Review

Plant-driven selection of microbes in the rhizosphere and plant-microbe feedbacks

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Abstract

Plant impacts on soil microbial communities and plant-microbe feedbacks have become the focus of much research. Recent advances in plant-microbe interactions investigations show that plants are able to shape their rhizosphere microbiome through diverse mechanisms. In this review, we gather findings from across multiple studies on the role of plants in altering the structure and functions of microbes in the rhizosphere. In addition, we discuss the roles of diverse phytochemicals in mediating these effects. Finally, we highlight that selective enrichment of specific microorganisms in the rhizosphere has either negative feedbacks, with pathogen accumulation in the rhizosphere; or, perhaps most importantly, positive feedbacks as a result of the recruitment of a beneficial microflora. Insights into the mechanisms that underpin plant selection of microbial communities with positive feedbacks will provide new opportunities to increase crop production.

Keywords: Plants, microbes, rhizosphere, feedbacks.

Résumé

L'effet des plantes sur les microorganismes du sol et les rétroactions entre les microbes et les plantes sont devenus le focus de beaucoup de recherche. Les dernières avancées dans le domaine des interactions plantes-microbes montrent que les plantes sont capables de façonner le microbiome de leur rhizosphère via des mécanismes divers. Dans cette revue, nous rassemblons des résultats de multiples études sur le rôle des plantes dans l'altération de la structure et des fonctions des microorganismes au niveau de la rhizosphère. En outre, nous discutons les rôles de différentes substances phytochimiques dans la médiation de ces effets. Finalement, nous soulignons que l'enrichissement sélectif de microorganismes spécifiques a aussi bien des rétroactions négatives, avec l'accumulation de pathogènes dans la rhizosphère, que positives, suite au recrutement de microflore bénéfique. Une meilleure compréhension des mécanismes qui régissent la sélection de microorganismes ayant des rétroactions positives ouvrira de nouvelles possibilités pour l'amélioration de la production agricole.

Mots-clés: Plantes, microorganismes, rhizosphère, rétroactions.

INTRODUCTION

A broad range of biotic and abiotic forces shape soil microbial communities. Within a given soil type and set of climatic conditions, there is compelling evidence that plants set the stage for growth conditions experienced by soil microbial communities through a variety of mechanisms (Dini-Andreote and van Elsas, 2013). In particular, plants are capable of modulating microbial population density, identity, and relative abundance; and influencing the functional activities that are carried out by soil microbial communities. These characteristics are inter-related, although specific relationships between microbial community structure and function are often unclear (Fuhrman, 2009). Understanding the factors that promote and maintain microbial diversity is a critical task for enhancing ecosystem processes and functioning. Significant role may be played by plants in this regard, through plant direct impacts on microbial activity and fitness, or through indirect alterations of soil properties or microbial interactions.

Interactions between soil microorganisms and plants occur primarily in the rhizosphere (Barea et *al.*, 2005; Prithiviraj et *al.*, 2007). The root system, which was long considered only as a means of anchorage and uptake of nutrients and water from the soil, is now consensually recognized as a key element in the interplay between plants and their milieu (Bais et *al.*, 2006), making the root environment the most likely place to observe effects of plants on associated soil microbial communities (Kowalchuk et *al.*, 2002; Bais et *al.*, 2006). Indeed, the rhizosphere is a biologically and chemically highly diverse environment where complex and dynamic interactions occur among plant roots, microbes, and the soil (Hartmann et *al.*, 2009). Compelling evidence was reported on the ability of plants to alter associated soil microbial communities through the well-known rhizosphere effect, wherein microbial populations and activity are markedly higher in soil adhering to plant roots compared to bulk soil (Starkey, 1958). Within this habitat, plants and microbes have evolved intimate relationships that enable them to coexist (Hartman et *al.,* 2009).Specifically, plants provide nutrient resources to the rhizosphere that support

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microbial activities. In turn, microbes provide a wide range of services that impact directly plant health and productivity (Nihorimbere et *al.*, 2011).

A coupling of the concepts that plants are capable of exerting selection on associated microbes and that associated microbes may impact plant fitness, suggests the existence of interactions in which plants achieve fitness benefits through targeted manipulation of associated microbes. Such interactions are likely to be dependent upon the provision of resources to soil microbes, suggesting a selective force that may explain the seemingly inefficient loss of nutrients through plant roots. Expanding our knowledge on the specific mechanisms by which plants influence microbes and the resulting consequences for plant fitness will provide valuable insight into novel strategies for enhancing plant productivity in agricultural systems. Here; we (i) provide an overview on plant-driven impacts on soil microbial community characteristics (density, composition and structure, and function), (ii) explain mechanisms by which plants exert substantial effects on associated microbes,and (iii) examine plant response to rhizosphere microbiome, known as plant-microbe feedbacks.

