CHAPTER

Compost use for plant disease suppression

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1. Introduction

1.1 History of organic amendments used for plant disease suppression

Farmers have used manures and composts for thousands of years to maintain plant health and yield. Even so, the first experimental data which proved that “barnyard” cow manure applications could successfully control diseases caused by a soilborne plant pathogen was not published until the 1930s. Application of manure increased cotton yields but also controlled an epidemic of root rot caused by *Phymatotrichum*, although disease control was incomplete because some roots still were affected by the disease. Scientists speculated that beneficial microorganisms on plant roots competed with the plant pathogen in the soil and reduced its activity through production of antibiotics. They even suggested that roots on plants in the manured plots were more resistant to disease based on the presence of many infected roots, but the plants did not die from root rot, as was the case in controls. It was recognized even then that there was an interaction between the crop, beneficial microorganisms, and the organic amendment that might play a role in this “muck and magic” type of biological control of plant diseases. Only much later, have these ideas been supported scientifically through published research, starting in the late 1950s for example in East Germany (Bochow and Seidel, 1961) (Fig. 17.1).

Large scale disease control with compost applications began during the 1950s when the nursery industry in the US and Australia developed lower-cost potting mixes and soil amendments for woody ornamentals that were bark-based rather than peat-based products (Hoitink and Ramos, 2004). Several growers found that composted bark could suppress root rots caused by *Phytophthora cinnamomi* for which effective resistant varieties or chemical control procedures other than

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FIGURE 17.1

Taxus plants produced in a bark-based potting mix naturally suppressive to *Phytophthora* root rot. Note the uniform growth of the plants and the absence of root rot symptoms. This photo was taken before systemic fungicides for control of this disease were available. It was impossible to grow this crop on a commercial scale in peat-based mixes until after such fungicides became available.

Source: Courtesy of Harry A. Hoitink.

methyl bromide were unavailable. The nursery industry discovered that the same composts could also control this disease in field soil but only if ideal drainage was provided. Without compost, Phytophthora root rot was particularly severe in heavy soils, in peat-based potting mixes, and in soils amended with fresh sawdust (Fig. 17.2). Thus, it was recognized early that not all sources of organic matter were effective for disease control.

During the 1970s, plant pathologists performed the first controlled experiments in the US and Australia that confirmed growers' experiences (Hoitink and Ramos, 2004). Phytophthora root rot of rhododendron in potting mixes and Phytophthora root rot of avocado in field soil were early examples. Peat-based mix stimulated release of zoospores by sporangia of *P. cinnamomi* but the zoospores died in potting mixes amended with composted bark. It was realized early that composts did not kill all pathogens. Researchers did not know whether the pathogen was inactivated by a toxin or other means. Only later, was it understood that pathogens are suppressed primarily by microorganisms in compost-amended soils.

FIGURE 17.2

Typical crop losses in azaleas caused by *Phytophthora cinnamomi* in 1971, before composted bark was used.

Source: H.A. Hoitink.

Since the early 1990s, animal manures have reclaimed their value with farmers for a variety of reasons, including that livestock farmers began to add value to raw manures through composting. Compost could solve problems with nutrient management and improve soil health. The types of experiments performed on Phymatotrichum root rot of cotton were repeated with composted manures across the globe in hundreds of tests for numerous crops and for many soilborne diseases. In general, these studies show that composted manures reduced the severity of diseases caused by essentially all types of soilborne plant pathogens including bacteria, fungi, Oomycota, and some nematodes. However, diseases also can be more severe after compost application if immature compost is used or if the timing of compost application is not synchronized with crop needs (Termorshuizen et al., 2006). Therefore, several factors must be addressed to obtain disease control consistently.

Research conducted in the 1990s demonstrated that composts applied to soil could also suppress foliar diseases, but the effect was often minor (Hoitink and Ramos, 2004). It was discovered that specific microorganisms in the rhizosphere of plants (the interface between plant roots and surrounding soil) can reduce the severity of diseases on the entire plant. In a study from Germany, composted cow manure applied to soil with small grains and grapes suppressed powdery and downy mildew, respectively. Other early reports from Florida and Ohio showed that application of composted municipal waste or composted yard wastes to field soil reduced the severity of bacterial spot (*Xanthamonas*) and of early blight (*Alternaria*) of tomato. Several foliar diseases of beans and cucumber were reduced by incorporating composted paper mill sludge into a sandy Wisconsin soil. Although composted sludge was effective, fresh paper mill sludge did not have this effect.

What the early research has shown is that biological elements in composts, at least some composts, can suppress plant disease. The missing piece is understanding the mechanism(s) by which compost microorganisms suppress plant pathogens and disease. Subsequent studies confirmed that different compost types can stimulate plant defense responses. Although scientists are starting to reveal the diversity of compost organisms, much remains to be known about the ecological function of these microorganisms (Vacheron et al., 2013; Lugtenberg and Kamilova, 2009; Andrews, 2018). Furthermore, our current understanding of the relationships between compost chemistry and the induction of systemic resistance in the plant is limited.

