Annual Review of Phytopathology

Organic Amendments, Beneficial Microbes, and Soil Microbiota: Toward a Unified Framework for Disease Suppression

Giuliano Bonanomi,[1,4] Matteo Lorito,[1,2,4]
Francesco Vinale,[1,2] and Sheridan L. Woo[2,3,4]

[1] Department of Agricultural Sciences, University of Naples Federico II, 80055 Portici (NA), Italy; email: lorito@unina.it

[2] Institute for Sustainable Plant Protection, National Research Council (IPSP-CNR), 80055 Portici (NA), Italy

[3] Department of Pharmacy, University of Naples Federico II, 80131 Napoli (NA), Italy

[4] Task Force on Microbiome Studies, University of Naples Federico II, 80131 Napoli (NA), Italy

Annu. Rev. Phytopathol. 2018. 56:1–20

First published as a Review in Advance on May 16, 2018

The *Annual Review of Phytopathology* is online at phyto.annualreviews.org

https://doi.org/10.1146/annurev-phyto-080615-100046

Keywords

soil microbiota, beneficial microbes, biocontrol, soilborne pathogens, ^{13}C-CPMAS NMR

Abstract

Organic amendments (OAs) and soilborne biocontrol agents or beneficial microbes (BMs) have been extensively studied and applied worldwide in most agriculturally important plant species. However, poor integration of research and technical approaches has limited the development of effective disease management practices based on the combination of these two bio-based strategies. Insights into the importance of the plant-associated microbiome for crop productivity, which can be modified or modulated by introducing OAs and/or BMs, are providing novel opportunities to achieve the goal of long-term disease control. This review discusses novel ways of functionally characterizing OAs and how they may be used to promote the effect of added biocontrol agents and/or beneficial soil microbiota to support natural suppressiveness of plant pathogens.

INTRODUCTION

Increasing public awareness about sustainable crop and vegetable production has prompted research into low-input agricultural management practices. However, considerable losses are still caused by soilborne plant pathogens, which are difficult to control with synthetic chemical pesticides. The global ban of methyl bromide, which is associated with restrictions on the use of alternative soil fumigants (74), has further increased the need for methods providing acceptable levels of disease control but limited side effects on the environment.

In this context, the use of organic amendments (OAs), possibly integrated with applications that introduce or promote the activity of beneficial microbes (BMs), has been proposed but its potential is not yet fully explored. Control of soilborne pathogens has been obtained by using green and animal manure (61), organic wastes from agro-industry (28), compost (40), and, more recently, biochar (31). The list of affected pathogens includes bacteria (e.g., *Ralstonia solanacearum*), oomycetes (e.g., *Phytophthora* spp. and *Pythium* spp.), and fungi (e.g., *Fusarium* spp., *Rhizoctonia solani*, *Sclerotinia* spp., *Sclerotium* spp., and *Verticillium dahliae*) (11). In the case of BMs, their usefulness is illustrated by the large number of products available worldwide (69).

Despite the recognized potential value of OAs and BMs, lack of predictability and consistency still limit their adoption in commercial agriculture. It has been reported that OAs are not effective for disease control and in quite a few cases may enhance plant disease intensity (77, 103, 121). Undesired side effects of BMs seem to be less frequent, but their efficacy can vary greatly when applied to different cultivation systems and soil types or in diverse climatic conditions (114). Therefore, an improved understanding of the mechanisms that regulate OA-based suppressiveness, as well as pathogenic and antagonistic microbe interactions, will help to develop new, more-reliable product applications.

This review explores the opportunity provided by powerful chemical and genetic tools to study OA nature, application, and mechanisms of action in relation to the current understanding of microbial ecology in the soil. The two topics are linked by addressing the issue of the nutritional role of OAs and the effect on the virulence and aggressiveness of soilborne plant pathogens, BMs, and native microbiota. Finally, we discuss the principles for applying effective combinations of different OA types and BMs.

HISTORICAL OVERVIEW

Organic Amendment for the Control of Soilborne Pathogens

In the past 70 years, hundreds of papers, based on thousands of experiments, have reported the suppressive effect of different OA types on 78 plant pathogen species (**Figure 1**). Early scientific evidence dates back to the 1940s and 1950s, when crop residues and N-rich organic wastes were found capable of controlling *R. solani*, *Fusarium oxysporum*, and *Verticillium albo-atrum* (97, 116). In the 1960s, the research effort led by G.C. Papavizas studied the effect of crop residues on *Fusarium* species, *R. solani*, and *Thielaviopsis basicola*, among other pathogens (1, 86). With the exception of a few papers linking OAs to soil fungistasis (67), interest in the biocontrol properties of OAs declined in the 1970s. It recovered in the next two decades thanks to the work of the Hoitink group on the suppressiveness of some peat-based potting mixes and compost (26, 44, 70). According to a meta-analysis of this topic based on 2,423 experiments, OAs were indeed suppressive in 45% of cases and had a nonsignificant effect in 35% of cases, although there was a significant increase in disease incidence in 20% of the tests (11).

Compost remains the most widely studied OA type, with more than 1,000 related papers, followed by crop residues, organic wastes from the agro-industry (e.g., from olive, paper, and fish

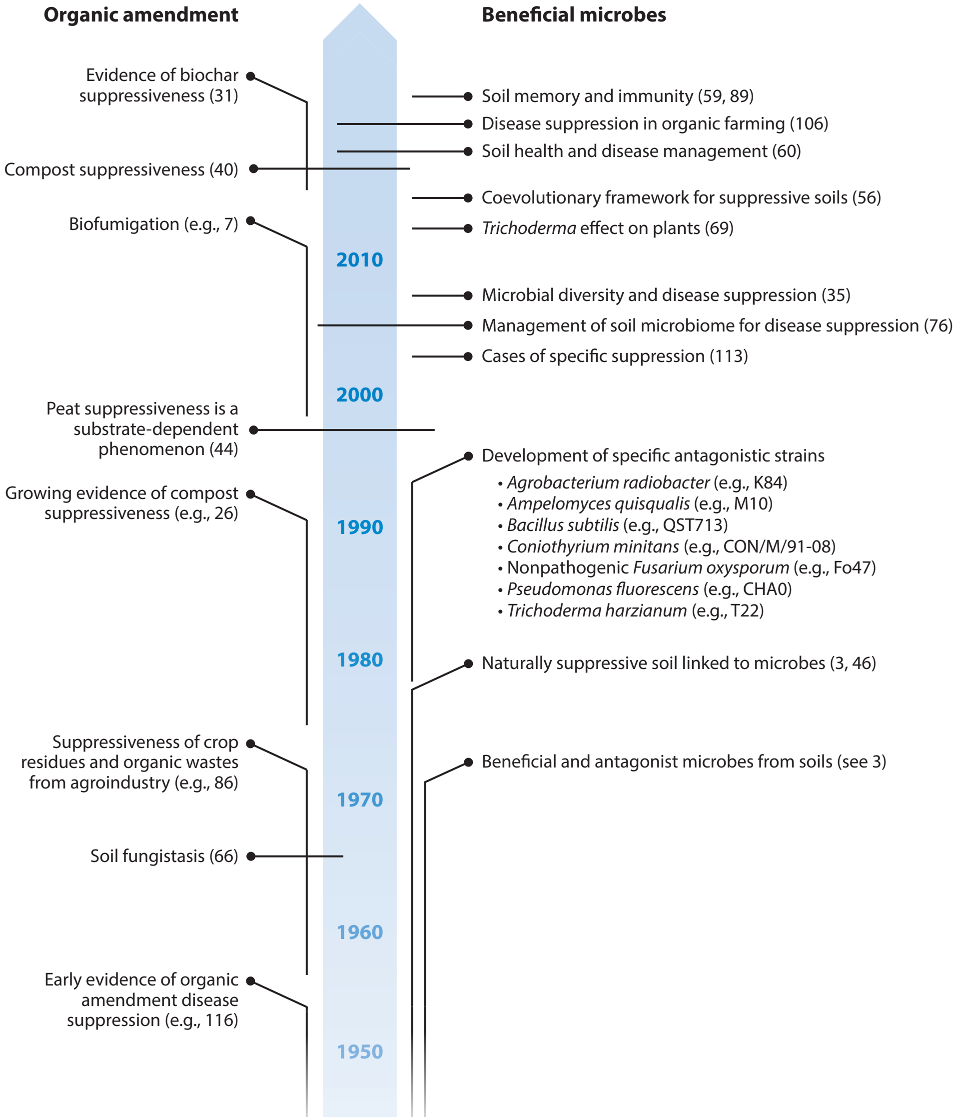

Figure 1

Historical perspective of the research and main scientific achievements on organic amendments and beneficial microbes for control of soilborne pathogens. The length of crossing horizontal lines indicates the level of integration between the two main topics.

and meat meal), and peat-based substrates (11). In addition, OAs made of biochar have received considerable attention because of their activity on both soilborne and airborne diseases (31, 80). The most popular plant pathogen target in the OA-related literature has been *R. solani*, with more than 700 experiments published, followed by *Pythium* (473), *Fusarium* (259), and *Phytophthora* species (186). The number of papers reporting tests performed with *Verticillium* spp., *Sclerotinia* spp., *T. basicola*, *Sclerotium rolfsii*, or *Macrophomina phaseolina* is less than 100 (11).