PLANT-DERIVED IMPACTS ON SOIL MICROBIAL COMMUNITIES

Methods for assessing plant effects on soil microbes

A wide variety of techniques, ranging from traditional approaches to modern molecular methods, have been used to evidence differential host plant selective effects. These techniques have been reviewed extensively in previous work (Mazolla, 2004; Rastoji and Sani, 2011). Traditional culture-based approaches have been effective in demonstrating effects of particular plant species on soil bacterial populations (Loranger-Merciris et *al.*, 2006). However, the major drawback of culture-based techniques is that >99% of the microorganisms in any environment observed through a microscope are not cultivable by standard culturing techniques (Hugenholtz, 2002). This limits comprehensive understanding of community structure and functions. Further insight into differential influence of plant host on microbial community can be reached through community profiling based on the characterization of biomolecules such as lipids without relying on culturing (Banowetz et *al.,* 2006). Indeed, fatty acids are present in a relatively constant proportion of the cell biomass, and fatty acid signatures that can differentiate major taxonomic groups within a community exist in microbial cells. Specifically, soil microbial phospholipid fatty acid (PLFA) profiles and fatty acid methyl ester (FAME) profiles have been used to detect distinct microbial footprints and show specific microbial responses to various plant hosts (Germida et *al.*, 1998; Carney and Matson, 2006). With recent advances in the development and application of molecular tools, the fields of microbial ecology and plant-microbe interactions have made an unprecedented bound. The use of techniques such as denaturing/temperature gradient gel electrophoresis (DGGE/TGGE),ribosomal intergenic spacer analysis (RISA), terminal restriction fragment length polymorphism (TRFLP), real-time PCR, amplicon sequencing, and metatranscriptomics of environmental DNA showed that specific microbial communities are associated with distinct plant species, and that plant species have significant effects on the structure and function of resident soil microbial community (Miethling et *al.*, 2000; Kuske et *al.*, 2002; Broeckling et *al.*, 2008; Garbeva et *al.*, 2008; Micallef et *al.,* 2009; LeBlanc et *al.*, 2015).

Effect of plants on soil microbial density

Plant host identity exerts significant impact on the density of associated microbes. Not only does plant community above-ground biomass correlates positively with soil microbial biomass (Wang et *al.*, 2011), plant hosts also differ in the density of soil microbes that are supported in their rhizosphere. This has been demonstrated for particular taxa as well as for overall microbial population densities. For example, alfalfa supported larger populations of inoculated *Sinorhizobium meliloti* compared to rye (Miethling et *al.*, 2000), and the population density of antibiotic producing *Pseudomonas* in soil was found to differ among plant hosts (Bergsma-Vlami et *al.*, 2005a). In addition, some prairie perennial plant species were shown to differ in the density of antagonistic *Streptomyces* associated with their rhizospheres (Bakker et *al.*, 2014). Furthermore, past work in recently deglaciated soils showed that plant species have differential effects on soil microbial biomass (Bardgett and Walker, 2004). Consistent with this, higher bacterial cell counts were found to be associated with wild oat roots than bulk soil (DeAngelis et *al.*, 2006). Taken together, these findings from across multiple systems prove that some plant species support denser soil microbial communities than others. The difference in impact on soil microbial biomass among plant species suggests that the composition, structure, and function of soil microbial community will depend on the identity of plant host.

Effect of plants on soil microbial community composition, structure, and function

For several years, great research efforts have been devoted to depict the impact of plant host on soil microbial community composition, structure, and function. Regardless of the investigation tools and approaches, findings from diverse studies seem to support the validity and ubiquity of plant-derived effects on soil microbial communities (Figure 1). For instance, plant hosts have been shown to alter the identity of ammonia-oxidizing bacteria (Briones et *al.*, 2002) and denitrifying bacteria present in soil (Bremer et *al.*, 2009). Clear impact of plant species effects on the composition, structure, diversity and taxonomic identity of pathogen-antagonistic microbial groups was also found (Berg et *al.*, 2002; Berg et *al.*, 2006). Interestingly, the strength of selective effect has been shown to differ among host plants. Specifically, compared to microbial communities associated with tomato, flax caused a greater shift away from the baseline conditions of uncultivated soil (Lemanceau et *al.*, 1995). The ability of host plants to differentially select among soil microbes is also suggested by host specificity in mycorrhizal associations, although partners in such interactions span a continuum from specialist to generalist. That is, some mycorrhizal fungal species associate with specific plants, while others have a broad host range (Johnson et *al.*, 2005).Furthermore, invasive plants have been shown to significantly alter soil microbial communities in invaded soils (Batten et *al.*, 2006) and occasionally reduce significantly soil microbial diversity (Broz et *al.*, 2007). Monitoring soil microbial communities over the course of a change in plant cover can also reveal the selective effect of host plant. In some cases, it appears that the soil microbial community stabilizes after a period of adaptation to a host plant, with subsequent host switching leading to dramatic microbial community shifts (Badri et *al.*, 2008). The study of the temporal dynamic of plant host effects on associated microbes,supported meta-transcriptomics data on potato associated microbes, suggests development-dependent changes over time in the rhizobiomes (Rasche et *al.*, 2006; Chaparro et *al.*, 2014).

