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The Role of Soil Microorganisms in Plant Mineral Nutrition

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ABSTRACT

Plants, in their natural environment, are part of a diverse ecosystem that includes numerous and diverse microorganisms in the soil. Some of these microbes, such as mycorrhizal fungi and nitrogen-fixing symbiotic bacteria, have long been recognised for their importance in plant performance by improving mineral nutrition. However, the full range of microbes associated with plants, as well as their potential to replace synthetic agricultural inputs, has only recently been discovered. In recent years, significant progress has been made in understanding the composition and dynamics of rhizospheric micro biomes. Plants shape micro biome structures, most likely through root exudates, and bacteria have developed various adaptations to thrive in the rhizospheric niche. The mechanisms of these interactions, as well as the processes that drive the changes in micro biomes, are, however, largely unknown. This review focuses on the interaction of plants and root-associated bacteria that improves plant mineral nutrition, summarising current knowledge from several research fields that can converge to improve our understanding of the molecular mechanisms underlying this phenomenon

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1.1 INTRODUCTION

Although plant physiologists sometimes consider soil to be nothing more than a source of nutrients for plants, it is actually a complex ecosystem that is home to bacteria, fungi, protists, and animals (Bonkowski et al., 2009; Muller et al., 2016). Plants engage in a wide range of interactions with these soil-dwelling organisms, spanning the entire range of ecological possibilities (competitive, exploitative, neutral, commensal, and mutualistic). Most interaction studies in modern plant science have focused on mitigating pathogenic effects such as herbivory and infection (Strange and Scott, 2005; Zhang et al., 2013), or reducing the effects of abiotic stress (Yaish et al., 2016; Meena et al., 2017). However, there has long been a desire to understand the positive ecological interactions that promote plant growth. For example, mycorrhizal fungi and bacteria found in modulated legumes were both recognised as root symbionts as early as the second half of the nineteenth century (Morton, 1981). Crop seeds were coated with bacterial cultures (Azotobacter chroococcum or Bacillus megaterium) as early as the 1950s to improve growth and

yield (Brown, 1974). By the 1980s, numerous bacterial strains, primarily Pseudomonas but also Azospirillum, had been identified as having effects that promote plant growth (Burr et al., 1978; Teintze et al., 1981; Lin et al., 1983). Since the 2000s, the emphasis of research has shifted away from individual microbial strains and toward documenting the abundance and diversity of the root micro biome via met genomics. According to the findings of such sequencing studies, the rhizospheric niche is a hotspot of ecological richness, with plant roots hosting a diverse array of microbial taxa (Bulgarelli et al., 2013). In recent years, research has shifted toward the formation of rationally designed synthetic communities (SynComs) composed of strains representing the dominant rhizospheric taxa, with the goal of under controlled experimental conditions, re-capitulating favourable microbial functions (Busby et al., 2017). One major goal of this research field is to gain a mechanistic understanding of how soil microbes promote plant growth and defence, and then use this knowledge to inform the optimal design of microbial communities tailored to perform specific functions.

1.2 MICROBIAL TRAITS AND THE BIOAVAILABILITY OF NUTRIENTS FOR PLANTS

Three mechanisms are typically proposed to explain how microbial activity can boost plant growth: (1) manipulating plant hormonal signaling (Verbon and Liberman, 2016); (2) repelling or outcompeting pathogenic microbial strains (Mendes et al., 2013); and (3) increasing soil-borne nutrient bioavailability (van der Heijden et al., 2008). This review will concentrate on the third mechanism, in which soil microbes metabolise recalcitrant forms of soil-borne nutrients in order to liberate them for plant nutrition. Most nutrients, such as N, P, and S, are bound in organic molecules in natural ecosystems and thus have a low bioavailability to plants. Plants rely on the growth of soil microbes such as bacteria and fungi to access these nutrients Fungi are organisms that have the metabolic machinery to depolymerize and mineralize organic forms of N, P, and S. The contents of these microbial cells are then released, either through cell turnover and lysis or through protozoic predation (Bonkowski, 2004; Richardson et al., 2009). This releases inorganic N, P, and S forms into the soil, as well as ionic species like ammonium, nitrate, phosphate, and sulphate, which are the preferred nutrient forms for plants (van der Heijden et al., 2008). These microbial nutrient transformations are key drivers of plant growth in natural settings, and can sometimes be the rate-limiting step in ecosystem productivity (Schimel and Bennett, 2004).

