

Harnessing the rhizosphere microbiome through plant breeding and agricultural management

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Abstract

Background The need to enhance the sustainability of intensive agricultural systems is widely recognized. One promising approach is to encourage beneficial services provided by soil microorganisms to decrease the inputs of fertilizers and pesticides. However, limited success of this approach in field applications raises questions as to how this might be best accomplished.

Scope We highlight connections between root exudates and the rhizosphere microbiome, and discuss the possibility of using plant exudation characteristics to selectively enhance beneficial microbial activities and microbiome characteristics. Gaps in our understanding and areas of research that are vital to our ability to more fully exploit the soil microbiome for agroecosystem productivity and sustainability are also discussed.

Conclusion This article outlines strategies for more effectively exploiting beneficial microbial services on agricultural systems, and calls attention to topics that require additional research.

Keywords Rhizosphere · Exudates · Plant-driven selection · Beneficial microbes · Plant breeding

Introduction

Agricultural productivity rests on a foundation of microbial activity, much of which takes place in soil. The soil has long been understood to harbor enormous microbial diversity (Torsvik et al. 1990), and contemporary research has reinforced this fact (Roesch et al. 2007). There is a growing appreciation of the genetic potential and the functional importance of the soil microbiome (Morales and Holben 2011). Within a given soil type, resident plants exert selective forces on this enormous pool of biodiversity, shaping and restructuring microbial communities in the rhizosphere [reviewed in (Berg and Smalla 2009)]. At the same time, plants are also sensitive to microbial activity, and may experience either enhanced or compromised performance depending on the activities of associated microbes. This dynamic, two-way exchange of effects between plants and soil microbes is significant in agricultural systems, and enhancing our ability to manipulate or direct these interactions could offer progress toward sustainability through development of crop varieties that selectively enhance beneficial functions within the soil microbiome. However, significant gaps in our understanding of the forces that influence the structure and functioning of plant-associated soil microbial communities pose an obstacle to realizing this goal. In this article, we review

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the current state of knowledge and highlight areas of future research that are vital to our ability to more fully exploit the rhizosphere microbiome for maximum, sustainable agricultural crop production.

Plants and the soil microbiome

Root exudation

In the rhizosphere of actively growing plants, root exudates are of particular importance to plant-microbe interactions (Badri and Vivanco 2009). The composition of root exudates varies by plant species, and even cultivars within a species (Kowalchuk et al. 2002; Högberg et al. 2006; Micallef et al. 2009), and as a result so does the soil microbial community (Grayston et al. 1998; Kuklinsky-Sobral et al. 2004; Salles et al. 2004). Variation in root exudation among plant species and genotypes suggests the potential for manipulation of root exudation in agricultural cultivars, in order to create specific selective effects on the rhizosphere microbiome.

Root exudates are made up of sugars, amino acids, flavonoids, proteins, and fatty acids (Badri and Vivanco 2009). These substances can serve as growth substrates or signals for suitable microbial partners, and as antimicrobials or growth deterrents for other microbes (Bais et al. 2006). In several classic examples of symbiosis, a very sophisticated interplay of chemical signaling mediates plant-microbe interactions. For example, legumes release flavonoids that alter patterns of gene expression in rhizobia, initiating a series of complex and specific interactions that ultimately lead to the fixation of atmospheric nitrogen inside of nodules (Oldroyd and Downie 2008). An important task ahead is to determine whether chemical signaling also has a role more broadly in plant-microbiome interactions in the rhizosphere. Evidence supports the idea that cross-kingdom interactions may be commonly mediated by chemical signaling. For instance, plants have been shown to interact with the acyl-homoserine lactone signaling mechanisms involved in bacterial cell-to-cell communication (Teplitski et al. 2000; Gao et al. 2003; Mathesius et al. 2003; Delalande et al. 2005) and to enhance anti-fungal gene expression in root-associated bacteria (Jousset et al. 2011). Plants have also been shown to perceive and respond to signals of microbial origin. For instance, the rhizobacterium *Pseudomonas fluorescens* CHA0 was shown to trigger

induced systemic resistance in *Arabidopsis thaliana*, through the production of the compound 2,4-diacetylphloroglucinol (Iavicoli et al. 2003).

