. Actinorhizas have central vasculature and can fix the same amount of N_2 as rhizobia nodules (Mus et al. 2016). Another group of bacteria called cyanobacteria, especially filamentous cyanobacteria (mainly *Nosotc* and *Scytonema*), are able to fix N_2 with cells which are known as heterocysts. Cyanobacteria create this symbiotic association with a variety of higher and lower plants, algae, and fungi (Merks and Elhai 2002). Moreover, there are some other N-fixing bacteria, such as *Azospirillum* spp. and *Azoarcus* spp., that can colonize nonlegume plants without any nodule formation (Elmerich and Newton 2007), and these bacteria are known as N_2-fixing endophytes (Döbereiner 1992; Baldani and Baldani 2005). Consequently, it may be important to create more symbiotic associations between N_2-fixing bacteria and nonlegume plants, especially in different crops, thereby reducing the use of chemical N fertilizer and better manage greenhouse gases fluxes.

5.2 Plant Growth-Promoting Bacteria (PGPR)

Kloepper and Schroth (1978) were the first authors who coined the term "plant growth-promoting rhizobacteria" (PGPR) for bacteria inoculated on seeds that successfully colonized the plant root and promoted plant growth. Antoun and Kloepper (2001) reported that only a few bacteria (1–2%) have an aptitude to promote plant growth. PGPR are propitious free-living bacteria which can colonize the rhizosphere and rhizoplane and within the root itself (Gray and Smith 2005). Moreover, based on this colonization, PGPR can be divided into two subcategories: (i) bacteria which colonized the rhizosphere or rhizoplane are called extracellular PGPR (ePGPR) and (ii) those positioned inside root tissues are known as iPGPR (intracellular PGPR) (Viveros et al. 2010). To date, several different bacterial genera have been recognized as PGPR, many of them mainly belong to the *Proteobacteria* and *Firmicutes* phyla (Lugtenberg and Kamilova 2009; Drouge et al. 2012), though *Bacillus* spp. and *Pseudomonas* spp. are predominant (Podile and Kishore 2006).

PGPR can induce plant growth in two different ways, directly as biofertilizer or indirectly as biopesticide/biocontrol. Direct plant growth induction includes enhanced nutrient supply such as N, phosphorus, and potassium and increases in Fe through the release of siderophore, etc. or by modulation of phytohormones such as auxin and cytokinins (Arora et al. 2012; Bhardwaj et al. 2014). Indirect plant growth promotion entails control over the inhibitory effect of phytopathogens by producing antibiotics or trigger induced systemic resistance (Glick 1995; van Loon et al. 1998; Van Loon 2007). Colonization of a microbial community on the root surface was erratic, and interaction with roots occurred in various patches (McNear 2013). Nutrient availability and root surface physicochemical variations are key factors that induce changes in the abundance and structure of microbial communities (McNear 2013). Root exudation provides chemical compounds for microbes which leads to the formation of microcolonies on the root surface. Danhorn and Fuqua (2007) reported that root epidermal cell junctions, root hairs, axial grove, cap cells, etc. are common sites for the formation of bacterial colonies. Furthermore, microcolonies expand into larger bacterial biofilms which later become wrapped into an exopolymeric matrix (McNear 2013). Rudrappa et al. (2008) showed that bacterial abundance (PGPR) is one of the key factors controlling plant growth promotion. During the plant growth promotion time course, microbial biofilms act together performing quorum sensing and synchronize discharges of various compounds that directly or indirectly promote plant growth (Mcnear 2013). Each plant growth promotion mechanism and function (direct or indirect) have been discussed in detail (Gupta et al. 2015; Vecheron et al. 2013). Some recent findings also suggest that PGPR can also be used in the phytoremediation of contaminated soil (Zhuang et al. 2007; Shukla et al. 2011; Tak et al. 2013; Meena and Yadav 2015), as some PGPR enable improved plant resistance against abiotic factors, including heavy metal contamination, and in some way help plants to enhance resistance to heavy metals (Jing et al. 2007; Saharan and Nehra 2011; Tak et al. 2013).

