CHAPTER ELEVEN

The Plant Microbiome

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Abstract

How do we define the 'plant microbiome' and what is its significance to the plant genome? Before addressing what the microbiome is in relation to plants, it is important to first understand the concept of the microbiome; what this means in relation to the host becomes an extension of this working concept. Conceptualizing the microbiome requires a fusion of microbial ecology and bioinformatics, integrated with an understanding of both host biology and ecology. The analysis of microbiome structure and function was pioneered in studies of human hosts and has become widely recognized as essential to understanding genetic and functional capacity otherwise attributed to the host, including important aspects of metabolism and physiology. Plants are teeming with microbial organisms, including those that colonize internal tissues, in addition to those that adhere to external surfaces. Combined with the vast diversity of microorganisms in the soil rhizosphere, these plant–soil-associated microbes comprise the plant microbiome. The microbiome is intricately involved in plant health and serves as a reservoir of additional genes that plants can access when needed. Understanding the regulation of plant trait expression, hence plant performance and how this in turn impacts ecosystem function, requires that we study the impacts of the plant microbiome. Herein, the importance of the plant microbiome to plant

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genomics is addressed by defining the plant microbiome in relation to the ecology of the system with emphasis on habitats occurring belowground at the plant–soil interface, where focus is on the role of exudates as currency in this system.

1. BACKGROUND

The concept of the microbiome and the relevance it has to host health, diseases state, and immune function have been the focus of research over the past decade that has led to significant advances in our understanding of the enormous power of the small unseen majority—the microbes. Coinvolvement of the microbiome, the environment, and host genetics and immunity is now recognized to produce several human disease states. Each individual human has a 'personalized' microbiome when examined at fine scales (genus level and below), but at the group and phylum level, there are characteristic trends in abundance that have value in defining a 'healthy-state' microbiome from disease states such as obesity, irritable bowel (Greenblum, Turnbaugh, & Borenstein, 2012), and atherosclerosis (Koeth et al., 2013). The Human Genome Project has referred to this concept as the 'supraorganism'. Turnbaugh et al. (2007) stated it in this way: 'If humans are thought of as a composite of microbial and human cells, the human genetic landscape as an aggregate of the genes in the human genome and the microbiome, and human metabolic features as a blend of human and microbial traits, then the picture that emerges is one of a human "supraorganism"'.

To then borrow from those that pioneered the human microbiome project (Turnbaugh et al., 2007), the concepts of their definition can be expanded to centralize upon plants rather than humans. Here then, the core plant microbiome comprises the set of genes present in a given habitat associated with a given plant (which can be further scaled based on plant phylogeny, phenology, etc.). This begs the question of defining the habitat, which is scaled over a range—from the whole organism (plant as an individual) to specific regions of the macroorganism (e.g. roots, leaves, shoots, flowers, and seeds), including out to zones of interaction between roots and the adhering/surrounding soil, the rhizosphere. The rhizosphere refers to the zone of influence created by the roots through their exudates and by the exudates of the microorganisms within the soil matrix (discussed in detail in the succeeding text) and is not merely the soil in contact with the roots (or other belowground structures of the plant); exudates effectively extend the functional boundary of the

belowground plant–microbe interface. The plant microbiome can be further compartmentalized and subdivided to zoom in on and observe these interactions as information highways (Bais, Park, Weir, Callaway, & Vivanco, 2004) at the interface where plants and microbes exchange information. These habitats of the microbiome include the rhizosphere, as well as the plant organs (below- to aboveground structures) where microbes can interact in an associated, adherent (epiphytic), or internal (endophytic) manner.

Thinking about the soil–microbe–plant interface is not new—however, the concept of the plant microbiome perceives this interaction more along the lines of the 'microbe–soil–microbe–plant–microbe interface' rather than the 'soil–microbe–plant interface'. What is the difference? The difference is understanding that the microbiome is comprised of genomes vastly more complex than that of the plant alone, and by the nature of microbial interactions, these genomes serve as an extension of the plant's genetic compendium—effectively coined the plant's 'second genome' (Bernedsen, Pieterse, & Bakker, 2012).

Focusing on the belowground habitats within the plant microbiome, the subsections of bulk soil, rhizosphere, rhizoplane, epiphyte, and endophyte (Fig. 11.1) are addressed. Bulk soil technically refers to areas of soil not penetrated by roots. This region is beyond the plant's zone of influence through root exudation. A large body of research on plant root exudates has documented higher concentrations of organic compounds consistently reported in the rhizospheres and not found in bulk soils (reviewed by Jones, 1998). The rhizosphere is a key habitat documented to contain vast microbial diversity (Egamberdiyeva et al., 2008; Mendes et al., 2011), where soil functions as the medium in which complex signalling occurs among microbes and plants, accomplished by exudates, creating zones of interaction between roots and the adhering/surrounding soil. Influenced by climatic factors, the rhizosphere in turn impacts the plants and microbiota that utilize this habitat as an information highway (Bais et al., 2004). Moving closer into proximity with the plant, the next habitat is the rhizoplane, which refers to the surface of the plant tissues in contact with the soil (i.e. roots and rhizomes). Microbes that can exist in an adherent form to the plant tissues are termed epiphytes. Endophytes refer to the microbial genomes located inside plant tissues (Bulgarelli, Schlaeppi, Spaepen, Ver Loren van Themaat, & Schulze-Lefert, 2013). It is important to understand that microbial lifestyles are complex and many microorganisms are not restricted in their interactive potential, thus enabling them to exist as facultative epiphytes and endophytes, as dictated by other biotic and abiotic factors. The interrelation