1.3 FERTILIZATION PRACTICES AND ENVIRONMENTAL SUSTAINABILITY

Mineral fertilizers are used to provide macronutrients in the majority of modern agricultural systems. Unsustainable fertilisation practises, on the other hand, are contributing to large-scale changes in Earth's biogeochemical cycles via mechanisms such as soil degradation, waterway eutrophication, and greenhouse gas emissions (Amundson et al., 2015; Steffen et al., 2015). Furthermore, known phosphate rock reserves are rapidly depleting and are expected to be depleted within a few decades (Cordell and White, 2014), while N-fertilizer production via the energy-intensive Haber–Bosch process is dependent on fossil fuels, exacerbating global warming and natural resource depletion (Erisman et al., 2013). Because of the magnitude and severity of these fertilizer-related issues, agricultural science is

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currently focusing on developing alternative methods of sustaining agriculture Plant nutrition with significantly lower mineral fertiliser inputs (Foley et al., 2011). One such possibility is to supplement plants with specific root-associated microbes that depolymerize and mineralize organic-bound nutrients, in place of mineral fertilisers. The logic behind this idea is that organic inputs can be obtained more sustainably than mineral fertilisers because a variety of agricultural, industrial, and municipal processes generate massive amounts of nutrient-rich "waste" that is currently disposed of but could potentially be composted and applied as fertilisers (Paungfoo-Lonhienne et al., 2012). Another consideration is that organically bound nutrients are more stable in soil than mineral fertilisers, making them less susceptible to leaching and volatilization (Reganold and Wachter, 2016). Organic farming systems already use bio-fertilizers However; there is currently little mechanistic understanding behind the selection of plant cultivars and microbial inoculants (Bender et al., 2016; Reganold and Wachter, 2016). This lack of precision is caused by two major knowledge gaps: (1) it is unknown what strategies plants use to recruit beneficial microbes and how much genetic variation exists for this trait; and (2) it is unknown which specific microbes are best partners for boosting plant nutrition from organic sources of N, P, and S.

We want to know how microbes contribute to plant nutrition and how plants shape their micro biome to get the most out of this interaction. In this review, we summarise current progress in approaches to dissecting the interconnection of plants and bacteria in mineral nutrition, with an emphasis on plant and microbe metabolic capacities. When reviewing this field, it is important to note that there is a substantial body of literature examining how certain plants can receive nutritional benefits through symbiotic relationships with mycorrhizal and modulating bacteria. To avoid duplicating some excellent recent reviews (Smith and Smith, 2011; Udvardi and Poole, 2013; Garcia et al., 2016; Kamel et al., 2017), we do not concentrate on these well-studied symbiotic interactions Instead; we concentrate on how plant nutrition can be linked to the entire rhizospheric micro biome, an emerging field that is rapidly expanding. The review focuses on bacteria, but most of the concepts apply to other soil organisms, particularly fungi. We argue for a multidisciplinary approach that integrates plant and microbial genetics with biochemistry and metabolic modelling. Together, these tools can improve our mechanistic understanding of plant-microbe interactions and how these processes can be optimized to drive plant nutrition with lower mineral fertiliser applications.

1.4 EFFECTS OF PLANT NATURAL VARIATION ON THE RHIZOSPHERIC MICRO BIOME

The genetic components of this trait must first be discovered in order to selectively breed plants for optimized nutritional interactions with soil microbes. Sequence analyses revealed differences in the composition of bacterial taxa in soil, plant rhizospheric, and entophytic fractions, indicating that plants select for specific bacterial taxa and thus have some control over their micro biomes (Bulgarelli et al., 2012; Turner et al., 2013; Zgadzaj et al., 2016). The next step is to identify the key genetic determinants that govern how various plant genotypes interact with rhizospheric bacteria. Decades of research have revealed that plant susceptibility to pathogenic microorganisms is highly dependent on the plant genome, both between and within species additions to the same one (Zhang et al., 2013). Similarly, Arabidopsis accessions differed greatly in their ability to support the growth of the rhizospheric

