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MICROBIAL DIVERSITY IN SOIL: Selection of Microbial Populations by Plant and Soil Type and Implications for Disease Suppressiveness

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Key Words soil microbial diversity and community, plant effect, soil type, management regimes, soil suppressiveness

■ **Abstract** An increasing interest has emerged with respect to the importance of microbial diversity in soil habitats. The extent of the diversity of microorganisms in soil is seen to be critical to the maintenance of soil health and quality, as a wide range of microorganisms is involved in important soil functions. This review focuses on recent data relating how plant type, soil type, and soil management regime affect the microbial diversity of soil and the implication for the soil's disease suppressiveness. The two main drivers of soil microbial community structure, i.e., plant type and soil type, are thought to exert their function in a complex manner. We propose that the fact that in some situations the soil and in others the plant type is the key factor determining soil microbial diversity is related to the complexity of the microbial interactions in soil, including interactions between microorganisms and soil and microorganisms and plants. A conceptual framework, based on the relative strengths of the shaping forces exerted by plant and soil versus the ecological behavior of microorganisms, is proposed.

INTRODUCTION

Microorganisms in soil are critical to the maintenance of soil function in both natural and managed agricultural soils because of their involvement in such key processes as soil structure formation; decomposition of organic matter; toxin removal; and the cycling of carbon, nitrogen, phosphorus, and sulphur (124). In addition, microorganisms play key roles in suppressing soilborne plant diseases, in promoting plant growth, and in changes in vegetation (29).

Although microbiologists have been investigating the impact of microbial diversity on the stability of ecosystem function since the 1960s (47), there is now heightened interest in the effect that the diversity of microbial communities has on ecological function and resilience to disturbances in soil ecosystems. Relationships

are often observed between the extent of microbial diversity in soil, soil and plant quality, and ecosystem sustainability. Moreover, several studies have documented the relationship between the degree of soil suppressiveness to plant diseases and the diversity or abundance of soil microbial communities (4, 85).

That the treatment or management of soil affects microbial community structures has long been recognized. Application of pesticides (50), amendment with chitin (46), compost (99) or manure, and the introduction of genetically modified microorganisms (26, 75) have all been shown to affect soil microbial community structures. The physicochemical properties of soil (64), soil particle size distribution (94), the presence and age of specific plant species (38, 43), and crop rotations (128) are key determinative factors.

Thus, although we know that both plant (crop) type and soil can direct the structure of microbial communities, the details of these interactions are incompletely elucidated and warrant further study. For instance, will it be possible to develop a predictive model on the functioning and effect of the two potential drivers of soil microbial diversity? What are the mechanisms behind the steering force of plants or soils and can we distinguish the relative strengths of the forces they exert? How do microbial diversity and microbial community structure relate to the suppressiveness of plant pathogens?

Soil microbial communities are often difficult to fully characterize, mainly because of their immense phenotypic and genotypic diversity, heterogeneity, and crypticity. With respect to the latter, bacterial populations in soil top layers can go up to more than 10^9 cells per g soil (115), and most of these cells are generally unculturable. The fraction of the cells making up the soil microbial biomass that have been cultured and studied in any detail are negligible, often less than 5% (15, 114). As direct DNA-based methods offer the possibility to assess the total microbial diversity present, thus bypassing the limitations of cultivation-based studies, recent years have seen the rapid development of such cultivation-independent methods for analyzing the microbial communities in soil (6, 88). The direct methods have become indispensable in such studies; however, we have to be cautious about what they tell us (129).

We focus in this review on recent data relating to how microbial diversity of soil is affected by plant type, soil type, or soil management. We then address the implications of these effects for the disease suppressiveness of soil. The data supporting our conclusions were generally obtained by either cultivation-based or cultivation-independent (often DNA-based) techniques. We therefore address briefly the merits of these techniques.

Soil, Microbial Diversity, and Community Structure

THE SOIL HABITAT Soil represents a highly heterogeneous environment for the microbiota inhabiting it; the different components of the solid fractions in soil (sand, silt, clay, and organic matter) provide myriads of different microhabitats (124). The organisms resident in soil are exposed to abiotic and nutritional

conditions that may vary even over the micrometer scale, i.e., the scale experienced as their biosphere. In a "stable" system, one can hypothesize that each microhabitat is occupied by organisms that were best able to colonize the niche and become established. These organisms collectively are the underlying catalysts of the biochemical processes in soil. Thus, the microbial processes in soil, including those resulting in disease suppressiveness, clearly take place at the scale of microhabitats and organismal biospheres. These processes are susceptible to major changes in the surroundings, whereby a measurable effect will be the result of individual shifts at the micrometer scale. Three major and inherently complex factors, plant type, soil type, and soil management or treatment, have been selected for discussion here because these factors can have major repercussions on soil quality, as reflected in suppressiveness of soil to plant diseases.

MICROBIAL DIVERSITY VERSUS COMMUNITY STRUCTURE The term biodiversity has been defined in various ways. In microbial terms, it describes the number of different types (species) and their relative abundance in a given community in a given habitat. In molecular-ecological terms, it can be defined as the number and distribution of different sequence types present in the DNA extracted from the community in the habitat. However, the term "community structure" implies that information is included on the numbers of individuals of different recognizable taxa (71). These divergent terms are often used interchangeably in publications on soil microbial diversity. We will, as much as possible, adhere to the definitions given above. With respect to microbial diversity, the number of types present and the evenness of their distribution are important. A habitat with a larger number of species is more diverse, whereas an evenly distributed community is more diverse than an unevenly distributed community with the same number of species (49).

Methods for the Assessment of Soil Microbial Diversity

CULTIVATION-BASED METHODS Traditionally, methods to analyze soil microorganisms have been based on cultivation and isolation (122); a wide variety of culture media has therefore been designed to maximize the recovery of diverse microbial groups. A Biolog-based method for directly analyzing the potential activity of soil microbial communities, denoted community-level physiological profiling (CLPP) (37), has also been introduced. Unfortunately, as a result of biases favoring copiotrophic organisms, the resulting metabolic fingerprints are unlikely to represent accurately the *in situ* functional diversity in a natural microbial community (103). Cultivation-based methods are limited in that only a small fraction of the microbial cells in soil are accessible to study, although a recent study claimed that this percentage can be raised substantially by using special cultivation techniques (62).

