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The Soil-Borne Identity and Microbiome-Assisted Agriculture: Looking Back to the Future

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ABSTRACT

Looking forward includes looking back every now and then. In 2007, David Weller looked back at 30 years of biocontrol of soil-borne pathogens by *Pseudomonas* and signified that the progress made over decades of research has provided a firm foundation to formulate current and future research questions. It has been recognized for more than a century that soil-borne microbes play a significant role in plant growth and health. The recent application of high-throughput omics technologies has enabled detailed dissection of the microbial players and molecular mechanisms involved in the complex interactions in plant-associated microbiomes. Here, we highlight old and emerging plant microbiome concepts related to plant disease control, and address perspectives that modern and emerging microbiomics technologies can bring to functionally characterize and exploit plant-associated microbiomes for the benefit of plant health in future microbiome-assisted agriculture.

Key words: disease suppressive soils, rhizosphere, root exudates, root immune response, soil fungistasis

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INTRODUCTION

In looking back to the future, it is most appropriate to start by quoting Lorentz Hiltner who stated in 1904: “However, I am convinced that soil bacteriology will finally provide results that are not only of explanatory nature, but will also directly affect and determine agricultural practice” (translated from German in Hartmann et al., 2008). Also his declaration: “I would like to state from the very first, that apart from some sporadic exceptions, the main goal of our joint effort to make the results applicable in practice, has not been reached so far,” is still relevant. Microbial communities that are associated with plants are nowadays widely recognized as being crucial for plant performance and health (Berendsen et al., 2012). Since the publication of the first next-generation sequencing-based papers on the plant microbiome (Mendes et al., 2011; Bulgarelli et al., 2012; Lundberg et al., 2012), the number of plant microbiome studies increases at a rapid pace (Berg et al., 2020; Fitzpatrick et al., 2020). The term microbiome was first used by Whipps et al. (1988) in the context of plant disease control and defined as “a characteristic microbial community occupying a reasonably well-defined habitat which has distinct physico-chemical properties” (Eisen, 2015). Most commonly, studies refer to Lederberg and McCray (2001) who use the term microbiome “to signify the ecological community of commensal, symbiotic, and pathogenic microorganisms that literally share our body space and have been all but ignored as determinants of health and disease.” Here, we adopt the definition of plant microbiome as the collective communities of plant-associated microorganisms, also referred to as the plants’ second genome (Berendsen et al., 2012; Mendes et al., 2013; Turner et al., 2013). Thus, instead of plants being viewed as autonomous entities, they are considered as holobionts that consist of the plant host plus the interactions with its associated microbiota (Bordenstein and Theis, 2015; Vandenkoornhuyse et al., 2015). The functional repertoire of the plant is thereby increased to a great extent and helps the plant to adapt to its biotic and abiotic environment (Bakker et al., 2018). In this perspective we focus on a number of established concepts that emerged in the past century in relation to root-associated microbiota and their functions in plant health, and especially on how

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modern microbiomics technologies can help to decipher complex processes that govern the assembly and functioning of the root microbiome.

Microbial diversity in soils is enormous with estimates that range from thousands to a million microbial species in several grams of soil (Allison and Martiny, 2008). Plant roots deposit 10%–44% of the carbon that is photosynthetically fixed by the plant into a narrow zone of soil around the root, creating an environment that stimulates the development of active microbial communities that are selected and assembled from the soil microbial community (Bais et al., 2006). It has been postulated frequently that plants select specific microbes and microbial functions that can alleviate the specific stress conditions that the plant encounters by selectively adjusting the chemical composition of their root deposits (Rudrappa et al., 2008; Castrillo et al., 2017; Verbon et al., 2017; Stringlis et al., 2018a; Bakker et al., 2018; Berendsen et al., 2018; Hu et al., 2018; Sasse et al., 2018; Huang et al., 2019; Koprivova et al., 2019; Pascale et al., 2020). To get back to Lorentz Hiltner's quote on the applicability of soil microbiology: we are now at the brink of effective exploitation of long-standing and emerging concepts of plant–microbiome interactions in agricultural practice. Over the last few decades, we have questioned and dissected the rhizosphere microbiome with application in mind. However, with the exciting new next-generation sequencing-based approaches, biological principles underlying plant–microbiome interactions can be unraveled in detail at the molecular level (White et al., 2017; Fitzpatrick et al., 2020), thereby bringing the development of more sustainable, microbiome-assisted agricultural systems within reach (Finkel et al., 2017; Toju et al., 2018).