Not only do different plant species have disparate effects on soil microbes, but also variants within the same species show distinct selective effects on soil communities. For instance, significantly distinct rhizosphere communities were found to be associated with specific genotypes of *Arabidopsis*, barley, canola, maize, potato, and sugar cane (Siciliano et *al.*, 1998; Rasche et *al.*, 2006; Micallef et *al.* 2009; Bulgarelli et *al.*, 2012; Peiffer et *al.*, 2013; Bulgarelli et *al.*, 2015; Lebeis et *al.*, 2015; Yeoh et *al.*, 2015). Additionally, studies of genetically modified plants have demonstrated that small changes in plant genotype within the same species can result in significant impacts on associated microbial communities (Giovanni et *al.*, 1999). In one fascinating example, the culture of opine-producing transgenic lotus plants induces an increase in the rhizosphere of bacterial communities that are able to utilize these molecules as sole carbon source. The density of members of these was about 10,000 times higher in the rhizosphere of the opine-producing plants than in that of wild-type (control) (Oger et *al.*, 2004). This is suggestive of strong and rapid plant-imposed selection on soil microbial communities.

The effects of host plants extend to many functional measures of soil microbial activity. Plant induced effects can span from very general functions, as was seen for total microbial respiration (Innes et *al.*, 2004), to specific microbial functional traits. For example, plant identity and presence were found to exert substantial impact on soil denitrifying microbial communities; in bare soil, the denitrifying enzyme activity was 80% lower than in planted soil (Bremer et *al.*, 2009). The plants influenced enzyme activity indirectly through their effect on the composition of the denitrifier community. Consistent with this, Alfalfa and rye supported microbial communities with significantly different community level physiological profiles (Miethling et *al.*, 2000). Additionally, the proportion of auxin-producing *Pseudomonads* was higher for heterozygous maize plants compared to either of the parent lines (Picard and Bosco, 2005). Further, rice cultivars supported different amounts of activity by associated ammonia-oxidizing bacteria (Briones et *al.*, 2002). Pathogen antagonism and related functional traits have been specifically studied as variables that respond to plant host selection. Recently, compelling evidence of plant host and plant community richness impact on soil *Streptomyces* nutrient use profiles and growth dynamics has been reported, suggesting that *Streptomyces* respond to selection imposed by plants (Essarioui et *al.*, 2014, 2016). The proportion, composition, richness and diversity of pathogen-antagonistic microbes have been shown to be plant species and plant diversity dependent (Garbeva et *al.*, 2008). An enhanced proportion, but reduced diversity of *Verticillium* antagonists, was found in rhizosphere compared to bulk soil (Berg et *al.*, 2006). This lowered antagonist diversity in the rhizosphere is an evidence of plant-driven selection favoring some microbes over others (Berg et *al.*, 2005). Cultivars of wheat differed in their ability to support antibiotic producing *Pseudomonads* (Mazzola et *al.*, 2004). In other work, *Streptomyces griseoviridis* was shown to colonize the root surface of turnip rape (*Brassica rapa* subspecies *oleifera*) more readily than of carrot (Kortemaa et *al.*, 1994) and the ability of various antibiotic producing *Pseudomonad* genotypes to colonize the rhizosphere of sugar beets was shown to be variable (Bergsma-Vlami et *al.*, 2005a). Furthermore, the amount of antibiotic produced on a per cell basis by *Pseudomonads* in the rhizosphere differed among plant species (Bergsma-Vlami et *al.*, 2005b).These find-

