

Manipulating the soil microbiome to increase soil health and plant fertility

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Abstract A variety of soil factors are known to increase nutrient availability and plant productivity. The most influential might be the organisms comprising the soil microbial community of the rhizosphere, which is the soil surrounding the roots of plants where complex interactions occur between the roots, soil, and microorganisms. Root exudates act as substrates and signaling molecules for microbes creating a complex and interwoven relationship between plants and the microbiome. While individual microorganisms such as endophytes, symbionts, pathogens, and plant growth promoting rhizobacteria are increasingly featured in the literature, the larger community of soil microorganisms, or soil microbiome, may have more far-reaching effects. Each microorganism functions in coordination with the overall soil microbiome to influence plant health and crop productivity. Increasing evidence indicates that plants can shape the soil microbiome through the secretion of root exudates. The molecular communication fluctuates according to the plant development stage, proximity to neighboring species, management techniques, and many other factors. This review seeks to summarize the current knowledge on this topic.

Keywords Microbiome · Root exudates · Plant growth promoting rhizobacteria (PGPRs)

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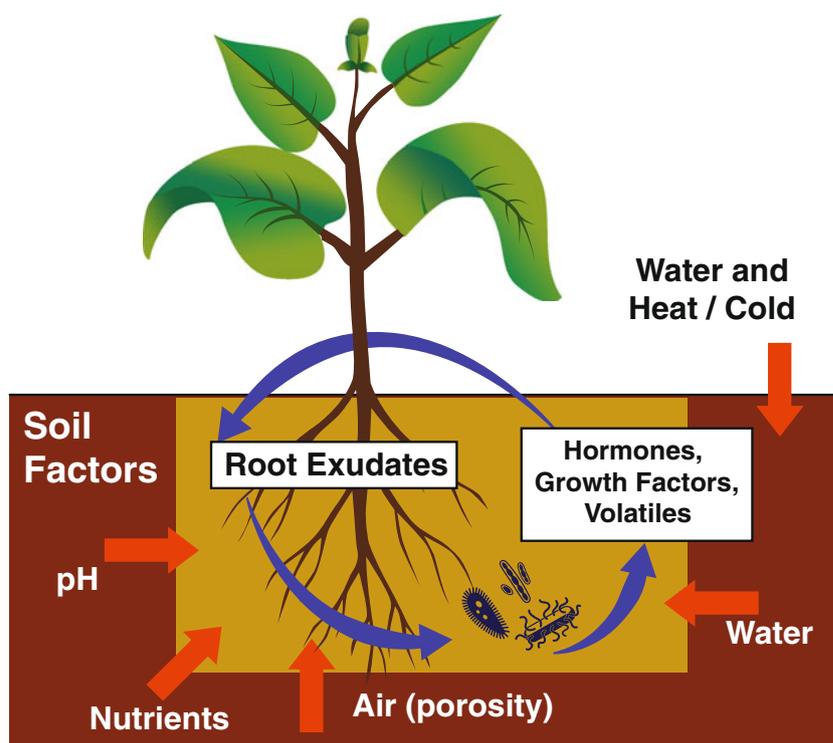
Introduction

The relationship between plants and their surroundings is a complex one that, for centuries, has been the focus of much research. For much of this time, the focus was on the plants with little focus on the beneficial plant–microbe interactions (Berg 2009). Plants and microbes have evolved intimate relationships that enable them to coexist (Nihorimbere et al. 2011). Many experiments have tried to answer these questions by simplifying the interactions that occur to an individual plant–microbe relationship, but in reality, these interactions are much more complex, involve a vast array of microbes, and often produce synergistic effects (Mendes et al. 2011). It is necessary to move away from the potentially simplistic view of individual plant–microbe interactions and take into account all the factors that influence this complex ecosystem. The plant, the soil, and the soil microbes all work together to mediate and influence the various exchanges (see Fig. 1) that contribute to plant health and productivity. An understanding of how each component manipulates and influences each other is needed. Recent advances in “-omics” research can help us answer these questions and allow us to see how all these interactions relate and influence one another (Morales and Holben 2011). Here, we focus on the soil microbiome and its impact on plant health and productivity.