Beneficial and Antagonistic Microbes

The link between soil suppressiveness and the presence of BMs acting by such mechanisms as nutrient competition, direct antagonism, parasitism, and antibiosis was suggested by studies in the 1930s (38, 109), confirmed in the 1950s and 1960s (83), and finally established by the work of Baker & Cook and others in the 1970s (3) (**Figure 1**). Concurrently, the development of ever more sophisticated techniques for microbe isolation and characterization allowed identification of a variety of bacteria and fungi able to act beneficially when proliferating in the soil for disease control and plant-growth promotion. Species reported in the 1970s included those belonging to the *Agrobacterium*, *Pseudomonas*, *Bacillus*, *Streptomyces*, and *Trichoderma* genera. The following step (from the mid-1980s and through the 1990s) was to study and select particularly active strains for use in converting soils or growth substrates from conducive to suppressive. This led to the marketing of a broad range of plant protection products, which are officially registered in no fewer than 100 countries worldwide, with the most successful based on one or two BMs (see Reference 118 for a review of *Trichoderma*-based products). It took approximately 10 more years to generally recognize that often the same strains or species found useful for pathogen control could also act as plant growth–promoting agents able to increase yield and/or improve quality in both conventional and organic farming. Results have focused on understanding the mechanism of interaction between soil microbes (e.g., beneficial versus pathogenic) or the biocontrol agent and the plant (69). The fruits of such efforts have provided accurate genetic information linked to specific functions, microbial compounds positively affecting plant metabolism, and more effective and reliable BM strains. However, the rush for the best strain or BM-active principle appears to have become disconnected from the idea of exploiting soil general suppressiveness, as demonstrated by the relative scarcity of studies that link the two topics (**Figure 1**). Finally, the entry of biocontrol-related research into the microbiome area promises to close this gap, reconnecting research on selected BMs and the broader microbial community. The next technology advancement may come from the recognition that (*a*) soil- and plant-related microbiomes are shaped by the plant and define its health status and modulate the efficacy of both pathogens and specific BMs even following an inundative application; (*b*) beneficial properties of the soil microbiome and the activity of biocontrol agents can be enhanced by using a well-characterized OA; and (*c*) the availability of powerful chemical and genetic analysis tools may allow identification of the main factors that determine the outcome of the complex plant-microbe interactions following BM and OA application.

ORGANIC AMENDMENTS: FROM SNAKE-OIL REMEDY TO A RELIABLE TOOL FOR DISEASE CONTROL

Practical application of the capacity of OAs to control plant diseases is still limited despite the thousands of published supporting tests. The main reasons lie in the inconsistency of results and difficulty predicting the effect in different pathosystems (93, 102). A key issue is the lack of knowledge regarding the chemical, biochemical, and biological factors responsible for effective OA-based disease suppression. A meta-analysis that compared 81 parameters, based on 643 correlations between OA traits and suppressiveness, found only weak relationships (10), with the most promising factor being the rate of fluorescein diacetate (FDA) hydrolysis or soil respiration, total microbial biomass, and population density of fluorescent pseudomonads and *Trichoderma*. Thus, an in-depth understanding of the interactions between pathogens, BMs, and native microbiota may help to apply OAs successfully. In this context, we believe that an improved definition of OA chemical composition and properties could assist in using OAs successfully to promote microbial activity related to disease control.

Suppressive Effect of Organic Amendments: The Importance of Chemical Composition

Various mechanisms have been described to explain OA suppressiveness, including the release of fungitoxic compounds, such as glucosinolates from Brassicaceae (61) or ammonia (101), during decomposition in the soil. In most cases, however, the activity of soil microbiota is more directly involved. OAs increase biomass and thus may enhance antagonism of the resident microbes against pathogens, with a suppression effect found in the spermosphere and rhizosphere (84). By modulating BM populations, OAs can also induce a systemic resistance in the host plants, as already demonstrated for compost (122) and biochar (32).

The link between OA chemical composition, BM activity, and disease suppression was first demonstrated in a simplified system. Dark peat was not as suppressive to *Pythium* damping-off when compared to light peat because of its low carbohydrate content (8), a property that made dark peat unable to sustain the life of biocontrol agents such as *Pseudomonas* species. Light peat was richer in carbohydrates and promoted microbial activity, as measured by fluorescein diacetate, indicating that disease suppression is a substrate-dependent phenomenon (44).

Defining Organic Amendment Quality: Beyond the C:N Ratio

OAs made from a broad variety of materials have been used, including raw crop residues and organic wastes, substrates like peat and compost, and biochar, i.e., the material generated through pyrolysis at temperatures ranging from 200°C to more than 1,000°C. Consequently, the organic carbon fraction of such materials is chemically heterogenic. In the 1950s and 1960s, OA chemistry was defined using parameters such as cellulose and lignin content, and the C:N ratio index. Even today, most publications on this topic still use the C:N ratio as the main descriptor of organic matter quality. However, the latter parameter was originally developed to measure the kinetics of organic matter decomposition in soil (100), and its use as a quality index has been heavily criticized. According to studies on C-cycling in natural ecosystems, the C:N ratio is a poor predictor of leaf litter decomposition in tropical (42) and temperate forests (17). Moreover, the limited usefulness of C:N ratio measurements to predict the impact of OAs on some ecosystem functions has been recently demonstrated, including effects on phytotoxicity toward root proliferation (16), soil structural stability (92), soil water repellency (25), and organic C-cycling (49). The C:N ratio refers to the total amount of organic C independent of the biochemical composition, which may range from simple sugars to highly aromatic materials recalcitrant to decomposition, such as lignin or biochar. This alone could explain the unsuccessful use of the C:N ratio to predict soilborne disease suppression by OAs (10). Indeed, OAs with similar C:N ratios might demonstrate completely different properties in the soil. Some compounds (e.g., simple sugars, cellulose, and sawdust powder) with a high C:N ratio may stimulate proliferation of microbes competing for mineral N, thus impairing the saprophytic growth and infection by *F. solani* (97). However, some wood biochars with very high C:N ratios do not induce N starvation or limit the saprophytic growth of phytopathogens. Conversely, several studies have shown that the temporary accumulation of ammonia or nitrous acid in acidic soils, following application of meat meal with a very low C:N ratio (below 10–12), kills the microsclerotia of *V. dahliae* (101). Moreover, this index is unable to discriminate meat meal from stabilized composts or humus-like materials, which, despite the low C:N ratio, mineralize N very slowly. In addition, the C:N ratio of OAs is not related to the response of soils in terms of fungistatic activity. This has been demonstrated recently in a study using 42 OAs, where the recovery of the inhibitory effect, which is typically lost, after the typical reduction occurring in the early phase following the application, was independent of the C:N ratio (15).

^{13}C Cross-Polarized Magic Angle Spinning Nuclear Magnetic Resonance–Based Characterization

The limited value of the C:N ratio as a predictor of disease suppression makes it necessary to achieve better characterization of OA chemistry. Several high-throughput methods have been used to characterize organic matter, including pyrolysis–gas chromatography/mass spectrometry (47), near-infrared reflectance (37), and Fourier-transform infrared spectroscopy (48). However, none of them have proven useful to describe OA composition in relation to disease suppression. Although these methods provide a very detailed description of OA composition at a molecular level (110), they have provided information that is difficult to convert into a user-friendly index that can be understood and used by agronomists and farmers.

In this regard, the ^{13}C cross-polarized magic angle spinning nuclear magnetic resonance (^{13}C-CPMAS NMR; hereafter, ^{13}C NMR) spectroscopy is considered to have several advantages over other techniques. It is carried out in solid state by using the raw organic substrate, which permits direct evaluation of OA chemical composition without the bias due to an extraction procedure (63). Furthermore, and most importantly, ^{13}C NMR is able to identify key chemical features that characterize the different OAs, and these data are relatively simple to analyze and relate to soil functions. In general, ^{13}C NMR spectra are usually divided into seven main regions associated with different C types (57, 75); i.e., 0–45 ppm alkyl C; 46–60 ppm methoxyl and N-alkyl C; 61–90 ppm O-alkyl C; 91–110 ppm di-O-alkyl C; 111–140 ppm H- and C-substituted aromatic C; 141–160 ppm O-substituted aromatic C (phenolic and O-aryl C); and 161–190 ppm carbonyl C. Measuring the relative abundance of these regions may provide a rapid and effective description of the C chemical quality of OAs (**Figure 2**). For instance, sawdust or grass crop residues are very rich in the O-alkyl C and di-O-alkyl C fractions that are mainly associated with simple sugars and carbohydrates. Biologically stabilized OAs such as peat and compost usually have lower O-alkyl C and di-O-alkyl C fractions but contain an alkyl C component related to lipids (**Figure 2**). Lignin-rich materials like sawdust, as well as lignified crop residues, have considerable peaks in the aromatic regions. The OAs derived from animal tissues (e.g., meat and fish meal) can be easily distinguished by their high relative content in carbonyl C and alkyl C fractions, combined with the low relative abundance of O-alkyl C type (**Figure 2**). Finally, biochar of any origin produced at temperatures greater than 500°C demonstrates a unique spectrum, with a major peak at 125–130 ppm characteristic of aromatic C produced during pyrolysis. Biochar produced at lower temperatures (e.g., 300°C) has a different profile, showing two main peaks in the aromatic and alkyl C types (**Figure 2**).