CULTIVATION-INDEPENDENT METHODS Recent advances in molecular technology have aided in the development of cutting-edge studies of soil microbial communities. These molecular techniques are generally based on PCR or RT-PCR of specific

or generic targets in soil DNA or RNA. The 16S and 18S ribosomal RNA (rRNA) or their genes (rDNA) represent useful ecological markers for prokaryotes and eukaryotes, respectively. However, the shortcomings of these techniques and their related problems have also been well documented (62, 129). PCR products generated with primers based on conserved regions of the 16S or 18S rDNA from soil DNA or RNA yield a mixture of DNA fragments representing all PCR-accessible species present in the soil. The mixed PCR products can be used for (a) preparing clone libraries (15, 80), and (b) a range of microbial community fingerprinting techniques.

Clone libraries Clone libraries are useful to identify and characterize the dominant bacterial or fungal types in soil and thereby provide a picture of diversity. However, to accurately describe the microbial diversity within a soil sample, clone libraries usually need to be quite large. There are as yet few studies in which the representativeness issue has been satisfactorily resolved, and hence microbial diversity has not been adequately covered in most studies to date. Rarefaction analysis, calculation of coverage values, or other statistical techniques are needed to evaluate whether the number of screened clones is sufficient to realistically estimate the true diversity (23, 95). Great progress can be expected in this area, as our capacity for rapid sequencing of large numbers of clones increases and as statistical techniques to determine representativeness improve.

Microbial community fingerprinting techniques A range of techniques has been developed to fingerprint soil microbial communities. These include denaturing or temperature gradient gel electrophoresis (DGGE/TGGE) (52, 82, 83), amplified rDNA restriction analysis (ARDRA) (79), terminal restriction fragment length polymorphism (T-RFLP) (72), single-strand conformational polymorphism (SSCP) (98), and ribosomal intergenic spacer length polymorphism (RISA) (93). Although these PCR-based methods are in principle reproducible and robust, they are susceptible to the potential biases described above that are inherent in both nucleic acid extractions and PCR amplifications (see Table 1).

PCR-DGGE is probably the most widely used among the methods to study microbial communities in environmental samples. The DGGE profiles of microbial communities in soil and rhizosphere are often very complex when analyzed with universal (bacterial) primers, and as a result, less abundant organisms may escape detection (14, 39). Group-specific PCR-DGGE systems have been developed recently that allow a better understanding of specific subgroups of complex environmental communities. Group-specific PCR-DGGE systems are now available for studying prokaryotic groups such as Actinomycetes (52), *Bacillus* (36), *Paenibacillus* (24), *Pseudomonas* (35, 45), the α - and β -Proteobacteria (42), methanotrophic bacteria of the α - and β -Proteobacteria (51), ammonia-oxidizing bacteria (66), and N_2 -fixing bacteria (73). Systems for other specific groups are under development. In addition, a promising new development is the application of DNA microarray technology to the analysis of microbial communities and

TABLE 1 Advantages and disadvantages of culture-independent PCR-based microbial community fingerprinting methods

Advantages

- Dependence on efficient cell lysis only and not on the physiological status of cells
- Direct picture of the diversity of dominant microbial types, including the unculturables
- Direct assessment of shifts in microbial community structure
- Ease in handling. Simultaneous analysis of high sample numbers
- Reproducible results
- Generation of sequences resulting in identification and specific probes to track the specific organism in the ecosystem

Disadvantages

- Incomplete lysis of some species, notably gram-positive spore-formers
- Possible biases in DNA extraction and PCR amplification, inhibition by soil compounds
- Possible presence of one particular sequence or band in different organisms
- Heterogeneous bands that may originate from one bacterial strain due to heterogeneity in the rDNA genes
- Phylogenetic information only is usually obtained, and the link to functional information is difficult

selected genes in the environment (60, 112). Space limitations preclude discussing this issue here, other than to point to its potential in future work and to note that, as it is based on hybridization, it faces all well-documented intricacies of probe-based studies, especially the need for careful selection of sufficiently specific probes to allow a reliable description of the soil microbial community.

METABOLICALLY ACTIVE COMMUNITIES Some authors have claimed that, by using rRNA (rather than rDNA), information can be obtained about metabolically active members of the microbial community in soil (34). However, the abundance of ribosomal targets may be related in different ways with microbial activities. A more convincing method, in which microbial activity can be linked to phylogenetic information, is to incorporate 5-bromo-2'-deoxyuridine (BrdU) into DNA, followed by fingerprinting of the active communities (116, 136). In addition, ¹³C incorporation (stable isotope labeling) followed by separation and fingerprinting has been proposed as a way to assess the metabolically active fractions (10). Such activity-oriented methods may allow us to identify organisms with an active function in soil, and to better correlate knowledge of microbial community structure in soil with that of how the system functions. Despite these recent advances, improved methods are still needed to assess specific activities in soil, e.g., on the basis of specific messenger RNA.

POLYPHASIC APPROACH Although culture-dependent techniques are limited for studies on the composition of natural microbial communities in soil when used alone, they are nevertheless useful for understanding the growth characteristics,

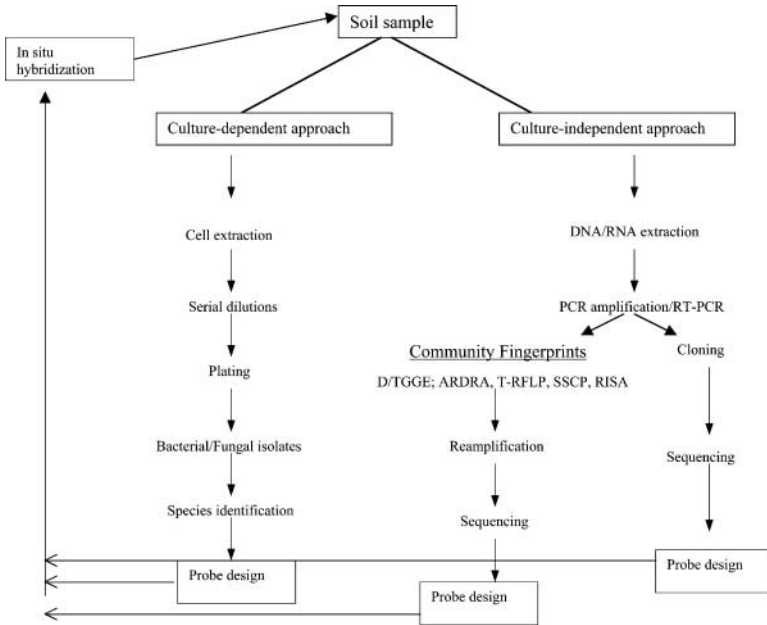


Figure 1 Outline of cultivation-dependent and cultivation-independent approaches to studying microbial diversity in soil and rhizosphere.

potential ecological behavior, and function of microorganisms from soil habitats. A polyphasic approach, using culture-based and culture-independent methods, is likely to produce more complete information on the composition of soil microbial communities (53, 69) (Figure 1).