The effect of plants on the soil microbiome

The interaction between plants and their surroundings is a dynamic process in which plants monitor their environment and react to changes. The root system, which was traditionally thought to only provide anchorage and uptake of nutrients and water, is a key element to a plant interacting with its

Fig. 1 Schematic illustration of how soil factors influence both plant roots and soil microbes which in turn reshape the soil environment through a dynamic exchange of chemical responses to living and non-living stimuli



surroundings (Bais et al. 2006). Chemical signals emitted by soil microorganisms are received and recognized by plants and then addressed through the release of chemical compounds in the form of root exudates. Secretion of these compounds varies between different plant species (Rovira 1969), ecotypes (Micallef et al. 2009), and even distinct roots within a plant (Uren 2007). The diverse compounds released by plants as root exudates create a unique environment in the rhizosphere and include sugars, amino acids, flavonoids, aliphatic acids, proteins, and fatty acids (Badri et al. 2009b). All these different compounds are able to attract and initiate both symbiotic and pathogenic interactions within the rhizosphere (Bais et al. 2006). Root exudate composition and concentration change according to the signals received from the environment and the rhizosphere, age of the plant (De-la-Pena et al. 2010), soil type (Rovira 1969), and biotic and abiotic factors (Flores et al. 1999; Tang et al. 1995). For example, De-la-Pena et al. (2010) observed that the protein composition of the root exudates changed when the plant grew alone as compared to when the plant interacted with pathogens or with symbiotic microbes. Root exudates are used as growth substrates (Vandenkoornhuysen et al. 2007) by soil microbes and can act as antimicrobials (Bais et al. 2006; Perry et al. 2007); therefore, as the composition and concentration of the exudates change, so do the microbes that inhabit the rhizosphere (Badri et al. 2009a; Micallef et al. 2009).

Root exudates are released by a variety of mechanisms. Diffusion, ion channels, and vesicle transport are the primary mechanisms of root exudation and require little to no energy input (Bertin et al. 2003; Neuman and Romheld 2007).

Recently, it has been demonstrated that ATP-binding cassette (ABC) transporters are also involved in root exudation (Badri et al. 2008). Micallef et al. (2009) demonstrated that naturally occurring ecotype accessions of *Arabidopsis* exuded a unique suite of compounds into the rhizosphere, with each genotype supporting a different soil bacterial community. This is a clear example of how root exudates can have a significant effect on the soil microbiome. Rhizodeposition, which encompasses border cells, root debris, and root exudates is the major source of organic C to enter the soil (Uren 2007). It comes at a high C cost to the plant, with young seedlings typically releasing about 30–40 % of their fixed C (Whipps 1990). Why would the plant use such a large percentage of its energy to produce and release these rhizodeposits? Perhaps it is to attract microorganisms that service the plant through secreting growth promoting hormones, preventing disease, or acquiring nutrients via the excretions of a biochemically active root system. For example, Hamilton and Frank (2001) demonstrated that a grazing tolerant grass, *Poa pratensis*, is capable of concentrating microbes that facilitate the uptake of a limiting soil resource needed for growth, in this case N, in its rhizosphere when under herbivore attack. White lupin, on the other hand, is able to discourage microbial growth by drastically decreasing the soil pH in the rhizosphere via the release of organic acids, lowering the competition for P acquisition (Weisskopf et al. 2006). At the same time, white lupin prevents microbial degradation of root exudates important for P acquisition (Weisskopf et al. 2006). The diversity and relative number of soil microbes was found to decrease with closer proximity to the rhizosphere of the invasive weed *Centaurea*

maculosa and changes in the soil microbial community extended to neighboring native grass species (Broz et al. 2007). The invasive weed *Chromolaena odorata* has been shown to accumulate high concentrations of native soil pathogenic fungi inhibiting the growth of the native plant species (Mangla and Callaway 2008). Other studies have demonstrated that similar disruptions in the microbial communities of native plants benefits the invasive species while diminishing the success of native plants (Klironomos 2002; Stinson et al. 2006). The altered soil microbiome appears to be a significant part of the strategy for invasive weeds to increase its own resources and exploit weaknesses in the native plant.