Boehm et al. (8) made the first successful attempt to use this technique to discriminate suppressive from conducive peat for the control of damping-off caused by *Pythium ultimum*, demonstrating that light peat, which is richer in the O-alkyl C fraction, was suppressive because of increased carbohydrate availability that supported the antagonistic activity of *Pseudomonas* species. By contrast, the much older brown peat depleted in the O-alkyl C fraction was unable to feed the antagonistic microbe that suppressed the pathogen. This pioneering study inspired further research, although ^{13}C NMR chemical characterization was not always useful in identifying the correlation between suppressiveness and organic C composition of compost and native soil organic matter (23, 85, 99). The meta-analysis performed on all the available studies confirmed this finding (10).

LINKING SOIL MICROBIOME FUNCTIONS TO ORGANIC AMENDMENT CHEMISTRY

It is clear that no single parameter, including data from ^{13}C NMR–based analysis, is sufficient to effectively predict the suppressiveness of OAs to soilborne pathogens. This may be due to the fact

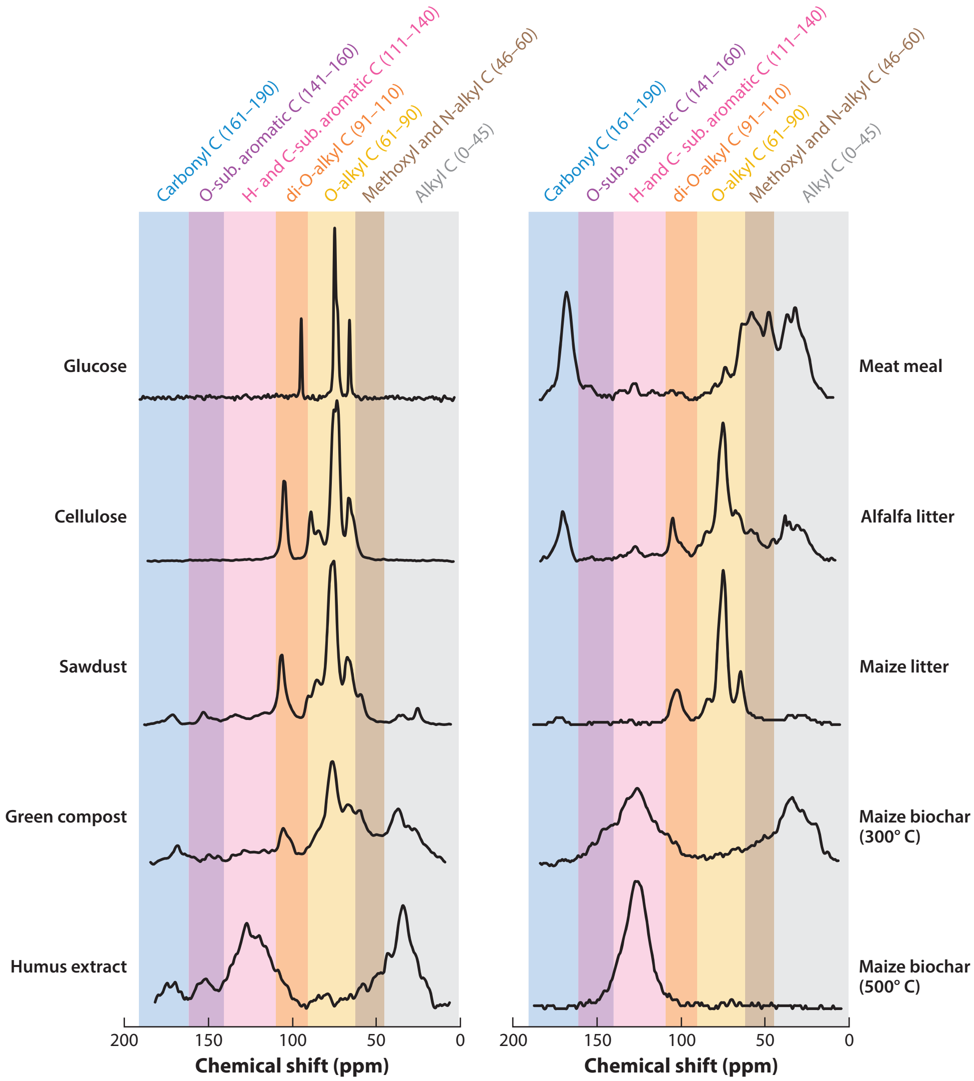

Figure 2

Chemical diversity of typical organic amendments used in agriculture defined by ^{13}C cross-polarized magic angle spinning nuclear magnetic resonance. Reference spectral regions and corresponding C types are included.

that the mechanisms of disease suppression are indirect, and, in most cases, the effect is mediated by BMs or the entire soil microbiome. In general, microbiome composition is determined by the chemical components of the native soil, with the main factors being soil organic matter (82), root exudates (5), and exogenously added OAs (65). This is analogous to what has been demonstrated in animals and humans, where gut microbiome composition is shaped by the diet (4) and the amount and quality of OAs may play a major role in defining the composition and functions of soil microbial communities. To this end, ^{13}C NMR spectroscopy could provide a powerful disease suppression prediction tool if the compound identification data are associated with activities and the structure of the soil microbiome.

Organic Amendment Controls the Soil Microbiome

The soil is a bioreactor containing a complex microbiota, possibly made up of thousands of bacterial and hundreds of fungal strains that coexist by exploiting a variety of organic carbon sources (33). Their scarcity, often found in agricultural soils, drives intense competition among microbes. By providing a diversified food base, OAs may alleviate starvation for organic C and, consequently, modify the interactions and equilibrium of microbe populations. This phenomenon was characterized in earlier studies as well as in more recent, next-generation sequencing-based research (2, 50, 65). The impact on the soil microbiome depends on timing, the OA type, and the amount and frequency of the application (24). It may be relatively fast, resulting in a dramatic shift in population composition only a few days after treatment (115), with the effect lasting months or even years (53). Long-term experiments in organic farming based on repeated applications of OAs confirmed that over time this practice promotes microbial diversity in the soil and crop yield (41, 71). Likewise, a more recent long-term study reported an increased abundance of acidobacteria, firmicutes, and especially enchytraeid worms (13).

The main question is how the potential of OAs to shape the soil microbiota can be reliably used to enhance the activity of BMs without stimulating pathogen populations and virulence. Recently, Inderbitzin et al. (50) reported that soil applications of broccoli residues and crab meal enhanced the relative abundance of *Pseudomonas* and *Streptomyces* with antagonistic activity toward wilt-causing *Verticillium*, thus contributing to disease suppression. In many cases, a simplified research strategy has been used, where OAs of different origins are applied and the subsequent changes in the soil microbiome determined. Obviously, for significant progress in our understanding of OA effects on the soil-plant microbiome, a new approach is required in which feeding preferences for OA-based nutrients of plants and saprophytic, beneficial, and pathogenic microbes are considered.

Unraveling the Feeding Preference of Microbes and Plants

When applied to the soil, OAs affect all living components, including plants and autotrophic, heterotrophic, and saprophytic microbes. An in-depth understanding of the effect of OAs upon each different trophic group would be an important step toward the sound use of such materials. However, our current understanding of the feeding preference, e.g., during the saprophytic phase of either pathogenic microbes or BMs, is generally inadequate for reliably predicting the impact of OAs. To fill this gap, recent studies have combined ^{13}C NMR–based characterization of many types of OAs with a multitrophic bioassay to distinguish the nutritional responses of different components of the soil system (12, 16, 19).