The Rhizosphere Effect

The notion that there is active interaction between plant roots and soil microbiota dates back more than 100 years. In his seminal publication, the previously mentioned Lorentz Hiltner (1904) introduced the term rhizosphere, describing the zone of soil that is influenced by plant roots. He envisioned that root exudates attract beneficial bacteria and that plant quality and health depend on the composition of the root microflora (Hartmann et al., 2008). Research on rhizosphere microbial communities revealed that microbial populations directly around plant roots are much larger than those in non-rooted bulk soil, a phenomenon known as "the rhizosphere effect" (Bakker et al., 2013) (Figure 1). By determining the abundance of colonies that developed on different agar media, Starkey (1929) reported higher populations of fungi, actinomycetes, and bacteria in soil sampled near roots than away from roots for different plant species. But the rhizosphere not only facilitates higher numbers of microbes, there is also selection of specific microbes from the bulk soil, as shown in studies on bacteria that are either based on isolation on agar media (Glandorf et al., 1993; Lemanceau et al., 1995) or cultivation-independent 16S rDNA amplicon analysis (Smalla et al., 2001). Moreover, plant type and soil composition significantly affect the bacterial and fungal rhizosphere microbiome (Edwards et al., 2015; Tkacz et al., 2015). Thus, as compared with the bulk soil, the rhizosphere microbiome has a higher microbial density and activity, but the microbial diversity in the rhizosphere is typically lower than that of the bulk soil (Philippot et al., 2013). Within the microbiome, microbial interactions affect population densities and functioning of the different microbiota. Studies in relation to plant performance have focused on those interactions that affect either plant beneficial microbes or plant pathogenic microbes. Enrichment for beneficial microbial functions in the rhizosphere can lead to improved root architecture, enhanced nutrient uptake, increased abiotic stress tolerance, and stimulate the plant's immune system (Castrillo et al., 2017; Fitzpatrick et al., 2020; Hacquard et al., 2017; Philippot et al., 2013; Pieterse et al., 2014; Xu et al., 2018; Yang et al., 2009) (Figure 1), therewith promoting plant growth and survival. Selected rhizosphere microbes can also directly suppress soil-borne pathogens, e.g., via antibiosis or siderophore-mediated competition for iron (Mercado-Blanco and Bakker, 2007). In this respect it has been postulated that the rhizosphere microbiome provides a first line of defense of the plant against soil-borne plant pathogens (Weller, 1988; Weller, 2007; Mendes et al., 2018b).

Soil Fungistasis

Microbial interactions frequently occur in soils, and one of the most well-known examples of such interactions is a phenomenon called "soil fungistasis," the inability of fungal spores to germinate in soil under conditions seemingly favorable for germination *in vitro* (Lockwood, 1977; Garbeva et al., 2011) (Figure 1). For soil-borne plant pathogenic fungi, fungistasis is important in their ecology as the fungal spores will not germinate in the absence of a host and thus survive in rest until a host plant root arrives. Soil fungistasis is a common feature that can be observed in microbially active soils, irrespective of their history. For example, spore germination of *Penicillium frequentans* and 14 other fungal species was completely inhibited in a wide range of fresh soils, and heat treatment of the soils annulled the inhibition (Dobbs and Hinson, 1953). Thus, microbial activity was postulated to be involved in inhibition of fungal spore germination and hyphal growth, and the mechanisms proposed are nutrient deprivation and the microbial production of inhibitory substances (De Boer et al., 2003; Garbeva et al., 2011). In the elegant study by Duran et al. (2018), the interkingdom interactions between bacteria and filamentous eukaryotic microbes they reported to be important for plant survival may well be a reflection of classical soil fungistasis as the authors basically followed an approach similar to that of Henry (1931). Henry applied a plant disease suppressive synthetic community of soil microbiota in a gnotobiotic plant system. In this pioneering study, a pathogen inhibitory soil was sterilized resulting in complete loss of pathogen inhibition. Addition of a trace of unsterilized soil restored the pathogen inhibition completely as did a combination of bacteria, actinomycetes, and fungi isolated from the soil.