1.2 Plant diseases prone to suppression by compost

Compost naturally suppresses Oomycota pathogens, *Pythium* and *Phytophthora,* which cause root rots on vegetables, fruit, woody ornamentals, and forest trees (Table 17.1). Wilt diseases on cereals and grasses caused by *Fusarium oxysporum* and *Verticillium dahliae* are manageable with composts. *Rhizoctonia solani*, which causes damping-off disease in most crops, has a more checkered history in relationship to control by compost. It is the most studied, but least consistently managed by compost of the major soilborne fungal pathogens. The taxonomy and genetics of *R. solani* reveal immense variation within the genus resulting in the original species being divided into multiple species.

Table 17.1 Soilborne pathogens demonstrated to be suppressed by compost.

Pathogen	Crop	Compost feedstock(s)	References
Aphanomyces euteiches	Snap bean	Paper mill waste, bark	Noble and Coventry (2005)
Aphanomyces euteiches	Root rot on pea	Sewage sludge, wood chips	Litterick et al. (2004)
Fusarium oxysporum f. sp. *lini*	Flax	Horse manure (20%) and green waste (80%) (wheat straw, corn straw, conifer bark)	Termorshuizen et al. (2006)
Fusarium oxysporum f. sp. *lini*	Flax	Yard waste (without grass)	Termorshuizen et al. (2006)
Fusarium oxysporum f.sp. *lycopersici*	Tomato	Municipal solid waste	Vida et al. (2020)
Fusarium spp.	Several hosts	Vegetal	Bonilla et al. (2012)
Fusarium wilt and stem rot	Cucumber	Greenhouse compost	Vida et al. (2020)
Microdochium nivale	Turf	Bark, poultry manure	Noble and Coventry (2005)
Phytophthora capsici	Pepper	Chitin in crab shell	Bonilla et al. (2012)
Phytophthora cinnamomi	Lupin	Spent mushroom compost (wheat straw 56%, chicken manure 39%, gypsum 5%)	Termorshuizen et al. (2006)
Phytophthora cinnamomi	White lupin	Chicken manure	Vida et al. (2020)

Table 17.1 Soilborne pathogens demonstrated to be suppressed by compost.—*cont'd*

Pathogen	Crop	Compost feedstock(s)	References
Phytophthora cinnamomi	Avocado	*Eucalyptus* trimmings	Bonilla et al. (2012)
Phytophthora cinnamomi	Avocado	Vegetal	Bonilla et al. (2012)
Phytophthora nicotianae	Tomato	Organic residue of wine grapes, green waste	Termorshuizen et al. (2006)
Phytophthora nicotianae	Tomato	Woodcut, plants, horse manure	Termorshuizen et al. (2006)
Phytophthora nicotianae	Tomato	Woody waste, poultry manure	Termorshuizen et al. (2006)
Phytophthora nicotianae	Tomato	Yard waste (without grass)	Termorshuizen et al. (2006)
Phytophthora nicotianae	Tomato	Yard waste (without grass)	Termorshuizen et al. (2006)
Phytophthora nicotianae	Tomato	Yard waste (woody materials, grass clippings)	Termorshuizen et al. (2006)
Pythium graminicola	Turf	Brewery and sewage sludges	Noble and Coventry (2005)
Pythium ultimum	Cucumber	Green vegetable waste, horse manure	Noble and Coventry (2005)
Pythium ultimum	Garden cress	Animal and vegetal	Bonilla et al. (2012)
Pythium ultimum	Garden cress	Bark	Bonilla et al. (2012)
Ralstonia solanacearum	Potato	Organic waste	Vida et al. (2020)
Rhizoctonia solani	Basil	Cow manure	Bonilla et al. (2012)
Rhizoctonia solani	Cauliflower	Wood chips, horse manure	Termorshuizen et al. (2006)
Rhizoctonia solani	Cauliflower	Wood chips 88%, manure 2.5%, clay 10%	Termorshuizen et al. (2006)
Rhizoctonia solani	Cauliflower	Yard waste (with grass)	Termorshuizen et al. (2006)
Rhizoctonia solani	Cauliflower	Yard waste (without grass)	Termorshuizen et al. (2006)
Rhizoctonia solani	Cauliflower	Yard waste (woody materials, grass clippings)	Termorshuizen et al. (2006)
Rhizoctonia solani	Garden cress	Viticulture waste	Bonilla et al. (2012)
Rhizoctonia solani	Pine	Urban biowaste	Termorshuizen et al. (2006)
Rhizoctonia solani	Pine	Wood chips, horse manure	Termorshuizen et al. (2006)

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Table 17.1 Soilborne pathogens demonstrated to be suppressed by compost.—*cont'd*