^{13}C NMR analysis reveals a clear difference in the feeding preferences of the diverse organisms, especially when plants and microbes are compared in terms of organic compounds utilized (**Figure 3**). In general, plant root development is inhibited by OAs containing a high content of labile C, i.e., O-alkyl C and di-O-alkyl C, as well as carbonyl C, whereas root proliferation was stimulated in substrates rich in aromatic C types. In contrast, the microbes thrive on OAs rich in sugars and cellulose, i.e., O-alkyl C and di-O-alkyl C fractions, and showed poor development on materials rich in lignin and aromatic C types. Growth of all tested fungal species was positively correlated with methoxyl and N-alkyl C and the O-alkyl C regions but negatively associated with the presence of two aromatic C regions (**Figure 3**). Interestingly, *Trichoderma harzianum*, *Aspergillus niger*, and *Fusarium oxysporum* showed only small differences in their responses. However, the soil-borne fungus *R. solani*, which may thrive as a plant pathogen as well as a saprophyte, produced a distinct intermediate pattern between plants and fungi. Compared to fungi, bacteria demonstrated a lower degree of correlations between nutritional response and the different C types found in the

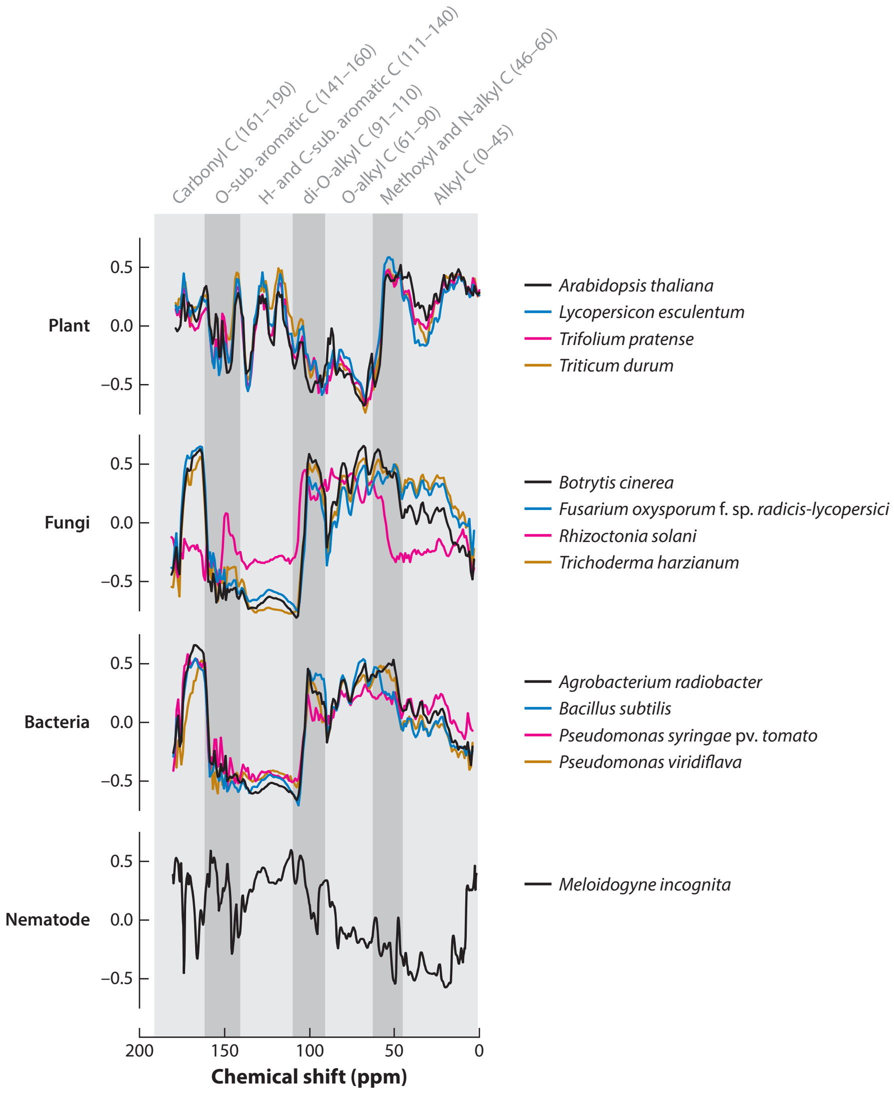

Figure 3

Response of plants (root proliferation), fungi (hyphal growth), bacteria (proliferation), and nematode (survival) to different C types of organic amendments. Data are correlations (Pearson's r) with ^{13}C cross-polarized magic angle spinning nuclear magnetic resonance spectral signals of organic amendments.

OAs. Interestingly, *Agrobacterium tumefaciens* showed poor saprophytic abilities and a distinct feeding preference comparable to that of BMs such as *Bacillus*, *Pseudomonas*, and *Lysobacter* (**Figure 3**). Some interspecific differences were also noticed within the *Pseudomonas* genera in comparisons of *Pseudomonas fluorescens*, *Pseudomonas viridiflava*, and *Pseudomonas syringae* pv. *tomato* (19). Recently, the response of the nematode *Meloidogyne incognita* was also investigated when challenged with a range of OA types. The nematode showed distinct preferences, demonstrating a response more similar to that of higher plants than to that of bacteria and fungi (**Figure 3**).

From a technical point of view, an extensive correlation analysis of all signals performed on restricted NMR spectra sections, as compared to the wider areas typically used in most studies (57, 75), allowed more detailed determination of the feeding preferences of different organisms (12, 49). Moreover, analysis of restricted (selected) resonance intervals within the alkyl C, methoxyl C, O-alkyl C, and di-O-alkyl C spectral regions may help gain insights into specific effects of OAs, such as why plant root growth is negatively affected by labile C but positively associated with signals related to plant tissue lignification. The opposite response was observed for bacteria and, particularly, fungi (12). Clearly, a more in-depth study that systematically compares microbial growth over a wide range of OA types is required. The great diversity of soil microbes and OA chemicals makes this a considerable research challenge, especially given the limited availability of solid-state ^{13}C NMR spectroscopy facilities for this type of investigation. Part of the solution is to make the data already obtained in various laboratories worldwide openly accessible.

COMBINING ORGANIC AMENDMENTS AND BENEFICIAL MICROBES FOR DISEASE SUPPRESSION

OA profiles of feeding preferences for plants and microbes may help to build reliable guidelines for a combined application of organic matter and BMs to suppress soilborne pathogens.

Positive and Negative Effects of Organic Amendments on Plants

Application of OAs to soil has direct effects on plant growth and development that range from inhibition to growth promotion. Characterization of more than 100 organic substrates by ^{13}C NMR associated with bioassays performed on more than 20 plant species allowed C types with inhibitory or stimulatory effects to be identified (12, 16). Undecomposed OAs, such as plant residues and by-products from agro-industrial processes, typically have broad nonspecific phytotoxic effects on root growth, as demonstrated by three studies made with 21 (68), 64 (16), and 65 (81) different plant residues, respectively. Bonanomi et al. (21) reported that phytotoxicity of leaf and root debris depends on the plant functional type or origin, with tissues from nitrogen-fixing species being the most toxic, followed by forbs, woody species, and grasses. Root growth was generally negatively associated with O-alkyl C and di-O-alkyl C contents of OAs but stimulated by the presence of lignified plant tissue. Raw, N-rich organic wastes from animal origins such as meat and fish meal were particularly phytotoxic and could be easily identified by ^{13}C NMR because of their very high carbonyl C content.

Decomposition due to microbes plays a key role in determining the phytotoxic effect of OAs by modulating the relative abundance and activity of inhibitory compounds in the soil ecosystem. A number of studies have established that the phytotoxicity of plant residues and undecomposed organic waste is a transient phenomenon that lasts from a few days to several weeks (91, 104). For example, 5 to 30 days is the typical toxic time lag of crop residues when soil environmental conditions are within the normal range for moisture and temperature, followed by a quick decline and complete disappearance of toxicity after 60 to 90 days of decomposition (21). Unsurprisingly, after months (e.g., compost) or millennia (e.g., peat) of decomposition, biologically stabilized OAs show no phytotoxic effects. ^{13}C NMR may also be useful in identifying the state of maturation of OAs (98), where a progressive decrease in O-alkyl C together with an increase in the alkyl C region are indicators of biological stabilization of organic substrates.

A recent report suggests that crop residues may also have a species-specific, long-lasting inhibitory effect on plant growth (78). The specificity of the process has been associated with the release of extracellular DNA (exDNA) in the soil during the decomposition of plant debris. The study proposes that accumulation of fragmented (fragment size between 50 and 2,000 bp) extracellular self-DNA (i.e., DNA originating from conspecifics) produces species-specific inhibitory effects. Similar findings were also reported for bacteria (6) and fungi (79).

Considering both the short- and long-term nonspecific phytotoxicity of OAs, as well as the species-specific toxicity of crop residues, is important for sound, effective implementation at the field level. For example, seeding or seedling transplant should be delayed at least 2–3 weeks after the application of raw OAs. This avoids the risk of phytotoxicity or increased incidence of soilborne pathogens, as reported for different formae speciales of *F. oxysporum* (119, 120), *Pythium* spp., and *R. solani* (9). Indeed, meta-analysis of the literature (11) indicates that this was the case in many experiments.

Managing Diseases and Shaping Beneficial Microbiota in the Soil

The addition of OAs to the soil may provide a food base for BMs but may also support the growth of pathogens. In terms of saprophytic capabilities, soilborne fungi are simply classified as strong (e.g., *R. solani*, *F. oxysporum*, some *Pythium* species) or weak saprotrophs (e.g., *V. dahliae*, *T. basicola*, several *Phytophthora* species). Limited knowledge is available on how these microbes exploit complex food sources such as crop residues, compost, and biochar. Instead, the feeding preference profiles allow substantial differences among species with radically different habits to be appreciated (e.g., pathogens such as *R. solani* versus antagonists such as *T. harzianum*) (**Figure 3**). However, in contrast to plants, only a handful of feeding preference profiles are available for microbes and are based on fewer than 20 organic substrates characterized by ^{13}C NMR. This limits the possibilities of improving OA-based field applications to regulate populations of beneficial and pathogenic microbes. In contrast, green manuring (i.e., the incorporation of crop residues in soil) may increase populations of pathogens, as found with residues from N-fixing legumes, which controlled *T. basicola* but stimulated *Pythium* spp. and *R. solani* (72, 90). The effect depends on the plant origin of the residue and its (*a*) functional group (e.g., herbaceous, nitrogen-fixing legumes, Brassicaceae, and grasses); (*b*) effect on soil biogeochemical properties (e.g., nitrogen-fixing legumes, brassica); (*c*) category (monocots versus dicots) and taxonomic groups (e.g., cereals and legumes); and (*d*) tissue maturity level. ^{13}C NMR analysis would allow, for example, selection of the appropriate plant origin and tissue maturity level to reduce the risk of negative side effects on disease incidence.