In some soils, the effect on plant pathogens is more specific and even when both a virulent pathogen and a susceptible host are co-cultivated, plants hardly get diseased. In this case soils are classified as "disease suppressive." Many examples of disease suppressive soils have been reported and were described by James Cook and Kenneth Baker (1983) in their monumental book "The Nature and Practice of Biological Control of Plant Pathogens."

The Soil-Borne Legacy

A prerequisite for disease suppressive soils to develop is a severe outbreak of disease after which disease incidence declines and

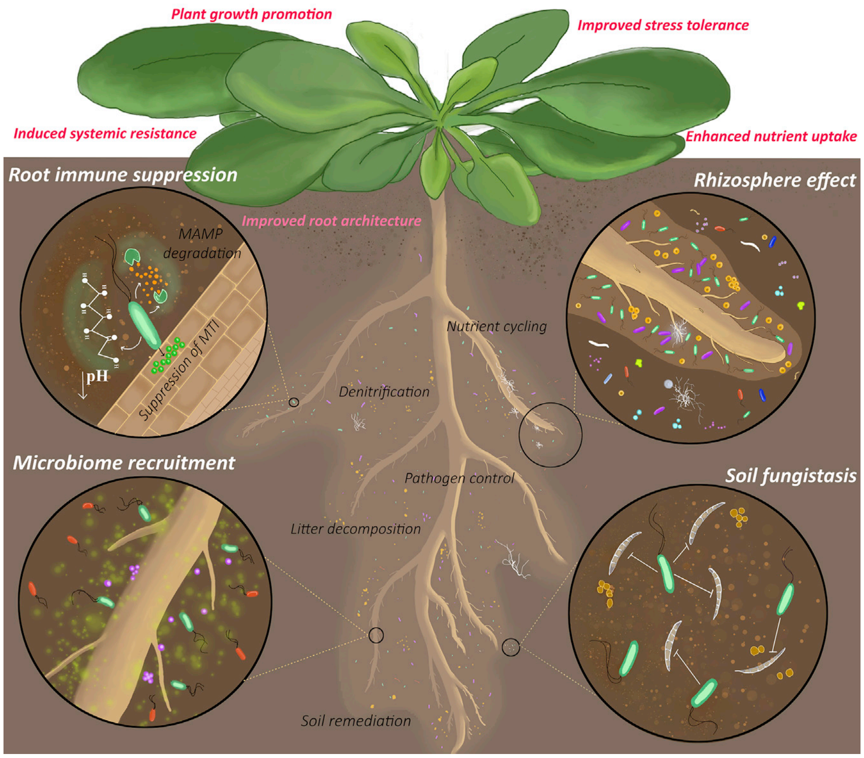

Figure 1. Key Concepts in Plant–Microbiome Interactions.

The rhizosphere is a microbial hotspot. Microbial activity in the rhizosphere stimulates processes such as nutrient mobilization, denitrification, litter decomposition, soil remediation, and biocontrol of soil-borne pathogens. Microbial activities in the rhizosphere provide important services to the plant, such as enhanced nutrient uptake, promotion of plant growth, abiotic stress tolerance, and increased resistance against pests and pathogens. The blow outs represent artist impressions of four prominent rhizosphere microbiome processes. *Rhizosphere effect*: plants nurture a vast community of commensal and mutualistic microbes in the rhizosphere. Root exudates and other rhizodeposits shape the microbial community in the rhizosphere. This typically results in a higher microbial density, and a lower microbial diversity than in bulk soil. *Soil fungistasis*: in microbially active soils, soil microbiota (represented by green bacteria) inhibit germination of spores of soil-borne fungal pathogens (represented by gray spores). This soil fungistasis is important in the ecology of fungal pathogens as the spores will not germinate in the absence of a host and thus survive in rest until a host plant root arrives and chemically stimulates its germination. *Microbiome recruitment*: in response to biotic or abiotic stress, such as foliar pathogen infection or nutrient starvation, plants can actively reshape their root microbiome and recruit specific beneficial microbes to their roots (represented by green bacteria) that can aid in the alleviation of the experienced stress, while repressing others (represented by red bacteria). Root secreted metabolites, such as coumarins, benzoxazinoids, camalexin, and triterpenes recently emerged as important players in root microbiome assembly. *Root immune suppression*: the rhizosphere is a MAMP-rich environment. To prevent continuous activation of MAMP-triggered immunity, which would hamper colonization by beneficial microbes and result in chronic growth repression due to defense-growth tradeoffs, beneficial rhizosphere microbiota can evade or suppress MAMP-triggered immunity in roots, making this an important function of the root microbiome. Different mechanisms can be involved, including host immune evasion via microbial protease-mediated degradation of MAMPs, and host immune suppression via delivery of microbial effector proteins or local lowering of environmental pH via microbially produced gluconic acid.