Pathogen	Crop	Compost feedstock(s)	References
Rhizoctonia solani	Radish	5:5:3 ratio of manure/silage: hardwood bark: softwood shavings resulting in a C:N ratio of 34:1	Neher et al. (2017)
Rhizoctonia solani	Radish	20% food residuals, 10%–15% hardwood bark/mixed wood chips, 10% hay, ≤ 5% shredded paper, ≤ 2% dry sawdust/shavings, 50%–60% mixed horse/cattle manure with bedding	Neher et al. (2017)
Rosellinia necatrix	Avocado	Vegetal	Bonilla et al. (2012)
Sclerotium minor	Garden cress	Municipal biowaste, cow manure	Bonilla et al. (2012)
Typhula incarnata	Tomato	Cotton gin trash	Vida et al. (2020)
Typhula incarnata	Turf	Sewage sludge	Noble and Coventry (2005)
Verticillium dahliae	Turf	Bark, poultry manure	Noble and Coventry (2005)
Verticillium dahliae	Eggplant	Horse manure (20%) and green waste (80%) (wheat straw, corn straw, conifer bark)	Termorshuizen et al. (2006)

All of the above soilborne pathogens have many host plants and are distributed globally. Pathogenic and nonpathogenic strains of *Pythium*, *F. oxysporum*, and *R. solani* can coinhabit a given soil. This coexistence complicates diagnostics given similar fungal morphology and disease symptoms. Environmental properties likely affect relative pathogenicity. For example, pH influences suppression of *Phytophthora nicotianae* on tomato and Fusarium wilt on carnations.

Soilborne pathogens are masters of survival, making them difficult to kill. They exist primarily in dormant forms (e.g., spores), which allows them to survive for a decade or more. They are stimulated to germinate, grow, and infect roots when they sense nutrition available through root and seed exudates or added nutrients. Soilborne pathogens produce different enzymes to obtain nutrition. The biochemical properties of the enzymes determine their ability to compete with other species. Poor competitors, such as *Pythium* and *Phytophthora* species, thrive in high nutrient conditions and easily degradable simple carbohydrates (e.g., sugars). In contrast, *R. solani* is more competitive than *Pythium* and *Phytophthora* because it can also metabolize starches and cellulose, both of which are abundant in compost (Scotti et al., 2020).

Between growing seasons, many pathogens live as saprophytes to varying abilities. Saprophytes survive on plant debris and detritus. Mature composts, especially containing wood chips and/or bark, contain microorganisms with strong saprophytic ability that can outcompete soil pathogens with weak saprophytic ability (e.g., *Verticillium dahliae*, *Thielaviopsis basicola*). The composition of carbon sources in compost differentially attracts specific species of bacteria and fungi that naturally colonize the compost during the cooling phase of the process and are antagonistic to pathogens (Hadar and Papadopoulou, 2012; Neher et al., 2013). These saprophytic microorganisms in compost may also suppress foodborne pathogens such as coliforms, *Listeria*, or *Salmonella* species (Limoges et al., 2020). Similar antagonism against animal pathogens has also been observed in animal bedding that has been composted or allowed to compost in place (Box 17.1).

Box 17.1 Biological control of animal pathogens in bedding

Compost-bedded pack barns (CBPs) are receiving increasing attention as a housing system for dairy cows that has potential to improve animal welfare. Bedded-pack barns not only provide comfort and better foot and leg health but also microorganisms in the bedded pack have potential to decrease animal pathogens (Leso et al., 2020). Dairy farmers identify mastitis as a top animal health challenge area. Prevention is critical to limiting mastitis, particularly on organic dairy farms, where efficacy of products approved to treat infections is limited. Organic dairy farmers report less incidence and severity of mastitis on cows bedded on compost-bedded pack. Traditionally, bedded packs have been thought to increase risk of mastitis due to the presence of pathogenic bacteria and the favorable moisture and temperature for the growth of these pathogens. However, there is empirical evidence that bedded-pack systems do not increase the prevalence of mastitis, and potentially change the ability of these communities to buffer against disease (Andrews, 2018). These packs are also home to large populations of predaceous mites that prey upon fly larvae.

This system requires excellent pack and ventilation management for barns to perform well. Because of the high bacterial concentrations in bedding, regular additions of ample bedding and excellent teat preparation procedures in milking are recommended. Repeatedly adding bedding materials generates a layering of bedding and animal excrement. CBP use wood chips or sawdust as bedding instead of straw. The wood residue binds the excrement and daily aerating incorporates the manure and starts the composting process. Researchers and dairy producers from Minnesota suggest that dry, fine wood shavings, or sawdust, preferably from pine or other softwoods, are the choice bedding materials in CBP. The size of bedding particles is particularly important for regulating microbial access to the food source. Additionally, shavings or sawdust provide structure that can be easily stirred and remain fluffy enough to assure oxygen transfer within the bedding material. Especially under cold and humid weather conditions, large amounts of bedding may be necessary to keep the pack adequately dry and comfortable for the cows. Published estimates range from 8.2 to 25.6 m^3/cow per year (Leso et al., 2020). Dairy cow feces have a low C:N ratio, ranging from 15:1 to 19:1 and the most commonly used bedding materials are dry and have a very high C:N ratio. In CBP, adding fresh bedding may be necessary to absorb excessive pack moisture and to keep the pack C:N ratio within the optimal range. Otherwise, composting is inhibited in CBP if the C:N ratio decreases to 15:1 or below.