A similar approach could be followed to improve the usefulness of fortified compost and other biofertilizers. In several cases, the combination of BMs with OAs resulted in a synergistic positive effect in terms of plant-growth promotion and disease control (34, 96). For example, *Fusarium* wilt of banana was inhibited by using *Bacillus* raised in a solid fermentation on a manure substrate (95). However, OA-BM combinations have been mostly made by using locally available materials and simply tested by monitoring their performance over time. Also in this context, ^{13}C NMR–based nutritional profiling would aid in the preliminary identification of OA properties that could support the growth of different antagonistic microbes according to their feeding preferences.

Induction of systemic resistance in plants by compost was first demonstrated in cucumber by Zhang et al. (122) for soilborne (i.e., *P. ultimum* and *Pythium aphanidermatum*) and airborne pathogens (i.e., *Colletotrichum orbiculare*). Subsequent studies confirmed that different compost types (55, 87) and biochar (32) can stimulate plant defense responses. However, current understanding of the relationships between OA chemistry and the induction of systemic disease resistance in the plant is limited. This process is known to be activated by chemical compounds, including some found in OAs, that are applied exogenously or produced by plant-associated nonpathogenic microbes. For instance, enhanced resistance was obtained when compost was added to a peat mixture that was previously colonized by a biocontrol strain of *Trichoderma hamatum*, with the authors concluding that in this case only the fungus activated a systemic response in the plant (45). Thus, selected OAs could modulate the activity of biocontrol agents in terms of both direct and plant-mediated pathogen inhibition.

Organic Amendment Decomposition and Disease Suppression

Once incorporated into potting mixtures or soil, all OAs, because of microbial decomposition, release compounds that support or stimulate various biological processes. The activity of heterotrophic microbes that feed on organic matter progressively alters OA chemistry, which in turn promotes a microbial turnover that further changes OA composition. This process makes the disease suppression ability of OAs a dynamic and continuously modified trait. In this regard, the meta-analysis performed by Bonanomi et al. (10) indicates that the OA decomposition stage had a significant effect in 73% of the studies analyzed ($N = 426$) and thus plays an important role.

Early investigations recognize that after the application of OAs, soil suppressiveness may dramatically change over time, either increasing, decreasing, remaining unchanged, or demonstrating more complex responses, e.g., U-shaped or ∩-shaped dynamics (28, 39, 93). Decomposition-driven changes are well known only for peat because this material generally loses its suppressiveness during the process of aging (8). In contrast, the complex relationship between OA maturity and suppressive activity is poorly understood for compost, crop residues, and organic wastes. For instance, Tuitert et al. (105) found that undecomposed as well as mature composts were suppressive to *R. solani* damping-off, whereas partially decomposed materials were conducive. In the case of crop residues, an analysis of nine studies of comparable duration indicates that disease suppression toward *Pythium* spp. consistently increases during decomposition, whereas inhibition of *R. solani* often decreases during breakdown (10). Such different outcomes make it difficult to predict the persistence of significant disease suppression in the short (days), medium (weeks), and long (months to years) term after OA application. Again, a detailed description of initial OA chemistry made by ^{13}C NMR may help to predict the modifications, and the consequent effects on the microbiome, that the material will undergo when introduced into the soil. For instance, amendments rich in N and labile C, such as meat and fish meal, are subjected to deep changes in a time frame of hours and days (101), whereas biochar remains stable in the soil for decades or even centuries (111).

A Case Study: Disease Suppression by Application of Biochar and Terra Preta Substrates

The disease-suppressive properties of peat (44), crop residues (11), and compost (40) have been comprehensively presented elsewhere. Here, we focus on biochar, an OA that has recently received considerable attention. Biochar is a material generated through pyrolysis at temperatures ranging from 200°C to more than 1,000°C. It can be readily identified by ^{13}C NMR because of a prominent peak at 125–130 ppm in the aromatic C region (**Figure 2**). However, the quality of the initial organic feedstock (e.g., crop residues, wood, municipal waste, sewage sludge, manure, and animal bones) and pyrolysis conditions (i.e., temperature and oxygen availability) can deeply change its chemical profile. For instance, low-temperature biochar produced from wood and crop residues contains a considerable amount of bio-oils (**Figure 2**) (62).

In the past ten years, biochar has been reported to be capable of suppressing diseases caused by airborne and soilborne fungal pathogens, including *Botrytis cinerea*, *Leveillula taurica*, and *Podosphaera aphanis*; several formae speciales of *F. oxysporum*, *P. aphanidermatum*, *Phytophthora* *cactorum*, *Phytophthora cinnamomi*, and *R. solani* (31); the parasitic weed *Phelipanche aegyptiaca* (30); and the nematode *Pratylenchus penetrans* (36). The mechanism of action differs substantially from that of other OAs because biochar does not provide a readily available food base for soil microbes, whether pathogenic or beneficial (20, 58). During biomass pyrolysis, the rapid disappearance of easily degradable carbon sources and the enrichment of aromatic fractions make biochar an organic material capable of stimulating plant growth but not of acting as a food base for microbes. Instead, its porous structure can physically sustain soil microbe colonies by providing sites not reachable by grazers or predators such as mites, collembola, protozoans, and nematodes (64, 112). For the same reason, biochar can be used as a carrier for a variety of BMs. Postma et al. (88) reported that biocontrol agents (i.e., *Pseudomonas chlororaphis*, *Bacillus pumilus*, and *Streptomyces pseudovenezuelae*) extensively colonized the pores of bone biochar, and the combined formulation applied to the soil effectively reduced the incidence of diseases caused by *P. aphanidermatum* and *F. oxysporum* f. sp. *lycopersici* in tomato. Systemic induced resistance has also been considered as part of the biochar mechanism of disease suppression. However, to date, few studies have provided scientific support for this hypothesis (80).

A promising but still untested possibility for the development of novel biocontrol products is to combine biochar, BMs, and an appropriate organic food source. The application of biochar with other nonpyrolyzed OAs (e.g., manure, compost, and plant residues) has generated a number of commercially applied formulations termed terra preta–like planting substrates (e.g., see 117). In fact, specific combinations of biochar with nonpyrogenic OAs have been found to be very effective in promoting plant growth (18, 52), whereas their ability to suppress diseases remains untested. It is tempting to speculate that biochar and nonpyrogenic OA mixtures could provide both safe sites and food substrates for biocontrol agents, which would be important in the early phases of soil or rhizosphere colonization. Also in this case, defining the feeding profile preference could be very useful for identification of the best combination of treatments. Recent findings indicate that soil amendments containing a combination of wood biochar and alfalfa leaf litter applied for two consecutive years dramatically change the composition of the soil microbiome and suppress diseases on lettuce caused by *F. oxysporum* f. sp. *lactucae* or *Sclerotinia sclerotiorum*. Even more interesting, a statistically significant ($P < 0.01$) reduction of spotted wilt virus infection was detected on tomato (G. Bonanomi, G. Cesarano, D. Alioto, F. Scala, unpublished data).

Overall, biochar should be considered a promising tool to support soil suppressiveness to pathogens. In a few cases, biochar has been associated with undesired effects (27). However, the limited number of pathosystems tested and poor chemical characterization of the material used in most published studies do not currently allow the potential of biochar to be exploited as a safe, effective, and affordable tool for controlling plant pathogens.

Effect of Application Frequency of Organic Amendments

To adapt OA application to conventional agricultural practices, most studies have tested disease suppression effects after a single initial application, eventually followed by once per year treatment in the event of a long-term trial (73). This practice resulted in a pattern of alternating boom and bust of microbial activity, causing fluctuations and instability in the functionality of the soil system (43, 108). Interestingly, the few studies that examined the relationship between OA application frequency and soil microbiota demonstrated that frequent treatments increase enzymatic activities (29) and the presence of a biologically active microbial biomass (54). Unfortunately, because of the scarcity of specifically designed studies, it is not yet clear how the application frequency of OAs may influence disease suppression. In a recent report (14), repeated applications (i.e., every two days) of four OA types were able to increase soil fungistasis on *A. niger*, *B. cinerea*, and *Pyrenochaeta* *lycopersici* by shortening the time required for its restoration. Furthermore, it was confirmed that soil amendments have a time-dependent effect on fungistasis and pathogen inhibition, as the result was negative in the short term (e.g., hours to days) and positive in the medium term (e.g., weeks). Repeated applications of OAs reduced the time required for fungistasis restoration and hence the window of opportunity for pathogens to attack the plant. Moreover, the recurrent addition of easily decomposable organic compounds enhanced respiration and specific catabolic capabilities of the soil (14). The conclusion is that application frequency has the potential of significantly enhancing the usefulness of OAs as a soilborne pathogen biocontrol tool if the relationship between OA chemistry and efficacy is fully understood. Studies should take into account the duration of the soil-conditioning phase, the frequency and quantity of treatments, the variety and extent of the positive effects that OAs may have on the conditioned soil, and the time that applications remain effective.