Whether mediated through differential provision of energy- and nutrient-rich substrates [as in (Oger et al. 2004)], or through more complex inhibitory and signaling interactions, chemical compounds released by the roots are likely the basis for the selective effect of host plant genotype on the rhizosphere microbiome. Comparative studies across plant hosts have provided clues to root exudation traits that may be relevant to the shaping of soil microbial communities (Lesuffleur et al. 2007). Stable isotope probing techniques have been employed to address questions related to root exudation and rhizosphere microbial communities (Prosser et al. 2006). However, this technique has been focused on identifying microbial taxa that respond to plant hosts (Paterson et al. 2006), rather than on identifying particular exudation characteristics that are most important in plant-driven restructuring of soil microbial communities. Stable isotope probing has been helpfully applied to the study of spatial variation in exudation (Lu et al. 2007) and of the fate of particular compounds in soil. Though these compounds have most often been contaminants (Mahmood et al. 2005), the technique could also be applied to study incorporation of exudate components into microbial biomass.

There is a need for a much more detailed understanding of the relative importance of various root exudate components. Can selective effects be explained by a small number of high-impact compounds? How important are the diversity, quantity, or consistency of exudation to host plant selective effects? The impact of particular aspects of root exudation on soil microbes has begun to be addressed for model plant species (Badri et al. 2008, 2009), but this should be made a priority for agriculturally relevant species as well.

An important bottleneck to advancing concepts related to interactions between root exudates and soil microbes has been the ability to study root exudation *in situ*. However, recent developments are advancing this area. For instance, anion exchange membranes have been used to capture exudates, with comparisons between bulk and rhizosphere soil accounting for compounds coming from soil (Chiang et al. 2011). Putting anion exchange membranes in contact with roots allows for the repeated sampling of root exudates from the same roots over a period of time, and when

coupled with image analysis, can allow for calculations of exudation rates (Shi et al. 2011). Exudates have also been collected from intact live roots by flushing with an aqueous solution to collect soluble exudate components (Phillips et al. 2008).

Extent of plant-driven change to the soil microbiome

Host plant effects have been detected in the bulk soil microbiome (Carney and Matson 2006; Bremer et al. 2009), indicating that it may be possible to use plants to shape soil microbial communities more broadly than just in the rhizosphere. This potential is significant in agricultural systems: as host plants are switched during crop rotation, microbial colonizers for the newly forming rhizosphere are drawn from the bulk soil community (Jones et al. 2004). The availability of beneficial colonizers in a newly forming rhizosphere may depend on the selective effects of the previous crop. However, agricultural application of plant-driven influence in bulk soil microbial communities will require a more detailed understanding of the mechanistic basis for such effects. For instance, are bulk soil effects driven more strongly by plant litter inputs or by downstream outcomes of rhizosphere effects? The rhizosphere is dynamic in extent, fading into bulk soil with root death and forming again with the emergence of new roots (Jones et al. 2004). Thus rhizosphere turnover offers one pathway for plants to extend influence beyond the root zone to shape the bulk soil microbiome. Importantly, the degree to which rhizosphere populations carry over to impact bulk soil microbial community structure likely differs among microbial taxa, depending on the degree of specialization to the rhizosphere environment and the capacity for quiescence.

Plant-microbiome co-adaptation

Host plant effects on the soil microbiome become more pronounced over time, and it is probable that microbial partners undergo adaptation to their host plant. At least in cases of tight mutualistic symbioses, there is evidence of co-evolution between plants and rhizosphere microbes (Lambers et al. 2009). Although data demonstrating widespread microbial adaptation to match root exudation are remarkably sparse, some suggestive evidence has been reported. For example, root colonizers more efficiently utilized dominant

exudate components compared to randomly selected rhizobacteria (Kamilova et al. 2006). In some cases, soil microbes have also shown an enhanced ability to degrade the biomass of their host plant species relative to that of other plant species (Ayres et al. 2009; Madritch and Lindroth 2011). Pairing near-isogenic bacterial strains differing in catabolic capacity with transgenic plants producing novel substrates, has demonstrated that the ability to catabolize plant-supplied resources impacts rhizosphere population densities under competition (Savka and Farrand 1997).