remains at a very low level (Raaijmakers and Mazzola, 2016). Early reports on the microbial origin of disease suppressiveness relied on elimination of microbes by heat treatments (Broadbent and Baker, 1974) and in addition the transferability of suppressiveness by mixing small amounts of suppressive soil with conducive soil (Cook and Rovira, 1976). The latter reflects the disease suppressive effect of fecal microbiota transplants from healthy human donors to patients with a bacterial bowel infection (Van Nood et al., 2013). The isolation of microbes from suppressive soils and subsequently testing them for control of the disease in conducive soil identified microbes that were potentially responsible for disease suppressiveness. For example, fluorescent *Pseudomonas* in take-all decline soils (Weller et al., 2002) and non-pathogenic *Fusarium oxysporum* in a Fusarium wilt-suppressive soil (Alabouvette, 1999). In more recent studies, identification of microbes associated with disease suppressiveness is based on analysis of the microbiome by amplicon sequencing, often in combination with experimental procedures that eliminate suppressiveness, such as heat or gamma radiation (Mendes et al., 2011; Cha et al., 2016). Using a metagenomics and network interference approach, Carrion et al. (2019) elegantly demonstrated in sugar beet that infection by the soil-borne pathogen *Rhizoctonia solani* resulted in the recruitment of specific endophytes possessing biosynthetic gene clusters that are needed for disease suppressiveness. Whereas studies on disease suppressiveness have focused on soil-borne pathogens that infect plant roots, recent studies show that, also for aboveground plant pathogens, infection in the leaves can trigger changes in the rhizosphere microbiome that can protect a next generation of plants against the pathogen. This microbial "soil-borne legacy" was demonstrated in *Arabidopsis thaliana* for the oomycete pathogen *Hyaloperonospora arabidopsidis* (Berendsen et al., 2018) and for the bacterial pathogen *Pseudomonas syringae* pv. *tomato* (Yuan et al., 2018). Hence, an infected plant can create a soil-borne microbial memory that provides protection in a next generation of plants. Similar soil-borne legacy effects have been reported affecting flowering time (Panke-Buisse et al., 2015) or drought tolerance (Lau and Lennon, 2012). The identification of plant cues that govern this soil-borne legacy is a next crucial step to further exploit this phenomenon for agricultural purposes (Bakker et al., 2018).