Interactive Effects of Organic Amendments with Agronomic Practices

In experimental trials, OAs are usually applied using standard agricultural management practices, which include agronomic and crop protection treatments often based on fungicides, mineral fertilizers, herbicides, and insecticides that are known to have an impact on soil microbiota (22, 53, 107). Fumigants, for instance, indiscriminately kill both pathogenic microbes and BMs, altering the species composition and thus reducing the diversity and functionality of soil microbiota (94). The decreased biological diversity may change the outcome of competitive interactions of soil microbiota feeding on native organic matter, exogenous OAs, and root exudates, which may lead in some cases to a dissemination of aggressive pathogenic species. The use of soil fumigation following OA applications, an erroneous technique still practiced in several farming regimes, alters the soil microbiome, which could abolish the suppressiveness induced by OAs, thus favoring the long-term incidence and spread of soilborne diseases. Fungicides, as well as mineral fertilizers, have also been demonstrated to reduce microbiota diversity and functionality (24, 51). Clearly, there is a need for gaining insights into the compatibility of OA application with other agronomic practices in terms of beneficial effects on soil microbial functions.

CONCLUSIONS

To achieve the necessary reduction of chemical inputs, synergistic combinations of bio-based practices should be developed and widely applied. Well-characterized OAs used together with highly effective BMs can address the increasing problem of soilborne pathogen control, with an action mediated by and associated with the promotion of beneficial soil microbiota. Finally, both OAs and BMs could be produced by using wastes, residues, and a variety of organic materials, thereby supporting a green approach to a circular economy.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

This work was supported by the following grants: MIUR – PON (Linfa 03PE_00026_1 and Marea 03PE_00106); MIUR – GPS (DM29156 Sicura); BIP (Rete delle biotecnologie in Campania); Regione Puglia (SIX 1410-12/06/2015); and KENYA-AID (10306/CEFA/KEN).

LITERATURE CITED

1. Adams PB, Papavizas GC. 1969. Survival of root-infecting fungi in soil. X. Sensitivity of propagules of *Thielaviopsis basicola* to soil fungistasis in natural and alfalfa-amended soil. *Phytopathology* 59:135–38
2. Allard SM, Walsh CS, Wallis AE, Ottesen AR, Brown EW, et al. 2016. *Solanum lycopersicum* (tomato) hosts robust phyllosphere and rhizosphere bacterial communities when grown in soil amended with various organic and synthetic fertilizers. *Sci. Total Environ.* 573:555–63
3. Baker KF, Cook RJ. 1974. *Biological Control of Plant Pathogens*. San Francisco: W.H. Freeman
4. Bäumler AJ, Sperandio V. 2016. Interactions between the microbiota and pathogenic bacteria in the gut. *Nature* 535:85–93
5. Berendsen RL, Pieterse CM, Bakker PA. 2012. The rhizosphere microbiome and plant health. *Trends Plant Sci*. 17:478–86
6. Berne C, Kysela DT, Brun YV. 2010. A bacterial extracellular DNA inhibits settling of motile progeny cells within a biofilm. *Mol. Microbiol.* 77:815–29
7. Blok WJ, Lamers JG, Termorshuizen AJ, Bollen GJ. 2000. Control of soilborne plant pathogens by incorporating fresh organic amendments followed by tarping. *Phytopathology* 90:253–59
8. Boehm MJ, Wu T, Stone AG, Kraakman B, Iannotti DA. 1997. Cross-polarized magic-angle spinning ^{13}C nuclear magnetic resonance spectroscopic characterization of soil organic matter relative to culturable bacterial species composition and sustained biological control of *Pythium* root rot. *Appl. Environ. Microbiol.* 63:162–68
9. Bonanomi G, Antignani V, Barile E, Lanzotti V, Scala F. 2011. Decomposition of *Medicago sativa* residues affects phytotoxicity, fungal growth and soil-borne pathogen diseases. *J. Plant Pathol.* 93:57–69
10. Bonanomi G, Antignani V, Capodilupo M, Scala F. 2010. Identifying the characteristics of organic soil amendments that suppress soilborne plant diseases. *Soil Biol. Biochem.* 42:136–44
11. Bonanomi G, Antignani V, Pane C, Scala F. 2007. Suppression of soilborne fungal diseases with organic amendments. *J. Plant Pathol.* 89:311–24
12. Bonanomi G, Cesarano G, Lombardi N, Motti R, Scala F, et al. 2017. Litter chemistry explains contrasting feeding preferences of bacteria, fungi, and higher plants. *Sci. Rep.* 7:9208
13. Bonanomi G, De Filippis F, Cesarano G, La Storia A, Ercolini D, et al. 2016. Organic farming induces changes in soil microbiota that affect agro-ecosystem functions. *Soil Biol. Biochem.* 103:327–36
14. Bonanomi G, Gaglione SA, Cesarano G, Sarker TC, Pascale M, et al. 2017. Frequent applications of organic matter to agricultural soil increase fungistasis. *Pedosphere* 27:86–95
15. Bonanomi G, Gaglione SA, Incerti G, Zoina A. 2013. Biochemical quality of organic amendments affects soil fungistasis. *Appl. Soil Ecol.* 72:135–42
16. Bonanomi G, Incerti G, Barile E, Capodilupo M, Antignani V, et al. 2011. Phytotoxicity, not nitrogen immobilization, explains plant litter inhibitory effects: evidence from solid-state ^{13}C NMR spectroscopy. *New Phytol*. 191:1018–30
17. Bonanomi G, Incerti G, Giannino F, Mingo A, Lanzotti V, et al. 2013. Litter quality assessed by solid state ^{13}C NMR spectroscopy predicts decay rate better than C/N and lignin/N ratios. *Soil Biol. Biochem.* 56:40–48
18. Bonanomi G, Ippolito F, Cesarano G, Nanni B, Lombardi N, et al. 2017. Biochar as plant growth promoter: better off alone or mixed with organic amendments? *Front. Plant Sci.* 8:1570
19. Bonanomi G, Ippolito F, Cesarano G, Vinale F, Lombardi N, et al. 2018. Biochar chemistry defined by ^{13}C-CPMAS NMR explains opposite effects on soilborne microbes and crop plants. *Appl. Soil Ecol.* 124:351–61
20. Bonanomi G, Ippolito F, Scala F. 2015. A "black" future for plant pathology? Biochar as a new soil amendment for controlling plant diseases. *J. Plant Pathol.* 97:223–34
21. Bonanomi G, Sicurezza MG, Caporaso S, Esposito A, Mazzoleni S. 2006. Phytotoxicity dynamics of decaying plant materials. *New Phytol*. 169:571–78
22. Cai F, Pang G, Li RX, Li R, Gu XL, et al. 2017. Bioorganic fertilizer maintains a more stable soil microbiome than chemical fertilizer for monocropping. *Biol. Fertil. Soils* 53:861–72
23. Castaño R, Borrero C, Avilés M. 2011. Organic matter fractions by SP-MAS ^{13} C NMR and microbial communities involved in the suppression of Fusarium wilt in organic growth media. *Biol. Control* 58:286–93