Soil properties influence microbial diversity

The forces that shape the rhizosphere microbial community cannot be completely understood without a discussion of the influences of the soil environment. Soils are highly diverse allowing for habitation by equally diverse communities of microorganisms with as many as 10,000–50,000 species of microbes existing in 1 g of soil (Schloss and Handelsman 2006). Unique bacterial and fungal communities have been associated with soils of varying texture (Girvan et al. 2003), N content (Frey et al. 2004), P content (Faoro et al. 2010), and soil pH (Fierer and Jackson 2006; Lauber et al. 2008; Rousk et al. 2010). Recent evidence suggests that out of all these factors, soil pH may have the most influence on the bacterial community in the soil (Fierer and Jackson 2006). Rousk et al. (2010) collected soil samples across a long-term liming experiment where the pH varied from 4.0–8.3 while all other factors and variables that compose soil variability were controlled. A strong correlation between soil pH and the diversity and composition of bacterial communities was seen across biomes and was a greater driver of bacterial community composition than dispersal limitations (Rousk et al. 2010). It is hypothesized that the reason for this connection between pH and soil bacterial community structure has to do with the sensitivity of bacterial cells to pH, as bacterial taxa exhibit a relatively narrow pH growth tolerance (Rousk et al. 2010). Other evidence refutes pH as a driver for soil microbial diversity, indicating that P content, altitude, and the ratio of cations in the soil (Ca^{2+} , Mg^{2+} , and Al^{3+}) are more influential (Faoro et al. 2010). Clearly, many influences converge to create the ultimate effect on the soil microbial community and multiple soil factors potentially exhibit synergistic effects.

Although soil factors provide a strong influence on microbial communities, root exudates have been shown to also strongly influence the soil microbial community. Close ties between the composition of soil microbial communities and host plants were found (Broeckling et al. 2008). Soil fungal communities changed composition and decreased in total

biomass after planting with a non-native model plant or applying the non-native plant's exudates (Broeckling et al. 2008). Two model plant species, *Arabidopsis thaliana* and *Medicago truncatula*, were grown in their native soil and in the other plant's soil, non-native. *Arabidopsis* plants or root exudates added alone maintained the native fungal community in its native soil but not in non-native soil. In non-native soil, some microbial species increased while others diminished. Total fungal biomass was also affected when treated with root exudates alone or grown with *Arabidopsis* plants. The same was observed with *Medicago*. These results strongly suggest that plant root exudates and, therefore, plants themselves are able to affect the composition and total population of soil microflora.

Role of soil microbes in soil health and plant productivity

The purpose of this review is not to cover all of the beneficial effects of soil microbes on plant health and the associated mechanisms of action; these have been covered adequately in other reviews (Babalola 2010; Cummings 2009; Esitken 2011; Lugtenberg and Kamilova 2009; Maheshwari 2011). Instead, the aim is to highlight some of the more recent advances made in this rapidly developing field and emphasize potential practical applications for sustainable and integrated approaches to agriculture. For example, adding beneficial microorganisms to those already present in the soil can maximize plant nutrient uptake (Kirankumar et al. 2008), increase plant growth (Cummings 2009; Guiñazú et al. 2009), confer resistance to abiotic stress (Selvakumar et al. 2012), and suppress disease (De Vleeschauwer and Höfte 2009). These living microorganisms are dynamic and potentially self-sustaining, reducing the need for repeated applications, and can avoid the problem of pests and pathogens evolving resistance to the treatments (Lucas 2011). A possible management technique is to apply plant growth promoting rhizobacteria (PGPRs) as an agricultural treatment to minimize niche vacancy and effectively fill vacant niches. It has been shown that PGPRs colonize particularly and effectively in soils with low microbial biomass (Fliessbach et al. 2009) so inoculations are more likely to be successful. Beneficial microorganisms that thrive in this environment can more quickly take up space and nutrients made available for potential pathogen invaders and assist with achieving sustained niche occupancy (Kaymak 2011). In addition to “sealing off” open ecological niches and increasing the soil's resistance to pathogen invasion, PGPRs offer benefits of increased yields, nutrient acquisition, stress tolerance, and disease resistance to the plant host (Lugtenberg and Kamilova 2009). As an example of the potential of microbial inoculation, consider the outcome of a greenhouse study using tomato plants inoculated with PGPR