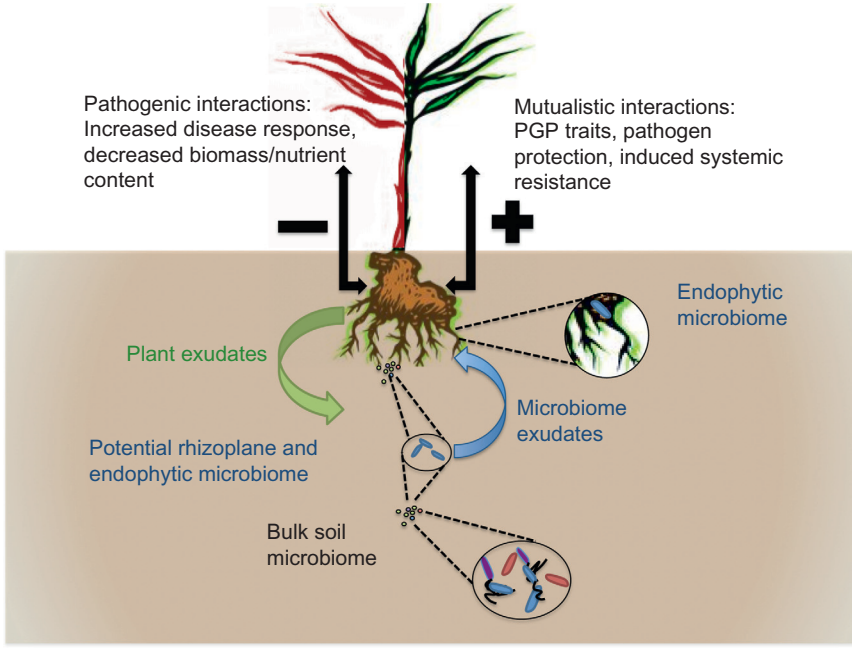

Figure 11.1 Model of the plant microbiome, with emphasis on the belowground habitats. The belowground regions of the plant microbiome include microorganisms inhabiting areas surrounding the plant roots at the root–soil interface or rhizosphere, those that are adherent to the root surface referred to as the rhizoplane, and those that colonize the internal root tissues that are known as endophytes. The microbial community residing in the bulk soil is primarily under the influence of environmental factors and is not under the direct influence of the plant (roots and exudates).

and importance of epiphytic and endophytic lifestyles to the plant microbiome is critical and thus is explored in detail herein.

Due to this interplay, the rhizosphere–rhizoplane is a dynamic environment. Microbiome structure is both influenced by and has an influence on the rhizosphere, contributing to some of the major differences between rhizosphere and bulk soil. Immobile cations, such as phosphorus, potassium, and ammonium, will be quickly depleted in the rhizosphere, while more mobile ions can be restored (Neumann and Romheld, 2002). The pH of the rhizosphere can differ up to 2–3 units from bulk soil as a direct result of biological activity, which can likewise impact the relative solubilities of essential nutrients—for example, phosphorus occurs in soils most abundantly in insoluble inorganic forms that can be solubilized through the actions of plants and microbes (Neumann and Romheld, 2002).

Extrapolating commonalities from current measurements of rhizosphere biota using structural assessments has been difficult to apply with any success across biogeographical contexts or over spatial and temporal fluxes. This suggests that local variations and adaptations of the rhizosphere biota are occurring, and evidence of this effect is demonstrated in invaded ecosystems where nutrient cycles are altered in a consistent but seemingly paradoxical way (Rout and Callaway, 2009, 2012). The implications of this are that the plant microbiome can influence ecosystem functions, increasing plant-available forms and soil stocks of carbon and nitrogen.

Ecosystem services are intricately linked to plant functional traits, of which several are likely mediated by microbes including soil formation, decomposition of organic matter, nutrient mineralization, and primary productivity (de Bello, Lavorel, Diaz, Harrington, & Cornelissen, 2010). The impact of the rhizosphere microbiome on plant productivity has not escaped those that are familiar with crops, where nodulating soybean (*Glycine max*) cultivars have been historically manipulated to enhance yield through alterations to their interactions with various *Rhizobium* microbial partners (Harris, Pacovsky, & Paul, 1985; Heath and Tiffin, 2009; Kiers and Denison, 2008). There are many examples of microbially mediated plant-growth-promoting (PGP) activity in the literature. The PGP activities that many rhizosphere-dwelling prokaryotes provide to plants include nitrogen (N_2) fixation (James, 2000; Martinez-Romero, 2006), phosphate solubilization, and production of plant-growth hormones (reviewed by Hardoim, van Overbeek, & van Elsas, 2008).

Clearly, any contribution from the microbiome to plant hormone signalling pathways has huge implications for plant genomics. Changes in the plant microbiome ecosystem that confer novel functionality may be closely associated with macroevolutionary events in the host, such as genome duplication (polyploidization). Whether from a macro (plant-centric) or a micro (microbiome-centric) perspective, the plant microbiome can exert influences on plant trait expression through top-down and bottom-up interactions. To understand the dynamics within ecosystem function and the regulation of plant trait expression accounting for plant performance, we must study the impacts of the microbiome. Herein, the plant microbiome is defined and discussed in relation to the currency of the complex communication pathways that occur within it, the ecology of the habitats of the plant microbiome with emphasis on those occurring belowground, and the importance of the plant microbiome to plant genomics.

2. CURRENCY OF THE MICROBIOME: EXUDATES

Exudates in the soil rhizosphere are defined here as those chemicals released from plants (primarily root cap cells) or from microbes. Through exudates, plants are able to communicate with microorganisms to elicit assistance in environmental acclimation to alleviate stresses, such as pathogen attack, drought-limiting nutrient acquisition, and metal toxicity to name a few. Microbes benefit from plant exudates by using them as a resource, in many cases carbon but also other nutrients. Through the exudate currency, the plant microbiome serves as an extension of the plant genome. A discussion of plant and microbial exudate uptake/release and impacts on plant and microbial functions are addressed.

2.1. Plant uptake and release

Plant exudate structure and constituents can be quite varied and often plant-species-specific and include high-molecular-weight molecules (e.g. sugars, lipids, and proteins) and low-molecular-weight signalling molecules (e.g. organic and amino acids) (Badri and Vivanco, 2009). Sugars and amino acids comprise the majority of plant root exudates (Jaeger, Lindow, Miller, Clark, & Firestone, 1999), and they serve a variety of functions including as antimicrobials, allelopathic molecules, and pathogen/herbivore defences. Many of these exudates also serve as an energy source for the microbiome; prokaryotes can utilize many different sources of carbon, including many of the plant exudates. For example, in the invasive grass *Sorghum halepense*, the exudate sorgoleone is the dominant chemical exuded from root hairs (Czarnota, Paul, Dayan, Nimbal, & Weston, 2001; Kagan, Rimando, & Dyan, 2003) and has well-known allelopathic properties (Czarnota, Rimando, & Weston, 2003; Nielsen and Moller, 1999). Further work using mineralization kinetics confirmed that rhizosphere microbes in invaded soils were capable of utilizing this allelopathic molecule as a carbon source (Gimsing et al., 2009). The multiple functions of this exudate reiterate the importance it serves as multiple currencies of the plant microbiome. Studies of the feedbacks between the influence of the microbiome and plant production of this and other allelochemical exudates are important, yet currently unknown, aspects of the functional contribution of the plant microbiome.