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bacterium Pseudomonas fluorescens in a hydroponic system (Haney et al., 2015). Sequence analyses have confirmed different micro biome structures across plant taxa, with greater differences in more distant species and a greater contribution of environment and soil to variation (Turner et al., 2013; Schlaeppi et al., 2014; Zgadzaj et al., 2016). Genotypic effects on micro biome structure have been observed when comparing accessions or varieties of the same species in Arabidopsis, maize, and barley (Bulgarelli et al., 2012, 2015; Peiffer et al., 2013). In terms of leaf micro biota, Leaf micro biomes differed significantly across 196 Arabidopsis accessions (Horton et al., 2014). Plant-genome variation was especially high for the most abundant operational taxonomic units (OTU). The variation was investigated further using a genome-wide association study (GWAS), which used the number of reads for individual OTUs as quantitative phenotypes (Horton et al., 2014). GWAS revealed that many of the significant SNPs associated with bacterial OTU structure were classified as defence response, which was the most overrepresented gene ontology term among the candidate genes. Furthermore, genes involved in cell wall synthesis and kinase activity were found to be overrepresented (Horton et al., 2014). Despite the fact that there are several candidate genes that affect the although the leaf micro biome was identified, no further confirmatory tests of mutants of these genes were reported, so the functionality of the genes in shaping the micro biome remains to be demonstrated. Because the leaf and root micro biomes overlap (Bai et al., 2015) and may be shaped by similar processes, the leaf micro biome GWAS could be very useful for understanding rhizospheric processes. Bodenhausen et al. (2014) used an alternative approach to GWAS by monitoring changes to SynComs inoculated onto the leaves of Arabidopsis accessions and mutants of a priori selected genes (Bodenhausen et al., 2014). In the 10 accessions and several mutants, a clear genotype effect on microbial taxonomic composition was observed. The effects were consistent and reproducible in three mutants, two of which Mutants were found to be involved in cuticle synthesis and ethylene signalling (ein2) (Bodenhausen et al., 2014). Given that only 40 mutants and highly simplified SynComs were tested, the approach appears promising for root micro biome analysis as well, especially if mutants in nutrient uptake and assimilation are investigated.

1.6 GWAS OF BACTERIA-MEDIATED PLANT TRAITS

The sequence analyses, on the other hand, focus solely on the taxonomical composition of the plant micro biome, without taking into account the entire bacterial genome or addressing the functions that these microbes perform. The analysis of variation in susceptibility of Arabidopsis accessions to the plant growth-promoting rhizobacterium Pseudomonas simiae WCS417r is the best attempt so far to assess how plant genotype affects functional interaction with rhizobacterium (Wintermans et al., 2016). The researchers grew 302 accessions with and without the bacterium, which promotes changes in root architecture and growth via volatile emission. The accessions differed significantly in all three phenotypes measured: fresh weight gain, lateral root proliferation, and primary root elongation (Wintermans et al., 2016). Statistical GWAS analysis revealed several highly significant associations despite some good correlation between fresh weight and root architecture data, none of the positive SNPs were found to be associated with multiple phenotypes. The analysis resulted in the identification of several candidate

genes, but no further verification or confirmatory experiments were conducted (Wintermans et al., 2016). The results show that Arabidopsis GWAS is a viable approach for identifying genetic loci that control phenotypic variation in plant–microbe interactions. The challenge is to go beyond the relatively simple traits that have been studied thus far and design screens that will allow us to dissect the genetic architecture of the complex signalling and metabolic networks that lead to variation in the composition of root associated micro biota in different plant genotypes.

1.7 PLANT ROOT EXUDATES—A SOURCE OF MOLECULAR SIGNALS

Metabolic Signals to Recruit Favorable Microbes

Because the growth of soil microbes is typically carbon-limited, the large amounts of sugars, amino acids, and organic acids that plants deposit into the rhizospheric represent an important source of nutrition (Bais et al., 2006). However, the deposition of this labile carbon does not always promote the recruitment of beneficial microbes because pathogenic strains can use these molecules as growth substrates as well. As a result, it is possible that plants have evolved recognition mechanisms to distinguish beneficial microorganisms from those that must be repelled. In this case, the specific molecules present in root exudates that contribute to the structure of the microbial community are potential targets for plant breeding strategies that seek to engineer the structure of the microbial community micro biome of the rhizospheric Plant root exudates have been shown to contain components used in belowground chemical communication strategies, such as flavonoids, strigolactones, or terpenoids (Bais et al., 2006; Venturi and Fuqua, 2013; Massalha et al., 2017). Studies on the micro biomes of various plant species and accessions revealed significant differences, leading to the hypothesis that exudates play an important role in shaping plant–microbe interactions (Hartmann et al., 2009). Furthermore, it has been demonstrated that plants use root-derived signals to attract beneficial interaction partners (Neal et al., 2012; Lareen et al., 2016).

