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CHAPTER FIVE

Plant Communication With Associated Microbiota in the Spermosphere, Rhizosphere and Phyllosphere

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Abstract

Plants are surrounded with microorganisms whose abundance is promoted by the release of plant organic compounds and by the presence of niches favourable to microbial development and activities. These microorganisms thrive in three main plant compartments, i.e., spermosphere, rhizosphere and phyllosphere, which are interconnected. They are recruited from the environment (soil, atmosphere) and from the mother plant via the seed. Plants indeed modulate the composition and activities of the hosted microbial populations through complex communication trackways relying on trophic interactions and/or molecular signalization. The tuning of these interactions by the plant favours beneficial microbial populations and activities while depressing deleterious ones, which have a major impact on plant growth and health. This review presents the current knowledge of the plant communication with associated microorganisms in the spermosphere, rhizosphere and phyllosphere and of plant and microbial traits involved. Possible prospects of application of this knowledge for monitoring plant—microbe interactions in agroecological systems with reduced chemical inputs are discussed.

1. INTRODUCTION

In contrast with animals which have developed the ability to escape biotic and abiotic stresses, plants cannot move and have therefore evolved strategies to cope with them. These strategies rely in large part on the plant-associated microbiota. Long standing coevolution process has indeed led to reciprocal beneficial interactions between plants and microorganisms. The first evidence for such association dates back to 400 million years ago with the discovery of fossils of plant—fungus associations, including arbuscular mycorrhiza ancestors (Redecker, Kodner, & Graham, 2000). These associated microorganisms are heterotrophs or even biotrophs and are supported by the primary production of host plant photosynthesis. In turn, they contribute to the nutrition and health of the host plant. The stability of the association depends on the benefits generated for each partner.

Plants are surrounded with microorganisms whose abundance is promoted by the release of plant organic compounds and the presence of niches favourable to microbial development and activities. These microorganisms thrive in three main plant compartments, i.e., spermosphere, rhizosphere and phyllosphere, which are interconnected. They are recruited from the environment (soil, atmosphere) and from the mother plant via the seed. Plants indeed modulate the composition and activities of the hosted microbial populations through complex communication trackways relying on trophic interactions and/or molecular signalization. The tuning of these interactions by the plant favours beneficial microbial populations and activities while depressing deleterious ones.

The close connection of microorganisms with plants, and more generally with eukaryotes, has recently led to the emergence of the holobiont concept, defined as the host plus all of its associated microbes (Theis et al., 2016; Vandenkoornhuyse, Quaiser, Duhamel, Le Van, & Dufresne, 2015). The study of the holobiont has been recently boosted by the development of molecular tools allowing us to characterize the taxonomic and functional diversity of microbial communities, but also their location and interaction with the host at the molecular and cellular levels.

Below we review current knowledge of the plant communication with associated microorganisms in the spermosphere, rhizosphere and phyllosphere and of plant and microbial traits involved. Possible prospects of application of this knowledge for monitoring plant–microbe interactions in agroecological systems are further discussed.

2. PLANT COMMUNICATION WITH ASSOCIATED MICROORGANISMS IN THE SPERMOSPHERE

2.1 Acquisition of the Seed Microbiota

Seeds, defined here as sexually derived structures of spermatophytes, are not only decisive for transmission of genetic material from one plant generation to another but are also strongly linked to the vertical transmission of multiple microorganisms ranging from plant-growth promoting agents to plant pathogens (Darrasse et al., 2010; Quesada-Moraga, Lopez-Diaz, & Landa, 2014; Truyens, Weyens, Cuypers, & Vangronsveld, 2015). These microorganisms are associated with different seed compartments, such as the embryo (e.g., the embryonic axis and the cotyledons), the storages tissues (e.g., endosperm and/or perisperm) and the seed coat, representing distinct microhabitats. The colonization of these microhabitats is strongly dependent of the seed transmission pathway employed by microorganisms. To date, three main seed transmission pathways have been documented: (1) the internal pathway, in which microorganisms colonize developing seeds via the xylem or nonvascular tissue of the mother plant; (2) the floral pathway that represents microbial colonization of developing seeds through the stigma and (3) the external pathway, which corresponds to colonization of mature seeds via contact of the seed with microorganisms located on fruits or threshing residues (Maude, 1996, Fig. 1). Microorganisms transmitted by the internal and floral pathways are usually found in all seed compartments, while those transmitted through the external pathway are almost exclusively associated with the seed coat (Singh & Mathur, 2004). As the external pathway is more permissive than the internal or floral pathway,

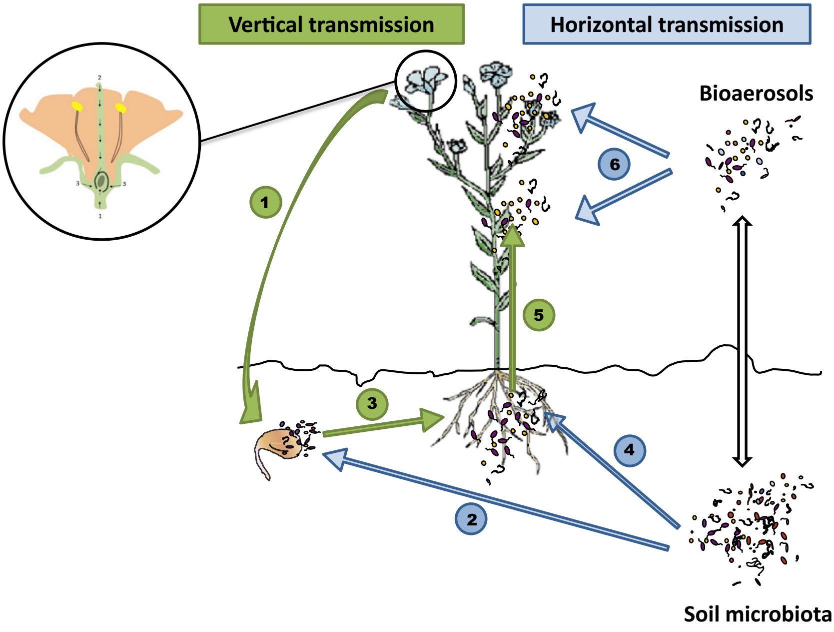

Figure 1 Schematic diagram representing the sources of microorganisms associated with the different plant compartments (spermosphere, rhizosphere and phyllosphere) and the continuum between them. Microorganisms in the spermosphere are recruited from flowers fruits and seeds (1) through internal, floral or external pathway and from soilborne communities (2) via trophic and signal communication; microorganisms in the rhizosphere are recruited from the spermosphere (3), and from soilborne communities via trophic and signal communication (4); microorganisms of the phyllosphere originate from the seed and rhizosphere (3, 5) but mostly from airborne communities upon their ability to adhesion to the plant surface and to resist to biotic and abiotic stresses (6). *Flower scheme adapted from Maude, R.B. (1996).* Seedborne diseases and their control: Principles and practice. *Wallinford, Oxon, UK: CAB International.*

microbial communities associated with the seed coat are usually more diverse than those associated with the endosperm or the embryo (Barret, Guimbaud, Darrasse, & Jacques, 2016).