5.3 Mycorrhizal Fungi

Among all microbial associations, fungi form symbiotic associations with plants, and between mycelial fungi and plants, the relationship is known as a mycorrhizal association. These words are derived from the Greek word *mikos* meaning fungi and *rhiza* meaning roots. In contrast to legume-rhizobia association, mycorrhizal association is pervasive and indiscriminative, resulting in colonization of nearly 80% of angiosperms and all gymnosperms. Mycorrhizal association is the earliest plant-microbe association, it first occurred approximately 450 million years ago, and this helps explain the pervasiveness of mycorrhiza overall the plant kingdom. Mainly the mycorrhizal association is a mutualistic association, where fungi provide phosphorus, water, and other micronutrient acquisitions by increasing the root surface; in return the fungi receive fixed carbon. Moreover, mycorrhizal fungi play a vital role in the fitness of natural plants (Allen et al. 1995).

Based on anatomical aspects, the mycorrhizal association is divided into two different subcategories, ectomycorrhizae and endomycorrhizae. In ectomycorrhizae (ECM), fungi grow and are colonized within root intercellular spaces by forming a *hartig* net around the root cortex (McNear 2013). In contrast, endomycorrhizae fungi are colonized within root cortical cells and form highly branched structures, called arbuscules (Harrison 2005). Moreover, endomycorrhizae fungi are subdivided into three subcategories, orchid, ericoid, and arbuscular mycorrhiza (AM), AM association being the most common occurring association. During association, fungal hyphae (hartig net or arbuscule) provide nutrients to the plant through the horizontal transfer and expanding the root surface area and exchanging photosynthetically fixed carbon from plants. While ECM prefers to associate with woody plants, AM fungi form a symbiotic association with various land plants, including many agricultural crops (Garcia et al. 2015). In stress conditions such as under extreme rainfall, the fungus can grow their hyphae outside soil nutrient-depleted zones, leading to expanded contact with the soil surface or particles which help to reach out into the soil for plant uptake (Barman et al. 2016; Datta et al. 2017). The mycorrhizal hyphal network also significantly affects soil quality by promoting soil aggregation and stability through various biochemical and biological mechanisms, which directly or indirectly increase plant productivity (Rillig and Mummey 2006).

Unlike the rhizobia symbiosis, the chemical signaling processes of mycorrhizae are less well understood. Much focus has been given to the ECM association since both partners can be grown easily, while endomycorrhizae is difficult to grow in vitro due to their obligate behavior (McNear 2013). Plant root exudates such as various flavonoids (mainly rutin) (Lagrange et al. 2001), abietic acid (Fries 1987), and strigolactones (only in AM fungus) (Akiyama et al. 2005) initiate the spore germination and hyphal growth and branching of the fungus by activation of genes in mycorrhiza fungus which produce lipochitooligosaccharides or short chitooligosaccharides, known as *Myc* factors (Maillet et al. 2011; Genre et al. 2013). There is some resemblance between *Myc* factors and nod factors (produced by rhizobia in the legume-rhizobia association) (McNear 2013), and this could explain the phenomena of “common symbiosis pathway” which originated in AM symbiosis, later adopted by legume-rhizobia association (Garcia et al. 2015). Due to these chemical dialogues, fungi interact with host plants and begin the hyphae proliferation into host plant roots, called hyphopodium (in AM), or growth between dermal cells (in ECM). Formation of arbuscules is the final step of the symbiotic process, and through these arbuscules, fungi enter into the root cell cytoplasm. Selosse et al. (2006) reported that two or more plants can share nutrients through the same mycorrhizae associations as fungal hyphae can create a “common mycorrhizal network” (CMN). Similar phenomena may occur in the ECM symbiosis, but more research is needed to understand the molecular mechanisms of ECM symbiotic associations.