Until now, the majority of knowledge about signal perception and transduction in plant–microbe interactions has come from the field of plant pathology Plant receptor-like kinases (RLKs) are important (Antoln-Llovera et al., 2012). Nodulation and mycorrhizal interactions serve as model systems for identifying recognition mechanisms between plants and microbes in mutualistic interactions (Delaux et al., 2015; Lagunas et al., 2015). In addition to the plant recognising the microbial interaction partner, microbes must recognise their mutual interaction partner (the plant root). It is widely accepted that root exudates help to establish the root micro biome (Massalha et al., 2017). The term "root exudates" refers to molecules secreted selectively by roots, as opposed to the sloughing-off of root border cells (Walker et al., 2003). Overall, the release Rhizodeposition refers to the incorporation of fixed carbon compounds (border cells and exudates) into the surrounding soil (Jones et al., 2004; Dennis et al., 2010). Data on Rhizodeposition range between 5 and 30% of total fixed carbon (Bekku et al., 1997; Hütsch et al., 2002; Dennis et al., 2010), implying a significant loss of reduced-C for biomass and having a significant impact on the carbon budget of individual plants as well as entire ecosystems (Badri and Vivanco, 2009; Bardgett et al., 2014). Hütsch et al. (2002) discovered remarkable differences in the amount of C-release among six different plant species using a 14C approach, ranging from 11.6 (wheat) to 27.7 mg C/g root dry matter (oil radish). The composition of these exudates

also differed between species, with oil radish exudates being high in organic acids and pea exudates being high in sugars. These findings suggest that different plant species modulate the chemical composition of their rhizospheric in different ways, which may have an impact on the associated microbial community. Beneficial microbe recruitment may be critical in environmental stress conditions such as nutrient limitation, pathogen attack, pests, high salt, or heavy metal stress.

1.8 ISSUES TO CONSIDER WHEN ANALYZING ROOT EXUDATES

To fully comprehend the dynamic interactions between soil microbes and plant roots, it is necessary to identify the specific molecules within root exudates that can attract beneficial microbial strains. This is a difficult problem in analytical biochemistry because a variety of biological and methodological issues must be addressed in order to conduct biologically insightful analyses of plant root exudates (Rovira, 1969). In terms of cultivation, artificial plant growth systems cannot replicate natural soil conditions, but it is difficult to decipher the relevant communication signals that occur in soil due to chemical interactions of metabolites with the soil matrix and background noise metabolites produced by organic matter decomposition or microbial exudation As a result, most studies recommend hydroponic cultivation, sometimes with an inert material to scaffold the roots. When collecting exudates, the experimenter must decide whether to collect them in deionized water or a more realistic medium containing mineral salts. Furthermore, it is practically impossible to devise an experimental approach capable of distinguishing exudates from sloughed-off border cells. Vranova et al. provide a comprehensive summary of exudate collection and influences (e.g., pH, re-uptake by roots, incubation period) (2013). Researchers are increasingly using unbiased mass spectrometry (MS) approaches for data acquisition, such as gas chromatography (GC)-MS and liquid chromatography (LC)-MS. However, due to physiochemical biases imposed by the chosen extraction method, sample clean-up procedure, matrix effects, and analytical technique, detection of all metabolites in a sample is impossible (Weston et al., 2015). As a result, different methods must be combined to provide a comprehensive view of the metabolite profile. The subsequent analysis of the derived MS data is a massive undertaking, beginning with data processing algorithms that enable feature detection, peak alignment, and various normalisation methods. These normalisation and scaling algorithms have a significant impact on the analysis's outcome (Worley and Powers, 2013). To confirm the identity of specific mass spectral features, fragmentation data (MS2 or MSn) are collected and analysed when compared to publicly available databases (Afendi et al., 2013; Misra and van der Hooft, 2016), or when compared to authentic standards (if available). Taken together, these difficulties indicate that a thorough examination of root exudates is not a simple task.

1.9 RECENT APPROACHES TO ANALYZE ROOT EXUDATE COMPOSITION

Several studies have described analyses of plant root exudates, with Phillips et al. (2008) developing a method to collect exudates from mature trees in the field, though microbial metabolism is likely to play a role in this non-sterile system. However, microbial nutrient uptake is an intriguing aspect of plant–microbe nutritional interactions,