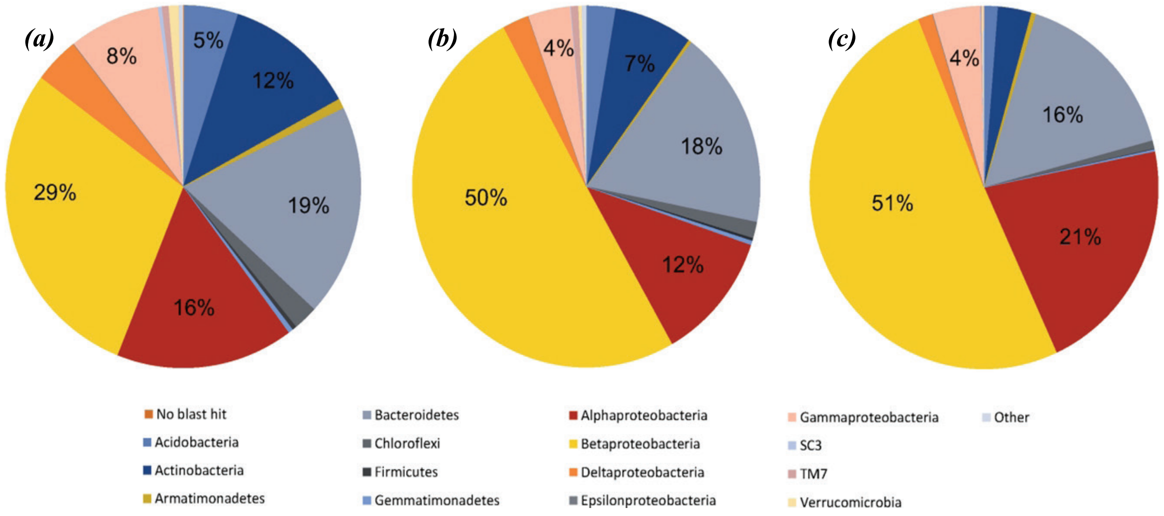

Figure 1: Example of plant host effect on associated microbes in the rhizosphere. Comparison of the average bacterial community composition and relative abundances, at the phylum level, in root samples from three different plant species; (a) Pilosella aurantiaca, (b) Leucanthemum vulgare, and (c) Trifolium hybridum. Data from Aleklett et al., (2015).

ings strengthen the view that specific microbial functional phenotypes are under significant selection by plant hosts in the rhizosphere.

Mechanisms underlying plant-derived impacts on soil microbial communities

The number of studies through the literature that have gone beyond measuring plant impacts on soil microbial community composition, structure and function, to explore the actual mechanisms underpinning microbe selection by plants remain limited. Results from across multiple plant-microbe interaction systems point to the chemical nature of resources provided by plants as the major driver of plant selection of microbes. However, few studies explicitly tested this assumption leaving a great gap of knowledge on the relative importance of plant originated resource inputs in shaping soil microbial communities.

Nutritional resources available to soil communities are largely of plant origin; sloughed-off roots, mucilage, leachates, senescent tissue, litter, and root exudates. A large body of work has emphasized root exudates as having a particular importance in determining rhizosphere microbial community characteristics (Walker et *al.*, 2003),although their significance relative to other rhizo-deposits has not always been clearly demonstrated (Dennis et *al.*, 2010). There is a general belief that root exudation may be the key determinant of microbial community structure in the rhizosphere, whereas inputs such as plant litter and senescent tissue may play a larger role in influencing bulk soil microbial communities.

Plants exude a wide range of compounds into the soil by diffusion, ion channels and vesicular transport (Bertin et *al.* 2003).Root exudates are often divided into two classes of compounds. Low-molecular weight compounds such as amino acids, organic acids, sugars, phenolics, and other secondary metabolites account for much of the diversity of root exudates, whereas high molecular weight exudates, such as mucilage (polysaccharides) and proteins, are less diverse but often compose a larger proportion of the root exudates by mass (Bais et *al.*, 2006).These compounds modify soil chemical properties and define microbial nutritional niches in the rhizosphere (Lynch and Whipps, 1990; Bardgett et *al.*, 1998; Vandenkoornhuyse et *al.* 2007; Bever et *al.*, 2012; Miransari, 2013).

The quantity and diversity of plant exudates vary among plant species and genotype (Haichar et *al.*, 2008; Micallef et *al.*, 2009; Compant et *al.*, 2010; Bever et *al.*, 2012; Philippot et *al.*, 2013; Pérez-Jaramillo et *al.*, 2015). Total nutrient inputs from plants will constrain microbial densities in soil, and the chemical variety of resources available to microbes will define in important ways microbial community composition, structure and function in the rhizosphere. The discovery that different plant species can have distinct microbial communities associated with their roots suggests that plant shape and dimension nutritional environment in the rhizosphere, and consequently create fitness penalties and rewards that are unequally distributed among taxa (Grayston et *al.*, 1998; Bertin et *al.*, 2003; Kumar et *al.*, 2007; Marshner et *al.*, 2011; Berendsen et *al.*, 2012). The provision of specific carbon substrates may offer a selective advantage to microbes with enzymatic capabilities to utilize those compounds. Methods for collecting plant root exudates in vitro have been previously described (Meharg and Killham, 1991; Nagahashi and Douds, 2000). This has opened new paths for studying the effects of plant exudates on soil microbial communities. Importantly, such collected exudates can have effects similar to whole plants when applied to soil (Badri et *al.*, 2008; Broeckling et *al.*, 2008). Quite recently, direct amendment of natural blends of phytochemicals, predominantly phenolic-related compounds, obtained from *Arabidopsis* to soil altered the bacterial community by stimulating or inhibiting different community members (Badri et *al.*, 2013).