Numerous studies have investigated the extent of phylogenetic overlap between organisms obtained by cultivation and those identified by direct molecular methods. The two methods generally sample different fractions of the soil microbial community and are thus complementary. On the basis of traditional cultivation studies, prokaryotic organisms typically found in soil were demonstrated to belong to, for example, the gram-positive bacteria (*Clostridium* spp., *Bacillus* spp., *Arthrobacter* spp., *Brevibacterium* spp., *Corynebacterium* spp.) or to different subgroups of the Proteobacteria (*Pseudomonas*, *Serratia*, *Enterobacter* and *Rhizobium* spp.) or the Cytophaga/Flavobacteria/*Bacteroides* (CFB) group. The genus *Pseudomonas* is easy to isolate by cultivation and is among the best-studied organisms in soil (35). Other genera commonly isolated from soil include *Acinetobacter*, *Agrobacterium* (α -Proteobacteria), *Alcaligenes* (β -Proteobacteria), and *Xanthomonas* (γ -Proteobacteria). The same lineages have been found with direct molecular methods, in particular the analysis of 16S rDNA gene clone libraries (74). A new bacterial division, *Acidobacterium*, has been found to be ubiquitously present in soil (106). This newly defined division was based on analysis of

sequences, and only few isolates have hitherto been obtained in culture. A study of the microbial communities of four acid soils from northern Arizona indicated that seven bacterial divisions were represented among the uncultured organisms and only three among the cultured isolates (32).

Like bacteria, reduced fractions of the fungi present in soil can be cultured. Several fungal taxa, such as the saprophytic basidiomycetes and arbuscular mycorrhizal fungi belonging to the Glomales, are difficult to isolate from soil by dilution plating (105, 110). In several studies, molecular techniques based on the 18S rRNA gene have been applied to assess the fungal diversity in soil (41, 68, 105, 117, 121). However, the amplified 18S rDNA is not always sufficient to identify fungal species as the fungal 18S rRNA sequence database is still underdeveloped. Using fungal 18S rDNA clone libraries, Gomes et al. (41) identified different members of the Ascomycota (Pleosporales, Hypocreales, Sordariales, and Eurotiales), Basidiomycota (Filobasidiales, Sporidiales), and Zygomycota (Mucorales) in soil.

Microbial Diversity of Soil—Effects of Plant Type, Soil Type, and Soil Management

In soil, a wide range of factors affect microbial life (126), but many relevant questions remain. What are the main factors controlling soil microbial community structure and diversity in soil? Can we distill general principles from the wide body of information that has accumulated over the years? In particular, can we make reliable predictions on how the selected parameters plant (crop) type and soil type, and the derived factor—soil management regime—will affect microbial diversity?

Three main hypotheses are addressed:

1. Plant type is a major determinant of the structure of microbial communities in soil, as plants are the main providers of specific carbon and energy sources;
2. Soil type is a major determinant of the structure of microbial communities, as the combination of soil texture and structure, organic matter, microaggregate stability, pH, and the presence of key nutrients, i.e., N, P, and Fe, determines the habitable niches in soil; and
3. Agricultural management regime, such as crop rotation, tillage, herbicide and fertilizer application, and irrigation, is the key determinant of microbial community structure in soil.

Conceptually, the extent to which plant and soil type influence the structure of microbial communities is dependent on their relative “strength,” which can be depicted on an arbitrary scale. In addition, the nature of the microbial type affected also is significant, as some organisms may turn out to be virtually refractory to change (e.g., typical K-strategists (slow growers) such as *Arthrobacter* types), whereas others are very prone to stimulatory or destimulatory effects (e.g., typical r-strategists (bacteria characterized by high growth rates under conditions of

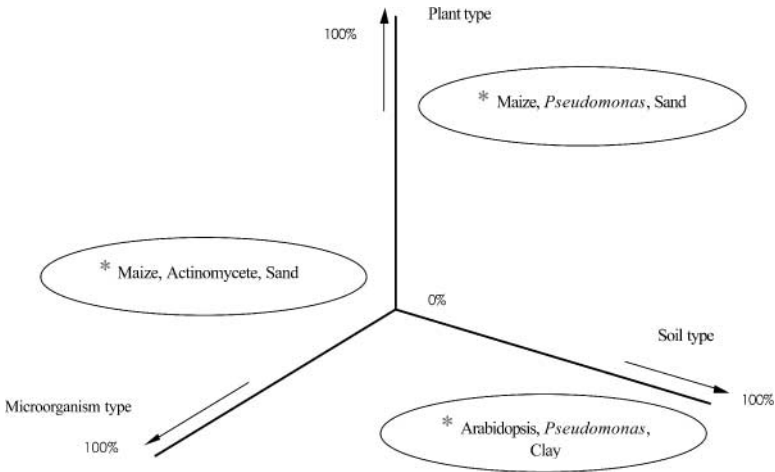


Figure 2 Conceptual depiction of relative strengths (scale 0–100%) of forces shaping microbial communities in soil and rhizosphere. Axes depict relative forces exerted by plant, soil, and microbial type. Maize (strong) versus Arabidopsis (weak), clay (strong) versus sand (weak), and Actinomycete (strong, recalcitrant) versus *Pseudomonas* (weak, low recalcitrance) were taken as models to illustrate the concept: Explanation: Maize, *Pseudomonas*, sand: strong plant effect, weak soil effect, organism of low recalcitrance; Arabidopsis, *Pseudomonas*, clay: weak plant effect, strong soil effect, organism of low recalcitrance; Maize, Actinomycete, sand: strong plant effect, weak soil effect, recalcitrant organism.

enhanced nutrient supply) such as the pseudomonads); these can also be depicted on a scale from 0 (refractory) to 100% (prone to change). Figure 2 depicts the interrelationships between the two drivers plant type and soil type, and the organisms affected; various situations can be inferred as, somewhat arbitrarily, indicated in the figure. We recommend the use of this depiction in the development of a conceptual framework that explains the effects of plant and soil type on diversity.