1.3 Compost organisms that suppress plant diseases

Every compost owes its disease suppressiveness to the microorganisms that inhabit it. These microorganisms naturally colonize compost during maturation and curing phases. Much scientific research has focused on identifying specific strains or species that control specific pathogens or diseases. Although some diseases can be suppressed by a single strain or species, inconsistencies may be attributed to the concept that mixtures of strains, organisms, or mechanisms are involved. Composts support a spectrum of microbial groups that offer multiple modes of action against a target pathogen or disease. Species of many biocontrol organisms that have been cultured and tested in bioassays are listed in Table 17.2. The list is likely to expand exponentially in the next decade with the use of molecular genetic tools that allow us to identify organisms from compost that are not culturable, yet prevalent and pivotal in disease suppression. Ideally, it would be most practical to have composts designed to suppress multiple pathogens and/or crop diseases.

1.4 Specific versus general compost-mediated disease suppression

Compost-mediated disease suppression ranges from specific to general. Specific suppression is provided by activities of a narrow spectrum of one or a few specific populations of beneficial microorganisms of which some do not colonize composts. General suppression results from the collective activity of many species of microorganisms in field or potting soils.

With specific suppression, the beneficial organisms deter pathogen growth through particular biological control mechanisms such as competition, parasitism, antagonism, and/or induced plant resistance. Suppression of damping-off caused by *R. solani* is an example. Other examples of specific suppression include *Streptomyces* A1RT on potato scab (*Streptomyces scabies*) and *Brachyphoris oviparasitica* (syn. *Dactylella oviparasitica*) on sugarbeet cyst nematodes. *Trichoderma* and other inoculants to control *Rhizoctonia* and *Fusarium* diseases are a proven practice for potted greenhouse crops. Strains of some *Trichoderma* spp. can kill sclerotia (resting structures) of *R. solani* (Coventry et al., 2006).

Companies that formulate, produce, and market specific antagonistic strains of microorganisms take advantage of specific suppression. Commercial products are limited to microbial species that can be cultured and have stable spores to extend shelf life (Grosch et al., 2004).

In contrast, no single species by itself is responsible for general suppression (Bonanomi et al., 2010). This type of suppression best explains biological control of root rots caused by *Pythium* spp. and *Phytophthora* spp. and some nematodes (e.g., lesion, root knot). General suppression relies on the activity and interaction among bacterial and fungal communities, and their chemical communication with the plant.

Table 17.2 Compost microorganisms identified as beneficial to biological control.

Microorganism	Disease or pathogen	Crop	Reference
Bacillus amyloliquefaciens Bg-C31	Capsicum bacterial wilt (*Ralstonia solanacearum*)	Pepper	Eljounaidi et al. (2016)
Bacillus amyloliquefaciens BZ6-1	Peanut bacterial wilt (*Ralstonia solanacearum*)	Peanut	Eljounaidi et al. (2016)
Bacillus subtilis	Large patch (*Rhizoctonia solani*)	Turf	Noble and Coventry (2005)
Bacillus subtilis	Rhizoctonia bottom rot (*Rhizoctonia solani*)	Lettuce	Grosch et al. (2004)
Bacillus subtilis Jaas ed1	Verticillium wilt (*Verticillium dahliae*)	Eggplant	Eljounaidi et al. (2016)
Bacillus subtilis strains	Damping-off (*Rhizoctonia solani*)	Carrot, cucumber, tomato	Grosch et al., (2004)
Brachyphoris oviparasitica (syn. *Dactylella oviparasitica*)	Southern root knot (*Meloidogyne incognita*)	Peach	Timper (2014)
Brachyphoris oviparasitica (syn. *Dactylella oviparasitica*)	Sugarbeet cyst nematode (*Heterodera schachtii*)	Sugar beet	Timper (2014)
Burkholderia cepacia (syn. *Pseudomonas cepacia*)	Rhizoctonia bottom rot (*Rhizoctonia solani*)	Lettuce	Grosch et al., (2004)
Enterobacter HA02	Verticillium wilt (*Verticillium dahliae*)	Cotton	Eljounaidi et al. (2016)
Fusarium oxysporum F2	Verticillium wilt (*Verticillium dahliae*)	Eggplant	Hadar and Papadopoulou (2012)
Fusarium oxysporum Fo162	Burrowing nematode (*Radopholus similis*)	Banana	Timper (2014)
Fusarium oxysporum Fo162	Southern root knot nematode (*Meloidogyne incognita*)	Tomato	Timper (2014)
Gliocladium virens G-21	Bottom rot (*Rhizoctonia solani*)	Lettuce	Grosch et al. (2004)
Hirsutella minnesotensis	Soybean cyst nematode (*Heterodera glycines*)	Soybean	Timper (2014)
Hirsutella rhossiliensis	Soybean cyst nematode (*Heterodera glycines*)	Soybean	Timper (2014)
Paecilomyces variotii MSW312	Fusarium wilt (*Fusarium oxysporum* f.sp. *melonis*)	Melon	Suárez-Estrella et al. (2013)
Paenibacillus K165	Verticillium wilt (*Verticillium dahliae*)	Eggplant, potato	Eljounaidi et al. (2016)
Pseudomonas fluorescens CHA0	Root knot nematode (*Meloidogyne javonica*)	Tomato	Timper (2014)
Pseudomonas fluorescens CHA0	Southern root knot (*Meloidogyne incognita*)	Soybean, mung bean, tomato	Timper (2014)
Pseudomonas fluorescens EB69	Eggplant wilt (*Ralstonia solanacearum*)	Eggplant	Eljounaidi et al. (2016)