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with Carlsen et al. (2012) observing a fast degradation of flavonoid glucosides when comparing the flavonoid content in two soils and after different legume cultivations. To avoid microbial impact on root exudate profiles, researchers have developed a variety of axenic hydroponic approaches cultivation systems (Badri et al., 2008; Oburger et al., 2013; Strehmel et al., 2014), which are easier to control, and plant responses may include stress reactions due to oxygen limitation and insufficient root support. Furthermore, hydroponics is well suited for exudate sampling because the total liquid can be taken directly for further sample preparation procedures while root damage is minimized. However, the timescale for collecting exudates and the medium used for collection vary greatly (nutrient solution or water). Badri et al. (2008) collected Arabidopsis thaliana root exudates in nutrient solution for 3 and 7 days for LC-MS analysis and discovered that most compounds are present only after the longer incubation period. It is possible this observation is thought to be the result of sloughed-off border cells. Nonetheless, they compared exudate composition to root composition and found an 80% difference based on detected molecular masses (Badri et al., 2008). Strehmel et al. (2014) also used a 7-day collection period in nutrient solution to obtain sufficient amounts of A. thaliana exudates. Carvalhais et al. (2010), on the other hand, used deionized water as the collection medium and only used a 6-hour exudate collection period on Zea mays plants to minimise the effect of sloughed-off border cells. A similar method was used to collect barley root exudates in deionized water for 4 hours (Tsednee et al., 2012). A large number of plants have been collected for a short-term exudate collection period from Arabidopsis It has been necessary to obtain sufficient quantities of exudates for LC-MS analysis (Schmid et al., 2014). A direct comparison of various plant cultivation and exudate collection techniques revealed that they had a significant impact on metabolite patterns (Oburger et al., 2013). Because of the high Trans membrane gradient of solutes in low ionic strength medium, long incubations in deionized water may result in overestimated exudation rates (Neumann and Römheld, 1999; Oburger et al., 2013). Most published data on exudates to date have focused on specific metabolite classes such as primary metabolites (Neumann and Römheld, 1999; Dakora and Phillips, 2002; Rudrappa et al., 2008; Carvalhais et al., 2010; Tan et al., 2013; Warren, 2015; Kawasaki et al., 2016), hormones (Foo et al., 2013), flavonoids (Graham, et al., 2006; Cesco et al., 2010), or phytosiderophores (et al., 2006) (Oburger et al., 2014) Although Strehmel et al. (2014) provided a comprehensive overview on secondary metabolites in Arabidopsis root exudates using LC-MS, non-targeted metabolite profiling approaches of root exudates have been used less frequently. In subsequent experiments, the data was supplemented with GC-MS data and expanded by a comparison of 19 Arabidopsis accessions (Monchgesang et al., 2016), co-cultivation with Piriformospora indica (Strehmel et al., 2016), and phosphate limitation data (Strehmel et al., 2016) (Ziegler et al., 2016) As MS technology advances, it is reasonable to expect that more studies will conduct untargeted analyses of root exudate profiles.

CONCLUSION

Plants rely on the metabolic activities of soil micro biota to access recalcitrant soil-borne nutrients. Given the environmental damage caused by current fertilisation practises, optimizing plant–microbe nutritional interactions for more sustainable agricultural systems is a current research priority. The specific mechanisms governing the

assembly of the plant micro biome and its modulation based on plant nutritional status, on the other hand, are extremely complex and difficult to predict. Despite the experimental challenges described here, we contend that many critical jigsaw puzzle pieces have been identified that will allow us to understand the mechanisms Dynamic plant–microbe interactions must be governed (Figure 5). Although soil is the most important determinant of the microbial community associated with plant roots, plants also have a significant impact on taxonomic assembly. As a result, comparative genetic approaches like GWAS hold the promise of identifying plant genes and processes that are important in controlling how plants shape the rhizospheric micro biome Genes in plant metabolic pathways that affect the composition of root exudates and thus the actual signals in the rhizospheric are particularly intriguing. As a result, continued advancements in our ability to collect and analyse exudates will be critical for determining the molecules plants use to communicate with soil microbes, as well as the pathways the microbes use to decrypt these signals.

Recent genomic studies are revealing the specific microbial strains that contain metabolic pathways beneficial to plant nutrition (Muller et al., 2016). The big question, however, is how much plants can attract specific microbes for specific environmental/nutritional conditions. The mechanisms of a number of microbes' plant growth promoting effects have been deciphered; however, it appears that almost every individual organism uses a different process. How do these various mechanisms interact with a diverse range of taxa in real soil? Rhizospheric micro biome research has already progressed from community description to community identification evaluating their dynamics as a result of changes in environmental conditions (Busby et al., 2017). However, little is known about which specific microbial strains contribute most to plant nutrition, or how nutrient availability affects the composition of the rhizospheric micro biome. How can we combine progress in individual areas of research to obtain a unified picture? Using different plant genotypes, we can already design experiments with synthetic microbial communities to identify processes important for the establishment of effective communities (Castillo et al., 2017). However, there is still a huge knowledge gap when it comes to developing a solid theory of plant–microbe interactions. The massive amount of data obtained from micro biome characterization clearly necessitates a modelling approach, for example, to construct nutritional models Plant and micro biota metabolic pathways are linked in networks. Such models would enable researchers to assemble various SynComs with defined metabolic capacities, facilitating dissection of the mechanisms that shape the composition and function of microbial communities. This understanding could help to guide the highly promising approaches to using microbes for more sustainable plant nutrition.

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