As it is difficult to study these factors independently, researchers are now addressing them simultaneously. A complex interaction has been shown between the various factors (see Tables 2, 3).

Plant Type as the Determinant of the Structure of Microbial Communities in Soil

Plant roots release a wide variety of compounds into the surrounding soil, including ethylene, sugars, amino acids, organic acids, vitamins, polysaccharides, and enzymes. These materials create unique environments for the microorganisms living in association with plant roots, in the rhizosphere. The rhizosphere was first described by Hiltner (1904) as the volume of soil surrounding plant roots influenced

TABLE 2 Effect of plant and soil type on microbial community structure

System and factors studied	Methods used	Results and conclusions	References
Plant species (chickpea, rape, and Sudan grass); soil type (sandy, sandy loam, and clay); root zone location	PCR-DGGE	Bacterial community structure in the rhizosphere is affected by a complex interaction between soil type, plant species, and root zone location	(77)
Soil type, plant type (clover, bean, alfalfa), plant age	PCR-TGGE	The plant species type had the greatest effect in determining microbial community structure	(133)
Soil type, plant type (wheat, rygrass, bentgrass, and clover)	Biolog CLPP	Plant effect with significant difference in microbial communities from the different plant species	(43)
Plant cultivar (maize) and soil-effect on a specific bacterial group <i>Paenibacillus</i>	PCR-DGGE	Soil type showed higher effect than plant cultivar type on <i>Paenibacillus</i> communities	(24)
Plant type (canola, wheat); soil type	FAME	Effect of plant type stronger than that of soil type	(40)
Plant (flax, tomato) and soil type; effect on fluorescent pseudomonads	Cultivation; REP-PCR, RFLP	Soil effect stronger than plant effect	(70)
Plant (maize) development, cultivar, and soil effect	Cultivation—plating enumeration	Between the factors studied, soil had the dominant effect on microbial diversity	(19)
Microbial community in the spermosphere as affected by soil type and seed type	Biolog CLPP; FAME	Soil type affected microbial community structure more than seed type	(18)

TABLE 3 Effects of major soil changes on microbial community structure

Soil management regimes	Impact	Reference
Organic, low-input, and conventional farming system	Increases in microbial biomass resulting from high organic matter inputs in the organic and low-input systems	(16)
Application of model herbicide 2,4-D in three different soils	The same population of 2,4-D degraders became dominant in the three soils	(111)
Long-term grassland management regimes (N-fertilizer application and soil drainage)	Grassland management practice impacts on community structure of specific bacterial groups. N fertilizer has significant impact on eubacterial and actinomycete community and soil drainage on actinomycetes and pseudomonad community	(21)
Unimproved, semi-improved, and improved grassland soil	Clear difference in microbial community between the three differently managed grasslands	(80)
Plots in sod and cropped to wheat. No-till, subtile, or plow managed	Cropped plots were higher in microbial biomass. Prevalence of mycorrhizal fungi in sod and sensitivity to tillage under wheat-fallow cropping	(30)
Change from forest to pasture vegetation	Shifts in bacterial community structure. Significantly higher G + C content in the pasture soil	(86)
Improved, unimproved, and semi-improved grassland pastures	Significant effect of soil management on diversity of ammonia oxidizer populations with higher diversity in unimproved soil	(131)
Permanent grassland, arable land under rotation and under monoculture of maize	Significant difference in microbial community structures. Higher diversities in the permanent grassland	(123)

by the living root. Bacteria respond differently to the compounds released by the plant root, and thus different compositions of root exudates are expected to select different rhizosphere communities. On the other hand, rhizosphere bacteria will also influence plants, as wide ranges of bacteria in the rhizosphere can promote plant growth via chemical signals such as auxins, gibberellins, glycolipids, and cytokinins. Genera such as *Pseudomonas*, *Agrobacterium*, *Bacillus*, *Variovorax*, *Phyllobacterium*, and *Azospirillum* are among the most efficient plant growth-promoting bacteria (13). For example, *Azospirillum brasilense* can exert a positive effect on the growth of common bean and soybean, and *Agrobacterium tumefaciens* can have a strong effect on plant root development (17, 81).

Scientific interest has long focused on the structure of microbial communities in the rhizosphere, assessed by cultivation-based studies. These studies have

shown that the microbial diversity in the rhizosphere is often extensive and that there are distinct differences in bacterial community structures between bulk (non-rhizosphere) soil and rhizosphere soil. Recently, several studies on different plant species in different locations, using a range of cultivation-based and molecular methods, indicated that plant type is indeed a major factor influencing the structure of microbial communities. In specific cases, bacterial communities were shown also to be influenced by plant genotype, root zone, or plant age. Using CLPP, Grayston et al. (43) compared the rhizospheres of wheat, ryegrass, bentgrass, and clover grown in two different soil types (dystic Cambisol and eutic gleysol) at two sites in Scotland. The two soils used had a similar crop history. A significant clustering of potential microbial activities along plant type (i.e., different plant species had different activities) was observed, but no differentiation was noted between microbial activities in the two soil types. This observation would indicate that the microorganisms selected in the Biolog plates had similar metabolic capacities, but is far from suggesting that the microbial communities were similar per se. Two studies by Germida (40) and Kaiser (63) and their associates with oilseed rape supported the hypothesis that crop type plays a major role in controlling the diversity of root-associated bacteria. Kaiser et al. (63) used cultivation-based and culture-independent (16S rRNA gene library) approaches, whereas Germida et al. (40) used a cultivation-dependent approach. Although the soil types were different between the two studies, both strongly indicated that the plant plays a major role in determining the composition of the bacterial community in the rhizosphere, whereas soil type seemed to play only a minor role. Kowalchuk et al. (67), using PCR-DGGE, also demonstrated clear plant-induced effects on bacterial community structures in soil. The effects appeared to be limited to the direct rhizosphere and to be highly plant-specific and reproducible for a given plant species. A major unresolved question from this and other studies is the extent to which, in space and time, the influence of plant roots remains visible. Smalla et al. (104) aimed, by using PCR-DGGE, to determine the degree to which the rhizosphere effect is plant-dependent and whether this effect is enhanced by growing the same crop for two consecutive years. Potato, strawberry, and oilseed rape were used. DGGE fingerprints of the bacterial communities showed plant-dependent shifts in the relative abundance of bacterial populations in the rhizosphere, which became more pronounced in the second year. Dominant populations were high G + C % gram-positive bacteria, such as actinomycetes. By contrast, Wardle et al. (130) showed that the removal of specific plant groups from a field affected the microbial community structure as described by PLFA patterns, but they found no differences in the total biomass of bacteria and fungi. Disappointingly when aiming for robust changes of the soil microbial diversity, this study thus indicated ephemeral root-induced effects.