Continued

Table 17.2 Compost microorganisms identified as beneficial to biological control.—*cont'd*

Microorganism	Disease or pathogen	Crop	Reference
Pseudomonas fluorescens PICF7	Verticillium wilt (*Verticillium dahliae*)	Olive	Eljounaidi et al. (2016)
Pseudomonas putida	Apple replant disease	Apple	Weller et al. (2002)
Pseudomonas putida B10	Take-all (*Gaeumannomyces graminis* var. *tritici*)	Wheat	Haas and Défago (2005)
Serratia marcescens UPM39B3	Fusarium wilt (*Fusarium oxysporum*)	Banana	Eljounaidi et al. (2016)
Serratia plymuthica HRO-C48	Verticillium wilt (*Verticillium dahliae*)	Oilseed rape	Eljounaidi et al. (2016)
Trichoderma hamatum	Damping-off (*Rhizoctonia solani*)	Radish	Chung et al. (1988)
Trichoderma hamatum	Rhizoctonia stem canker and black scurf (*Rhizoctonia solani*)	Potato	Beagle-Ristaino et al. (1985)
Trichoderma harzianum	Damping-off (*Pythium ultimum*)	Cucumber	Pugliese et al. (2011)
Trichoderma harzianum	Rhizoctonia bottom rot (*Rhizoctonia solani*)	Lettuce	Grosch et al. (2004)
Microorganisms that control multiple diseases			
Bacillus subtilis GBO3	*Rhizoctonia, Fusarium, Aspergillus,* and others	Seed treatment for cotton, peanuts, soybeans, wheat, barley, peas, beans	Fravel (2005)
Bacillus subtilis MBI 600	*Fusarium, Rhizoctonia, Alternaria,* and *Aspergillus*	Cotton, beans, barley, wheat, corn, peas, peanuts, soybeans	Fravel (2005)
Bacillus pumilus GB 34	Fusarium wilt and Rhizoctonia damping-off	Soybean	Fravel (2005)
Bacillus subtilis var. *amyloliquefaciens* FZB24	Fusarium wilt and Rhizoctonia damping-off	Shade and forest tree seedlings, ornamentals, shrubs	Fravel (2005)
Pseudomonas chlororaphis 63-28	*Pythium* sp., *Rhizoctonia solani*, *Fusarium oxysporum*	Vegetables, ornamentals	Fravel (2005)

Combinations of microorganisms that perform better than individual species or strains			
Trichoderma strains + bacteria	Fusarium wilt	Radish	Hoitink and Boehm (1999)
Trichoderma viride and/or *Trichoderma harzianum*	Root rot *(Phytophthora nicotianae)*	Tomato	Pugliese et al. (2011)
Trichoderma harzianum, *Verticillium chlamydosporium* + *Glomus mosseae*	*Heterodera cajani-Fusarium udum* wilt disease complex	Pigeonpea	Meyer and Roberts (2002)
Arthrobotrys oligospora and different unidentified bacteria	Root knot nematode (*Meloidogyne mayaguensis*)	Tomato	Meyer and Roberts (2002)
Anabaena oscillarioides C12 and *Bacillus subtilis* B5	Damping-off by combination of *Fusarium* sp*.*, *Pythium* sp. and *Rhizoctonia solani*	Tomato	Dukare et al. (2011)
Trichoderma virens G1-3 + *B. cepacia* Bc-F	*Rhizoctonia solani* and *Pythium ultimum*, alone or in combination with *Sclerotium rolfsii* and *Fusarium oxysporum* f. sp. *lycopersici.*	Tomato	Meyer and Roberts (2002)
Verticillium chlamydosporium + *Pasteuria penetrans*	Southern root knot nematode (*Meloidogyne incognita*)	Tomato	Meyer and Roberts (2002)
Escherichia coli S17R1 + *Burkholderia cepacia* Bc-B	*Pythium* and *Fusarium* spp.	Cucumber	Meyer and Roberts (2002)
Embellisia chlamydospora, *Verticillium chlamydosporium*, and a sterile fungus	Sugarbeet cyst nematode (*Heterodera schachtii*)	Sugar beet	Meyer and Roberts (2002)