2.2 Dynamics of the Seed Microbiota During Germination

Seed-associated microorganisms may either act as ephemeral colonizers of the seed habitat (seedborne microorganisms) or persist during the different plant developmental stages (seed-transmitted microorganisms). With the exception of microorganisms located within the embryo, the persistence of microbial plant interactions is strongly dependent of the outcome of intermicrobial competition occurring in the area of soil under the influence of germinating seeds (ranging from seed imbibition to radicle protrusion). This area of 'elevated microbial activity around a germinating seed' has been coined spermosphere (Verona, 1958) in analogy to the rhizosphere. During seed imbibition, multiple compounds such as carbohydrates, fatty acids, organic acids and amino acids are released to the surrounding soil (Nelson, 2004; Schiltz et al., 2015). The nature and quantity of these exudates are not only linked to the plant species but also to abiotic factors such as soil type and temperature (Nelson, 2004; Schiltz et al., 2015). The release of these organic compounds into the soil creates a zone densely populated with microorganisms that compete for resources and space. To protect itself against the myriad of microorganisms in its vicinity, seeds release antimicrobial compounds during the germination process such as flavonoids and peptides modulating microbial growth (Scarafoni et al., 2013; Terras et al., 1995).

Given the high competition for resources and space occurring within the spermosphere, only microorganisms with specific traits succeed in colonizing germinating seeds. The first set of traits important for successful spermosphere competence is related to trophic interactions. A prompt consumption of resources represents a major competitive advantage and explains why copiotrophic microorganisms are usually enriched during germination and seedling emergence (Barret et al., 2015). Chemotaxis-based motility towards seed exudates such as amino acids and organics acids has also been reported for multiple spermophere bacterial taxa including *Bacillus*, *Pseudomonas* and *Rhizobium* (Gamliel & Katan, 1992; Zheng & Sinclair, 1996). In addition to chemotactic ability, microbial populations with a versatile metabolic potential are favoured in the spermosphere. For instance, proteomics data suggest that transport and biosynthesis of 15 different amino acids are required for an optimal growth of *Salmonella enterica* on alfalfa seedling exudates (Kwan, Pisithkul, Amador-Noguez, & Barak, 2015). Moreover, carbohydrate catabolism is decisive for successful bacterial colonization as illustrated by the impaired proliferation of *Enterobacter cloacae* in the spermosphere of various plant species after mutation of the phosphofructokinase gene (*pfk*A) (Roberts, Dery, Yucel, & Buyer, 2000).

Attachment to seeds represents another crucial trait for spermosphere colonization by commensal (Deflaun, Marshall, Kulle, & Levy, 1994; Espinosa-Urgel, Salido, & Ramos, 2000) and pathogenic (Darsonval et al., 2009) bacteria. The attachment can be either mediated by flagellin (Deflaun et al., 1994) or by secreted bacterial adhesins (Darsonval et al., 2009; Espinosa-Urgel et al., 2000). Since these adhesins are involved in biofilm formation and are regulated by quorum-sensing (QS), transition from planktonic to sessile phenotype appears to be necessary for spermosphere colonization. This has been illustrated in several reports showing that seed colonizers, such as *Pseudomonas putida* or *Acidovorax citrulli*, require QS and biofilm formation for seed to seedlings transmission (Espinosa-Urgel & Ramos, 2004; Johnson & Walcott, 2013; Tian et al., 2015). Biofilm formation could also account for the microbial resistance to various antimicrobial compounds produced by the plant during germination or by microbial competitors. QS is also involved in the production of a number of antimicrobial compounds such as phenazines or 2,4-diacetylphloroglucinol (Nelson, 2004) and in the release of bacterial toxins through the Type VI secretion system (Tian et al., 2015).

Microorganisms associated with seeds represent the first populations to colonize seedlings and ultimately roots.

3. PLANT COMMUNICATION WITH ASSOCIATED MICROORGANISMS IN THE RHIZOSPHERE

3.1 Evidence for the Rhizosphere Effect

3.1.1 Description of the Rhizosphere Effect

Roots are indeed densely colonized at their surface by a myriad of microorganisms as the result of major release of organic compounds by the plant (i.e., rhizodeposits) which may represent as much as 5–21% of all fixed carbon (Bais, Weir, Perry, Gilroy, & Vivanco, 2006). Rhizodeposits include a wide variety of substances originating from sloughed-off root cells and tissues, mucilages, volatiles, and soluble lysates and exudates that are released from damaged and intact cells, respectively (Baetz & Martinoia, 2014; Curl &