In some cases, observed functional differences emanating from plant species and plant richness manipulation suggest plausible connections to root exudation. For example, carbon source utilization by soil microbes varied among host plant species, and the carbon substrates responsible for the observed patterns matched known major components of root exudates (Grayston et *al.*, 1998). Similarly, differences in soil bacterial community level physiological profiles among pioneering plant species were driven by the utilization of particular carbon compounds (Yan et *al.*, 2008), although it was not demonstrated that these compounds were constituents of the root exudates of the plants in question. Additionally, assumed differences in the chemical nature and diversity of rhizo-deposits among plant species and between monocultures and polycultures were linked to differential selections imposed by plant host and plant community richness on *Streptomyces* and *Fusarium* nutrient use profiles and antagonistic capacities (Essarioui et *al.*, 2014, 2016, 2017). Furthermore, plant community richness has also the potential to influence soil microbial interactions and function by defining their resource competitive environment through the quantity and diversity of resources they contribute to the soil. In recent a study, plant richness was found to impact *Fusarium* and *Streptomyces* resource niche overlap and inhibitory capacity in different ways(Essarioui et *al.*, 2017).*Fusarium* species had greater niche (nutrient) overlap with *Streptomyces* in monoculture than in polyculture, which was suggested to be a significant factor in generating highly antagonistic *Streptomyces* communities in monoculture. Conversely, *Streptomyces* had greater niche (nutrient) overlap with *Fusarium* in polyculture than in monoculture, which was hypothesized to result in selection for more inhibitory *Fusarium* populations in polyculture. This suggests that beyond their direct impact on soil microbes, plants are able to shape their microbiome indirectly via the mediation of cross-kingdom microbial interactions.

The emerging picture from multiple studies is that bioactive molecules with inhibitory properties from plants can also play a role in structuring rhizosphere microbiome by impacting negatively microbe fitness (Broeckling et *al.*, 2008; De-la-Pena et *al.*, 2008; Badri et *al.*, 2009; De-la-Pena et *al.*, 2010). For example, root glucosinolate content in *Brassica napus* was negatively correlated with root infection by *Azorhizobium caulinodans* (O'Callaghan et *al.*, 2000). Selective effects imposed by plants may also be indirect, resulting from changes to the physical or chemical environment, such as modifications to water content, soil pH (Starkey 1958) or other factors. For example, rice cultivars that supported differing activity levels by ammonia-oxidizing bacteria were also found to exhibit differences in oxygen availability in the root zone (Briones et *al.*, 2002), suggesting that the observed host plant effects were modulated through atmospheric chemistry.

Plants may also impact soil microbial communities via phytochemicals that act as signals and alter gene expression, change microbial phenotypes and modulate outcomes of microbial competitive interactions. Probably the best-deciphered plan-microbe signaling systems are those underlying the well-established symbioses involving nitrogen fixing bacteria in legumes and mycorrhizal fungi. The role of plant signals in the formation of root nodules have been deeply explored in the past decades, and the outcomes of these studies have been systematically reviewed and updated (Downie, 2010; Oldroyd, 2013;Venturi and keel, 2016). Legumes release flavonoids (2-phenyl-1.4-benzopyrone derivatives) that alter patterns of gene expression in rhizobia, initiating a series of complex and specific interactions that ultimately lead to the fixation of atmospheric nitrogen inside of nodules (Rossen et *al.*, 1985; Redmond et *al.*, 1986; Ding and Oldroyd, 2009). Specific plant derived flavoind compounds elicit also variable responses among distinct mycorrhizal partners during pre-symbiotic growth (Scervino et *al.*, 2005) resulting in specific plant-mycorrhizae associations driven by efficient chemical cross-talk. Other molecules secreted by plant roots act as signals for arbuscular mycorrhizal fungi (AMF) as well. For example, the strigolactone plant hormones have been recently shown to play a central role in initiating symbiotic relationships between plants and AMF (Ruyter-Spira et *al.*, 2013; Schmitz and Harrison, 2014). Additionally, cutin monomers have been implicated as a specific class of plant signaling factors which play a primary role in the stimulation of AMF (Gobatto et *al.*, 2012; Wang et *al.*, 2012).