The global exchange of agricultural plant species provides an interesting system for studying plant-microbiome adaptation (see Fig. 1). Near the center of origin for a particular crop, long-term association between plant host and microbial partners is possible. In contrast, movement of a crop species to a new part of the world brings together a soil microbiome and a host plant that may have no shared evolutionary history. The foreign host plant species may secrete a novel combination of exudates into the soil, some of which may have antimicrobial properties or serve as inefficient substrates for the local microbial community. Thus sudden replacement of host plants will change the selective pressures acting on the rhizosphere microbiome. Competitive advantage among microbes may switch, leading to a period of rearrangement such as has been observed in studies of invasive plants in their new habitats (Broz et al. 2007), through experimental host plant switching (Broeckling et al. 2008), and by using plants with genetic defects related to root exudation (Badri et al. 2009). Microbial community dynamics in response to perturbation are enormously complex and there remains tremendous progress to be made in modeling such changes. It is clear that microbes enact transcriptional changes in response to shifts in resource availability (Brandt et al. 2004), and that environmental conditions and initial population densities influence the outcomes of competitive dynamics in unpredictable ways (Buchanan and Bagi 1999; Powell et al. 2004), such that population dynamics can be chaotic (Fussmann and Heber 2002).

A lack of shared history between host plant and soil microbiome may retard the development of niche saturation in the rhizosphere, because of provision of resources by the plant for which microbial metabolic capacity has not developed or become common. Common root exudate components may be quickly exploited by a naïve

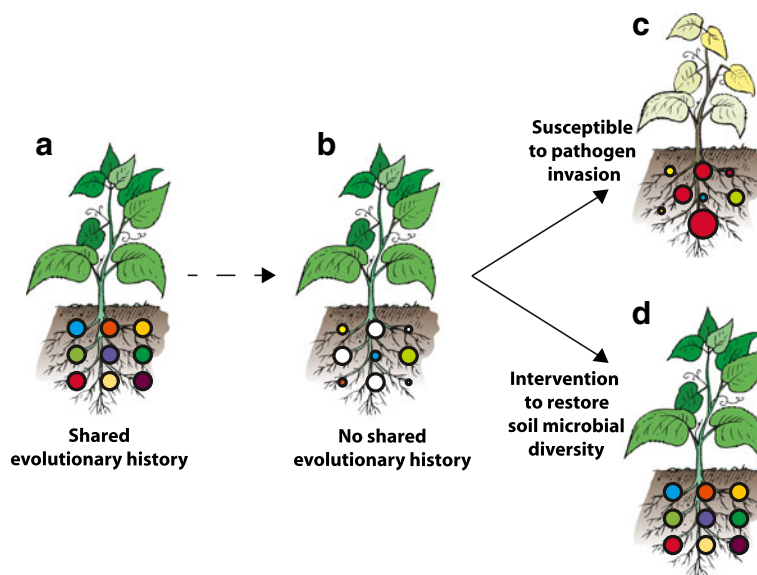


Fig. 1 Possible effects of disrupting plant-microbiome coadaptation on sensitivity to subsequent disease outbreaks. Colored shapes below the soil line represent different microbial taxa. Pathogenic taxa are indicated in red. **a** A plant growing in a location where there has been a long shared history between the plant and the soil microbiome. Although pathogens are present, their activity is greatly constrained. **b** A plant growing in

association with a naïve microbiome, which has no shared history or adaptation (e.g. after movement to a new part of the world for agriculture). **c** This un-adapted microbiome is less effective at preventing pathogen establishment, enhancing susceptibility to disease. **d** Management interventions may be able to foster microbiome characteristics that constrain disease

microbiome, but unfamiliar exudate components may be less readily accessible to extant microbial enzymes. Importantly, open niches left by incomplete resource utilization may provide a window of opportunity for pathogen establishment (see Fig. 1). Although the niches of pathogens and non-pathogens differ in some important ways, there are also common features. Pathogens and non-pathogens may compete, for example, for access to resources exuded from roots or for physical space on root surfaces. Rapid colonization of roots by a host-adapted microbiome may prevent pathogen establishment. We hypothesize that progressively tighter microbiome adaptation to a particular host results in niche saturation and thus more effective competitive exclusion of pathogens. This is consistent with the observation that long-term monoculture may lead to the development of disease suppressiveness over time. For instance, long-term monoculture of wheat (*Triticum aestivum* L.), potato (*Solanum tuberosum* L.) and melon (*Cucumis melo* L.) have all given rise to pathogen-suppressive soils (Sneh et al. 1987; Landa et al. 2006; Meng et al. 2012). Clearly this scenario represents only one possible outcome of repeated monoculture, and other trajectories are also possible, as discussed below.