Using PCR-TGGE, Wieland et al. (133) assessed the degree of variation of dominant bacterial populations in respect of soil type (silty sand and loamy sand), plant type (clover, bean, and alfalfa) and developmental stage of the plant. Plant species had the greatest effect on the rhizosphere microflora, whereas the plant developmental stage had the lowest effect. The effect of soil type exceeded that of

plant type in the soil habitat only, as the clustering of alfalfa plants in loamy sand was clearly distinct from the clustering of the same plants in the silty sand. Hence, the effect seen was dependent on the soil microhabitat sampled. Marschner et al. (77) examined bacterial community structures in the rhizosphere based on PCR-DGGE of soil rRNA genes, as affected by three factors: plant species (chickpea, rape, and Sudan grass), soil type (a sandy soil, a sandy loam, and a clay), and root zone location. All three factors, as well as the interaction between them, had significant effects on the community structures in the respective rhizospheres. The bacterial community associated with chickpea was influenced mainly by soil type, whereas the communities of rape and Sudan grass were more affected by root zone than by soil type. Hence, the effects exerted by the different plants were, to varying extents, controlled by soil type, which makes the interactions complex. Finally, studies have addressed the rhizosphere communities of genetically modified plants related to those of conventional plants. Dunfield & Germida (33), using both PLFA and CLPP, found differences between the bacterial communities associated with genetically modified *Brassica napus* and conventional varieties. This difference may be linked to differences in the exudation by these plants, as suggested by others (28, 101).

PLANT DEVELOPMENTAL STAGE The composition of root exudates is strongly affected by the plant developmental stage, which in turn can affect rhizosphere communities over time (135). Picard et al. (90) showed that the presence of 2,4-diacetylphloroglucinol (DAPG)-producing bacteria in the rhizosphere of maize was significantly affected by plant age. The frequency of DAPG producers was very low in the first stage of plant growth and increased over time. Plant age effects were also observed by di Cello et al. (27) and Seldin et al. (100), who showed that populations of *Burkholderia cepacia* and *Peanibacillus azotofixans* in the maize rhizosphere changed during plant growth. In both studies, cultivation was used. Also, the populations of *Burkholderia cepacia* decreased significantly during plant growth. Other studies, in the rhizospheres of maize as well as wheat, revealed that r-strategists (25) were dominant on young, immature roots, whereas K-strategists become dominant on mature roots (26, 84). Hence, bacterial communities not only adapt to plant type, but also change over time with the same plant type. The results obtained by Baudoin et al. (11) also revealed clear differences between bacterial communities on maize in dependency of growth stage. Furthermore, Gyamfi et al. (45) also confirmed that the plant growth stage had a strong impact on total bacterial as well as *Pseudomonas* communities. The fact that young plants contained bacterial communities that were distinct from those in other plant developmental stages was also observed by Duineveld et al. (31) with chrysanthemum. Root tips were compared with root base parts. Specifically, the PCR-DGGE analyses revealed higher similarities between samples derived from root tips and between samples from young plants (31). Yang & Crowley (135) later confirmed these observations. The main sources of easily accessible substrates are sites at root tips and young roots. Thus, young plants provide the highest amount of organic carbon

available for microbial growth. Young roots and root tips might therefore represent excellent niches suitable for colonization by r-strategists.

EFFECTS ON FUNCTION Plants can have strong effects on soil microbial communities viewed from the functional perspective. For example, DAPG producers occurred with lower frequencies in non-rhizosphere soil than in corresponding rhizosphere soil and are significantly affected by plant (maize) development (90). To explore the effect of different plant species on the abundance and diversity of bacteria antagonistic to plant pathogens, isolates originating from the rhizospheres of three host plants of *Verticillium dahliae*—strawberry, potato, and oilseed rape—and from soil were analyzed for their antagonistic properties (12). The abundance, taxonomic composition, and diversity of *Verticillium dahliae* antagonists were shown to be plant-species dependent. The proportion of isolates with antagonistic activities was highest for the strawberry rhizosphere (9.5%), followed by oilseed rape (6.3%), potato (3.7%), and bulk soil (3.3%). Hence, plants affect their associated communities also in a functional way. It is a challenge to unravel these effects and convert the data into a predictive database. Can we, for instance, establish a database of plant-induced functional effects useful to predict the pathogen-suppressive capabilities of soil?

Soil Type as the Determinant of the Structure of Microbial Communities in Soil

Given the powerful effect of soil on its microflora, soil type likely represents another important factor influencing the structure of microbial communities. Soil, on the basis of different particle size distribution, pH, cation exchange capacity, or organic matter content, thus can affect microbial community structure either directly, i.e., by providing a specific habitat that selects specific microorganisms, or indirectly, i.e., by affecting plant root functioning and exudation in a soil-specific manner.

Several relatively recent studies have indeed provided evidence that soil type can be an important determinant of the composition of microbial rhizosphere communities. Gelsomino et al. (39) observed differences in the grouping of DGGE fingerprints obtained from 16 different soils from different geographical locations. These authors suggested that soil type largely determines the structure of bacterial communities seen by direct PCR-DGGE, and that similar soil types tend to select similar communities. In a study of microbial biomass and activity in four grasses in the U.S. Northeast, soil texture was also shown to have a stronger effect than plant species (44). Other studies have also indicated that soil type can have a marked influence on the microbial populations in the rhizosphere of maize. Chiarini et al. (19) compared the influence of soil type, cultivar, and growth stage of maize on the population size and structure of bacterial communities associated with the roots of field-grown maize. The greatest effect on density and community structure was exerted by soil type, whereas no significant difference between

the effect of different maize cultivars was observed. In an analysis of the diversity of *Paenibacillus* populations in maize plants grown in two different soils, da Silva et al. (24) observed that soil type, rather than maize cultivar type, was the overriding determinative factor that influenced the community structures of paenibacilli in the rhizosphere. Latour et al. (70) studied the effect of soil type and host plant type (flax and tomato) on the diversity of the populations of culturable fluorescent *Pseudomonas* spp. Although both soil type and host plant affected the diversity of fluorescent *Pseudomonas* species, soil type was clearly the dominant factor.