Roots function to uptake nutrients and chemical signalling molecules from the rhizosphere while simultaneously depositing nutrients and

chemical signalling molecules into this same space. These exudates serve as a chemical currency to the plant, in turn providing a wide range of services to other components of the plant microbiome (e.g. as a nutrient substrate, a signalling molecule eliciting protective response, or other microbiome ecosystem service). The chemical components released by plants often are unique to a genus or family (Lesuffleur, Paynel, Bataille, & Cliquet, 2007) and can range in concentration and composition due to a wide variety of factors (Carvalhais et al., 2011; Matilla et al., 2010). Terpenoids, flavonoids, and isoflavonoids comprise many of the plant's antimicrobial defences (Hardoim et al., 2008). Isoprenoids are the most diverse group of plant metabolitic compounds both structurally and functionally. As primary metabolites, they regulate cellular processes. For example, the biological molecules that are the end result of isoprenoid metabolites are essential aspects of photosynthesis (as phytopigments) and seed emergence (as gibberellic and abscisic acids). As secondary metabolites, they provide a range of benefits to plants in the form of defences from pathogens and niche expansion through allelopathic molecules.

Environmental factors influencing root exudate composition and quantity can include elevated levels of CO_2, drought, and nutrient deprivation (particularly nitrogen and phosphorus). All of these factors can have profound impacts on the phytochemistry released as exudates. For example, increased carbon allocation to roots has been documented in CO_2-fertilization experiments, resulting in shifts in exudate composition and concentration that varied according to plant species (Cheng and Gershenson, 2007; Phillips, Fow, & Six, 2006). These species-specific impacts can result in increased yield, in no net productivity increase, or can be detrimental to plant growth and production. An example of this was shown in positive biomass responses in rye and clover to CO_2 fertilization, while maize showed no net biomass benefit (Phillips et al., 2006). However, maize demonstrated increased exudation of several amino acids under CO_2 fertilization. These findings are not surprising considering that the C4 photosynthetic pathway facilitates growth under high levels of CO_2; however, the impacts of increased release of amino acids into the rhizosphere by the C4 grass (maize) might play a role in a multitude of feedbacks between other plants and microbes (Bever, 1994; Klironomos, 2002). The extent of this latter aspect is largely unknown and is a major reason why many scientists are studying the plant microbiome.

Not all environmental stressors elicit the same responses from plant roots, and nutrient deprivation has been shown to have an inhibitory effect on root

exudation. As an example, maize plants grown under either nitrogen (N) or phosphorus (P) limitations exuded decreased quantities of amino and organic acids from roots (Carvalhais et al., 2011). An additional influence on exudate composition and quantity is exerted by the microbiome, whose members can (through their exudates) confer plant protection in addition to plant-growth promotion. We know less about the ways in which the microbiome utilizes plant exudates to up- or downregulate microbial gene expression, but research has shown clear roles of their involvement in mediating pathogen attack to plants (Boller and He, 2009; Doornbos, van Loon, & Bakker, 2012; Reading and Sperandio, 2006).

2.2. Microbial uptake/release

For the microbial communities, exudates are the primary means of communication within the environment. What served as currency to the plant can serve as a carbon or another resource for members of the microbiome. Sugars and organic and amino acids are abundant in the rhizosphere (Jones, 1998), which is likely driving the vast microbial diversity documented for this region of the microbiome (reviewed by Bernedsen et al., 2012). The uptake of exudates has been a major focus of decades of research in microbial ecology using various measurements of respiration or carbon substrate utilization assays, such as those using ECO MicroPlates™ (Biolog®). Microbial respiration dramatically increases with increased availability of smaller molecules, primarily organic acids (van Hees et al., 2005), suggesting microbial community shifts with increased or decreased concentrations of readily available nutrients that require minimal energy to assimilate. This has been demonstrated with soil amendments of amino acids, where microbes residing in the rhizosphere can access this form of substrate more easily than plants (Kielland, 1994; Owen and Jones, 2001). There appears to be a selective pressure in some prokaryotes for amino acid utilization at the cost of sugar uptake. For example, to maximize the utilization of amino acids, sugar metabolism must be shunted in *Pseudomonas putida* KT2440, where the plant-growth-promoting bacterium (PGPB) utilizes the same protein for amino acid uptake as it does for downregulating gene transcription necessary for sugar uptake (Moreno, Martines-Gomariz, Yuste, Gil, & Rojo, 2009).

Microbial exudation includes a vast array of chemicals, many of which perform essential roles in ecosystem function, in turn providing benefits such as nutrient uptake, protection from pathogens, and growth promotion to higher organisms such as plants. The role of the rhizosphere microbiome

in nutrient cycling is complex and involves a myriad of nutrient transformations in soils that all terrestrial life relies upon. Microbes are responsible for biogeochemical cycling, where microbial exudates can be catalysts for the chemical transformations in soils. These transformations include those to essential plant nutrients (N and P), alkaline metals (Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+}), and micronutrients (Zn^{2+}, $Fe^{2/3+}$, Cu^{+}, and Mn^{2+}) (for more complete microbial roles in soil biogeochemical cycling, see Stevenson and Cole, 1999). The role of microbes in nutrient cycling has been the subject of many reviews and books and will not be addressed adequately here. However, biogeochemical cycling is mentioned here since it demonstrates an important aspect of microbiomes—functional redundancy—this is commonly exhibited by many soil microbial communities involved in nutrient cycling, including those in bulk, rhizosphere, and rhizoplane habitats. To emphasize the importance of this aspect to the plant microbiome, some aspects of the soil nitrogen cycle are briefly discussed.

The transformation of nitrogen into its many oxidation states is essential for all higher organisms to survive; this process relies upon the activities of the rhizosphere microbiome. Conversion of nitrogen gas (N_2) into ammonia (NH_3) is made possible by N_2-fixing prokaryotes, thus making nitrogen bioavailable to primary producers. There is functional redundancy of this critically important role in the transformation and subsequent entry of nitrogen into the terrestrial ecosystem. This is demonstrated by the vast physiological and phylogenetic diversity among N_2-fixing prokaryotes, with a relatively highly conserved enzyme complex, nitrogenase (Howard and Rees, 1996), where a high degree of sequence similarity among this suite of genes is reported. Genes within the nitrogenase complex (*nif*) have been used to quantify the relative abundance (DNA) and activity (mRNA) of N_2-fixing organisms, whose biogeographic distribution has been found worldwide, in habitats ranging from anaerobic, to microaerophilic, to aerobic (Zehr, Jenkins, Short, & Steward, 2003). This broad biogeographic and phylogenetic distribution of the *nif* genes demonstrates the functional redundancy in microbial communities, particularly for functions related to critical ecosystem services, like nutrient cycling. The biogeochemical cycling of soil nutrients is the outcome of microbial uptake and exudation in the rhizosphere.

Some microbial exudates are excellent mimics of plant hormones, such as indole-3-acetic acid (IAA), or are enzymatically involved in regulating plant hormone signalling (e.g. 1-aminocyclopropane-1-carboxylate (ACC) deaminase). These hormone signalling molecules can promote plant growth.