In addition to the well-studied signaling pathways in the classical rhizobial and mycorrhizal symbiotic relationships with plants, patters of signal-driven plant-microbe cross-communication in the rhizosphere,albeit not in such close association, have been elucidated. Many plant-associated bacteria require density-dependent signaling mechanisms, known as quorum sensing (QS) (Fuqua et *al.*, 1994, 2001), for the regulation of gene expression involved in various traits that facilitate the colonization of the plant-associated environments. Examples of such phenotypes are virulence, conjugation, secretion of hydrolytic enzymes, and the production of secondary metabolites (Van Bomdon, 2003; Newton and Fray, 2004). Gene expression coordination at the bacterial community level occurs through the production and response to quorum levels of signals, mainly N-acyl-homoserine lactones (ALHs) (Fuqua et *al.*, 2001). Importantly, plant-produced compounds have been reported to mimic and interfere with QS acting as agonists or antagonists of bacterial AHLs QS systems (Teplitski et *al.*, 2000; Keshavan et *al.*, 2005; Subramoni et *al.*, 2011; Gonzales and venture, 2013), though only a few of these compounds have been identified and the significance of their interference is still an open question.

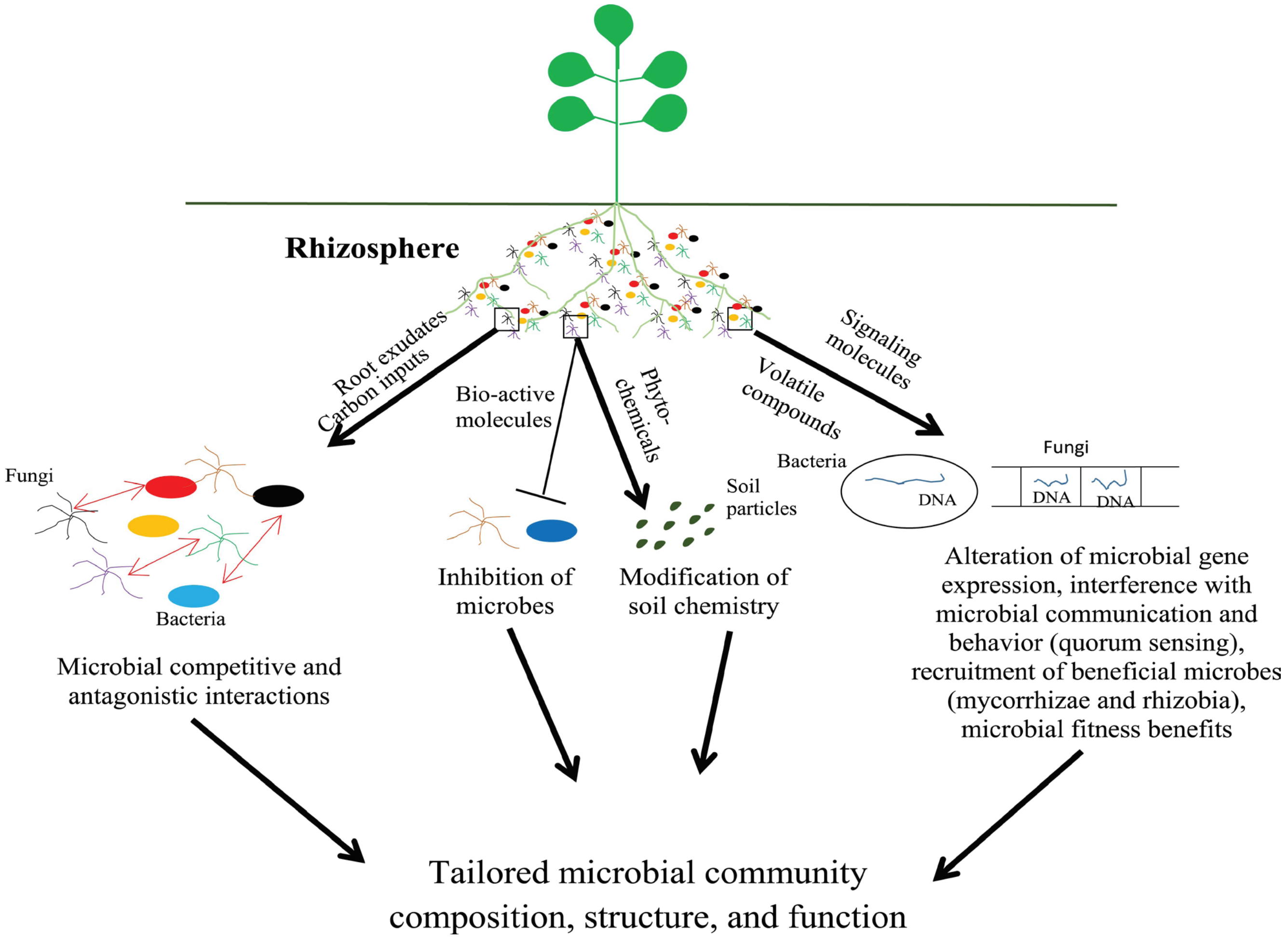

Figure 2: Mechanisms by which plants impact soil microbial community in the rhizosphere