Truelove, 1986; Dakora & Phillips, 2002; van Dam & Bouwmeester, 2016; Uren, 2001). The corresponding massive transfer of nutrients in the zone of soil surrounding roots, while soils are mostly mesotrophic/oligotrophic, induces a major impact on soil microbial communities, which are mostly heterotrophic. This zone of soil, termed rhizosphere (Hiltner, 1904), encompasses together plant roots (including endophytic microorganisms) plus environment surrounding or attached to and influenced by the roots (Hartmann, Rothballer, & Schmid, 2008). Rhizodeposits promote the abundance and activities of microorganisms in the rhizosphere by providing nutrient sources that support their growth, persistence and physiology (Fig. 1). However, not all the populations of the soil community are favoured in the rhizosphere, as indicated by a lower biodiversity in the rhizosphere than in the corresponding bulk soil (García-Salamanca et al., 2013; Lemanceau et al., 1995; Marilley, Vogt, Blanc, & Aragno, 1998; Semenov, van Bruggen, & Zelenev, 1999). Only the most competitive populations develop in the rhizosphere. Microbial competitiveness is greatly related to their carbon and energetic metabolism (Latour, Delorme, Mirleau, & Lemanceau, 2003); the populations having the enzymatic activities enabling to value the organic compounds from the rhizodeposits are favoured in the rhizosphere. Similarly, the most competitive populations of pseudomonads, a major beneficial group for the plants (Lemanceau, 1992), share the ability to use efficiently two different types of electron acceptors (iron and nitrogen oxides) (Ghirardi et al., 2012). Besides their carbon and energetic metabolism, they also share the ability to produce antibiotic compounds and N-acylhomoserine lactones (N-AHSL) mediating QS (Ghirardi et al., 2012). This is in agreement with the higher frequency of N-AHSL-producer pseudomonads in the rhizosphere than in bulk soil (Elasri et al., 2001). Preferential associations between plants and microorganisms are indeed not only regulated via trophic interactions but also via molecular signalization (1) from the plant, with the most documented Nod factors involved in the establishment of nitrogen-fixing symbiosis (see chapter: Commonalities in Symbiotic Plant-Microbe Signalling), (2) among microorganisms, with as example, the density regulation of bacterial activities and phenotypes (i.e., quorum-sensing) (Fuqua, Parsek, & Greenberg, 2001) and (3) through the so-called quorum quenching, an interference of the plant with this microbial communication (Grandclément, Tannières, Moréra, Dessaux, & Faure, 2016).

Plant communication leading to modifications of microbial diversity and activities in the soil surrounding roots and within roots (endophytes), collectively part of the so-called rhizosphere effect, will be reviewed herein.

3.1.2 *Impact of the Plant on the Rhizosphere Effect*

As expected from variations of rhizodeposits released by the host plant, microbial communities and populations significantly vary among plant species (Bulgarelli et al., 2015; Grayston, Wang, Campbell, & Edwards, 1998; Latour, Corberand, Laguerre, Allard, & Lemanceau, 1996; Pivato et al., 2007) and even genotypes of the same plant species (Inceoglu, Falcao Salles, van Overbeek, & van Elsas, 2010; Zancarini, Mougel, Terrat, Salon, & Munier-Jolain, 2013). They also differ between root zones (Baudoin, Benizri, & Guckert, 2002; Liljeroth, Burgers, & van Veen, 1991; Marschner, Crowley, & Rengel, 2011; Yang & Crowley, 2000) and during plant development (Chaparro et al., 2013; De-la-Pena et al., 2010; Mougel et al., 2006). The specificity of the rhizosphere effect remains strongly impacted by the soil communities and even physicochemical properties. Indeed, plants recruit populations from the soil reservoir whose composition is likely to vary according to the soil type (Ranjard et al., 2013). Latour, Philippot, Corberand, and Lemanceau (1999) have shown that the rhizosphere effect of a given host plant may vary from one soil type to the other, even when the sterilized soils were inoculated with the same pseudomonad community.

3.1.3 *Impact of Plant–Fungal Associations (Symbiotic and Pathogenic) on the Rhizosphere Effect*

Most of the plants from terrestrial ecosystems establish symbiotic associations with mycorrhizal fungi (for a review, see Smith & Read, 2008; see also chapter: Commonalities in Symbiotic Plant-Microbe Signalling). These associations are widespread and ancient, suggesting that they have evolved together with soilborne bacterial communities. This has been illustrated by the identification of bacterial groups (Comamonadaceae, Oxalobacteraceae) preferentially associated with mycorrhizal roots of *Medicago truncatula* (Offre et al., 2007, 2008; Pivato et al., 2009). In turn, bacteria preferentially associated not only with arbuscular mycorrhiza but also ectomycorrhiza (Frey, Frey-Klett, Garbaye, Berge, & Heulin, 1997) were showed to promote fungal symbioses (Frey-Klett, Garbaye, & Tarkka, 2007; Pivato et al., 2009). These bacteria were named mycorrhiza helper bacteria (MHB – Garbaye, 1994). These synergistic bacteria–mycorrhiza associations promote plant growth (Cusano et al., 2011; Gamalero et al., 2004; Pivato et al., 2009; Viollet et al., 2016). Plant roots are not only colonized by symbiotic fungi but may also be by pathogens which impact bacterial communities. A nice illustration is the take-all decline process during which wheat roots infected with the phytopathogenic fungus *Gaeumannomyces graminis* var. *tritici* select specific populations of fluorescent pseudomonads producing the 2,4-diacetylphloroglucinol antibiotic that inhibit the pathogen and therefore suppress the corresponding disease (Raaijmakers, Weller, & Thomashow, 1997; Raaijmakers & Weller, 1998).

3.1.4 Core Microbiome and Metagenomic Approaches to the Rhizosphere

Because of the importance of the associated microbiota, in terms of abundance, diversity and beneficial effects for the host plant, plants can no longer be considered as stand-alone entities and a more holistic perception is needed (Hacquard & Schadt, 2015; Theis et al., 2016; Vandenkoornhuyse et al., 2015). Plant fitness indeed results not only from plant traits but also from those of associated microorganisms, which with their plant host collectively form the holobiont. The core microbiome is defined as microbial phylotypes that are universally associated with a plant genotype or a plant species (Lundberg et al., 2012). For instance, Lundberg et al. (2012) identified a consistent presence of OTUs affiliated to Streptomycetaceae (Actinobacteria) in the *Arabidopsis thaliana* root endophytic compartment. However, composition of soil communities may to some extent impact the taxonomic composition of the core microbiome, as showed with *A. thaliana* (Bulgarelli et al., 2012; Lundberg et al., 2012). Therefore, a functional definition of the core microbiome has recently been proposed (Lakshmanan, Selvaraj, & Bais, 2014). It can be delineated using either a targeted approach (e.g., selection of antibiotic producers distributed in different genomic background of fluorescent pseudomonads according to the soils, see above) or an untargeted approach based on metagenomic or metatranscriptomic analyses to identify microbial functions (Mendes et al., 2011). The core microbiome is then defined by the shared microbial functions distributed in different microbial taxa.

3.2 Plant Traits Involved in the Rhizosphere Effect

Considering the importance of the rhizosphere effect for plant growth and health (Philippot, Raaijmakers, Lemanceau, & van der Putten, 2013), there is a major effort made by the scientific community in identifying plant traits involved in the selection of specific microbial populations and activities to ultimately monitor them through plant breeding. Among these traits a special attention is given to trophic mediated and signal-mediated communications between plant roots and microorganisms.