Plant-soil feedbacks and diffuse mutualisms

Ecological studies of plant-soil feedbacks offer insights that may be relevant to agriculture. In contrast to the previously cited observations, accumulation of pathogens after repeated cultivation has also been observed in agricultural systems, forming the basis for crop rotation (Hwang et al. 2009). This type of negative plant-soil feedback has received more attention than positive plant-soil feedbacks. Systems have been observed in nature in which growth of a particular plant species enhances the subsequent performance of that same species (Reynolds et al. 2003; Callaway et al. 2004; Bonanomi et al. 2007; Grunsvén et al. 2009). More attention should be given to drawing applications for agriculture from such systems. By deciphering relevant plant traits and identifying organisms [as in (Mendes et al. 2011)] or microbiome characteristics that are responsible for positive plant-soil feedbacks, we may be able to replicate these processes in agricultural systems.

Where positive plant-soil feedbacks are rooted in beneficial microbial services, a kind of associative symbiosis may be at play: plant hosts provide resources or

mediate microbial interactions in a way that favors particular microbes. In turn, these microbes provide services that enhance plant performance. Studies of the canonical plant-microbe mutualisms, such as mycorrhizae and the legume-Rhizobium symbioses (West et al. 2002; Kiers et al. 2011), have demonstrated that the stability of mutualisms depends on the aligning of fitness benefits for both partners and imposing sanctions against partners that ‘cheat.’ For diffuse mutualisms between plants and free-living rhizosphere microbes, this suggests the need for fine sensing of the beneficial functions provided by microbial partners, with concomitant fine control of root exudation. Many aspects of the exudation process are under active plant control, including the potential for re-uptake of exuded compounds (Jones et al. 2004). Variable exudation characteristics have been demonstrated among root types, as for lupine (*Lupinus albus* L.) cluster roots (Weisskopf et al. 2005), and in response to particular nutritional demands such as phosphorus deficiency (Shen et al. 2001). However, studies of root exudation at the microbial scale are needed in order to determine the extent and specificity of plant response to rhizosphere partners. It should also be noted that plant-beneficial microbial activities may not always bear a cost to the producer, and so ‘cheaters’ may not necessarily enjoy a fitness advantage. In this case, the host plant may be able to select for beneficial microbial functions without the need for sophisticated ability to impose sanctions against cheaters. Furthermore, even unstable mutualisms may be exploited in agriculture. For instance, populations of beneficial microbes can be augmented by external application or by provision of resources to periodically boost flagging populations.

Beneficial microbial activity

There are many mechanisms by which rhizosphere microbes may positively impact plant performance. Wherever host plants can capture services provided by the microbiome, agricultural productivity may be enhanced by more fully exploiting beneficial microbial functions. Microbial services may include the production of phytohormones (Ping and Boland 2004), provision of nutrients (Janos 2007), enhanced tolerance to abiotic stresses (Redman et al. 2002), induction of the plant innate immune response system (Jain et al. 2011), alteration of plant functional traits (Friesen et al. 2011)

or tissue chemistry (Larsen et al. 2006), and perhaps other mechanisms as well.