and mycorrhizal fungi. It showed that inoculated plants that received less than 75 % the full rate of fertilizer had yields identical to uninoculated plants that received full fertilizer treatments (Adesemoye et al. 2009). Furthermore, an awareness of the existing soil fertility level is critical to realizing PGPR benefits, as a diminishing effect is seen when starting N, P, and K levels are high (Shaharoon et al. 2008).

Recent discoveries have shown that plants also interact with a variety of PGPRs that are capable of increasing photosynthetic capacity (Xie et al. 2009; Zhang et al. 2008b), conferring drought and salt tolerance (Dimkpa et al. 2009; Xie et al. 2009; Zhang et al. 2008a, 2009a, 2010), increase disease suppression (Chithrashree et al. 2011; Jetiyanon and Kloepper 2002; Okubara and Bonsall 2008), plant growth (Hayat et al. 2010; Lim and Kim 2009), and improving the effectiveness of the plant's own iron acquisition mechanisms (Zhang et al. 2009a). These discoveries may offer potential for PGPR applications to improve agricultural production and sustainability. Currently, producers are faced with a need to reduce inputs like water and fertilizer applications while simultaneously increasing production. In addition, these PGPR traits promise considerable value in biofuel cropping considering the need to produce biofuel crops in areas unsuitable for agricultural production (Tilman et al. 2009) where drought and salt tolerance may become especially important. Given the wide variety of effects and mechanisms of action, it's not surprising that a combination of PGPR treatments has been shown to be even more effective than one treatment alone in suppressing disease (Ahemad and Khan 2011; Berg 2009; Pérez-Piqueres et al. 2006; Yang et al. 2011). One example of combined inoculations includes the PGPR *Pseudomonas putida* added in combination with nodule-inducing *Sinorhizobium meliloti* in the legume *Medicago sativa*, which resulted in increased nodulation and significantly increased plant biomass (Guiñazú et al. 2009). Another study analyzed the benefits of combining PGPR strains. Greenhouse studies showed that the dry weight of tomato transplants were higher when a combination of two PGPR strains, and 75 % fertilizer was used when compared to the control (100 % fertilizer with no PGPR inoculants) (Hernandez and Chailloux 2004). When these experiments were performed in the field, the treatments with PGPR, mycorrhizal fungi, and 50 % fertilizer exhibited a greater yield than the control (100 % fertilizer) (Hernandez and Chailloux 2004). This combination of beneficial microbes also had the added effect of stimulating plant N and P absorption (Hernandez and Chailloux 2004). Formulations of compost with beneficial bacteria have also shown the ability to suppress plant pathogens (Pugliese et al. 2011; Yang et al. 2011). The ability of formulations of multiple beneficial microbes to increase plant productivity and health hint at the potential of the entire microbiome and plants working together with mutually beneficial outcomes.