3.2.1 Trophic Mediated Communication

Carbon forms present in rhizodeposits are essential for plant–microbe trophic interactions. Chemically recalcitrant to degradation, polymeric carbon forms like cellulose or lignin and more labile sugars are present in the rhizosphere in different proportions; different chemical forms can be present and differ with plant genotypes and environmental factors (Neumann et al., 2014; Nguyen, 2003). Soil microbial taxa respond differently to various carbon sources (Eichorst & Kuske, 2012; Goldfarb et al., 2011; Shi et al., 2011). Only few soil bacterial taxa, such as Burkholderiales and Pseudomonales, are favoured by both labile and chemically recalcitrant substrates (Goldfarb et al., 2011). These groups appear to be commonly associated with plants (e.g., Bakker, Berendsen, Doornbos, Wintermans, & Pieterse, 2013; Bodenhausen, Horton, & Bergelson, 2013; Mendes, Garbeva, & Raaijmakers, 2013), suggesting that the presence of both chemically recalcitrant polymeric carbon forms and more labile sugars in the plant rhizosphere would favour these bacterial groups. The types of sugar molecules released by the plant may also impact the microbial diversity. Even if fluorescent pseudomonads are known for their ability to use a wide range of sugars, there is a high metabolism diversity among these populations. As examples, only some of these pseudomanad populations are able to use trehalose (Latour & Lemanceau, 1997; Raaijmakers et al., 2001) and as a result are favoured in the tomato rhizosphere (Latour et al., 1996) expected to produce the corresponding sugar; furthermore trehalose users were indeed shown to be efficient root colonizers of tomato rhizosphere (Ghirardi et al., 2012). Amino acids are the second most abundant class of compounds released in the rhizosphere behind sugars. They impact rhizosphere microorganisms both as nutrient sources and signal molecules modulating microbial activities such as biofilm formation (Moe, 2013). The most important trophic source for its impact on microbial communities seems to be the organic acids (Shi et al., 2011). Phenolic compounds may also impact the composition of the rhizosphere microbiota by either promoting or depressing a range of microbial taxa depending on their chemical structure (Badri, Chaparro, Zhang, Shen, & Vivanco, 2013). The interaction between plants and the pathogen *Agrobacterium* spp. represents a well-documented trophic mediated communication. These pathogenic bacteria cause crown gall tumours induced after transfer and insertion of bacterial genes (T-DNA) into plant genome (Platt, Morton, Barton, Bever, & Fuqua, 2014). As a result tumour cells produce xenotopic compounds (opines), usually not found in noninfected plant cells, that favour specific microorganisms able to use opines in the infected plant rhizosphere. These low molecular weight molecules (e.g., ordinary secondary amine derivatives derived from the condensation of amino acid and sugar) provide both C and N to these microorganisms. T-DNA found in the genome of tobacco ancestors that probably results from ancient bacterial transfer encodes synthesis of protein involved in opine production (Chen et al., 2016).

Plants not only impact rhizosphere microbiota via the release of nutrient but also via scavenging nutrients. As an example, the hyperaccumulation of iron by a transgenic tobacco deregulated in the ferritin synthesis led both to a depletion of that element in the rhizosphere and to the selection of pseudomonads populations highly competitive for this element, thanks to the synthesis of specific siderophores (Robin et al., 2006, 2007).

3.2.2 Signalling-Mediated Communication

Plant molecules, even present in small amount, such as hormones and hormone-like compounds, impact the composition of rhizosphere microbiome, microbial activities and behaviour. Some phytochemicals can indeed be key signals in well-known molecular communication described in symbiotic or parasitic interactions such as flavonoids involved in the establishment of the nitrogen-fixing symbiosis between legumes and rhizobia (see chapter: Commonalities in Symbiotic Plant-Microbe Signalling) and strigolactones essential in mycorrhizal symbiosis (see chapter: Commonalities in Symbiotic Plant-Microbe Signalling). Phytoalexins and plant phenolics such as acetosyringone are also known to be involved in parasitic interactions between plants and phytopathogenic bacteria (Ahuja, Kissen, & Bones, 2012; Baker et al., 2005; Jeandet, Clément, Courot, & Cordelier, 2013; Subramoni, Nathoo, Klimov, & Yuan, 2014).

Plants may also interfere with the QS pathway among bacteria by degrading acylhomoserine lactones (AHL) via lactonase synthesis that consequently disturb the QS resulting in a pathogenicity decrease of phytopathogenic bacteria (Kalia, 2013). Phytohormones, such as auxin, cytokinins, or gibberellins are involved in the regulation of parasitic and symbiotic plant—microbial interactions (Foo, McAdam, Weller, & Reid, 2016; Foo, Ross, Jones, & Reid, 2013; Groβkinsky et al., 2011; Miri, Janakirama, Held, Ross, & Szczyglowski, 2016; Ng, Perrine-Walker, Wasson, & Mathesius, 2015).

Hormones involved in plant immunity also shape the rhizosphere microbiome. A key hormone mediating plant defence reactions, salicylic acid (SA), impacts the root microbiome of *A. thaliana*, and the enrichment of specific taxa was further ascribed to their ability to use SA (Lebeis et al., 2015). Organic acids, such as citric acid and/or malic acid, also act as signals by inducing bacterial chemotaxis towards plants as showed with various species of plant-growth promoting rhizobacteria (Ling, Raza, Ma, Huang, & Shen, 2011; Rudrappa, Czymmek, Paré, & Bais, 2008; de Weert et al., 2002; Zhang et al., 2014; see also chapter: Chatting With a Tiny Belowground Member of the Holobiome: Communication Between Plants and Growth Promoting Rhizobacteria by Sharifi & Ryu, 2017). Organic acids also promote biofilm formation and therefore root colonization (Rudrappa et al., 2008; Zhang et al., 2014). Biofilm formation is indeed known to favour root bacterial colonization by creating an ecological niche that protects bacteria against biotic and abiotic stresses (Bogino, de las Mercedes Oliva, Sorroche, & Giordano, 2013). The production of QS molecules is also required for the production of mature biofilm, and consequently modulation of QS signalling may affect the ability to this production. Finally, not only these acids but also phenolics regulate expression of bacterial genes such as those encoding synthesis of antibiotics active against fungal phytopathogens (Pérez-Jaramillo, Mendes, & Raaijmakers, 2016).