Increased root development, and hence increased nutrient uptake, has been documented after inoculation of wheat with rhizosphere bacteria expressing ACC deaminase activity (Shaharoona, Naveed, Arshad, & Zahir, 2008). The mode of action of this enzyme is suppression of ethylene production in growing roots by catalysing the cleavage of ACC, the immediate precursor of ethylene in plants, to α-ketobutyrate and ammonia (Honma and Shimomura, 1978). The bacteria capable of producing ACC deaminase essentially shunt plant ACC away from synthesis in the form of ethylene, thereby minimizing impacts of various environmental stresses, which typically trigger increased ethylene production (Glick et al., 2007; Hardoim et al., 2008). The interplay in hormone signalling between the plant and the microbiome will be further explored in the following sections where the ecology of the microbiome is dissected.

Microbial exudates comprise much of the basis of modern antibiotics and antifungals. The excretion of antimicrobial substances is a common feature found in prokaryotic and eukaryotic microorganisms, and only a miniscule fraction of these organisms are cultivable (Piel, 2011), making the development of metatranscriptomics and metabolomics research more imperative. It might be that the complexity of these antimicrobial interactions within the microbiome actually maintains the astounding diversity previously documented in soils (Buée et al., 2009; Curtis, Sloan, & Scannell, 2002; Torsvik, Goksøyr, & Daae, 1990; Torsvik, Øvreås, & Thingstad, 2002). The complexity of these antimicrobial interactions was demonstrated by a research that found that nearly 35% of *E. coli* strains produce the antimicrobial compound known as colcin. Findings indicated that most tested strains were sensitive to at least one form of colcin, multiple resistance was found to be common among strains, and nearly one-fourth of the strains showed total resistance to all compounds tested (Achtman et al., 1983; Riley, 2011; Riley and Gordon, 1992). These findings support the hypothesis that antimicrobial interactions within microbial communities serve to maintain diversity; this idea was developed using simulation models (Czaran, Hoekstra, & Pagie, 2002). In addition to exuding antimicrobials that assist in plant immunity, microbes also exude low-molecular-weight effector molecules detectible to plants through what are known as pathogen- or microbe-associated molecular patterns in plants that trigger the immune response (Boller and He, 2009). Thus, microbial exudates in the rhizosphere can act directly on other microbes within the microbiome in suppressive mechanisms or can act directly on the plant to stimulate immune responses, often triggering plant exudation.

As our ability to detect and quantify these microbial exudates in the soil matrix improves, we are discovering multiple functions of the same microbiological substances. This should not be surprising considering that functional redundancy is a hallmark of soil microbial communities, one that again is demonstrated by the nitrogen cycle in soils (e.g. the range of bacterial taxa that perform N_2 fixation and denitrification in rhizospheres). The multiplicity of function is a complementary aspect of functional redundancy in microbial communities.

2.3. Impact on plant functions

The microbiome of plant roots was best summarized with the analogous reference to the microbiome of the human gut; both provide similar functional roles to their respective hosts (Bernedsen et al., 2012). These roles include nutrient uptake (Van der Heijden, Bardgett, & van Straalen, 2008), protection from pathogens (Doornbos et al., 2012), and regulation of host immunity (Neal, Ahmad, Gordon-Weeks, & Ton, 2012; Neal and Ton, 2013; Van der Ent et al., 2009). There are also costs to the plant to participate in nutrient exchange and exudate communication, and these logically vary depending upon the molecule and the energy required for the plant (alone or through help from the microbiome) to acquire and/or release exudate currency. High-molecular-weight compounds like those documented in many plant phenolic exudates require active transport mechanisms to cross the plasma membrane and gain release into the rhizosphere (Badri and Vivanco, 2009). One of the primary active transport systems, the ATP-binding cassette transporter, seems to play an important role in root exudation composition and concentration (Badri et al., 2009). Low-molecular-weight molecules can be released through membrane diffusion as in the case of amino acids or through protein channels (Badri and Vivanco, 2009; Jones and Dangle, 2006). There are many factors influencing plant exudation; thus, estimating the costs to the plant becomes both impossible and irrelevant outside of the context of a given system. Regardless, it is clear that plants can benefit from interactions with the microbiome through the direct effects of diminished pathogenic and/or enhanced mutualistic interactions and indirect effects manifest through alterations of ecological and ecosystem processes (i.e. enhanced nutrient availability).

Plants are often the beneficiaries of antimicrobial exudates provided from the microbiome. Recent research has indicated that plants can actively construct the rhizosphere microbiome and that this community is, at least to some

degree, regulated or recruited by the plant to serve as protection from pathogens (Bernedsen et al., 2012; Friesen et al., 2011). An example of this is found in the bacterial production of enzymes that degrade *N*-acyl-L-homoserine lactones (AHLs), commonly found among several prokaryotic genera, which inhibit quorum sensing. Research has shown that plants were capable of recruiting beneficial bacteria expressing high levels of AHL-degrading enzymes when exposed to a pathogen, thus suppressing virulence gene expression (Reading and Sperandio, 2006). Plants also recruit activity within the microbiome specifically to stimulate AHL degradation (Teplitski, Robinson, & Bauer, 2000). Another example is demonstrated by fluorescent pseudomonads, many of which are capable of producing the antimicrobials 2,4-diacetylphloroglucinol (2,4-DAPG) and derivatives of phenazine (Phz). These bacteria are common to the rhizosphere of a diverse array of plant species (Mavrodi, Mavrodi, Parejko, Weller, & Thomashow, 2011). Both antimicrobials are broad spectrum and provide protection against a wide range of plant pathogens, many of which are fungal (Raaijmakers, Paulitz, Steinberg, Alabouvette, & Moenne-Loccoz, 2009). Pathogen success is a function of the soil microbial community, and in some systems, pathogen suppression can persists for extended lengths of time. This suppressive activity can be induced through recruitment of microbes that secrete valuable antimicrobials. The build-up of 2,4-DAPG in the rhizosphere has been observed in many ecosystems and is correlated with the suppression of the disease known as take-all in wheat (Mendes et al., 2011; Raaijmakers et al., 2009; Weller, Raaijmakers, Gardener, & Thomashow, 2002). Interestingly, recent research suggests that 2,4-DAPG and Phz derivatives also serve to reduce mineral content in the rhizosphere, perform plant regulatory and signalling functions that include alterations to exudate profiles, and play a role in the induction of plant systemic resistance (Doornbos et al., 2012; Matilla, Espinosa-Urgel, Rodriguez-Herva, Ramos, & Ramos-Gonzalez, 2007; Mavrodi et al., 2011).