Biological evolutionary processes endowed plants to also produce and secrete a wide range of volatile compounds from their leaves, flowers, fruits, and roots (Dudariva et *al.*, 2006). These chemicals are mainly represented by terpenoids, phenylpropanoids, and fatty acid and amino acid derivatives. Volatile compounds provide the producer with fitness benefits by acting against herbivores and pathogens, and conferring reproductive advantages. Specifically, volatiles can serve as antimicrobial molecules or as attractants for enemies of root-feeding herbivores (Rasmann et *al.*, 2005). This highlights the role that plant produced volatiles are likely to play in structuring soil microbial communities.

In summary, root exudates, bioactive molecules, signaling molecules, and volatile compounds have been recognized as major phytochemicals by which plant tailor their rhizomicrobiome (Figure 2). This complex and intimate communication suggest feedback loops between plants and microbes, which ultimately will alter soil processes and impact both partners fitness.

PLANT-MICROBE FEEDBACKS

The modulation of soil microbiome propounds the view that some plants invest more than others in broadening the spectrum of supported microbes for potentially greater beneficial feedbacks. This can lead to selective enrichment of specific microbial species and functional phenotypes in the rhizosphere with the potential to improve overall plant health and development. Recent work suggests that plants maintain high microbial densities to sustain a level of competition that will reduce pathogen viability (Kinkel et *al.*, 2011). For example, increased populations of *Bacillus subtilis* was shown to correlate with the suppression of the pathogen *Ralstonia solanacearum* in pepper, *Capcicum anuum* (Lee et *al.*, 2012). As a corollary of microbial enrichment in the rhizosphere, strong resource competition may also impact microbial coevolutionary trajectories and end up selecting for highly antagonistic phenotypes, critical to pathogen suppression at the root level (Kinkel et *al.*, 2014; Essarioui et *al.*, 2017). Additionally, Recruitments of mutualistic microbes improve nutrient supply to plants and enhance their growth. Beside symbiotic associations with AMF and rhizobia that facilitate phosphate and nitrogen uptake, plant select through their root exudates for siderophores-producing microbes that enhance soluble iron availability in the soil (Hartmann et *al.*, 2009; Carvalhais et *al.*, 2013).These findings and many others from multiple studies (Bertin et *al.*, 2003; Akiyama et *al.*, 2005; Hassan and Mathesius, 2011) suggest the possibility of plant-microbe feedbacks having positive outcomes for plant fitness. However, negative feedbacks can exist as well between plants and soil microbial communities (McCarthy-Neumann and Kobe, 2010b), with pathogens