Other plant compounds may interfere with microbial activities central for soil functioning. As an example, plants may inhibit nitrification (biological inhibition of nitrification, BNI) via suppressors consisting in nonesterified fatty acids, corresponding methyl esters and a cyclic diterpene (Philippot & Hallin, 2011; Skiba, George, Baggs, & Daniell, 2011; Subbarao et al., 2009, 2012). These plant compounds inhibit nitrification by suppressing microbial enzymatic pathways which catalyze the essential reactions of ammonia oxidation (Subbarao et al., 2012).

3.3 Microbial Traits Favoured in the Rhizosphere

As indicated above, elements or molecules, released or scavenged by plants, impact microbial communities in the rhizosphere. Microbial populations favoured by the plant exhibit the ability to (1) feed on specific nutrients and/or signal molecules released by the plant, (2) adapt to deprivation of nutrients scavenged by the plants, (3) respond by positive chemotaxis and (4) establish biofilms. Many studies relied on colonization studies of introduced strains (Pérez-Jaramillo et al., 2016). As an example, Ghirardi et al. (2012) compared the colonization of tomato rhizosphere in a natural soil of a collection of *Pseudomonas* strains representative of a wide diversity (plants, soils). These best colonizers share in common their ability to use a wide range of organic compounds, supporting the results of Goldfarb et al. (2011) following a community approach. These efficient colonizers were also able to efficiently use iron and nitrogen oxides as electron acceptors

(Ghirardi et al., 2012); this efficiency was related to the synthesis of specific siderophores and of nitrogen oxide reductases, respectively. These results confirmed the importance of the ability to adapt to iron starvation shown by Robin et al. (2007) and are in agreement with reported increased level of denitrification rates in the rhizosphere (Philippot et al., 2013).

Taken together, these studies underline the importance of the carbon and energetic metabolism in the adaptation of soilborne bacteria in the rhizosphere (Latour & Lemanceau, 1997), which is in agreement with the properties of that specific environment: (1) increased availability and forms in organic compounds (electron donors) and (2) decreased availability of oxygen and ferric iron as electron acceptors (Philippot et al., 2013; Robin et al., 2008).

Knowledge of plant–microbiota communication in the rhizosphere mostly relies on targeted studies using specific bacterial strains and considering specific traits hypothesized to play a major role. Over the last decade, progress in molecular methodologies has allowed the analysis of changes in microbial communities (Maron, Ranjard, Mougel, & Lemanceau, 2007) associated with different rhizosphere conditions (e.g., plant genotype, mycorrhizal root or not). Overall, these studies pinpointed taxa that are favoured or depressed in different environments (recently reviewed in Lakshmanan et al., 2014) without information on possible bacterial traits involved in the community shift with some exceptions such as the recent report of Lebeis et al. (2015) showing the enhancement of populations using SA. Reciprocally, plant traits accounting for community changes upon variations of the rhizosphere environment are rarely understood. As an example, rationale for the increased occurrence of pseudomonads harbouring type three secretion systems (T3SS) in the rhizosphere (Mazurier, Lemunier, Siblot, Mougel, & Lemanceau, 2004) as related to mycorrhization (Viollet et al., 2011) is not understood despite the beneficial effect of these bacterial populations on the fungal symbiosis and plant growth (Viollet et al., 2016).

3.4 Prospects for Monitoring Rhizosphere Microbiota via the Host Plant

Demonstration that the composition and activities of the microbial communities in the rhizosphere are regulated by the host plant through communication processes opens stimulating prospect for monitoring rhizosphere microbiota to promote populations the most favourable for plant growth and health. This relies on the knowledge of plant traits involved in the corresponding communication as described in

Sections 2.2 and 2.3. Knowledge of these traits may result from targeted or untargeted approaches.

3.4.1 Targeted Approaches

These approaches consist in engineering root exudation (Ryan, Dessaux, Thomashow, & Weller, 2009; Savka, Dessaux, Oger, & Rossbach, 2002) to make the host plant releasing molecules either interfering with bacterial signalling and resulting activities or promoting specific beneficial microbial populations.

Interference with bacterial signalling. Manipulating plants to express AHL-lactonase lead to a decreased pathogenicity of phytopathogenic bacteria requiring QS to express their virulence. This interference of the host plant with bacterial communication therefore decreases disease severity (Helman & Chernin, 2015; Kalia, 2013).

Promotion of specific populations. Agrobacterium—plant interaction represent a well-studied manipulation of the host plant by the bacteria to make it produce compounds (opines) that favour specific bacterial populations. This manipulation relies on the transfer of bacterial T-DNA to induce opine synthesis by the modified host plant giving to the pathogenic bacteria a competitive advantage with the creation of a specific niche (Dessaux, Petit, Farrand, & Murphy, 1998). The 'Opine concept' proposed by these authors stipulates that opines favour the pathogen growth with strain specific pattern as these molecules differ upon Agrobacteria strain and more specifically upon the nature of bacterial carrying tumour-inducing plasmid (pTi) transferred in the host plant. To discriminate the specific role of various opines on microbiota, a range of transgenic plants producing these different opines was generated by transfer to the plant of T-DNA from *Agrobacterium* and opine-degrading populations were characterized (Oger, Petit, & Dessaux, 1997), with different soils and plant species (Mansouri, Petit, Oger, & Dessaux, 2002). An increasing opine carbon bias was tested in artificial exudation systems (with artificial root exudate with increasing amount of octopine) and genetically modified plant rhizospheres that exuded octopine (Mondy et al., 2014). *Ensifer* and *Pseudomonas* spp. were significantly promoted in soil amended with these artificial exudates and in the rhizosphere of octopine-producers transgenic lines. However, the density of *Pseudomonas* was increased as a response to carbon supplementation while that of *Ensifer* only correlated with octopine concentrations suggesting two opposed colonization strategies for rhizosphere bacteria. *Pseudomonas* would be representative of bacteria using the copiotrophic strategy and *Ensifer* of bacteria using the oligotrophic one. Moreover 16S metabarcoding analysis showed that *Ensifer* became dominant in soil supplemented with the highest amount of octopine, indicating a strong reshape of bacterial community in response to octopine supply.

These two examples represent nice proofs of concept of the possibility to monitor microbial populations and activities via the host plant (i.e., engineering the rhizosphere, Dessaux, Grandclément, & Faure, 2016).