Buyer et al. (18) studied the effect of soil and seed type on the microbial community structure around germinating seeds. They examined two loamy sand soils with differences in pH and in humic content, and five seed types: maize, cucumber, radish, soybean, and sunflower. Soil type was shown to exert a greater effect on the spermosphere microbial community structure than seed type. This is in line with the presumed soil origin of the spermosphere-colonizing bacterial communities and with the assumption that the bacterial diversities of the two soils were different. In addition, the soil with higher organic matter content had a greater microbial biomass.

The observed dominant effect of soil type on microbial communities in the rhizosphere can thus be explained by the impact of the soil fabrics on the soil-inhabiting communities, which are the sources for rhizoplane and rhizosphere colonization. Also, soil texture may affect the rhizosphere microflora by limiting the availability of root exudates.

Agricultural Management Regime as the Determinant of the Structure of Microbial Communities in Soil

In conformity with earlier knowledge, several recent studies have shown that soil-management practices, such as crop rotation, tillage, fertilizer, compost, manure, or pesticide applications and irrigation greatly affect soil microbial parameters (8, 87, 99, 107). Inasmuch as the effects of the treatments are complex, the outcome is often not easily explainable. For instance, Bossio et al. (16) showed that different farming regimes, i.e., organic, low-input, and conventional, influence soil PLFA profiles. In particular, mono-unsaturated fatty acids increased with organic input in organic and low-input systems. In addition, the relative importance of environmental variables on the PLFA profiles was determined. Tiedje et al. (111) compared the responses of microbial communities in three soils of different history to the application of 2,4-D [2,4-dichlorophenoxyacetate]. They hypothesized that different land use practices will yield different microbial responses to the applied herbicide. However, the same population of 2,4-D degraders became dominant in three soils of different land use history, indicating that 2,4-D was a stronger selector than was soil use history. Steenwerth et al. (108) evaluated soil microbial community structure for nine land uses, including irrigated and non-irrigated agricultural

sites, nonnative annual grassland and relict, and never-tilled or old field perennial grassland. The results showed a distinct grouping of microbial communities from different treatments and suggested that nonnative annual grasses may be associated with a unique microbial community. In fact, all sites that supported annual grassland had similar PLFA profiles. The impact of long-term grassland management regimes (N-fertilizer application and soil drainage) on microbial community structure was assessed by Clegg et al. (21) using PCR-DGGE and PLFA profiling. N fertilizer was found to exert a significant impact on the total bacterial and actinomycete community structures, whereas soil drainage had a significant impact on the actinomycete and pseudomonad communities. This study strongly indicated that grassland management practice has an impact on the community structure of specific bacterial groups. McCaig et al. compared bacterial communities in grassland under different management regimes by 16S rDNA clone libraries and PCR-DGGE (80). The authors hypothesized that high nutrient input and low plant diversity in "improved" grassland lead to a less diverse bacterial community than the community in "unimproved" grassland, with the "semi-improved" grassland community being intermediate. The results based on 16S rDNA library did not indicate a difference in bacterial community structure between the different grasslands, whereas DGGE profiles demonstrated that there were clear differences among the three grassland types. Nusslein & Tiedje (86) showed soil bacterial community shifts correlated with a change from forest to pasture vegetation in a tropical soil. The G + C content of the pasture soil DNA was significantly higher than that of the forest soil DNA. Although α - and β -Proteobacteria dominated in the pasture soil, fibrobacter types were dominant in the forest soil. Palmer & Young (89) also showed clear effects of soil-management regime on rhizobial diversity in soil, as a higher diversity of *Rhizobium leguminosarum* was measured in arable soil than in grassland soil. Four soils from eastern Washington State with contrasting soil management (no-till and conventional till) and environmental conditions were analyzed by PLFA and DGGE (61). The results indicated that no-till soil practices improved the biological condition. This conclusion was based on the fact that high microbial biomass was determined by PLFA analysis and greater diversity of ammonia-oxidizing bacteria was associated with no-till soil.

In a long-term experiment performed in our groups (123), permanent grassland was studied adjacent to farmland under rotation or under monoculture of maize. To assess the microbial community structure in these soils, several complementary methods were used, e.g., conventional enumeration on four different agar media for enumeration of culturable fungal, bacterial, *Bacillus*, and *Pseudomonas* populations, PCR-DGGE assessment of microbial diversity using universal bacterial, fungal, and group-specific primers (for *Bacillus* and *Pseudomonas*), and 16S and 18S rDNA clone libraries obtained from different treatments. The results obtained by all methods showed clear differences in microbial community structures between different treatments (Table 4). Moreover, higher microbial diversities and biomass were measured in the permanent grassland than in the arable land under monoculture or under rotation (35, 36, 123).

TABLE 4 Some data from a field experiment with differently treated plots* (year 2001)

Measurements/Treatments	G	GA-R	GA-M	A-R	A-M
Bacterial and fungal cfu/g soil	No significant differences between the treatments of the culturable population of bacteria (R2A media), actinomycetes (COA) and fungi (PDA)				
Log cfu/g soil <i>Bacillus</i>	5.65 (0.3)	5.35 (0.2)	5.40 (0.2)	4.65 (0.3)	4.8 (0.2)
<i>Pseudomonas</i>	6.0 (0.3)	5.8 (0.2)	5.9 (0.2)	5.1 (0.1)	5.2 (0.2)
R-/K-strategists	In all treatments, the percentage of fast-growing bacteria (r) was higher than that of the slow-growing (K) bacteria				
EP ^a -indices	0.495 (0.01)	0.441 (0.03)	0.431 (0.02)	0.306 (0.02)	0.361 (0.04)
E-evenness	0.36	0.32	0.31	0.21	0.26
Antagonistic isolates (%) <i>Bacillus</i> (B)	B 18 (±2)	B 23 (±3)	B 23 (±1)	B 10 (±4)	B 11 (±3)
and <i>Pseudomonas</i> (P)	P 19 (±4)	P 22 (±2)	P 25 (±3)	P 6 (±1)	P 15 (±2)
Chitinolytic <i>Pseudomonas</i> spp.	17 (±2)	20 (±3)	22 (±1)	6 (±2)	14 (±4)
SW ^b (PCR-DGGE)					
Total bacteria	3.24 (0.01)	3.51 (0.02)	3.51 (0.03)	3.10 (0.02)	3.10 (0.01)
Total fungi	3.35 (0.03)	3.24 (0.04)	3.24 (0.02)	3.02 (0.03)	2.92 (0.03)
<i>Bacillus</i>	2.85 (0.01)	2.85 (0.01)	2.85 (0.01)	2.13 (0.02)	2.25 (0.01)
Actinomycetes	2.34 (0.04)	2.55 (0.01)	2.75 (0.02)	2.40 (0.02)	2.45 (0.03)
Extension of <i>R. solani</i> AG3 ^c	8.5 (0.4)	8.3 (0.3)	8.1 (0.7)	15.1 (0.4)	10.5 (0.4)

Abbreviations: G-, permanent grassland; GA-M, grassland recently turned to arable land monoculture of maize; GA-R, grassland recently turned to arable land under rotation; A-R, long-term arable land under rotation; and A-M, long-term arable land under monoculture of maize. The results are presented as an average of three plots; the numbers in parentheses are standard deviations. The data were considered to be different at $P < 0.05$.