The challenge with general suppression is that it establishes in place; it cannot be transferred, and it can be disrupted by changes in management. Therefore, the degree and longevity of disease suppression can vary greatly. The efficacy and duration of suppressiveness depend on a number of compost and soil factors, including feedstocks from which compost is prepared, the thermophilic and curing process, maturity and phytotoxicity, salinity and nutrient content, and the microorganisms that colonize composts after peak heating and before planting in soil (Box 17.2).

Box 17.2 Biological Character of Organic Matter

In the 1950s and 1960s, organic amendment chemistry was defined using parameters such as cellulose and lignin content, and the ratio of total carbon to total nitrogen (C:N). These measures provided estimates of decomposition rate and are a component of compost recipe development but only have limited usefulness to predict the impact of compost on disease suppression (Neher et al., 2015). One explanation is that not all carbon is alike. Carbon substrates differ in water repellency, hydrocarbon content, and biochemical composition (simple sugars to highly aromatic materials recalcitrant to decomposition). There are now several high-throughput methods available to characterize organic matter, including pyrolysis−gas chromatography/mass spectrometry, near-infrared reflectance, and Fourier transform infrared spectroscopy. These methods provide a detailed view of organic matter composition that changes our understanding of the mechanisms of decomposition. They also help identify what properties of organic matter offer disease suppression more than others. Organic matter acquires beneficial characteristics soon after it begins to decay. Beneficial saprophytic microorganisms derive their nutrition and energy from this decaying material. The particle size, particle density, and age (degree of decomposition) of soil organic matter seem to set limits on disease suppression. The largest, least decomposed particles of organic matter do not seem to contribute directly to disease control, but as they decrease in particle size through decomposition, their effectiveness increases. However, there is a point of diminishing returns on particle size. Clumps that resemble soil aggregates (roughly 6 mm or ¼-inch in diameter) contain beneficial biocontrol organisms that can be lost by very fine screening (Neher et al., 2019a). Several reports suggest that the finest, most stable fraction (humus) also does not contribute to long-term biological control. This fraction is so biologically stable that it cannot nutritionally support populations of beneficial microorganisms. However, stable materials like biochar provide a porous structure that can physically sustain colonies of biocontrol organisms such as *Pseudomonas chlororaphis*, *Bacillus pumilus*, and *Streptomyces pseudovenezuelae* to suppress diseases caused by *Pythium aphanidermatum* and *F. oxysporum* f. sp. *lycopersici* in tomato (Bonanomi et al., 2018).

The composition of carbon compounds in the final product differentially selects a suite of microorganism species that colonize and are antagonistic to pathogens (Hadar and Papadopoulou, 2012). Wood-based composts have higher lignin: cellulose ratios than hay or straw carbon-based composts. Tree bark and other woody materials also contain tannins and waxes that resist decomposition. Sophisticated ^{13}C CPMAS-NMR spectroscopy methods have identified phenolic carbon and methoxyl carbon molecules associated with suppressive mechanisms (Pane et al., 2013). Both phenolic and methoxyl carbon are products of lignin degradation in woodchips. Intermediate products and residues from lignin degradation contribute to the humified matter in composts. Phenol and methoxyl carbons are unique soil carbons, requiring specialty enzymes that only a subset of saprophytic microorganisms can produce under conditions of carbon or nutrient limitations. Lignin is a complex molecule that requires a suite of 14 different enzymes to completely degrade (Chapter 4). The white-rot fungi of the Basidiomycota are among the main group that can fully degrade lignin.

Maintaining high levels of organic matter (e.g., greater than 6%) using mature compost is perhaps the single most reliable way to establish and preserve general suppression (Fig. 17.3). There are interactions between the level of organic matter decomposition and soil physical conditions, and those interactions affect disease incidence and severity in some crops. Partially decomposed organic matter improves soil structure. This transformation results in better water retention under dry conditions and improved drainage during periods of high precipitation. The improved soil conditions, in turn, lead to natural root rot suppression in wet soils in ridge tillage systems and some degree of suppression of wilt diseases in dry soils. Examples are Phytophthora root rot, which is prominent in wet soils, and the early dying disease of potato, caused by a complex involving nematodes and *Verticillium* in dry soils. These levels of organic matter require a combination of compost amendments, minimal to no tillage, and maintaining continuous vegetation cover to promote a more complex food web of abundant and active microorganisms that can suppress the incidence and severity of root diseases.