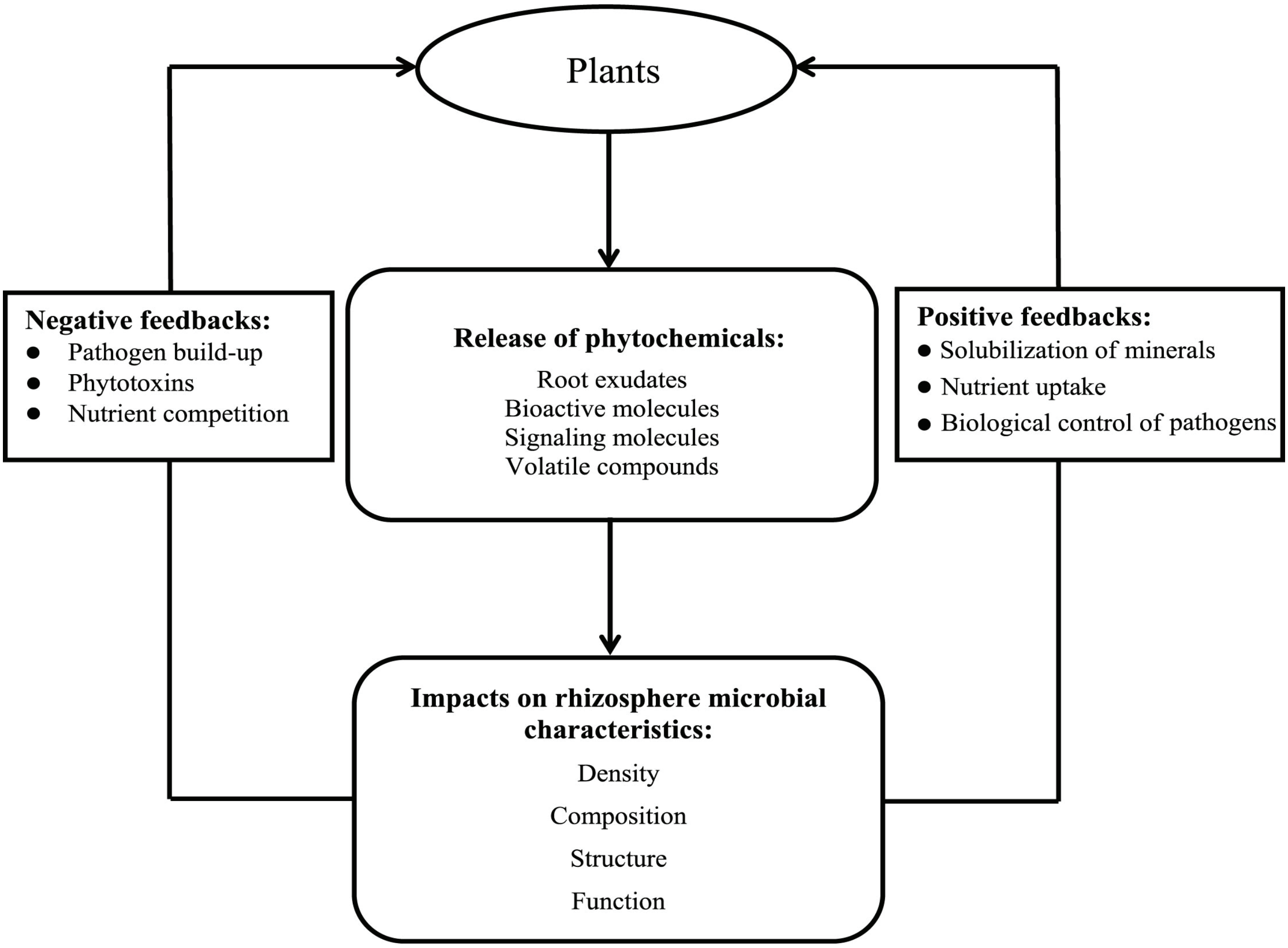

Figure 3: Schematic representation of plant-microbes interactions and feedbacks in the rhizosphere. Plants communicate with microbes through the secretion of a variety of phytochemicals. Microbes respond with positive or negative feedbacks, impacting thereby plant fitness

accumulating over time in the presence of a given host plant. Plant-microbe communication strategies are prone to hijacking by microbial plant parasites to increase their fitness. For example, isoflavones, that facilitate the recruitment of endosymbiotic nitrogen-fixing bacteria, were found to attract also the oomycete pathogen *Phytophtora sojae* and guide its growth towards the host (Morris et *al.*, 1998; Subramanian et *al.*, 2007; Cameroun et *al.*, 2013). Despite the potential exploitation by opportunistic and parasitic microbes, creating an advantageous rhizosphere milieu may allow plant to select for microbial functional phenotypes that are more likely to provide a variety of fitness benefits and enhance their ecological competitiveness.

Plant-microbe feedbacks are also believed to be important to plant community dynamics (Reynolds et *al.*, 2003), where the relative impact among plant species is the critical factor (McCarthy-Neumann and Kobe, 2010a); feedbacks may be species-specific, or may be more general, affecting all plants similarly (Casper et *al.*, 2008). Invasive plant-induced change in microbial community may contribute to a positive feedback loop that selectively improve invasive plant performance and lead to the exclusion of native plant species that experience relatively poorer performance under the new microbial environment (Batten et *al.*, 2007). On the other hand, specific negative feedbacks may slow competitive exclusion and work to sustain plant diversity (Bever et *al.*, 2010).

CONCLUSIONS AND PROSPECTS

Accumulating evidence demonstrates the importance of plant-microbe interplays in structuring soil microbial communities in the rhizosphere and impacting plant fitness (Figure 3).Considerable progress has been made with regard to bringing into focus the significance of these relationships to plant development and health. This highlights the agricultural potential of plant-microbe interactions management in inducing plant-beneficial microbial communities in soil and, thus, enhancing sustainable plant productivity. However, much research has focused only on plant impact on individual microbial strains and their feedbacks to that specific plant. Yet, there is increasing consensus that plant-microbe interactions are highly complex and involve consortia of plant and microbial species in a given assembly. Additionally, a wide range of factors such as edaphic conditions, climatic conditions, and microbe-microbe interactions, can influence plants, microbes, and the outcomes of their interactions. Therefore, further work is still needed to unravel the intricacies of the multipartite communication between microbes and hosts all along with the factors that govern their interactions. A greater understanding of the dynamics of root microbial communities has the potential to allow for the development of agricultural practices that support the recruitment of beneficial microbial communities. Overall,soil microbiome can be an-as-yet untapped resource to ameliorate plant health and productivity and promote global food security.

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