3.4.2 Untargeted Approaches

In their pioneer study, Smith, Handelsman, and Goodman (1999) evidenced that ability of inbred lines of tomato to promote the survival of biocontrol bacterial strain and their efficiency to suppress damping-off induced by *Pythium* differed, suggesting that plant traits may influence survival and activities of beneficial bacterial strains. More recently, plant quantitative loci from *A. thaliana* involved in the beneficial effects (root architecture and shoot growth) of a PGPR bacterial strain, *Pseudomonas simiae* WCS417r, were identified by comparing the response of 302 *Arabidopsis* accession to the bacterial effects (Wintermans, Bakker, & Pieterse, 2016). Several of the underlying candidate genes described by the authors have been assigned to important plant growth-related processes.

Attempts are also being made to identify plant traits that select beneficial microbial populations from soilborne communities and/or functional microbial genes encoding beneficial activities by comparing the rhizosphere metagenome associated to plant genotypes chosen for their genetic distances and or for their ecophysological dissimilarities (Lambers, Mougel, Jaillard, & Hinsinger, 2009; Moreau et al., 2015; Zancarini et al., 2013). Root traits mediating plant nutrition appear to be involved in plant–microbial community interaction, as supported by (1) the significant differences of bacterial communities in the rhizosphere of plants with ecophysiological profiles corresponding to different nutritional strategies (Zancarini et al., 2013) and (2) the promotion of nitrate-reducing microbial community in the rhizosphere of plants with a slow nitrogen uptake rate (Moreau et al., 2015).

4. PLANT COMMUNICATION WITH ASSOCIATED MICROORGANISMS IN THE PHYLLOSPHERE

The above-ground parts of plants also sustain an active microbial life (Vorholt, 2012). These microbial communities, which are at the interface between the plant and the surrounding atmosphere, have not fully been integrated into the global change research agenda yet, although they can mediate plant responses to climate change (Vacher et al., 2016). The phyllosphere can be considered as the above-ground homolog of the rhizosphere. It can be defined as '*the microenvironment extending from the leaf surface outward to the outer edge of the boundary layer surrounding the leaf and inward into the leaf tissues*' (Morris, 2002). According to this definition, the phyllosphere microbiota comprises all microorganisms living on the lower and upper leaf surface (i.e., leaf epiphytes) and inside the leaf tissues (i.e., leaf endophytes). The phyllosphere microbiota is composed of bacteria, fungi, Oomycetes and, less frequently, Archaea and Nematodes (Lindow & Brandl, 2003; Vorholt, 2012). These microorganisms interact with the host plant (Baker et al., 2010; Melotto, Underwood, & He, 2008) and with each other (Agler et al., 2016; Jakuschkin et al., 2016; Kemen, 2014). They also interact with viruses, such as mycoviruses (Marzano & Domier, 2015) and bacteriophages (Koskella, 2013; Koskella & Parr, 2015), and with herbivorous arthropods (Crawford, Land, & Rudgers, 2010; Humphrey, Nguyen, Villalobos, & Whiteman, 2014).

4.1 Acquisition of the Phyllosphere Microbiota by the Plant

The colonization of the phyllosphere by microorganisms starts at seedling emergence and starts over every year at leaf flush in the case of perennial plant species. Most phyllosphere microorganisms are acquired horizontally, from the environment. Some of them can also be transmitted vertically, from maternal plants onto offspring via seeds (Fig. 1).

4.1.1 Horizontal Transmission

Phyllosphere microorganisms can originate from various environmental sources, including soil and litter of the germination environment (Barret et al., 2015; Copeland, Yuan, Layeghifard, Wang, & Guttman, 2015) and bioaerosols (Bulgarelli, Schlaeppi, Spaepen, Ver Loren van Themaat, & Schulze-Lefert, 2013) (Fig. 1). Bioaerosols themselves originate from various sources, including aquatic environments, soil, animals (Bulgarelli et al., 2013) and of course neighbouring plants (Wilson, Carroll, Roy, & Blaisdell, 2014). Raindrops, irrigation water (Morris, 2002) and leaf-dwelling insects (Osono, 2014) can also bring some microorganisms onto plant leaves. In the case of perennial plants, the phyllosphere can also be colonized at bud burst by the microorganisms associated to the perennial organs of the plant, such as twigs (Osono, 2014).

4.1.2 Vertical Transmission

In addition, some phyllosphere microorganisms are transmitted from maternal plants onto offspring via seeds (Fig. 1). The transmission can occur via the seed tissues or the exterior of seed coats. Some beneficial bacteria inoculated on maize seeds have for instance been retrieved from leaves, after having colonized the rhizosphere, the roots and the stems (Fig. 1) and have been shown to significantly increase maize tolerance to drought (Naveed, Mitter, Reichenauer, Wieczorek, & Sessitsch, 2014). Such vertical transmission is also common in the endophytic fungal species protecting plants against herbivory (Hodgson et al., 2014; Rodriguez, White, Arnold, & Redman, 2009). Some species of *Epichloë*, for instance, are transmitted via the seeds of temperate grasses. The mycelium first colonizes the stems, rhizomes and leaf tissues of the mother plant. It may also be present on the leaf surface. Then it colonizes the inflorescence, grows into ovules and colonizes the embryo within the seed (Rodriguez et al., 2009). Some foliar endophytes of forbs have also been found in and on pollen grains, suggesting that the transmission to seeds can also occur via the pollen tube (Hodgson et al., 2014).

4.2 Evidence for the Phyllosphere Effect

Phyllosphere microbial communities are significantly different from airborne microbial communities, although they are in direct contact with the atmosphere surrounding the plant (Vokou et al., 2012). Each leaf indeed creates a specific environment in which only some microorganisms can thrive (Vacher et al., 2016; Vorholt, 2012). This selective effect of leaves on microbial communities can be termed the phyllosphere effect, by analogy to the rhizosphere effect (See Section 2.2).

4.2.1 Differentiation Between Foliar, Airborne and Soil Microbial Communities

A first line of evidence of the phyllosphere effect comes from the seasonal dynamics of phyllosphere microbial communities. At the beginning of the vegetative season, phyllosphere microbial communities are strongly influenced by the communities of surrounding environmental sources (soil and air, in particular). Then, they gradually acquire a higher proportion of leaf-specific taxa (Copeland et al., 2015; Maignien, DeForce, Chafee, Eren, & Simmons, 2014). The environmental source influencing the initial assemblage depends on the plant growing conditions. For instance, Maignien et al. (2014) found that phyllosphere microbial communities of

A. thaliana plants growing in sterile soil initially mirrored airborne communities. In contrast, Copeland et al. (2015) showed that phyllosphere microbial communities of several annual crop species growing in field conditions were initially influenced by soil microbial communities. In both cases, phyllosphere microbial communities subsequently differentiated from those of environmental sources, indicating that the leaf selects for specific microbial species.