In some cases, application of a microbial organism that confers benefit may not even be necessary. Sometimes, the

same effect can be achieved by applying a microbial elicitor, which is a compound produced by the microorganism that causes the desired effect. For example, exogenous application of the *Bacillus subtilis*-derived elicitor, acetoin (3-hydroxy-2-butanone), was found to trigger induced systemic resistance (ISR) and protect plants against *Pseudomonas syringae* pv tomato pathogenesis (Rudrappa et al. 2008). Similarly, adding low doses of *Chryseobacterium balustinum* AUR9 cell wall lipopolysaccharides, another bacterial elicitor, to *A. thaliana* reproduced systemic induction (Ramos Solano et al. 2008). Determining the precise compounds and dosages necessary for application would allow for commercial development of a non-living application providing the same benefits as the PGPRs themselves. Such treatments could avoid some of the potential complications associated with developing commercial PGPR applications such as low survivability due to competition and adverse environmental conditions (Cummings 2009). While it might be easier to come to market sooner with more consistent results, the potential advantages of being self-sustaining and avoiding evolution of resistant super-organisms would probably be lost with such products. Applications of living microbes or their elicitors has potential use for agricultural priming, the induction of ISR (Conrath and Loon 2009), which has been shown as an efficient way to increase pathogen resistance with little cost to the plant (De Vleeschauwer and Höfte 2009). An important addition to strategic management practices will be the development of crop species that are able to accomplish their own priming and ISR induction, which will reduce the use of microbial applications. Although, ideally, adding PGPRs as inoculants into the rhizosphere to exploit the immense benefits they provide is, potentially, an easy fix, there is still much inconsistency in their performance at the field scale (Mark et al. 2006; Morrissey et al. 2004). Research has begun to focus on how to cater the rhizosphere environment for PGPR rhizosphere colonization by means of rhizosphere engineering (Ryan et al. 2009). By understanding which PGPR traits are essential for rhizosphere competence (Barret et al. 2011), or by considering which indigenous soil microbial communities respond most favorably to inoculation (Bernard et al. 2012).

Role of the microbiome in plant health and productivity

While it's tempting to focus on characterizing microorganisms and their associated functions on the species level, logistically, this proves difficult (Nee 2004). Soil microbes are capable of both directly and indirectly influencing the productivity, diversity, and composition of plant communities (Barea et al. 2002; Fitzsimons and Miller 2010; Lau and Lennon 2011; van der Heijden et al. 2006, 2008). As a result, some characterizations now focus on aspects of

community structure that influence plant function. Recently, increasing soil microbial species richness was shown to be a predictor of plant health and productivity (Lau and Lennon 2011; Schnitzer et al. 2011; van der Heijden et al. 2008; Wagg et al. 2011). Plant productivity, diversity and nutrient acquisition have all been shown to increase with soil fungal diversity (Jonsson et al. 2001; Maherali and Klironomos 2007; van der Heijden et al. 1998; Wagg et al. 2011); however, we are unaware of similar research using soil bacteria alone or in combination with soil fungi. Other studies have indicated that the reduction of microbial diversity (as measured by species richness) does not result in decreased soil ecosystem functions and that other microorganisms can carry out the same function without affecting plant productivity (Nannipieri et al. 2003). Perhaps the key aspect determining this relationship is not taxonomic diversity, but rather functional diversity. In other words, it is not who is present but what they are doing that is more informative and revealing (Andren and Balandreau 1999; Bardgett and Shine 1999; Nannipieri et al. 2003). Advances in technology have shed light on the importance and need in determining microbial functional diversity along with microbial species diversity in the rhizosphere (Nannipieri et al. 2003, 2008). For example, one study found that plant productivity increased only when increased fungal diversity spanned a range of functional groups, not taxonomic groups (Maherali and Klironomos 2007). In support of this possibility, decomposition rates have been shown to be promoted through increased microbial functional diversity (Balser et al. 2002; Bonkowski and Roy 2005). While the soil microbial community exerts changing effects on the plant community, it also changes in response to host plant productivity and community characteristics resulting in a feedback response. For instance, Zak et al. (2003) demonstrated that changes in microbial community biomass, activity, and composition were a direct result of increased plant production. Another study linked plant community evenness with increased microbial biomass which in turn increased microbial functions (Lamb et al. 2011). Therefore, it is important to determine microbial functional activity in the rhizosphere. Functional activity has been closely linked to organic C mineralization (Nannipieri et al. 2008). Rhizodeposition is the major source of organic C to enter the soil (Uren 2007). This results in higher enzymatic activity in the rhizosphere soil than the bulk soil, but this increase in enzymatic activity does not always correlate with higher microbial diversity (Nannipieri et al. 2008). There is much debate on the actual influence of plant species on microbial diversity (de Ridder-Duine et al. 2005; Dennis et al. 2010; Garbeva et al. 2004). Yet, recent studies using six publicly available rhizosphere microbiomes (Markowitz et al. 2008) were used to analyze the functional content of the assembled and unassembled reads from rhizosphere and bulk soil (Barret et al. 2011). Comparing these six microbiomes demonstrated that a small