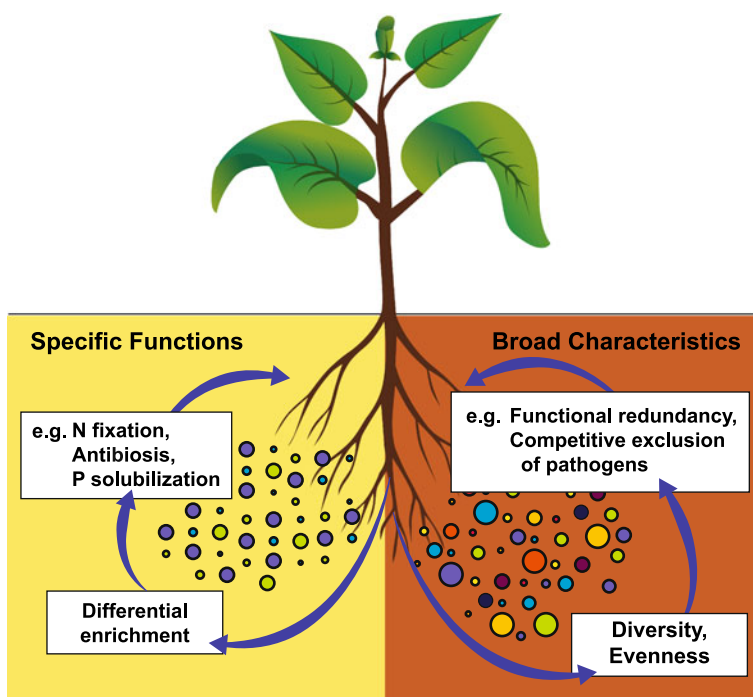
Specific functions

One strategy is to shape the microbiome for optimal provision of very particular services (Fig. 2, left side), such as by offering a competitive advantage to particular microbes in order to enhance the rate of certain enzymatic transformations. From this perspective, the goal is to develop plants able to select particular beneficial microbes from amongst a broader community that includes many members without beneficial function. Unfortunately, however, there may be a mismatch between microbial features that are accessible to selection, and those that benefit plant performance. It becomes difficult to devise mechanisms for specifically enriching beneficial microbial functions when those functions are performed by a subset of the members of many different taxa. It would be extremely valuable to identify characteristics that are linked to the provision of beneficial services (e.g., phosphorus solubilization, pathogen suppression) and that are also susceptible to selection, either by the host plant or through agricultural management practices. For instance, is it possible to manipulate environmental conditions in such a way as to induce the provision of beneficial services by a disparate collection of organisms?

Broad microbiome characteristics

As an alternate approach to enriching for very particular microbial functions, it may be possible to develop plants that shape the soil microbiome in a broadly beneficial fashion (Fig. 2, right side), defining community-level characteristics that promote plant health. For instance, rhizosphere microbial richness and evenness may be particularly important to plant performance. Increasing microbial richness equates to greater community-level trait diversity and/or functional redundancy, and should lead to more consistent functioning across variable environments (Loreau et al. 2001). However, because rare members of the microbiome may be unable to effectively perform important functions, the evenness (relative abundance) of members of the microbiome is also important (van Elsas et al. 2008). In the case of disease suppression, for instance, maximizing overall microbial activity or niche saturation may be important to competitive

Fig. 2 There may be alternate paths to realizing the goal of using plants to enrich beneficial microbial functions. For instance, one could target particular microbial taxa or services (left side), or one could aim for broad microbiome characteristics that may promote plant performance (right side). Colored shapes below the soil line represent different microbial taxa



exclusion of pathogens. Increasing microbial biomass and/or diversity have been commonly found to accompany enhanced pathogen- or disease-suppressiveness (Larkin and Honeycutt 2006; Ochiai et al. 2008; Postma et al. 2008) and to limit successful invasion by introduced organisms (van Elsas et al. 2012). It has been noted that only a portion of the soil microbial pool is in a metabolically active state (Pennanen et al. 2004). This is an important caution, but we expect that increasing over all diversity will typically correspond to an increasing diversity of metabolically active microbes as well.

Although evenness has received less attention than richness or diversity, evidence supports an important role for evenness in community functioning, particularly under stresses or perturbations (Wittebolle et al. 2009). A field study showed that increasing evenness of predators and pathogens was important to the successful biocontrol of insect pests of potato (Crowder et al. 2010). Evenness of plant species abundance reduces weed invasion (Tracy and Sanderson 2004) via more complete resource utilization that reduces niche space available for invaders (Knops et al. 1999; Naeem et al. 2000). Low soil microbial evenness has been associated with reduced plant productivity (Wilsey and Potvin 2000). The richness and

evenness of the soil microbiome are central to providing stability, resilience to stress and disease, and high levels of internal nutrient cycling (Elliot and Lynch 1994). Importantly, soil microbial evenness can be modified by agricultural management practices (Fließbach et al. 2009; Sugiyama et al. 2010).

Future work should investigate plant characteristics that are related to microbiome richness and evenness. For instance, how important are adaptation or long-term association in maintaining evenness among rhizosphere microbes? Over long time scales, does rhizosphere microbial evenness increase as many microbial community members undergo adaptation or niche differentiation in the context of a stable assemblage of interacting organisms? Does increasing exudate diversity sustain greater microbial richness in the rhizosphere? Or, can simple exudates be transformed by microbial activity into sufficiently diverse metabolites to allow for niche differentiation of many microbes? If so, simply increasing exudate quantity may be as effective in maintaining a rich microbiome as increasing exudate diversity. The relative importance of carbon source quantity, identity and diversity have begun to be explored through simple studies of resource amendment using defined compounds (Orwin et al. 2006), but much more work of this sort is needed.