In recent studies, several metabolites in root exudates emerged as important players in the assembly of root microbiomes (Pascale et al., 2020) (Figure 1). The untargeted metabolite profiling of non-sterile rhizospheres (Petriarcq et al., 2017) that was used in the study by Cotton et al. (2019) revealed benzoxazinoids in maize root exudates as important regulators of rhizosphere microbiome composition. In another study, benzoxazinoids produced by a first generation of maize plants were shown to influence the rhizosphere microbiome composition of a next generation of maize plants, therewith positively affecting plant performance and defense against herbivore attack (Hu et al., 2018). In *A. thaliana*, microbiome analyses of wild-type and mutant variants recently revealed coumarins (Stringlis et al., 2018a; Voges et al., 2019), camalexin (Koprivova et al., 2019), and triterpenes (Huang et al., 2019) as potent root exudate-derived metabolites that influence microbiome composition. Coumarins possess selective antimicrobial activity and can act as semiochemicals (Stringlis et al., 2019; Stassen et al., 2020). In *A. thaliana*, the coumarin scopoletin was shown to selectively influence growth of different members of the microbiome, and favoring selected plant beneficial microbes, while suppressing selected soil-borne pathogens (Stringlis et al., 2018a). An experimental evolution study on *Pseudomonas protegens* in the rhizosphere of *A. thaliana* revealed a role for scopoletin in the "domestication" of this plant root colonizing bacterium. The bacteria rapidly diversified in the rhizosphere and variants that stimulate plant growth became dominant over the neutral ancestor. These dominant variants upregulated a transcription factor in the plant roots that is involved in regulation of scopoletin production. At the same time, the dominant variants were less sensitive to the antimicrobial activity of this coumarin, suggesting that the plant provides the selective pressure (Li et al., 2020). Thus, plants do not only select for plant beneficial microbes, they also seem to be able to domesticate them for their own advantage. This opens new avenues for the design of strategies that are directed toward microbiome management of our future crops.

The Soil-Borne Supremacy

In recent years, the plant microbiome has been portrayed as an additional layer of the plant immune system (Hacquard et al., 2017; Teixeira et al., 2019). Indeed, disrupting the genetic network that regulates plant immunity leads to dysbiosis of endophytic microbiota and, consequently, to disease (Chen et al., 2020). The proposed role of the microbiome in plant immunity is in line with evidence that microorganisms in the rhizosphere provide the front-line defense for plant roots against attack by pathogens (Weller, 1988) and can stimulate an induced systemic resistance that is effective against a broad spectrum of plant pathogens, also in aboveground plant parts (Pieterse et al., 2014). Plant disease resistance against soil-borne pathogens appears to be often microbiome driven. In potato cultivars differing in their susceptibility to *Verticillium dahliae*, bacteria antagonistic to this fungal pathogen were more commonly associated with the roots of resistant cultivars (Azad et al., 1985, 1987). This suggests that the first line of defense of the resistant cultivar indeed relies on its associated root microbiome. These findings are supported by the observation that, in common bean cultivars differing in susceptibility to Fusarium, resistance to this pathogen is associated with higher abundance of plant beneficial bacterial families (Mendes et al., 2018b) and higher expression of microbial genes associated with the biosynthesis of antifungal compounds (Mendes et al., 2018a). When comparing root-associated microbiomes of wild crop relatives and domesticated accessions of bean, *Bacteroidetes* were relatively more abundant on roots of wild relatives, while in the rhizospheres of domesticated plants *Actinobacteria* and *Proteobacteria* were more abundant (Perez-Jaramillo et al., 2017). An exciting question is whether such shifts are also functionally important and if such information can be used to improve the performance of cultivated crops (Cordovez et al., 2019). Domestication of crop species led to a reduction in genetic diversity, which has been shown to affect root microbiome assembly (Bulgarelli et al., 2015; Perez-Jaramillo et al., 2017). Hence, plant genes associated with the selection of protective microbiome-encoded traits might be found by the comparative analysis of wild versus domesticated crop species (Perez-Jaramillo et al., 2018; Oyserman et al., 2019).

These observations support the notion that plant genotype can navigate the composition of the root microbiome toward fitness benefits for the host plant. Using a diversity panel of wild *A. thaliana* accessions, Haney et al. (2015) demonstrated that small plant genotype-mediated effects on microbiome composition can have significant effects on host health. Defense-related phytohormones, such as salicylic acid and jasmonic acid, which are produced upon pathogen or insect attack, have been shown to affect the composition of the root microbiome (Carvalhais et al., 2013; Lebeis et al., 2015). Integrating novel plant traits that promote rhizosphere microbiome-encoded functions with impact on plant immunity in future disease resistance breeding strategies, will open new avenues for the design of future crops that are less dependent on harmful agrochemicals (Pieterse et al., 2016).