4.2.2 Variations in Phyllosphere Microbial Communities Among Plant Species and Genotypes

A second line of evidence of the phyllosphere effect comes from the influence of the host plant genotype on phyllosphere microbial communities. Plant species growing in the same location, and therefore submitted to the same inoculum, develop distinct phyllosphere microbial communities (Arfi, Buée, Marchand, Levasseur, & Record, 2012; Dees, Lysøe, Nordskog, & Brurberg, 2015; Inácio, Ludwig, Spencer-Martins, & Fonseca, 2010; Kembel & Mueller, 2014; Kembel, Connor, Arnold, Hubbell, & Wright, 2014; Kim, Singh, Lai-hoe, Chun, & Adams, 2012; Laforest-Lapointe, Messier, & Kembel, 2016; Lambais, Lucheta, & Crowley, 2014; Redford, Bowers, Knight, Linhart, & Fierer, 2010; Sapkota, Knorr, Jørgensen, O'Hanlon, & Nicolaisen, 2015). Similarly, within the same plant species, the composition of phyllosphere microbial communities differs among plant genotypes growing in the same location (Bálint et al., 2013; Balint-Kurti, Simmons, Blum, Ballaré, & Stapleton, 2010; Bodenhausen, Bortfeld-Miller, Ackermann, & Vorholt, 2014; Cordier, Robin, Capdevielle, Desprez-Loustau, & Vacher, 2012; Horton et al., 2014; Hunter, Hand, Pink, Whipps, & Bending, 2010; Hunter, Pink, & Bending, 2015). These variations in phyllosphere microbial communities among plant species and genotypes can be explained by variations in foliar functional traits among plant genotypes; each plant species or genotype has its own foliar features, which selects for specific foliar microbial communities.

4.3 Functional Traits and Signalling Molecules Underlying the Phyllosphere Effect

Phyllosphere microbial communities differ from soil and airborne microbial communities, and among plant species and genotypes, because the host plant exerts a selective pressure on microbial communities (Vacher et al., 2016). This selective pressure (i.e., the phyllosphere effect) depends both on plant and microbial traits. The plant traits define the features of the microbial habitat, whereas the microbial traits underlie the ability of microorganisms to thrive in that habitat.

4.3.1 Plant Traits Shaping Phyllosphere Microbial Communities

Leaf anatomy and chemistry. At the beginning of the vegetative season, many microbial cells and spores reach the leaf via airborne dispersal. Only microorganisms able to attach to the leaf cuticle then have a chance to survive and multiply in the phyllosphere. The structure and composition of the cuticle is thus expected to have a major influence on phyllosphere microbial communities. Mutant lines of *A. thaliana* were used to test this hypothesis; the results confirmed the significant effect of cuticular chemistry on the composition of phyllosphere bacterial communities (Bodenhausen et al., 2014; Reisberg, Hildebrandt, Riederer, & Hentschel, 2013). Several other foliar morphological traits have been studied (Hunter et al., 2010; Yadav, Karamanoli, & Vokou, 2005), but surprisingly they have little influence on phyllosphere microbial communities. For instance, the presence of trichomes does not influence the composition and diversity of phyllosphere bacterial communities (Reisberg, Hildebrandt, Riederer, & Hentschel, 2012), whereas leaf size does not influence the richness of phyllosphere fungal communities (Kinkel, Andrews, Berbee, & Nordheim, 1987). Artificial leaf surfaces, that mimic the leaf surface topography down to the nanometre resolution, constitute a promising tool for better understanding the selective pressures exerted by leaf anatomy on phyllosphere microbial communities (Doan & Leveau, 2015).

Leaf primary metabolism. Among the microorganisms able to attach to the leaf cuticle, only those able to use the nutrients available in the phyllosphere have a chance to thrive and reproduce. These nutrients include the carbohydrates produced by photosynthesis and exported to the leaf surface through leaching and guttation and some volatile organic compounds such as the methanol emitted during leaf growth (Vacher et al., 2016). The nature and abundance of the foliar nutrients is expected to have a major influence on phyllosphere microbial communities. Accordingly, several studies showed that the leaf nitrogen content, which is related to the maximum photosynthetic rate (Cornelissen et al., 2003), correlates with the structure of phyllosphere microbial communities across plant species (Kembel & Mueller, 2014; Kembel et al., 2014; Laforest-Lapointe et al., 2016). In addition, the higher abundance and activity of the genus *Methylobacterium* in the phyllosphere than in the rhizosphere indicates that the foliar production of methanol shapes the composition of phyllosphere bacterial communities (Iguchi, Yurimoto, & Sakai, 2015; Knief et al., 2012).

Leaf secondary metabolism. Finally, only the microorganisms able to cope with the harsh microclimate of the leaf surface and with the foliar defences can thrive and reproduce in the phyllosphere. The genetic and molecular pathways involved in the foliar recognition of pathogens, the foliar production of antimicrobial compounds, the regulation of stomatal aperture and the maintenance of cell wall integrity are expected to have a major influence on phyllosphere microbial communities. Accordingly, Horton et al. (2014) showed that plant loci responsible for defence and cell wall integrity are the main drivers of both phyllosphere fungal and bacterial communities in *A. thaliana*. For instance, a locus involved in the production of callose, a polysaccharide used by the plant for sealing wounds during fungal infection, was found to drive variations in phyllosphere fungal communities (Horton et al., 2014). The structure of phyllosphere microbial communities is also controlled by the production of ethylene (ET) and GABA, two signalling molecules known for mediating the interactions between plants and a variety of organisms (Balint-Kurti et al., 2010; Bodenhausen et al., 2014). Recently, Vogel, Bodenhausen, Gruissem, and Vorholt (2016) showed that the protective ability of some phyllosphere commensals against foliar pathogens is related to the induction of defence-related genes. The colonization of *A. thaliana* by the commensal *Sphingomonas melonis*, which confers protection against the pathogen *Pseudomonas syringae* (Innerebner, Knief, & Vorholt, 2011), changed the expression of almost 400 plant genes, including genes encoding pathogenesis-related proteins and antimicrobial proteins. Among them were genes involved in the salicylic acid (SA)- and ET-dependent defence-signalling pathways. Interestingly, Vogel et al. (2016) showed that *A. thaliana* mutants impaired in the recognition of microbe-associated molecular patterns were less protected by the commensal strain, indicating that the protective ability of *S. melonis* depends on its molecular recognition by the plant. Other commensals did not trigger the same changes in the leaf trancriptome, suggesting that the structure of phyllosphere microbial communities and their impact on plant performance are regulated by fine-tune molecular interactions between the leaf and its microbiota.