5.4 Pathogenic Microorganisms

In contrast to beneficial (symbiotic/naturalistic) associations with the rhizosphere microbiota, plants can also interact with some soil microbes that inhibit plant growth and health, commonly referred as pathogenic microbes or phytopathogens. These can include fungi, bacteria, viruses, oomycetes, and nematodes. Phytopathogens are one of the major constraints to global food production and security. While many of soil-borne pathogens survive and grow into bulk soil, the rhizosphere is a key niche where pathogenic microbes form parasitic associations with plant roots. Soil-borne pathogens are more persistent when compared to pathogens associated with above-ground parts of the plant (Bruehl 1987). While information has been available on how root exudates modulate/regulate plant-symbiont association, the limited focus has been given on how rhizodeposition can attract and activate the phytopathogens. Agrios (2005) has divided plant pathogens into four main groups: virus, bacteria, fungi, and nematodes. Among these four groups, fungi are the main soil-borne pathogens compared to others. Bacteria and viruses need natural openings or wounds to enter into plant tissues. Furthermore, the soil is not a suitable habitat for nonspore-forming bacteria, while some filamentous bacteria such as *Streptomyces* spp. can grow easily in soil and able to cause infection to host plants. *Ralstonia solanacearum* (*Pseudomonas*) can colonize the xylem and cause wilt to a variety of plants, mainly tomato (Genin and Boucher 2004), pepper, and eggplants. While *Agrobacterium tumefaciens* is well known for causing crown gall (Nester et al. 2005), through the transmission of DNA (T-DNA), these two are the best-understood examples of soil-borne pathogenic bacteria. Only a few viruses can infect plant roots, as they required a vector for transmission and in soil nematodes (e.g., Nepoviruses; Brown et al. 1995), and some zoosporic fungi such as *Olpidium* (Campbell 1996) are the main vectors for viral transmission. Nematodes can be free-living worms that normally ingest other microbes such as bacteria or fungi or other nematodes. However some can form parasitic relationships with host plants. There are three main types of associations that nematodes form with host plants: (i) ectoparasitic, in which nematodes contact with only the outer body of roots; (ii) endoparasitic, in which nematodes are able to reach out the inner body of plant roots; and (iii) sedentary endoparasitic, in which nematodes persist in the inner body of roots for reproduction process (Raaijamakers et al. 2009).

Fungi and oomycetes can be soil-borne phytopathogens. While oomycetes are phylogenetically closer to blue algae, their morphological characteristics are identical to fungi, and their parasitism and diseases have similar symptoms to fungi (Raaijamakers et al. 2009). Most of the soil pathogenic fungi and oomycetes are necrotrophic, and only a few of them are biotrophic such as *Plasmodiophora brassicae* (cause of cabbage "clubroot") and *Plasmopara halstedii* ("downy mildew" in sunflower, Friskop et al. 2009). *Phytophthora sojae* is semi-biotrophic and causes powdery mildew and rusts, especially in soybean. Due to their generalist behavior, necrotrophic pathogens have a wider selection of hosts and can easily infect many plants. Fungi penetrate the host plants through the germ tubes or zoospores and infect epidermal root cells (tips, hairs, etc.) or strike at emerging shoots or seed radicles. *Pythium*, fast-growing and important soil-borne pathogen, affects tree seedling production through attacking plant seeds even before they start to emerge; the disease is called "damping off" (Vaartaja 1975; Weiland et al. 2013). Fungi produce degrading enzymes or use hydrostatic pressure to enter into host root cells (young or juvenile roots) and further colonized into the root cortex. After cortex colonization, fungal mycelia still continue to spread to other parts of the plant and sometimes grow externally and can also cause disease in adjoining plants. *Fusarium oxysporum* and *Verticillium dahlia* and other fungi can spread into the plant vascular tissues through the root endodermis and blocking water flow that causes wilting. This fungal problem can infect many different plants including potato, cotton, tomato, and eggplants and some tree species such as olive (Beckman 1987). A number of different diseases are caused by a fungus such as decay, rot, damping off, and wilt; among all of them, root rot is often the first stage. By infecting or destroying plant roots, plant water and nutrient uptake capacity is decreased causing nutrient deficiency symptoms, reduced size, and drought stress (Raaijamakers et al. 2009).

6 Concluding Remarks and Future Applications

The rhizosphere represents a plethora of interactions between plant-microbes, plant-soil, microbe-soil, and microbe-microbe, and because this network is highly complex, we can affirm that the study of this environment is still in its infancy (Zheng et al. 2017; Berendesen et al. 2012; Sihag et al. 2015). A pivotal and strong link is highlighted among soil-microorganism-plant, thereby creating a *hotspot* in which to study and improve crop health and NUE. In the present work, we have discussed the dynamic processes in the rhizosphere and especially how root exudates, as well as the rhizobiota, are influenced by biotic and abiotic factors to understand and thus improve nutrient use efficiency in the context of more sustainable agriculture. Moreover, the emphasis was given to the role of the roots both in the selection of microbes and in the efficiency of use of resources focusing particularly on nitrate as nutrient and signal.

Rhizosphere interaction studies include measurements of the microbiota, root morphology, and rarely their interactions, especially in field condition. Our limited knowledge is presented on how the plants control the microbe communities present in the soil and how different root types influence the availability of nutrients and also their absorption by rhizobiota. Furthermore, new omic technologies will contribute to identifying new signaling compounds which allow us to set new strategies for promoting plant growth and health.

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