24. Cesarano G, De Filippis F, La Storia A, Scala F, Bonanomi G. 2017. Organic amendment type and application frequency affect crop yields, soil fertility and microbiome composition. *Appl. Soil Ecol.* 120:254–64
25. Cesarano G, Incerti G, Bonanomi G. 2016. The influence of plant litter on soil water repellency: insight from ^{13}C NMR spectroscopy. *PLOS ONE* 11:e0152565
26. Chen W, Hoitink HAJ, Madden LV. 1988. Microbial activity and biomass in container media for predicting suppressiveness to damping-off caused by *Pythium ultimum*. *Phytopathology* 78:1447–50
27. Copley TR, Aliferis KA, Jabaji S. 2015. Maple bark biochar affects *Rhizoctonia solani* metabolism and increases damping-off severity. *Phytopathology* 105:1334–46
28. Croteau GA, Zibilske LM. 1998. Influence of papermill processing residuals on saprophytic growth and disease caused by *Rhizoctonia solani*. *Appl. Soil Ecol.* 10:103–15
29. Dick RP, Rasmussen PE, Kerle EA. 1988. Influence of long-term residue management on soil enzyme activities in relation to soil chemical properties of a wheat-fallow system. *Biol. Fertil. Soils* 6:159–64
30. Eizenberg H, Plakhine D, Ziadne H, Tsechansky L, Graber ER. 2017. Non-chemical control of root parasitic weeds with biochar. *Front. Plant Sci.* 8:939
31. Elad Y, Cytryn E, Harel YM, Lew B, Graber ER. 2012. The biochar effect: plant resistance to biotic stresses. *Phytopathol. Mediterr.* 50:335–49
32. Elad Y, David DR, Harel YM, Borenshtein M, Kalifa HB, et al. 2010. Induction of systemic resistance in plants by biochar, a soil-applied carbon sequestering agent. *Phytopathology* 100:913–21
33. Fierer N. 2017. Embracing the unknown: disentangling the complexities of the soil microbiome. *Nat. Rev. Microbiol.* 15:579–90
34. Fu L, Penton CR, Ruan Y, Shen Z, Xue C, et al. 2017. Inducing the rhizosphere microbiome by biofertilizer application to suppress banana Fusarium wilt disease. *Soil Biol. Biochem.* 104:39–48
35. Garbeva PV, Van Veen JA, Van Elsas JD. 2004. Microbial diversity in soil: selection of microbial populations by plant and soil type and implications for disease suppressiveness. *Annu. Rev. Phytopathol.* 42:243–70
36. George C, Kohler J, Rillig MC. 2016. Biochars reduce infection rates of the root-lesion nematode *Pratylenchus penetrans* and associated biomass loss in carrot. *Soil Biol. Biochem.* 95:11–18
37. Gillon D, Joffre R, Ibrahima A. 1999. Can litter decomposability be predicted by near infrared reflectance spectroscopy? *Ecology* 80:175–86
38. Glynne MD. 1935. Incidence of take-all on wheat and barley on experimental plots at Woburn. *Ann. Appl. Biol.* 22:225–35
39. Grünwald NJ, Hu S, Van Bruggen AHC. 2000. Short-term cover crop decomposition in organic and conventional soils: soil microbial and nutrient cycling indicator variables associated with different levels of soil suppressiveness to *Pythium aphanidermatum*. *Eur. J. Plant Pathol.* 106:51–60
40. Hadar Y, Papadopoulou KK. 2012. Suppressive composts: microbial ecology links between abiotic environments and healthy plants. *Annu. Rev. Phytopathol.* 50:133–53
41. Hartmann M, Frey B, Mayer J, Mäder P, Widmer F. 2015. Distinct soil microbial diversity under long-term organic and conventional farming. *ISME J.* 9:1177–94
42. Hättenschwiler S, Coq S, Barantal S, Tanya I. 2011. Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis. *New Phytol.* 189:950–65
43. He M, Tian G, Semenov AM, Van Bruggen AH. 2012. Short-term fluctuations of sugar beet damping-off by *Pythium ultimum* in relation to changes in bacterial communities after organic amendments to two soils. *Phytopathology* 102:413–20
44. Hoitink HAJ, Boehm MJ. 1999. Biocontrol within the context of soil microbial communities: a substrate-dependent phenomenon. *Annu. Rev. Phytopathol.* 37:427–46
45. Hoitink HAJ, Madden LV, Dorrance AE. 2006. Systemic resistance induced by *Trichoderma* spp.: interactions between the host, the pathogen, the biocontrol agent, and soil organic matter quality. *Phytopathology* 96:186–89
46. Hornby D. 1983. Suppressive soils. *Annu. Rev. Phytopathol.* 21:65–85
47. Huang Y, Stankiewicz BA, Eglinton G, Snape CE, Evans B, et al. 1998. Monitoring biomacromolecular degradation of *Calluna vulgaris* in a 23-year field experiment using solid state ^{13}C-NMR and pyrolysis-GC/MS. *Soil Biol. Biochem.* 30:1517–28

48. Inbar Y, Chen Y, Hadar Y. 1989. Solid-state carbon-13 nuclear magnetic resonance and infrared spectroscopy of composted organic matter. *Soil Sci. Soc. Am. J.* 53:1695–701
49. Incerti G, Bonanomi G, Giannino F, Cartenì F, Spaccini R, et al. 2017. OMDY: a new model of organic matter decomposition based on biomolecular content as assessed by ^{13}C-CPMAS-NMR. *Plant Soil* 411:377–94
50. Inderbitzin P, Ward J, Barbella A, Solares N, Izyumin D, et al. 2018. Soil microbiomes associated with Verticillium wilt suppressive broccoli and chitin amendments are enriched with potential biocontrol agents. *Phytopathology* 108:31–43
51. Jacobsen CS, Hjelmsø MH. 2014. Agricultural soils, pesticides and microbial diversity. *Curr. Opin. Biotechnol.* 27:15–20
52. Kammann C, Glaser B, Schmidt HP. 2016. Combining biochar and organic amendments. In *Biochar in European Soils and Agriculture: Science and Practice*, ed. S Shackley, G Ruysschaert, K Zwart, B Glaser, pp. 136–64. New York: Routledge
53. Kanaan H, Frenk S, Raviv M, Medina S, Minz D. 2018. Long and short term effects of solarization on soil microbiome and agricultural production. *Appl. Soil Ecol.* 124:54–61
54. Kandeler E, Stemmer M, Klimanek EM. 1999. Response of soil microbial biomass, urease and xylanase within particle size fractions to long-term soil management. *Soil Biol. Biochem.* 31:261–73
55. Kavroulakis N, Ehaliotis C, Ntougias S, Zervakis GI, Papadopoulou KK. 2005. Local and systemic resistance against fungal pathogens of tomato plants elicited by a compost derived from agricultural residues. *Physiol. Mol. Plant Pathol.* 66:163–74
56. Kinkel LL, Bakker MG, Schlatter DC. 2011. A coevolutionary framework for managing disease-suppressive soils. *Annu. Rev. Phytopathol.* 49:47–67
57. Kögel-Knabner I. 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biol. Biochem.* 34:139–62
58. Kolton M, Graber ER, Tsehansky L, Elad Y, Cytryn E. 2017. Biochar-stimulated plant performance is strongly linked to microbial diversity and metabolic potential in the rhizosphere. *New Phytol*. 213:1393–404
59. Lapsansky ER, Milroy AM, Andales MJ, Vivanco JM. 2016. Soil memory as a potential mechanism for encouraging sustainable plant health and productivity. *Curr. Opin. Biotechnol.* 38:137–42
60. Larkin RP. 2015. Soil health paradigms and implications for disease management. *Annu. Rev. Phytopathol.* 53:199–221
61. Larkin RP, Griffin TS. 2007. Control of soilborne potato diseases using Brassica green manures. *Crop Prot*. 26:1067–77
62. Lehmann J, Joseph S. 2015. *Biochar for Environmental Management: Science, Technology and Implementation*. London: Routledge
63. Lehmann J, Kleber M. 2015. The contentious nature of soil organic matter. *Nature* 528:60–68
64. Lehmann J, Rillig MC, Thies J, Masiello CA, Hockaday WC, et al. 2011. Biochar effects on soil biota: a review. *Soil Biol. Biochem.* 43:1812–36
65. Ling N, Zhu C, Xue C, Chen H, Duan Y, et al. 2016. Insight into how organic amendments can shape the soil microbiome in long-term field experiments as revealed by network analysis. *Soil Biol. Biochem.* 99:137–49
66. Lockwood JL. 1964. Soil fungistasis. *Annu. Rev. Phytopathol.* 2:341–62
67. Lockwood JL. 1977. Fungistasis in soils. *Biol. Rev.* 52:1–43
68. Lopez-Iglesias B, Olmo M, Gallardo A, Villar R. 2014. Short-term effects of litter from 21 woody species on plant growth and root development. *Plant Soil* 381:177–91
69. Lorito M, Woo SL, Harman GE, Monte E. 2010. Translational research on *Trichoderma*: from 'omics to the field. *Annu. Rev. Phytopathol.* 48:395–417
70. Lumsden RD, Lewis JA, Millner PD. 1983. Effect of composted sewage sludge on several soilborne pathogens and diseases. *Phytopathology* 73:1543–48
71. Mäder P, Flieβbach A, Dubois D, Gunst L, Fried P, et al. 2002. Soil fertility and biodiversity in organic farming. *Science* 296:1694–97
72. Manici LM, Caputo F, Babini V. 2004. Effect of green manure on *Pythium* spp. population and microbial communities in intensive cropping systems. *Plant Soil* 263:133–42