In addition to suppression of pathogens, plant trait expression can also be a function of the interplay with the microbiome. Microbes mediate plant functional traits by providing novel biochemical capabilities and through altering existing plant pathways. Compared to the plant hosts, microbes have a far more diverse metabolic library, enabling them to synthesize biologically active chemicals that can mimic those produced by plants (e.g. hormones), or are totally novel to plants (e.g. specific antimicrobials). All plant hormones currently known can be produced by microbes (Friesen et al., 2011). This ability allows microbial communities to alter plant physiological pathways by producing or manipulating phytohormones. For example, production of IAA

has been reported in nearly 80% of bacterial taxa in plant rhizospheres (Loper and Schroth, 1986). Low concentrations of IAA promote root growth in many plants (Glick, 1999; Patton and Glick, 1996); high concentrations of IAA inhibit plant growth and cause developmental perturbations typical of plant pathogenic bacteria (Sarwar and Kremer, 1995). A support for this variation in IAA secretion has been documented for members of the microbiome associated with the invasive grass, *S. halepense*, where prokaryotes most closely related to known plant pathogens secreted high concentrations of IAA *in situ* compared to lower levels found in prokaryotes not closely related to known pathogens (Rout, Chrzanowski, DeLuca, et al., 2013). Fluctuations in the plant's need for increased or decreased levels of this hormone could also be driven by climate stresses and plant phenology. Selection pressures favour those PGP members of the microbiome that can influence plant traits in ways that increase abiotic stress tolerance and/or plant performance to ensure plant persistence, and empirical evidence supports this (as reviewed by Friesen et al., 2011; Kaplan et al., 2013). PGPB that contain and express multiple genes important for maintaining the plant–microbial association have been called 'competent' (Hardoim et al., 2008). This idea is similar to the 'dual trait' phenomenon where PGPB were more effective at promoting plant growth when they were capable of dual growth-promoting traits (i.e. phosphate solubilization and ACC deaminase production, Baig, Arshad, Shaharoona, Khalid, & Ahmed, 2012). Here again is an example of multiplicity of microbial function as a complementary aspect of functional redundancy.

2.4. Impact on bacterial functions

The preference for organic and amino acids (demonstrated as chemotaxis) is a common phenomenon among rhizosphere microbes (Nelson, 2004). Root exudates are known to induce a range of phenotypic expression in rhizosphere-dwelling bacteria and include chemotaxis and stress tolerance (Amador, Canosa, Govantes, & Santero, 2010), polychlorinated biphenyl degradation (Toussaint, Pham, Barriault, & Sylvestre, 2012), modulation of genes involved in competence and sporulation (Mader et al., 2002), and biofilm formation on plant roots (Rudrappa, Czymmek, Pare, & Bais, 2008). Root exudates (specifically, amino acids) are intimately involved in biofilm formation and disassembly of rhizosphere-dwelling bacteria (Kolodkin-Gal et al., 2010). The surface of roots and admission into the internal structures of plants are protected from many microbial inhabitants by plant exudates, such as terpenoids, flavonoids, and isoflavonoids

(Hardoim et al., 2008). Whether living adherent to roots (epiphytes) or internal to cellular structures (endophytes), these microbiome symbionts are able to persist for some period of their life cycle in these intimate relationships and include not only successful pathogens but also those that can typically promote plant growth through a variety of mechanisms (including hormone signalling).

3. ECOLOGY OF THE MICROBIOME

The aspects of the plant microbiome covered in this overview are restricted to the rhizosphere, rhizoplane (epiphytes), and internal endosymbionts (endophytes) of the belowground organs of the plant, to address the importance of the soil-associated plant microbiome to plant trait expression and ecosystem functions. However, to do so admittedly ignores the impacts of the rhizosphere microbiome on the aboveground interactions, including protection from herbivory, pollination, and seed predation, as well as pathogen attack from aboveground structures (see the review by Friesen et al., 2011). Clearly, all of these aboveground interactions exert an influence on the plant genome, and a complete integration of the 'microbe–soil–microbe–plant–microbe' microbiome will certainly need to be expanded to include the various pollinators (and potentially their microbiomes) for the complete biochemical network map. However, since the 'black box' concept of soils still persists, a key to dissecting the interactions in the rhizosphere will be through a deeper understanding of the plant microbiome that is in contact with this region of soil. Many factors driving plant microbiome structure are a function of the currency in this system—exudates. Three factors influence the currency; not surprisingly, these are three components of the system: soils, microbes, and plants. However, separating these three as independent aspects is both incomplete and unlikely to discover the underlying organization or functional hierarchy within the plant microbiome.

3.1. Rhizosphere and rhizoplane

Defining the microbial community of the rhizosphere in any form of a static or consistent description is impossible. While we are struggling to increase our understanding of the complexity of the rhizosphere microbiome through the use of 'next-generation' and now 'third-generation' technologies, we have known for quite some time that the rhizosphere influences plant health (Hiltner, 1904). The mechanisms enabling this interaction

are only now beginning to unfold, thanks to modern advances in molecular science permitting mining of environmental DNA for functional genes of interest. The magnitude of the differences in rhizosphere soils compared to bulk soils is largely a function of abiotic and biotic stresses influenced by climate. Thus, as stresses/disturbances increase at the macroscale (e.g. drought, plant invasion, pathogenic attack, and metal toxicities), these differences are manifested at the microscale and are demonstrated in the magnitude of difference in microbial community composition between these zones. This phenomenon has been repeatedly demonstrated in arid environments, where low microbial abundance and diversity are typical of bulk soils and rhizosphere soils contain abundantly diverse microbial communities (Aguirre-Garrido et al., 2012; Ben-David, Zaady, Sher, & Nejidat, 2011; Kaplan et al., 2013; Yu, Grishkan, & Steinbrener, 2012). In general, rhizosphere soils have higher water-holding capacity, increased nutrient availability, and greater microbial biomass compared to bulk soils (Schade and Hobbie, 2005). Spatiotemporal shifts have been documented in the rhizosphere microbiome (Houlden, Timms-Wilson, Day, & Bailey, 2008; Kaplan et al., 2013), but how much of this is driven by direct effects of abiotic impacts (seasonal stochasticity) and indirect effects of abiotic stressors as exhibited by biotic interactions (e.g. plant life stage and plant community structure) remains tightly entangled.