The soil microbiome in agriculture

Plant breeding

We have highlighted plants as selective agents that shape the soil microbiome, and how such effects might feed back to impact plant performance. In agricultural systems, plant genotype is carefully controlled through breeding and cultivar selection. It has been proposed previously that ‘rhizosphere engineering’ could yield many benefits to agriculture (Oger et al. 2004; Ryan et al. 2009). We reiterate this call for plant breeding to consider the beneficial functions afforded by the soil microbiome, and extend discussion on the topic. The strategy of using plants as selective agents to enrich beneficial microbial functions has the major advantage of not requiring any change in infrastructure or management; all of the required work is in the area of cultivar development, which could then be seamlessly integrated into existing production systems.

There are limited examples of breeding programs that have considered rhizosphere-related traits (Wissuwa et al. 2009), and those that have considered particular root exudation characteristics have had a very narrow focus, such as improving nodulation (Rengel 2002). We are not aware of any breeding program in the world that evaluates plant lines for broad interactions with the soil microbiome. This is unfortunate, as variation certainly exists for traits related to interactions with soil microbes (Smith and Goodman 1999). The impacts of transgenic crops on soil microflora have been evaluated [reviewed in (Bruinsma et al. 2003)], but this should become a routine consideration during crop breeding and development. For the first time, this is now a feasible proposal, as high throughput methods and new sequencing technologies allow for the simultaneous and economical profiling of hundreds of microbiomes (Erlich et al. 2009).

Difficulties associated with breeding for interactions with microbes

Variability across environments, soil types and microbial communities represents a substantial obstacle to the goal of using plants as selective agents to enrich beneficial microbial functions in soil. In fact, these variables compound with each other: different soil types not only shape the microbial communities present there (Ulrich and Becker 2006; Wakelin et al. 2008), but also impact plant

physiology (Taiz and Zeiger 2006), which will in turn further alter interactions with soil microbes. Obtaining a clear picture of just how difficult it may be to overcome such variability will require broad surveys that test particular plant genotypes across treatments in which environment, soil properties, and microbial communities are systematically and independently varied.

The exudation and re-uptake of compounds by plant roots are very complex processes, and specific targets for breeding are unclear. Should breeders aim to enhance the synthesis of particular compounds? Should they aim to increase the activity of particular transporter proteins? We do not yet have clear targets by which breeders might create plants with enhanced ability to foster beneficial microbial functions. However, traditional plant breeding often works in ignorance of the mechanisms which underlie a desired phenotype. Breeding for a beneficial microbiome will likely begin in the same way, with breeders selecting for outcomes (such as yield), but in an environment that is suitable for revealing the impacts of associated microbes. For example, this may mean limiting nutrient availability for plants during selection so that differences in microbial provision of nutrients become clear. Plants may not select for beneficial microbes, or the activity of those beneficial microbes may not be detectable, under high resource availability.

Breeders assess the performance of a given plant genotype across variable locations and environments. The soil microbiome is one aspect of this environmental variation and interaction with the local microbiome contributes some component of site-to-site variability in plant performance. From this perspective, selection for consistent plant performance across locations may have the effect of reducing host plant sensitivity to microbial activities. For instance, mycorrhizal dependence has been shown to be reduced in modern wheat cultivars relative to older landraces (Hetrick et al. 1993). To the extent that this has occurred, genes mediating beneficial interactions with associated microbes (Smith and Goodman 1999; Smith et al. 1999; Schweitzer et al. 2008) may need to be re-introduced into elite germplasm.

It is also possible that in modern cultivars the potential for benefit from microbial activity has been reduced in an absolute sense. For instance, although microbial production of phytohormones may benefit plant performance in some cases [reviewed in (Tikhonovich and Provorov 2011)], this microbial function overlaps with

innate plant functions. Overlapping function suggests that the beneficial microbial activity could be superseded by fine-tuning of the plant's own regulatory systems to optimize hormone production and distribution for best performance in a given environment. Importantly, however, many microbial functions are unique rather than redundant with innate plant capabilities. Thus considering interactions with microbial partners has the potential to enhance plant performance beyond the genetic capability of the host plant in isolation. Most notably, soil microbes possess novel enzymes for scavenging nutrients from soil and liberating nutrients from organic to mineral forms (Cairney 2011; Gaur and Khare 2011). Breeding for plants that are able to harness beneficial microbial functions could enhance agricultural sustainability: for instance, plants that more efficiently exploit microbial phosphorus solubilization may continue to yield well even when less exogenous phosphorus is applied.