^aEP, Eco-Physiological indices and E, evenness, calculated based on culturable bacteria counted from second till eighth day.

^bSW, Shannon-Weaver calculated based on the PCR-DGGE patterns.

^cExtension of *R. solani* AG3. The higher % of extension-lower suppression.

Microbial Diversity in Relation to Suppressiveness of Soil to Plant Pathogens

Some soils are inhospitable to plant pathogens, by limiting either the survival or the growth of the pathogens. Such soils are known as pathogen- or disease-suppressive and are found throughout the world. Suppressiveness has been defined as either “general” or “specific,” indicating either the absence or presence of information about the mechanisms involved. General suppression often reduces fungal and nematode attacks, whereas specific suppression is often effective against only one or a few pathogens. In specific disease suppression, the monoculture of one crop, e.g., wheat, can lead to an initial increase in disease followed by a spontaneous decline in disease. Examples of specific suppression are declines in potato scab, take-all, oat cyst-nematode, and in *Rhizoctonia solani*. Suppressiveness is further differentiated in accordance with their longevity in “long-standing suppression” and “induced suppression” (57, 58). Long-standing suppression is a biological condition naturally associated with the soil, its origin is not known, and it appears to survive in the absence of plants. Induced suppression is initiated and sustained by crop monoculture or by the addition of inoculum of target pathogen.

Several soilborne pathogens, such as *Fusarium oxysporum* (the cause of vascular wilts), *Gaeumannomyces graminis* (the cause of take-all of wheat), *Phytophthora cinnamomi* (the cause of root rots of many fruit and forest trees), *Pythium* spp. (a cause of damping-off), and others develop well and cause disease in plants growing in some soils (known as conducive soils), whereas they develop much less and cause no disease or milder disease symptoms in plants growing in other, suppressive, soils (7, 58, 65, 78, 132). The mechanisms by which soils are suppressive to different pathogens, although not always clear, can involve biotic (soil microflora) and/or abiotic factors (soil physicochemical properties); they may vary with the pathogen. Malajczuk (76) suggested that the main agents in soil suppressiveness are microbial, because sterilization by autoclaving, stem pasteurization, and irradiation rendered soils conducive to the pathogen studied.

Several studies indicated that mechanisms within the microbial activity of soil are responsible for the suppression of pathogens. For example, van Os & van Ginkel (125) showed a clear relationship between the suppression of *Pythium* root rot in bulbous *Iris* and soil microbial biomass and activity: high microbial biomass and activity induced suppression of *Pythium* growth through soil. Further, a relationship has been found between microbial diversity and root disease suppression (85, 134). Rovira & Wildermuth (97) indicated that the microbiota in a “rich” soil tends to reduce the severity of attack by many soilborne plant pathogens (general disease suppression).

Representatives of a range of bacterial (*Pseudomonas*, *Burkholderia*, *Bacillus*, *Serratia*, Actinomycetes) and fungal (*Trichoderma*, *Penicillium*, *Gliocladium*, *Sporidesmium*, nonpathogenic *Fusarium* spp.) groups have been identified as antagonists of soilborne plant pathogens. The mechanisms by which these microorganisms make soil suppressive can be divided into several categories: nutrient

competition, amensalism, microbial antagonism, parasitism, and systemic induced resistance. One of the most important groups containing antagonistic microorganisms is the group of fluorescent pseudomonads. Several antibiotic-producing *Pseudomonas* 6 pp. were isolated from soil suppressive to diseases such as take-all of wheat, black rot of tobacco and fusarium wilt. Naturally occurring root-associated fluorescent *Pseudomonas* spp. producing the antibiotic 2,4-DAPG were highly enriched in take-all-suppressive soil and are key components of specific suppression of *Gaeumannomyces graminis* var. *tritici* (91, 92). This suppression was lost when 2,4-DAPG-producing *Pseudomonas* spp. were eliminated and, conversely, conducive soil gained suppressiveness to take-all when 2,4-DAPG-producing *Pseudomonas* strains were introduced.

Tippett (113) provided an example of the importance of the soil microbiota for the level of suppressiveness. By adding soil containing large quantities of microorganisms to microbially deficient soil, they were able to eliminate *P. cinnamomi*. Many antagonistic microorganisms are naturally present in soil and exert a certain degree of biological control over plant pathogens regardless of human activities. However, this level of natural control is often insufficient for consistent, reliable disease-free cropping. Researchers are therefore attempting to enhance the effectiveness of antagonists ex or in situ, thus increasing suppressiveness (55).

CROPPING EFFECT Disease suppression can be influenced by cropping and management practice (59). For example, cultivating orchard soils with wheat prior to planting apple induced suppressiveness to *R. solani* AG5 by increasing the level of specific fluorescent pseudomonad genotypes antagonistic to *R. solani*. Continuous cultivation of the same crop in conducive soil, after some years of severe disease, can eventually reduce disease pressure by stimulating microorganisms antagonistic to the pathogen. Continuous cultivation of wheat or cucumber leads to a reduction of take-all of wheat and *Rhizoctonia* damping-off of cucumber, respectively. Long-term cauliflower monocropping results in the suppressiveness of *R. solani*, although the causative agents of suppression are not yet known (R. Scheper, personal communication). Next to cover crops, compost application, and tillage, crop rotation is important (3, 4, 22), as the densities of both soilborne pathogens and the antagonistic microorganisms are affected. Suppressiveness can also develop after rotation of appropriate crops for sufficient duration. Effective crop rotation results in the lack of positive selection of the pathogen and provides time needed for the biological destination of pathogen inoculum by antagonists residing in soil (5). Crop rotation and, in some cases, a specific crop sequence have thus been recommended to control *Rhizoctonia*. Other studies showed the importance of a cover crop, to serve as "green manure" that improves the physical characteristics of the soil (96), increases microbial activity, and reduces plant disease (48, 109). The cultivation of plants influences the microbial activity of the soil and, therefore, the suppressiveness. For example, the cultivation of the leguminous cover plant *Pueraria javanica* significantly enhanced the suppressiveness to Fusarium wilt of