percentage of the functions overlapped between the different rhizosphere microbial communities. This suggests that plant species identity is the dominant factor influencing the composition of the rhizosphere microbial communities, as has been previously determined (Berg and Smalla 2009; van Overbeek and van Elsas 2008). Although there was a common core of shared broad functions between the rhizosphere and bulk soil microbiomes, further analysis of the functional traits to the pathway level revealed that certain specific functions are more abundant in the rhizosphere than in the bulk soil (Barret et al. 2011). This added to the importance of these traits to rhizosphere competence.

Along with increasing plant productivity, the soil microbiome also provides an important role in disease-suppressive soils. The ability of a soil to suppress disease is of key importance in measuring soil productivity (Janvier et al. 2007). There are many PGPRs that aid in disease suppression via the release of antimicrobial or antifungal compounds that deter plant pathogens (Garbeva et al. 2004; Weller et al. 2002). For example, fluorescent pseudomonads produce the antibiotic 2, 4-DAPG which has been extensively studied as a protectant against soil-borne diseases and have been directly linked to disease suppression (Raaijmakers et al. 1997; Raaijmakers and Weller 1998). *B. subtilis* also releases the antibiotics, surfactin and iturin, into the rhizosphere that play a major role in plant disease suppression (Kinsella et al. 2009) while also conferring increased plant growth promotion. Many studies have focused on the disease-suppressive ability of particular taxons or group of microbes but this ability of soils to suppress disease has been linked to the soil community as a whole (Garbeva et al. 2004; Malajczuk 1983; Mendes et al. 2011). Recently, Mendes et al. (2011) determined that the soil microbiome as a whole and not an individual taxon or group of soil microbes is what drives the disease-suppressive ability of the soil.

To achieve healthy and productive plants, soil quality is of great importance. Soil quality has been defined as the “capacity of a soil to function within ecosystem boundaries to sustain plant–animal productivity, maintain or enhance water and air quality, and support human health habitation” (Karlen et al. 1997). This definition has been further refined to take into account the dynamic nature of soil as a living system to “sustain biological productivity” (Doran and Safley 1997). The soil microbiome can be used as an indicator of soil quality due to its sensitivity to small changes in the environment resulting from environmental stresses or natural perturbations (Sharma et al. 2010). Elevated levels in species richness and diversity produce high functional redundancy within the soil microbiome, allowing it to quickly recover during stress (Nannipieri et al. 2003; Yin et al. 2000). The high functional redundancy in soil microbial diversity also confers protection against soil-borne diseases (Brussaard et al. 2007; Garbeva et al. 2004; Mendes et al. 2011; Nannipieri et al. 2003). The increase in microbial diversity produces a

balanced microbiome that does not allow for pathogens to flourish since the high microbial diversity present in the soil keeps the pathogen “in check” (Garbeva et al. 2004; Maron et al. 2010; Mendes et al. 2011; Ochiai et al. 2008; Postma et al. 2008; Schnitzer et al. 2011; Shennan 2008).