73. Marschner P, Kandeler E, Marschner B. 2003. Structure and function of the soil microbial community in a long-term fertilizer experiment. *Soil Biol. Biochem.* 35:453–61
74. Martin FN. 2003. Development of alternative strategies for management of soilborne pathogens currently controlled with methyl bromide. *Annu. Rev. Phytopathol.* 41:325–50
75. Mathers NJ, Jalota RK, Dalal RC, Boyd SE. 2007. ^{13}C-NMR analysis of decomposing litter and fine roots in the semi-arid Mulga Lands of southern Queensland. *Soil Biol. Biochem.* 39:993–1006
76. Mazzola M. 2004. Assessment and management of soil microbial community structure for disease suppression. *Annu. Rev. Phytopathol.* 42:35–59
77. Mazzola M, Granatstein DM, Elfving DC, Mullinix K. 2001. Suppression of specific apple root pathogens by *Brassica napus* seed meal amendment regardless of glucosinolate content. *Phytopathology* 91:673–79
78. Mazzoleni S, Bonanomi G, Incerti G, Chiusano ML, Termolino P, et al. 2015. Inhibitory and toxic effects of extracellular self-DNA in litter: a mechanism for negative plant-soil feedbacks? *New Phytol.* 205:1195–210
79. Mazzoleni S, Cartenì F, Bonanomi G, Senatore M, Termolino P, et al. 2015. Inhibitory effects of extracellular self-DNA: a general biological process? *New Phytol.* 206:127–32
80. Mehari ZH, Elad Y, Rav-David D, Graber ER, Harel YM. 2015. Induced systemic resistance in tomato (*Solanum lycopersicum*) against *Botrytis cinerea* by biochar amendment involves jasmonic acid signaling. *Plant Soil* 395:31–44
81. Meiners SJ. 2014. Functional correlates of allelopathic potential in a successional plant community. *Plant Ecol.* 215:661–72
82. Mendes LW, Tsai SM, Navarrete AA, De Hollander M, van Veen JA, et al. 2015. Soil-borne microbiome: linking diversity to function. *Microb. Ecol.* 70:255–65
83. Menzies JD. 1959. Occurrence and transfer of a biological factor in soil that suppresses potato scab. *Phytopathology* 49:648–52
84. Nelson EB. 2004. Microbial dynamics and interactions in the spermosphere. *Annu. Rev. Phytopathol.* 42:271–309
85. Pane C, Spaccini R, Piccolo A, Scala F, Bonanomi G. 2011. Compost amendments enhance peat suppressiveness to *Pythium ultimum*, *Rhizoctonia solani* and *Sclerotinia minor*. *Biol. Control* 56:115–24
86. Papavizas GC. 1968. Survival of root-infecting fungi in soil. IV. Effect of amendments on bean root rot caused by *Thielaviopsis basicola* and on inoculum density of the causal organism. *Phytopathology* 58:421–28
87. Pharand B, Carisse O, Benhamou N. 2002. Cytological aspects of compost-mediated induced resistance against Fusarium crown and root rot in tomato. *Phytopathology* 92:424–38
88. Postma J, Clematis F, Nijhuis EH, Someus E. 2013. Efficacy of four phosphate-mobilizing bacteria applied with an animal bone charcoal formulation in controlling *Pythium aphanidermatum* and *Fusarium oxysporum* f. sp. *radicis lycopersici* in tomato. *Biol. Control* 67:284–91
89. Raaijmakers JM, Mazzola M. 2016. Soil immune responses. *Science* 352:1392–93
90. Rothrock CS, Kirkpatrick TL. 1995. The influence of winter legume cover crops on soilborne plant pathogens and cotton seedling diseases. *Plant Dis.* 79:167–71
91. Saadi I, Laor Y, Raviv M, Medina S. 2007. Land spreading of olive mill wastewater: effects on soil microbial activity and potential phytotoxicity. *Chemosphere* 66:75–83
92. Sarker TS, Incerti G, Spaccini R, Piccolo A, Mazzoleni S, et al. 2018. Linking organic matter chemistry with soil aggregate stability: insight from ^{13}C NMR spectroscopy. *Soil Biol. Biochem.* 117:175–84
93. Scheuerell SJ, Sullivan DM, Mahaffee WF. 2005. Suppression of seedling damping-off caused by *Pythium ultimum*, *P. irregulare*, and *Rhizoctonia solani* in container media amended with a diverse range of Pacific Northwest compost sources. *Phytopathology* 95:306–15
94. Sederholm MR, Schmitz BW, Barberán A, Pepper IL. 2018. Effects of metam sodium fumigation on the abundance, activity, and diversity of soil bacterial communities. *Appl. Soil Ecol.* 124:27–33
95. Shen Z, Ruan Y, Chao X, Zhang J, Li R, et al. 2015. Rhizosphere microbial community manipulated by 2 years of consecutive biofertilizer application associated with banana Fusarium wilt disease suppression. *Biol. Fertil. Soils* 51:553–62
96. Siddiqui Y, Meon S, Ismail MR, Ali A. 2008. *Trichoderma*-fortified compost extracts for the control of choanephora wet rot in okra production. *Crop Prot.* 27:385–90

97. Snyder WC, Schroth MN, Christou T. 1959. Effect of plant residues on root rot of beans. *Phytopathology* 49:755–56
98. Spaccini R, Piccolo A. 2007. Molecular characterization of compost at increasing stages of maturity. 2. Thermochemolysis–GC-MS and ^{13}C-CPMAS-NMR spectroscopy. *J. Agric. Food Chem.* 55:2303–11
99. Stone AG, Traina SJ, Hoitink HAJ. 2001. Particulate organic matter composition and *Pythium* damping-off of cucumber. *Soil Sci. Soc. Am. J.* 65:761–70
100. Taylor BR, Parkinson D, Parsons WFJ. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70:97–104
101. Tenuta M, Lazarovits G. 2004. Soil properties associated with the variable effectiveness of meat and bone meal to kill microsclerotia of *Verticillium dahliae*. *Appl. Soil Ecol.* 25:219–36
102. Termorshuizen AJ, van Rijn E, van der Gaag DJ, Alabouvette C, Chen Y, et al. 2006. Suppressiveness of 18 composts against 7 pathosystems: variability in pathogen response. *Soil Biol. Biochem.* 38:2461–77
103. Tilston EL, Pitt D, Groenhof AC. 2002. Composted recycled organic matter suppresses soil-borne diseases of field crops. *New Phytol.* 154:731–40
104. Tiquia SM. 2010. Reduction of compost phytotoxicity during the process of decomposition. *Chemosphere* 79:506–12
105. Tuitert G, Szczach M, Bollen GJ. 1998. Suppression of *Rhizoctonia solani* in potting mixtures amended with compost made from organic household waste. *Phytopathology* 88:764–73
106. Van Bruggen AHC, Finckh MR. 2016. Plant diseases and management approaches in organic farming systems. *Annu. Rev. Phytopathol.* 54:25–54
107. Van Bruggen AHC, He MM, Shin K, Mai V, Jeong KC, et al. 2018. Environmental and health effects of the herbicide glyphosate. *Sci. Total Environ.* 616:255–68
108. Van Bruggen AHC, Semenov AM, van Diepeningen AD, de Vos OJ, Blok WJ. 2006. Relation between soil health, wave-like fluctuations in microbial populations, and soil-borne plant disease management. In *Plant Disease Epidemiology: Facing Challenges of the 21st Century*, ed. S Savary, BM Cook, pp. 105–22. Dordrecht, Neth.: Springer
109. Walker JC, Snyder WC. 1934. Pea wilt much less severe on certain soils. *Univ. Wis. Agric. Exp. Stn. Bull.* 428:95–96
110. Wallenstein MD, Hess AM, Lewis MR, Steltzer H, Ayres E. 2010. Decomposition of aspen leaf litter results in unique metabolomes when decomposed under different tree species. *Soil Biol. Biochem.* 42:484–90
111. Wang J, Xiong Z, Kuzyakov Y. 2016. Biochar stability in soil: meta-analysis of decomposition and priming effects. *GCB Bioenergy* 8:512–23
112. Warnock DD, Lehmann J, Kuyper TW, Rillig MC. 2007. Mycorrhizal responses to biochar in soil and concepts and mechanisms. *Plant Soil* 300:9–20
113. Weller DM, Raaijmakers JM, Gardener BBM, Thomashow LS. 2002. Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annu. Rev. Phytopathol.* 40:309–48
114. Whipps JM. 1997. Developments in the biological control of soil-borne plant pathogens. *Adv. Bot. Res.* 26:1–134
115. Whitman T, Pepe-Ranney C, Enders A, Koechli C, Campbell A, et al. 2016. Dynamics of microbial community composition and soil organic carbon mineralization in soil following addition of pyrogenic and fresh organic matter. *ISME J.* 10:2918–30
116. Wilhelm S. 1951. Effect of various soil amendments on the inoculum potential of *Verticillium* wilt fungus. *Phytopathology* 41:684–90
117. Wolf R, Wedig H. 2007. Process for manufacturing a soil conditioner. *U.S. Patent No. WO 2010055139 A1*
118. Woo SL, Ruocco M, Vinale F, Nigro M, Marra R, et al. 2014. *Trichoderma*-based products and their widespread use in agriculture. *Open Mycol. J.* 4:71–126
119. Yang RX, Gao ZG, Liu X, Yao Y, Cheng Y. 2014. Root exudates from muskmelon (*Cucumis melon* L) induce autotoxicity and promote growth of *Fusarium oxysporum* f. sp. *melonis*. *Allelopath. J.* 33:175–87

120. Ye SF, Yu JQ, Peng YH, Zheng JH, Zou L. 2004. Incidence of Fusarium wilt in *Cucumis sativus* L. is promoted by cinnamic acid, an autotoxin in root exudates. *Plant Soil* 263:143–50

121. Yulianti T, Sivasithamparam K, Turner DW. 2006. Saprophytic growth of *Rhizoctonia solani* Kühn AG2–1 (ZG5) in soil amended with fresh green manures affects the severity of damping-off in canola. *Soil Biol. Biochem.* 38:923–30

122. Zhang W, Han DY, Dick WA, Davis KR, Hoitink HAJ. 1998. Compost and compost water extract-induced systemic acquired resistance in cucumber and *Arabidopsis*. *Phytopathology* 88:450–55

Annual Review of Phytopathology
Volume 56, 2018

Contents

Errata

An online log of corrections to *Annual Review of Phytopathology* articles may be found at http://www.annualreviews.org/errata/phyto