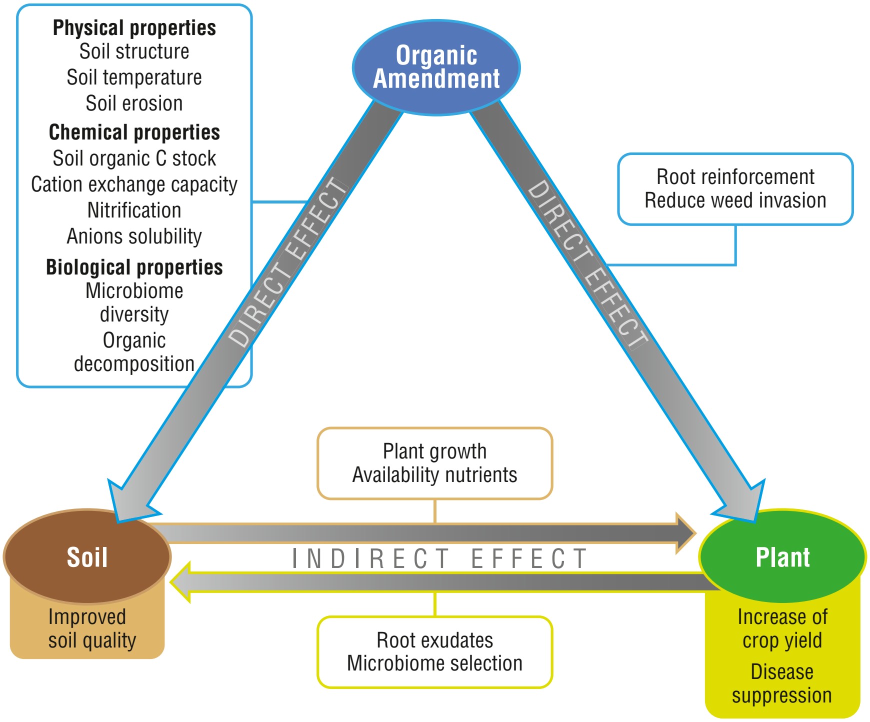

FIGURE 17.3

Interactions of compost, soil, and plants that support general suppression of plant diseases.

Adapted from Vida, C., De Vicente, A., Cazorla, F.M., 2020.

Rotating from a good host for a particular plant pathogen with crops that are nonhosts is an effective management strategy. In the years when a nonhost is planted, pathogen populations progressivly decline to low population densities. This decline, however, can be detrimental to microorganisms that are naturally antagonistic toward pathogens. A historical example of long-standing suppression is avocado root rot caused by *P. cinnamomi*, established in early 1940s in Queensland, Australia. The crop remained healthy after more than 40 years in soil infested with *P. cinnamomi* in an environment highly favorable for disease development, which was correlated with a diverse and abundant bacterial community that could antagonize the pathogen. A second example is "take-all" disease of wheat and barley caused by the fungus, *Gaeumannomyces graminis*. The suppressiveness was attributed to a build-up of populations of a specific *Pseudomonas fluorescence* strain that produced a broad-spectrum antibiotic that was especially active against the take-all pathogen. There are other examples of long-term, no-till monoculture with high organic matter content that suppress pathogens and pests, including soybean cyst nematodes (Neher et al., 2019b).

1.5 Compost factors that affect disease suppression

The degree of disease suppression experienced when soils are amended with organic amendments can vary greatly. Furthermore, organic amendments suppress diseases only for a limited period of time. The duration of suppressiveness and degree of efficacy, depend on a number of compost and soil factors, including:

- Feedstocks and characteristics,
- Composting process and curing,
- Compost decomposition level/maturity,
- Compost microorganisms and plant protection,
- Compost nutrient content,
- Compost salinity, and,
- Timing of compost application.

Extensive planning is required to implement strategies that maximize compost-induced disease suppression. This includes considering interactions among organic amendments, soils, and crops. Each of the factors will be reviewed here. Examples of disease control on several crops are used to illustrate reasons for success and failure in disease control.