The Soil-Borne Identity

Over the years, we have come a long way in analyzing the composition of plant-associated microbiomes and how different microbial- and plant-derived factors may affect this composition. The identity of the microbiome includes many activities and functions that benefit plant performance, which may be profitable for smart applications in future microbiome-optimized agriculture. An intriguing, long-standing question in the plant–microbe interactions research field is how plants can distinguish pathogenic from beneficial microbes. Both pathogenic and beneficial microbes have so-called microbe-associated molecular patterns (MAMPs) that are recognized by the plant through pattern-recognition receptors, resulting in energy costly MAMP-triggered immune responses that confer pathogen resistance at the expense of plant growth (Stringlis et al., 2018b; Yu et al., 2019b). Considering that the rhizosphere is a microbial hotspot with a large diversity of microbes that produce a myriad of MAMPs, one would expect that continuous activation of MAMP-triggered immune responses would seriously hamper plant growth. However, plants typically grow vigorously in microbially active soil. This could be explained by the recent finding that not only recognition of MAMPs suffices to induce immune responses in the roots but co-occurring damage to root cells is also required (Zhou et al., 2020). Moreover, microbes can evade immune recognition by degrading their MAMPs before they are recognized by the host immune system (Pel et al., 2014; Pel and Pieterse, 2013) (Figure 1). In addition, suppression of the MAMP-triggered root immune responses by rhizosphere microbes has been reported as a mechanism to avoid defensive host barriers (Millet et al., 2010; Stringlis et al., 2018b). Recent evidence suggests that active suppression of MAMP recognition is an important microbiome-encoded trait that can be induced by many members of the rhizosphere microbiome.

Using an *A*. *thaliana* root reporter system for the bacterial MAMP flagellin, it was shown that over 40% of the tested root microbiota were able to quench local root immune responses that were triggered by the flagellin epitope flg22 (Yu et al., 2019a). Mutant analysis of a plant growth-promoting *Pseudomonas* sp. uncovered that the observed root immune suppressive activity is based on the microbial production of gluconic acid, which locally lowers the environmental pH and desensitizes MAMP recognition (Yu et al., 2019a). Thus, suppression of MAMP-triggered root immune responses by beneficial members of the rhizosphere microbiome may be an important function of the root microbiome that not only allows plants to grow in a MAMP-dense environment, but also facilitates colonization by plant growth- and immunity-promoting microbiota (Figure 1). Dysbiosis of the rhizosphere microbiome might result in less-effective suppression of root immune responses leading to reduced plant growth. Yield loss in high-frequency monoculture cropping systems, where identical plant genotypes may not optimally match with the residing microbial community (Wallenstein, 2017), may be the result of such dysbiosis. Plant performance can be greatly hampered if crops are grown frequently in the same field. Growing crops in such so-called short rotations, is becoming more prevalent in agriculture and may help to intensify land-use to meet the growing demand for food and feed (Bennett et al., 2012). However, short rotations can seriously affect yield of key global crops due to accumulation of pathogens. Also, so-called deleterious microorganisms have been postulated to play an important role in such yield decline (Schippers et al., 1987; Bennett et al., 2012), but their identity has never been clearly established. The recently discovered function of the rhizosphere microbiome in the suppression of plant growth-inhibiting immune responses triggers intriguing new hypotheses to be investigated in relation to yield decline in high-frequency cropping.

Future Perspectives

Asking relevant questions is the main driver of science. This message should be kept very much alive in the era of fast technological developments, in which metagenomics, metatranscriptomics, microbial network analysis, synthetic communities, and keystone taxa can likely make everything possible. It is tempting to perform an analysis just because we can, but techniques alone should not be leading the direction of research questions. The necessity to increase crop production with less input in a sustainable way has been put forward by many researchers for decades, but the situation is getting more urgent every day taking climate change and world population growth into consideration. The notion that plants function in harmony with their associated microbiomes is now one of the leading themes in plant biology. Plants play a key role in shaping their microbiomes, and this can drive the selection of plant traits that sustain beneficial microbiomes. Because it takes two to tango, this may be an essential step needed to fully exploit the potential of plant-associated microbiomes. Lorentz Hiltner would probably be amazed by the progress we have made regarding the detailed information generated over the last century, but many of the questions that he and many scientists after him asked still remain unanswered fully. Hence, the current generation of young scientists is faced with a challenging but very exciting task. We have faith that when they look back to the future, microbiome-assisted agriculture will be flourishing.

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