Context dependence is an important characteristic of many microbially mediated benefits to plants. For instance, microbial interference with plant hormone signaling may be beneficial under drought conditions (Shaharouna et al. 2011), but is not necessarily so under other conditions. Thus, for optimal performance, plants should be able to quickly recruit or enhance particular microbial functions under conditions where they will have the greatest net benefit. Such adaptive plasticity in the host plant may be accommodated by the spatial and temporal variability that is already known to exist in root exudation (Baudoin et al. 2002; Mougél et al. 2006). Ideally, plant breeding would not only emphasize the ability to foster a beneficial microbiome, but also the ability to maximize net benefit by engaging microbial partners in a context-dependent fashion. For instance, pathogen attack has been shown to stimulate malic acid exudation by *Arabidopsis thaliana*, which in turn promotes colonization and biofilm formation by a beneficial *Bacillus* strain (Rudrappa et al. 2008).

In the future, cultivars or transgenic plants could be developed with exudation characteristics that encourage beneficial microbiome characteristics and microbial functions, while discouraging pathogens. Before this is possible, however, we will need a much more detailed understanding of the relative impact of various exudate components on shaping the soil microbiome. Comparative studies of plant hosts that differ

in specific root exudation characteristics have begun to address this deficit. For example, root exudates of an *Arabidopsis* mutant were found to contain relatively more phenolic compounds and fewer sugars compared to the wild-type plant, and this change led to a relatively greater abundance of beneficial soil bacteria, including plant-growth-promoting rhizobacteria, nitrogen-fixing bacteria, and bacteria involved in heavy metal remediation (Badri et al. 2009). However, much more work of this sort will need to be done before plant breeders will have clear and accessible targets for creating plants that foster their own beneficial microbiome.

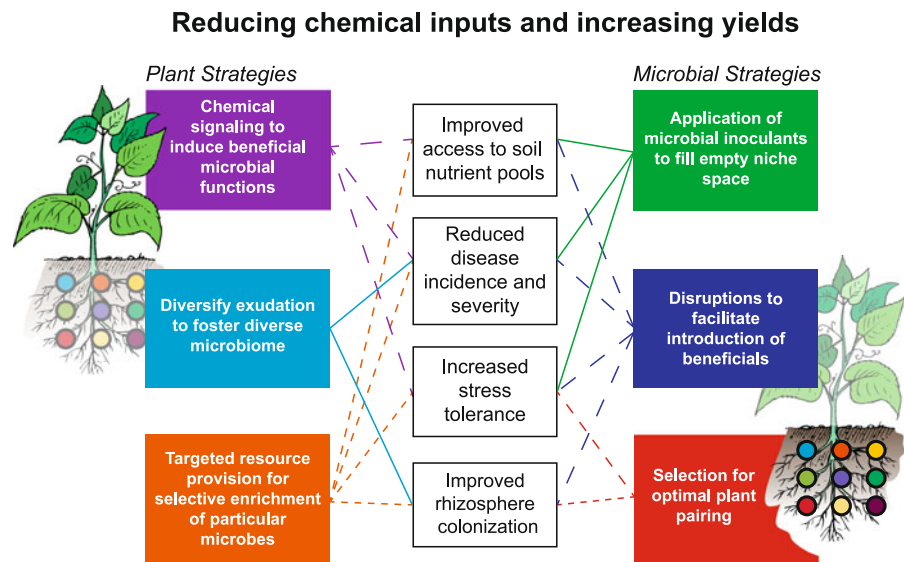
At the same time, manipulating root exudation is likely to create tradeoffs and may produce unexpected or undesirable outcomes. This is a natural result of our very incomplete understanding of the complex interactions that take place in the rhizosphere and of the fact that any one compound is likely to have multiple roles or activities. The strigolactones serve as a helpful illustration of this difficulty. These compounds were originally identified as germination stimulants for parasitic weeds [reviewed in (Xie et al. 2010)]. In isolation, this function would have suggested that breeding should attempt to eliminate the production of these compounds. However, it was subsequently discovered that strigolactones also play a role in establishment of mycorrhizae (Akiyama et al. 2005; Besserer et al. 2006). More recently, these compounds have been shown to be plant hormones playing a role in branching (Gomez-Roldan et al. 2008; Umehara et al. 2008). Since our knowledge is always incomplete, we may expect unexpected outcomes of breeding for particular exudation traits.