4.3.2 Microbial Adaptations to the Phyllosphere

Microbial adaptations to the phyllosphere have been extensively reviewed elsewhere (Vacher et al., 2016; Vorholt, 2012; Whipps, Hand, Pink, &

Bending, 2008). They include microbial traits favouring (1) adhesion to the leaf cuticle, (2) nutrient acquisition and (3) tolerance to biotic and abiotic stresses. The production of hygroscopic biosurfactants, for instance, benefits phyllosphere bacteria by increasing cuticle permeability, thus increasing the diffusion of nutrients to the leaf surface (Burch, Zeisler, Yokota, Schreiber, & Lindow, 2014; Schreiber et al., 2005). Some phyllosphere bacteria also produce multiple transporters, such as TonB-dependent transporters, to scavenge carbohydrates at low concentrations (Delmotte et al., 2009). The discovery of microbial rhodopsins in the phyllosphere suggests that some phyllosphere microorganisms have alternatively evolved a phototrophic lifestyle to cope with the scarcity of nutrients on the leaf surface (Atamna-Ismaeel et al., 2012). In addition, many microorganisms have evolved the ability to enter into the apoplast, which is richer in nutrients than the leaf surface. Some strains of the pathogenic bacteria *P. syringae*, for instance, synthesize phytotoxins regulating stomatal aperture. Stomata close upon molecular recognition of the pathogen by the guard cells but the phytotoxins reopen them, thus allowing the pathogen to colonize the apoplast (Baker et al., 2010; Melotto et al., 2008). Again, these findings show that the phyllosphere microbiota is shaped by the molecular communication between the plant and the microorganisms. Future research needs to better decipher these molecular interactions and to investigate whether the plant can control them to adjust its phyllosphere microbiota to environmental conditions (Vandenkoornhuyse et al., 2015).

5. CONCLUSIONS AND PROSPECTS

Plants are surrounded by microorganisms at the seed, root and shoot levels. There is a continuum between these three compartments: (1) microorganisms in the spermosphere originate both from the flowers and the soilborne microbial community, (2) microorganisms in the rhizosphere originate both from seedborne and soilborne microbial community, (3) microorganisms in the phyllosphere partly originate from the soil and the rhizosphere, as suggested by the overlap between phyllosphere and rhizosphere microbial communities (Bai et al., 2015; Bodenhausen et al., 2013), and from airborne communities (Fig. 1). The recruitment of microbial communities in these different spheres (i.e., spermosphere, rhizosphere, phyllosphere) relies on a subtle communication network between plant and microorganisms. This communication plays a major role in the plant selection of specific microbial populations, and there is growing evidence that the host plant is able to disturb communications among microorganisms to its advantage. There is also increasing awareness that the plant is not an autonomous entity and that it depends on microorganisms, at least some of them, for its growth, nutrition and health (Partida-Martínez et al., 2011; Vandenkoornhuyse et al., 2015). According to this new vision, the biomolecular network formed by the plant and associated microorganisms, termed the holobiont, has been proposed to be a unit of selection in evolution (Bordenstein & Theis, 2015; Zilber-Rosenberg & Rosenberg, 2008).

The properties of these spheres differ significantly, especially in their trophic state. Indeed while the spermosphere and rhizosphere are habitats with relatively abundant nutrients, the phyllosphere is a low-nutrient habitat. Therefore selection of microbial populations in the spermosphere and rhizosphere relies mostly on efficient resources uses, while selection of population in the phyllosphere is dependent on attachment and adaptation to biotic and abiotic stresses. In all cases, molecular signalization plays a major role in the plant selection of microbial populations. The stability of plant–microbe associations requires reciprocal benefices for the partners, the plant providing niches and nutrients to the microorganisms, mostly heterotrophic, and in return microorganisms, at least some of them, enhancing plant growth, nutrition and health. The association of all these bionts (plant and microorganisms) has been proposed to be called holobiont, this holobiont leading to a so-called extended phenotype since plant growth and development are significantly impacted by the associated microbiota (Partida-Martínez et al., 2011). According to this new vision, the biomolecular network formed by the plant and its microorganisms, i.e., holobiont, can be considered as a unit of selection in evolution (Bordenstein & Theis, 2015; Zilber-Rosenberg & Rosenberg, 2008). This network relies on molecular signalization mediated by phytochemicals, some of them being known but probably many remaining to be identified. Progress in metabolomics is expected to allow us to discover new signal molecules and to better detangle the complex communication between plants and associated microorganisms (van Dam & Bouwmeester, 2016).

Development of molecular approaches relying on nucleic acids extraction and analysis has also boosted research on plant–microbe interactions and open stimulating prospects in agroecology. Research on plant–microbe association as a whole (holobiont) is expected to give more insight to the impact of rhizosphere communities on those of the phyllosphere and reciprocally, with potential applications in plant health management (Lemanceau, Expert, Gaymard, Bakker, & Briat, 2009). A better knowledge of plant traits involved in the selection of beneficial microbial populations and its application to plant breeding is expected to allow us to decrease synthetic inputs by growing cultivars better valuing environmental biotic resources (Wissuwa, Mazzola, & Picard, 2009). This represents a major paradigm change since over the last decades agriculture has relied less on biodiversity and more on inputs (Philippot et al., 2013). Moreover, during that period, plant breeding may have led to the counterselection of plant traits involved in the selection of beneficial microbial populations (Bulgarelli et al., 2015; Pérez-Jaramillo et al., 2016; Schmidt, Bowles, & Gaudin, 2016; Wissuwa et al., 2009). Future research in plant breeding will have to reverse this trend, by fully taking the plant microbiota into account, and this will require a better knowledge of the communication network between plants and associated microorganisms.

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