Similar to the function of the gut, the rhizosphere region of the plant microbiome is informative about plant health, at both the individual and community level (particularly in monoculture crops), where a healthy versus diseased state of the plant community can be reflected in the composition of the rhizosphere microbiome (Burdon and Thrall, 2009). The rhizosphere and rhizoplane microbiomes are being tapped for a wide range of services (e.g. crops, bioremediation, and energy) to maximize quality, productivity, and sustainability. It is important to remember the context in which these microbes are interacting with the plant and surrounding members of the microbiome and that this interaction is where ecosystem functions become expressed, rather than being an intrinsic property of a specific, or suite of, microbe(s). For example, some members of the microbiome (particularly those classified as PGPB) stimulate induced systemic resistance (ISR) in plants, marked by priming of jasmonic acid-inducible genes in leaves (Van Wees, Van der Ent, & Pieterse, 2008), effectively stimulating immunity conferring resistance to a broad range of pathogens (Pineda, Zheng, van Loon, Pieterse, & Dicke, 2010; Van der Ent et al., 2009; Van Oosten et al., 2008). In turn,

plants with activated ISR display increased or enhanced defence signalling aboveground (Ahmad et al., 2011) and belowground (Neal et al., 2012; Neal and Ton, 2013). A network of communication begins to develop in the rhizosphere microbiome, and three-way interactions between multiple microbial partners and plants are as simple as we can hope for in the microbiome. As the largest reservoir of biological diversity currently known (Bernedsen et al., 2012; Curtis et al., 2002), the rhizosphere microbiome should pique the interest of anyone interested in venturing into the unknown to solve problems relevant to a changing climate, including bioremediation, maximization of crop yields (increased efficiency and sustainability), enhanced soil fertility of marginal lands, and discovery of novel antimicrobials, to name but a few.

3.2. Epiphytes and endophytes

The root epiphyte and endophyte communities can differ widely from those in the rhizosphere, which supports the concept of coevolution among host plant and microbial symbionts (Boller and He, 2009; Compant, Clement, & Sessitsch, 2010; Compant, Duffy, Nowak, Clement, & Barka, 2005), in which the plant engages in recognition and selection of microbiomes that promote a homeostatic relationship with the plant. The ability of the microbial members of the plant microbiome to colonize the plant tissues, whether in an adherent (epiphytic) or internal (endophytic) manner, is another complexity that we are beginning to catch glimpses of with molecular methods like metabolomics and metatranscriptomics.

The colonization process that occurs between microbes and plant hosts involves exudate communication through microbe–microbe signalling interactions (Deakin and Broughton, 2009; Elasri et al., 2001) in addition to those between microbes and plants (Boller and He, 2009; Deakin and Broughton, 2009; Friesen et al., 2011; Hardoim et al., 2008). The ability of a microbial partner to colonize the external root surfaces appears to be, at least to some degree, a coevolved communication exchange. For example, secondary metabolite root exudates in maize that were released due to an ISR response were responsible for the recruitment of the PGPB *P. putida*, based on chemotaxis preferences (Neal et al., 2012). Supporting this, genes for chemotaxis have been identified in a wide range of microbes inhabiting the rhizosphere, and expression of these genes is an essential step towards adherence and colonization of the root surface (Hardoim et al., 2008). Here again, a plant-mediated response is apparent as demonstrated by different plant chemical exudates used

to recruit beneficial PGPB; in tomato, organic acids are the major chemotactic agent (de Weert et al., 2002), while amino acids serve this function in rice (Bacilio-Jimenez et al., 2003). Several bacterial genes enabling establishment on plant roots have been identified and include those that code for the type IV pilus and twitching motility (Bohm, Hurek, & Reinhold-Hurek, 2007), isoflavonoid efflux pump (Palumbo, Kado, & Phillips, 1998), and DNA rearrangements affecting colony aggregation (Dekkers, Phoelich, van der Fits, & Lugtenberg, 1998).

One critical question at the crux of the communication pathways of the plant microbiome is how the plant detects a microbial mutualist from pathogen. This involves complex signalling between plants and microbes that trigger plant immune responses, the subject of several reviews (see Deakin and Broughton, 2009; Hardoim et al., 2008; or the May 2009 special issue in *Science* for starting material). Once adherent to the roots, biofilm and microcolony development proceeds (Compant et al., 2008; James et al., 2002), which potentially serve as gateways into internal colonization of the plant in an endophytic life stage (Hardoim et al., 2008).

The microbiome located inside plant tissues reflects the microorganisms living in an endophytic lifestyle (Bulgarelli et al., 2013). Many plant species have been shown to harbour endophytes, and these include domesticated crops (Compant et al., 2008; Hallmann, Quadt-Hallmann, Mahaffee, & Kloepper, 1997; James et al., 2002), and wild cultivars, including invasive species (Rout and Chrzanowski, 2009). Beyond a few well-known endophytic microbe–plant interactions (e.g. arbuscular mycorrhizal fungi and nodule-forming N_2-fixing bacteria in legumes), the importance of these endosymbionts to the plant microbiome is largely unknown. It should be noted that the importance of N_2-fixing bacterial endophytes in crop grasses of sugar cane and sorghum has been investigated for decades (Baldani et al., 1996; James, Olivares, Baldani, & Dobreiner, 1997; Kirchof et al., 2001).

Microbiome components demonstrating detectible plant-growth-promoting genes are of considerable interest to biotechnology and agriculture, where the motivating hypothesis is that multiple genes involved in establishment, persistence, and thriving of plant-beneficial microbes will be in higher abundance within these organisms. Some support for this is observed in phosphate-solubilizing *Bacillus* strains, where their effectiveness at plant-growth promotion was additive when the strain had the additional ability to produce the enzyme ACC deaminase (Baig et al., 2012). Other phosphate-solubilizing bacteria act in concert with mycorrhizal fungi to enhance plant-growth promotion (Zaidi and Khan, 2005), and while not

a dual trait from an individual organismic level, this does function as a dual trait from the microbiome perspective.

In general, putative epiphytic and endophytic microbes have to communicate with the plant for a series of interactions with the plant hosts that enable their establishment, persistence, and thriving. At the rhizosphere and bulk soil level, this is largely driven by soil factors, expanding to macroscale environmental inputs, such as climatic factors. On a microscale, this involves currency exchanges among plant and microbial exudates. Persistence is a function of timing of colonization. Therefore, it is not surprising that plant phenology is correlated with endophyte microbiome composition shifts (van Overbeek and van Elsas, 2008), and achieving persistence on or in the plant heavily relies upon colonization and compatibility (Hardoim et al., 2008). Shifts in endophyte communities as a function of plant developmental stage is a likely factor driving recruitment of PGPB that demonstrate high ACC deaminase activity to respond to high levels of ethylene in the plant, whether that be due to aspects of plant phenology (e.g. seedling emergence or fruit ripening) or as a response to abiotic stresses like high salinity (Cheng and Glick, 2007) and heavy metal toxicity (Zang et al., 2011). These findings support the viewpoint of others that the plant–endophyte relationship is coevolutionary (Boller and He, 2009; Compant et al., 2010, 2005) and suggest that cross-communication of plant developmental stage is conveyed through exudates. Potentially, these interactions achieve homeostasis. Simply stated, this is when the interaction leans more towards mutualism on the spectrum of symbiosis rather than towards parasitism. One confounding influence that epiphytes and endophytes can express on the plant genome is manifested through horizontal and vertical transmission of the symbionts.