a palm grove soil compared with soil that was kept uncultivated (1). The cultivation of *P. javanica* induced changes in the microbial balance, increasing the population of nonpathogenic *Fusarium* spp. Viaene & Abawi (127) found that Sudan grass was effective in reducing damage to lettuce plants by *Meloidogyne hapla*. Several studies further showed that root diseases are generally less severe in organic than in conventional farms, with reduction attributable to longer rotations, regular applications of organic amendments, and abstinence from, or reduction of, pesticide use (118, 119). Total populations of fungi and bacteria were significantly higher in organically than in conventionally farmed areas (102). Populations of specific groups, i.e., fluorescent pseudomonads and actinomycetes, were also higher in tomato rhizosphere soil from organic farms than in those from conventional farms (134).

In a long-term experiment, we studied fields that were subjected to different treatments: species-rich permanent grassland, grassland turned two years previously to arable land under rotation or monoculture of maize, and long-term arable land under rotation or monoculture of maize. The highest suppression of the soilborne pathogen *R. solani* AG3 was measured in grassland turned into monoculture of maize. Using in vitro screening for antagonistic isolates against *R. solani* AG3, higher numbers of such isolates were found in soil under permanent grassland and under grassland turned into arable land than in soil under arable land. The results supported our hypothesis of a positive correlation between microbial diversity and the disease-suppressive capacity of soil, as higher microbial diversities were measured in soil samples from the permanent grassland and grassland turned to arable land than in the long-term arable land under rotation. Moreover, by applying a quantitative real-time PCR assay to study the abundance of the *prnD* gene (the gene encoding the biosynthesis of the antibiotic pyrrolnitrin) in the different treatments, higher densities of these genes were detected in the permanent grassland and in grassland turned to arable land, whereas in the arable land the *prnD* genes were present at low densities or absent.

SOIL AMENDMENT AND TILLAGE Organic amendments such as manure, compost, and cover crops can positively affect the disease suppressiveness of soil. For instance, composts can suppress *Pythium* and *Phytophthora* root rot (54) as well as *Ralstonia solanacearum* (99). Organic amendments can be combined with the application of biocontrol agents such as *Trichoderma* or *Gliocladium* to control *Rhizoctonia* diseases, as shown with sheath blight control on rice (9). During decomposition of organic matter in soil, the soil ecosystem is subjected to "oligotrophication," and the ratio of oligotrophic (K-strategist) to copiotrophic (r-strategist) organisms changes during microbial succession (120). The range of this ratio has been associated with general disease suppression (119). Hoper et al. (56) modified the level of suppressiveness to *Fusarium* wilt by adding clay minerals to a conducive soil. Higher microbial densities resulted from this treatment and the degree of soil suppressiveness increased. Minimum-till or no-till cultivation may also lead to increased disease severity by pathogens that survive better when infested crop debris remain on or near the soil surface. For example, root rot and bare

patch disease of wheat caused by *R. solani* AG8 are favored by reduced or no-till treatments in the U.S. Pacific Northwest and in Australia. Abawi & Crosier demonstrated the influence of the reduced tillage practices on root rot severity and yield of snap beans, as beans grown in rototilled and chisel-plowed plots had significantly higher root rot severity than those grown in the conventionally plowed plots (2).

Knowledge on microbial communities and the major groups of microorganisms involved in the disease suppressiveness of soil is fundamental to a better understanding of the relevance of microbial diversity to disease suppression. Van Bruggen and Semenov (119) proposed that the microbial community structure and the time required to return to the initial state after application of various disturbances or stress could be characteristic for disease suppression in soil. Agricultural management can be directed toward maximizing the quality of the soil microbial community in terms of disease suppression, if it is possible to shift soil microbial communities.

CONCLUSIONS

Taken together, the studies discussed in this review indicate that the microbial community structure of soil does, in many instances, indeed have a bearing on the suppressiveness of plant pathogens. However, we are far from understanding the exact mechanisms in the complex microbial communities of soil that often underlie the enhanced disease suppression. Although suppressiveness is very likely to be related to microbial community structure with a basis in (antagonistic) functions, questions remain in respect to the organisms or combinations of organisms that are mechanistically involved and their activities that are important for the suppressive effects. The further development of molecular assessment tools, in particular including specialized DNA microarrays, to describe the antagonistic status of soil is a challenge for a future that may bring more understanding of, and "light" in, the dark aspects of soil.

Moreover, the two drivers of microbial community structure, plant type and soil type, exert their effects in a complex manner. The fact that in some situations the soil and in others plant type is the determining factor affecting the soil microbial community may relate to the effects being either stronger or weaker in accordance with the relative strength of the selective forces exerted by soil or the plant. Also, this determining factor may be related to the complex microbial interactions in soil, including interactions between microorganisms and soil and microorganisms and plants. We therefore propose that relative strengths, on a scale 0–100%, be attributed to the players in the tripartite relationship of plant-soil-microorganism (Figure 2). It might be possible, in our view, to use this concept as an emerging overarching model into which novel data might be fed as they appear. Such data would then serve to enable a better prediction of the effects of soil and crop management regimes on microbial communities as related to disease suppressiveness.

One key element, the effect of time and space in soil, remains somewhat undervalued so far in this review. Plants clearly affect microbial communities and

disease suppressiveness, but to what extent in time and space can we expect this effect to persist? An improved understanding of how far the beneficial effects of plants extend in space and time will be another major challenge for future work. Further, we have not considered how fluctuations in the abiotic conditions of soil (in particular soil moisture content and temperature) might confound the principles outlined and the relationships between the two main drivers of microbial community structure, plant and soil type, the microbial communities and the resulting disease suppressiveness of the system.

To obtain more knowledge in this broad and intricately related area, it is important to promote collaborations between soil microbial ecologists, plant pathologists, and agronomists. A multi-pronged approach is clearly needed, and given the complexity of the systems assessed, studies will have to be made on a case-by-case basis. This is certainly a promising, albeit pain-staking, endeavour on the road to devise wider practical applications.

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