There are many key factors involved in soil health. Recently, community evenness has also been identified as an important factor in community functioning, soil health, and plant productivity (Crowder et al. 2010; Wittebolle et al. 2009). Microbial evenness ensures that no individual microbial taxum is able to take over and flourish, upsetting the ecological balance (Elliot and Lynch 1994). Field studies using potato plants demonstrated that even biocontrol communities among natural enemies of the potato beetle allowed for the improved control of these pests. Treatments where both pathogens and predators of the pestiferous beetle were most evenly distributed also contained plants with the greatest biomass (Crowder et al. 2010). Since potato tuber yield is strongly correlated with above-ground productivity, this increase in biomass suggests that natural enemy evenness may also increase crop yield (Crowder et al. 2010; Donnelly et al. 2001). Increased competition found in diverse and even microbial communities reduces the niche spaces available for potential invaders (Hillebrand et al. 2008; Knops et al. 1999; Naeem et al. 2000), and a lack of community microbial evenness has been associated with reduced plant productivity (Wilsey and Potvin 2000), possibly due to an empty niche effect leaving some ecosystem services unfulfilled. It is suggested that when environmental fluctuations occur, even communities are quickly able to adapt to the new environment and sustain high productivity over time (Hillebrand et al. 2008; Wittebolle et al. 2009). These examples highlight the benefits of ensuring even and diverse microbial communities to produce healthy soil, high levels of nutrient cycling (Elliot and Lynch 1994) and to combat stress and disease (van Bruggen and Semenov 2000). In such an ecosystem where the synergistic interactions between the soil, the soil microbiome, and the plant are of great importance, it can be deduced that reduced evenness has potentially negative effects since synergistic interactions fail when one species completely dominates the assemblage (Hillebrand et al. 2008).

The strong ability of root exudates to mediate and maintain the soil microbiome allows for the possibilities of exploiting this mechanism. It could be foreseen that plants (i.e., engineered or selected) could cultivate specific soil microbes that are needed or of importance to plant health. Root exudates are a complex mixture of compounds (Uren 2007). If we could tease out which compounds attract which microbes, we could selectively culture beneficial microbes such as PGPRs. Recent studies have demonstrated how specific root exudates can attract specific microbes. Rudrappa et al. (2008) demonstrated that root-secreted

malic acid recruits *B. subtilis* to the root. This PGPR is known to be involved in plant growth promotion and plant protection against several plant pathogens. Chemotaxis is another means by which plants recruit PGPRs to the rhizosphere by means of the release of carbohydrates and amino acids (Somers et al. 2004). Root exudates have also shown the ability to influence flagellar motility in some rhizosphere bacteria (de Weert et al. 2002). The classic and most studied example of how plants are able to culture and attract beneficial microbes comes from the study of the legume *M. truncatula* and its relationship with its symbiont *S. meliloti*. Flavones and flavonols, released as root exudates by the legume, act as the “ice-breaker” for initiating symbiosis (Zhang et al. 2009b). To aid in the attraction of rhizobia to the legume, studies demonstrated that volatile organic compounds, specifically dimethyl sulfide, released by the legume are used to attract nematodes that transport the rhizobia to the legume for the purpose of symbiosis (Horiuchi et al. 2005). This example is only one of the potential multitrophic interactions that can exist in the rhizosphere. Such an example illuminates the potential influence plants have in manipulating their environment. For example, *Arabidopsis* mutants lacking an ABC transporter produced changes in root exudation profiles, the ratio of phenolics to sugars changed when compared to wildtype (Badri et al. 2009a). This change caused an overhaul of the natural microbial community. The changes in the root exudate chemical composition were able to culture beneficial bacterial communities enriched with PGPRs, N₂-fixing bacteria, and bacteria that are involved in heavy metal remediation (Badri et al. 2009a). If we can determine which chemicals are able to attract which microbes, we can selectively culture beneficial microbes and concurrently deter pathogenic microbes from colonizing the root.