The majority of known plant endophytes and epiphytes are horizontally transmitted (Friesen et al., 2011). This creates a potential fitness conflict where antagonistic coevolution of functional trait expression likely arises between the plant and microbial symbionts, where one downstream impact on functionality might be expressed as an altered ecosystem service. Horizontal transmission enables host-to-host transfer of endosymbionts without involvement of plant sexual reproduction. In turn, this often, but certainly not always, involves pathogenic interactions, and plants are challenged to coevolve mechanisms facilitating beneficial trait expression from these endosymbionts (Bever, Richardson, Lawrence, Holmes, & Watson, 2009; Kiers and Denison, 2008). This brings to mind the evolutionary shifts along the mutualism–parasitism trajectory, where horizontal transmission of endophytes might be a coevolutionary mechanism contributing to this range of interactions.

Vertical transmission of endophytes relies upon host fitness and is characterized in fungi as those demonstrating an asymptomatic lifestyle in the plant host (Clay and Schardl, 2002). Since this strategy involves the transfer of endosymbionts through sexual reproduction of the host, an increased likelihood for coevolutionary mechanisms between these partners exists. Some have suggested that vertically transmitted endophytes confer increased host benefits over those horizontally transmitted, and there is some evidence supporting this idea (Clay and Schardl, 2002; Sachs, Mueller, Wilcox, & Bull, 2004). However, it is unlikely that a generalizable rule can be extrapolated to the mode of transmission that will be applicable in a broad ecological sense, as a wide range of factors are likely to influence endophyte transmission, including host evolutionary relationship. For example, the invasive grass *S. halepense* is a relatively newly evolved polyploid hybrid (Feltus et al., 2004) that can transmit at least some of the N_2-fixing bacterial endophytes within the rhizomes both vertically and horizontally (Rout, Chrzanowski, DeLuca, et al., 2013; Rout, Chrzanowski, Smith, et al., 2013), indicating that this successful invader might be capable of regulating potential pathogenic responses expressed by these endosymbionts. Ecological theory suggests that horizontally transmitted organisms achieve maximal transmission when available hosts are within close proximity. Support for this theory has been shown, where horizontally transmitted endophytes were positively correlated with plant density dependence, while vertically transmitted endophytes did not show this trend (Rudgers et al., 2009). A hallmark of plant invasions is increased density, which often approaches near monocultures (Tilman, 2000). Thus, it is not surprising that endophytes of the *S. halepense* microbiome can be horizontally transmitted through plant rhizomes. This strategy will likely be a common one utilized by other invasive plants, particularly ones that clonally reproduce through rhizomes, as these organs have been shown to harbour endophytes in a wide range of plants (Baldani et al., 1996; James et al., 1997; Kirchof et al., 2001; Rout and Chrzanowski, 2009). A comprehensive and holistic consideration of the plant microbiome interface will be required to determine plant and microbial trait expression, genetics, and outcomes of their impacts on ecological functions.

4. IMPORTANCE OF THE MICROBIOME TO PLANT GENOMICS

A main goal of plant genomics is to uncover the mechanisms that regulate plant trait expression, ultimately to enhance plant performance.

Impacts of the plant microbiome community structure are clearly manifest in plant trait expression. For example, the plant microbiome influences plant root architecture (Morris and Djordjevic, 2006; Spaepen, Dobbelaere, Croonenborghs, & Vanderleyden, 2008), which should not be surprising given the repertoire of microbial phytohormones that the plant can elicit from the microbiome. Alterations to root architecture have important implications for overall plant health. Take, for an example, border cells in roots; increased numbers of border cells conferred increased resistance to fungal pathogen infection (Chen, Chen, & Wu, 2012), likely due to the function of border cells in extracellular trapping of microbes that has been shown to provide a defence for the root tip (Curlango-Rivera et al., 2013). Influencing plant architecture through enhancing root growth is a primary motivation behind mining the microbiome for this PGP trait, which is of interest to agribusiness. Enhanced root (and rhizome) growth is also of great ecological significance, since many successful invasive plants express increased belowground biomass in their nonnative ranges, and this serves as a primary means of niche expansion. Thus, it is possible that this ability confers an increased probability of invasiveness. Some evidence supports this notion, linking the microbiome to belowground growth in one of the world's worst invaders (Rout, Chrzanowski, DeLuca, et al., 2013; Rout, Chrzanowski, Smith, & Gough, 2013). Suppression of the invasive grass microbiome with antibiotics reduced belowground (rhizome) growth (over fivefold declines) compared to growth with an unsuppressed microbiome. The precise role(s) of the plant and the microbial contributions to the microbiome will be revealed in this system, and others like it, with the use of advances in molecular techniques, particularly the use of RNA-Seq allowing for separation of prokaryotic from eukaryotic mRNA in metagenomic samples. To what extent the microbiome drives traits associated with invasive plants and what generalities might be extrapolated across broad phylogenetic or biogeographic ranges remain to be determined. Nevertheless, the plant microbiome has been implicated in the mediation of over a dozen plant functional traits including root, vegetative, regenerative, stem, and leaf traits (reviewed by Friesen et al., 2011), so it follows that extremes in plant trait expression observed in the majority of invasive plants, including traits of physiology, leaf-area allocation, shoot allocation, growth rate, fitness, and biomass (detailed in the meta-analysis by van Kleunen, Weber, & Fischer, 2010), likely involve help from the microbiome.

The microbial members within the plant microbiome cause fundamental differences in expression of plant phenotypes, due to their influence on plant

functional traits. In turn, the plant microbiome also influences ecosystem functioning through an indirect mechanism, the plant as a community. The influence on the expression of individual functional traits impacts population dynamics, particularly for sessile organisms such as plants, best demonstrated through pathogen spread documented in wheat and rye (Burdon and Thrall, 2009). Besides assisting plants in niche expansion (or invasion spread) through enhanced root and rhizome production, the microbiome can impact plant ecology through influences exerted on plant–plant competition (Klironomos, 2002), pollination (Cahill, Elle, Smith, & Shore, 2008), herbivory, and defence (Friesen et al., 2011). Given that plant primary productivity is impacted by the availability of limiting nutrients and possessing the traits to enhance resource acquisition (Lambers, Raven, Shaver, & Smith, 2008), the role of the microbiome in soil biogeochemical cycles is a fundamental factor influencing plant productivity. Primary productivity is considered an aspect, or measurable outcome from a land management perspective, of ecosystem services.