It should also be noted that additional, previously unconsidered mechanisms might exist for plants to benefit from associated rhizosphere microbes. For instance, evidence has recently been proposed to demonstrate that plant roots may engulf microbial cells for digestion and use as a nutrient source (Paungfoo-Lonhienne et al. 2010). Thus future research is likely to suggest novel targets for plant breeding in order to enhance plant access to nutrient pools, improving plant growth performance in limited-input agricultural systems.

Direct microbiome manipulation

In the near term, a more feasible way to harnessing beneficial microbial functions in agricultural systems

Fig. 3 A variety of strategies could be used to promote beneficial services provided by soil microbial communities, with the aim of reducing chemical inputs while sustaining or improving crop yields. Manipulating plant traits that are related to interactions with microbes (left side), or manipulating soil microbial communities directly (right side), could improve conditions for plant productivity (center mechanisms)



would be to attempt to manipulate the soil microbiome directly (Fig. 3). Inoculation of microorganisms has been used for some time in agriculture. However, new approaches may enhance the success of introducing novel microbes into soil. For instance, deliberately imposing disturbances may increase soil vulnerability to invasion and enhance the establishment of exogenous beneficial organisms. This might take the form of disruption by fungicide application, crop rotation or tilling prior to the application of plant growth promoting rhizobacteria (Fließbach et al. 2009), mycorrhizal fungi (Gosling et al. 2006), or other beneficial microbes in the form of active compost or bio-preparations (Pérez-Piqueres et al. 2006).

An interesting approach would be to develop consortia of fungi and bacteria that are evolutionarily adapted to particular host plants. If applied with the plant, such consortia may serve to reduce the period of time required for the rhizosphere microbiome to achieve niche saturation and competitive exclusion of pathogens.

Hybrid approaches are also possible, tweaking both plant and microbiome characteristics in order to achieve a better fit. Attempts have been made to create plant genotypes that are tailored to particular microbes, such as engineering plants to produce novel carbon sources which are readily available to an inoculant strain (Savka et al. 2002). Alternately, information on the identity of beneficial microbial taxa could be used

to deduce probable substrates that could be supplied exogenously or via plant root exudation in order to enrich those particular taxa. For instance, recent work has identified microbial taxa and antibiotic biosynthetic genes associated with disease suppression (Mendes et al. 2011). Knowledge of the metabolic capacity of these organisms could be used to develop strategies for selective enrichment. At an even finer level, an understanding of the regulation of antibiotic biosynthetic gene expression in these organisms may allow for manipulation of relevant microbial functions through the introduction of appropriate signaling molecules.

Conclusion

Chemical pollution, a growing human population, and the depletion of resource and energy reserves have accentuated the need for sustainable agricultural practices. One path toward sustainability involves a greater reliance on the beneficial functions afforded by the soil microbiome. We have highlighted areas of research that are vital to our ability to more fully exploit the plant-associated microbiome in agricultural crop production, whether through direct manipulation, or by using crop plants as selective agents to enrich for beneficial microbes.

Box 1- Priorities for future research. Greater research attention should be given to these topic areas in order to advance the goal of more fully exploiting beneficial microbial functions in agriculture.

- Make positive interactions with the rhizosphere microbiome an explicit goal of plant breeding, and expand our understanding of the mechanistic basis for such interactions.
- Understand the impacts of plant genotype on the rhizosphere microbiome and on the ability of plants to interact with beneficial microbes.
- Develop strategies to selectively enrich for indigenous microbes performing beneficial functions.
- Identify root exudate components that have the largest or most consistent effects on shaping microbial communities. Clarify the relative importance of exudate identity, quantity, and diversity.
- Clarify the importance of chemical signaling (vs. resource provision) in plant-driven structuring of the rhizosphere microbiome.
- Expand study of mechanisms and extent of plant impacts on the bulk soil microbiome.
- Understand the extent and significance of microbial adaptation to host plants.
- Expand study of naturally occurring positive plant-soil feedbacks to draw new insights for agriculture.
- Investigate the importance of broad microbiome characteristics (such as richness and evenness) in promoting plant health.

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