Management practices influence the soil microbiome

Farm management practices fall into two general categories, organic or conventional; although, specific management objectives and/or styles exist within these categories. The choice of farming practices may lend themselves to different processes or steps to achieve a more diverse and even microbiome. The USDA defines organic farming as “an ecological production management system that promotes and enhances biodiversity, biological cycles and soil biological activity. Organic farming is based on the minimal use of off-farm inputs and on management practices that restore, maintain, and enhance ecological harmony” (Gold 1995). Whereas organic farming uses no synthetic fertilizers or added inputs to increase productivity, conventional farming does just the opposite; often using synthetic, chemical fertilizers, and pesticides to benefit crop protection and

productivity. Frequently, these treatments are aimed at the microbial “black box” that is the soil microbiome. For example, conventional agriculture may target plant pathogens through the use of pesticides/fungicides, with a potential side effect of reducing soil microbial community diversity and evenness (Crowder et al. 2010; Krauss et al. 2011; Liu et al. 2007; Sugiyama et al. 2010). Whereas, organic agriculture may seek to control plant pathogens through competition and/or antagonism by utilizing treatments that promote a more diverse and even microbial community (Sugiyama et al. 2010) such as the addition of varying types of organic matter. It is known that the structure of the soil microbiome is influenced by agricultural management practices (Crowder et al. 2010; Liu et al. 2007; Lumini et al. 2011; Reeve et al. 2010; Sugiyama et al. 2010), land use (Degens et al. 2000), and degrees of stress and disturbance (Degens et al. 2001). By understanding those influences that combine to create more diverse and even soil microbial communities, fertility and disease resistance can be inherently restored in depleted, disease-stricken soil environments.

Implications for agriculture

While improving crop productivity is a century-old agrarian goal, high energy prices, globalization and climate change are changing the landscape for seeking solutions. The problem is no longer simply to produce more food, but also to do so in environmentally and socially sustainable ways (Godfray et al. 2010; von Braun 2007). As discussed above, agriculture should consider maximizing the coadaptation between plants and microbes in an effort to promote soil microbial diversity. Although, this may reduce short-term productivity, we believe that it will maximize long-term yields while minimizing resource use.

Evidence showing the importance of coadaptation of plant-microbial communities in plant health and productivity continues to mount (Badri and Vivanco 2009; Hierro et al. 2005; Lambers et al. 2009; van der Putten et al. 2009; Wardle 2004). What implications does decoupling the coadapted plant-microbial relationship have on agriculture? The inability of plants to maintain the diversity and evenness of a microbiome that is not coadaptive has already been described (Broeckling et al. 2008). This loss of diversity and evenness is detrimental to ecosystem functioning and plant productivity. In a world where the demand for food increases by the second unhealthy crops with low productivity is unacceptable.

Conclusion

The growing human population, reduction in land and resources, and the need for more environmentally friendly

agricultural practices have highlighted the need for sustainable farming. There is evidence showing the close ties between plants and their microbiome. An even and balanced microbiome can be the answer for obtaining healthier and more productive plants. Recent studies have begun to hint at the importance of this relationship and have started to examine the system as a whole to better understand the intricacies of the plant-microbiome interaction and its impact on plant health and productivity. There is a complex conversation that occurs between soil microbes and plants, mediated by root exudates, but this conversation still needs a lot more translating. We realize that successful management of soil health and plant productivity is a combination of many factors and individuals coming together to provide optimal conditions for a healthy plant. PGPRs are known to increase plant productivity and health and we need to be able to improve the conversations between plants and those microbes. Root exudates, due to their use as signaling molecules and as substrates by microbes, can be the answer to manipulating this dialog (Ryan et al. 2009). We have seen that ABC transporters play a key role in root exudation, and the compounds exuded change when they are manipulated. Future studies should determine what key compounds and root exudate compositions will culture these beneficial microbes that produce healthy and more productive plants.

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