It is important to keep in mind that broader ecological aspects must also be considered when trying to disentangle the interactions within the plant microbiome. Ecosystems where we can measure shifts in microbiome community structure and function are the precise areas of attention that need focus. Ecology will dictate the adaptive traits required of the PGP microbiomes that enable plant persistence. Plant-invaded communities will likely provide many exciting insights about the plant microbiome, including the influence of the microbiome on invasive plant traits and their role in profound alterations to nutrient cycling documented in many invaded ecosystems and (Liao et al., 2008). Extreme environments, such as deserts, are another area where plant microbiome research efforts have correlated mechanisms of the microbiome permitting the plant to tolerate drought stress (Kaplan et al., 2013). To what extent plant communities regulate and are regulated by their microbiomes is an area that needs to be explored and raises questions regarding important mechanisms for acclimating and adapting to disturbances or tolerating stress.

Perception of the microbiome as a component of the plant genome is certainly evident in an obligate endosymbiotic relationship, such as the most well-known and evolutionarily significant one between plants and chloroplasts. This relationship occurred, presumably, over long periods of time when the bacterial organism switched between expressions of facultative–obligate endophyte lifestyles. When the parasitism–mutualism continuum is viewed in this way, it becomes clearer how the microbiome can impact the plant

genome without having to become a permanent component of the genome. We know that microbes of the rhizosphere can influence nearly every plant functional trait, resulting in impacts on plant trait variation of similar magnitude to those of the genotype (Friesen et al., 2011). Given the complexity of chemical communication capabilities within the microbiome, including microbial characteristics of multiple metabolic pathways for carbon utilization, the ability to utilize multiple terminal electron acceptors in addition to oxygen, and production of mimic plant phytohormones, the link between microbially mediated ecosystem process of nutrient cycling and plant productivity lies embedded in the rhizosphere matrix. Disentangling the plant–microbe communications in this matrix will enable us to determine the drivers of a vast array of desirable plant traits that will, potentially, be harnessed to address some of the many challenges currently facing our world, such as degradation of soil resources (Montgomery, 2007), depletion of water supplies (Rosegrant, Cai, & Cline, 2002), and losses of biodiversity (Pimentel, Lach, Zuniga, & Morrison, 2000) as examples. The human global population places many demands on the Earth beyond the need for increased food production, for example, an increased need to harvest more solar energy for fuel production (e.g. biofuel crops). This combination of events makes it likely that increased conversion of lands for agricultural uses will compete with human urbanization, a fact that we can already observe in most large U.S. cities. Balancing these two demands will inevitably require harnessing resources from fragile ecosystems or marginal landscapes (Tilman et al., 2009) while simultaneously maximizing plant productivity. The plant microbiome will likely play a prominent role towards achieving this requirement.

Clearly, the microbiome plays a huge role in plant function and performance. While microbiome analysis has only recently been widely recognized, it is now viewed as essential to understanding genetic and functional capacity otherwise attributed to host organisms, including important aspects of metabolism and physiology. High-throughput technologies of next- and third-generation sequencing will enable library construction of trait loci involved in plant phenotypic expression. Quantitative trait locus maps have been used in several plant species to identify genomic regions where genes responsible for a given trait of interest exist (e.g. ;Hu et al., 2003 Jang, Lemke, Tang, Bowers, & Paterson, 2008; Paterson, Schertz, Lin, Liu, & Chang, 1995). By knowing plant genes involved in phenotypic variation of a trait, the hormonal signalling pathways linked to trait expression can be tested for microbiome contributions to signalling cascades. The roles of microbiome in the regulation of plant hormone signalling cascades will also be influenced by

abiotic and biotic stresses such as drought, nutrient limitation, and pathogen attack. More complex still is deciphering the extent to which the microbiome is under selection by the host plant. Specific plant attributes and environmental factors that increase the plant's ability to select a microbiome are currently lacking from most plant ecology studies, but we know that plants can select their microbiome communities through the exudate currency shared among the plant and its colonizers (Doornbos et al., 2012).

5. CONCLUSIONS

Strong evidence illustrates the importance of understanding the multitude of plant microbiome associations that contribute to plant plasticity in a given environment (Friesen et al., 2011). Recognition of the plant microbiome as an integrated aspect of the plant genome expands on the ecological concept of 'feedbacks' (Bever, 1994). Feedbacks were certainly an important concept that forged the path ahead for integrating the soil–plant–microbe matrix. The reciprocity of the effects that soil biota and plants exert over this interaction varies over time as a function of attenuation of microbiome members that span the spectrum from parasitic to mutualistic in their interactions with plants (reviewed by Callaway and Rout, 2011). Disproportional accumulation of microbiome parasites (expressed as pathogenic effects) leads to negative feedbacks, while the disproportional accumulation of microbiome mutualists leads to positive feedbacks (Klironomos, 2002). Increased knowledge about these interactions and how shifts in biodiversity impact functions in the context of ecosystem services (plant productivity, biogeochemical pools, and fluxes) will be a critical factor for elucidating plant microbiome growth and gene expression patterns. Many of these patterns likely exhibit species-specific or other phylogenetically based distributions among plants. Rapid microbial generation times and the prevalence of horizontal gene transfer provide potential mechanisms for the development of regional genetic differences, or ecotypes, to arise in response to the effects of local plant species and communities (Rout and Callaway, 2012). As the integration of the plant microbiome unfolds, a new approach is emerging that includes aspects of microbial ecology, microbiomes, and transcriptomes into plant genetics. This is certainly motivated by the vast diversity documented in the rhizosphere microbiome (Bernedsen et al., 2012; Curtis et al., 2002) and correlated with the functional redundancy of genes responsible for essential nutrient transformations, like those involved in N_2 fixation (Zehr et al., 2003), previously discussed in earlier

sections. Selection favours the plants that can motivate/manipulate their microbiome in ways that favour plant persistence, particularly under a variety of stochastic disturbances (de Bello et al., 2010). Recent findings from many different plants in a wide range of ecosystems support this, as demonstrated by the ability of the plant to control the composition of the microbiome (reviewed by Bernedsen et al., 2012).

Understanding the regulation of such complex communication pathways within the plant microbiome involves detecting and quantifying the multiple functions of microbial and plant exudates and their impacts on gene transcription and translation. The holistic approach to understanding any organismic function and structure is to understand the organism in its entirety; the microbiome and its functional contribution are certainly integral for all higher organisms on the planet. This should not be a surprise. How the microbiome is influencing or being influenced by the plant will likely vary among species, as well as by environmental and genetic factors. Studies of the plant microbiome need to document microbial community structural and functional diversity and shifts in these metrics as a function of spatiotemporal changes associated with ecological habitats. Further development of functional screening that utilizes metagenomics and metatranscriptomics will lead us to predicting plant traits based on knowledge of the microbiome, in addition to knowing how and when this 'second genome' functions as an organ system of the plant.

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