1.5.1 Feedstocks and compost characteristics

There is no doubt that feedstocks determine the character of the compost and, thus, the compost's potential to suppress plant diseases and duration of the suppressive effect (Hoitink and Boehm, 1999). It is, however, difficult to prescribe or predict the effect of specific feedstocks on the disease-suppressive qualities of the resulting compost. With the exception of *Pythium* and *Phytophthora*, different compost recipes and maturity affect pathogen(s) and host crop(s) differently. Scientific results

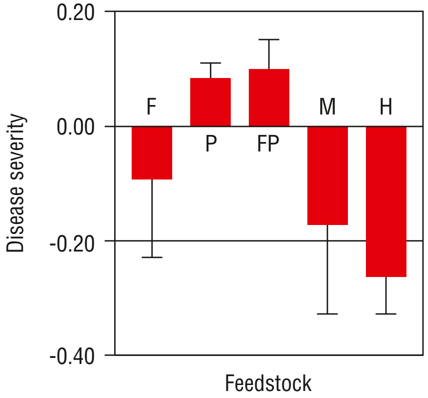

FIGURE 17.4

Disease severity of damping-off caused by *Rhizoctonia solani* in greenhouse studies, as affected by composting feedstock ($F = 0.59, 0.674$). Both controls and treatments were inoculated with virulent *Rhizoctonia solani*. Illustrated are means ± 1 standard error of percent change from noncompost control. *F*, Food waste; *FP*, Food waste + Poultry manure; *H*, Hardwood bark; *M*, dairy Manure; *P*, Poultry manure.

Source: Modified from Neher et al. (2017)

have provided some guidance but have so far fallen short of providing general recommendations regarding feedstock and disease suppression (Fig. 17.4). For example, composts made from green waste (yard trimmings, food scraps, animal manures, paper, and wood wastes) reduced damping-off caused by *R. solani* on tomato but had the opposite effect on lettuce (Noble, 2011). Another study compared two composts containing different vegetable residues amended with 10% wood chips. The compost containing rocket/arugula residues suppressed *R. solani* and *Sclerotinia minor* while another containing endive was conducive to disease (Scotti et al., 2020). Other studies examining the disease-suppressive effects of animal manure composts have generally shown positive but inconsistent results. Composts derived from poultry manure are particularly difficult to characterize because of the typically high ammonia content and salt concentrations.

One generalization is that the most reliable disease-suppressive composts are those made with woody materials, like tree bark, wood chips, and woody yard trimmings. Tree bark and other woody materials consist mostly of lignin, cellulose, tannins, and waxes, a mixture that resists decomposition. After composting, the disease-suppressive effects of composted barks last for several years in soil, depending on the tree species from which the bark was removed and how much compost was added to the soil. Decomposition of wood waste releases nutrients very slowly and produces humic acids (large molecular weight organic acids that are very complex and difficult to degrade). In contrast, food and feed wastes, animal manures and biosolids mostly consist of readily decomposable compounds and nutrients and produce fulvic acids (low molecular weight organic acids). Both fulvic and humic acids grab and bind (chelate) essential micronutrients and keep them available for uptake by plants. Chelates can strongly mediate the severity of diseases caused by soilborne plant pathogens. However, these beneficial effects usually do not last more than one or 2 years in soils.

1.5.2 Composting process and curing

Many composting feedstocks carry microorganisms that are pathogenic to plants and/or humans. Fortunately, pathogens and weed seeds are destroyed by the high temperatures achieved during the sanitization stage (e.g., pasteurization, PFRP) of composting (Neher et al., 2015). Therefore, properly prepared compost not only delivers the potential to suppress plant pathogens in the soil but also delivers few to no new pathogens to the plant environment.

Because numerous beneficial microorganisms contribute to biological control of plant diseases, the question becomes whether such organisms consistently colonize composts after peak heating. Chances of this happening are poor in large windrow or pile composting systems in which temperatures typically persist above 40°C (104°F) for prolonged periods after sanitation. Most biocontrol agents cannot grow or survive long-term in these temperatures, except for spores of *Bacillus* spp. Conversely, colonization is rapid when postsanitation temperatures are maintained below 35°C (95°F), especially at soil temperatures of 25°C (77°F) or lower. Bacterial biocontrol agents such as *Pseudomonas* spp. colonize the substrate fully in one to 2 days to establish general suppression. This does not occur, however, when the moisture content of the compost is below 30% on a weight basis. Dry composts become dusty and fungi become the principal colonizers. Some of these are nuisance fungi that delay or even inhibit plant growth. Therefore, it is important to manage moisture content during peak heating as well as during curing of compost to enhance the potential for natural colonization by the beneficial microflora during the process. Although most compost that is used in container media (predominantly made from bark, sawdust, etc.) is made in tall windrows/piles, these products still offer ideal opportunities for inoculation with specific biocontrol strains for use in greenhouse and nursery crops, as long as moisture and temperature regimes are managed appropriately.

The situation can be quite different for small windrow composting systems that are turned frequently, especially when the moisture content of the compost is maintained above 45%. These composts, especially those high in microbial activity such as manure composts, are much more likely to be colonized by a great diversity of biocontrol agents as the compost matures.

1.5.3 Level of organics matter decomposition

Fresh organic matter often has negative effects on plant health for some time after their application to soils. Fresh residues typically stimulate the growth of pathogens and increase disease incidence and severity for some time after their incorporation.

For example, the pathogens *R. solani* (causes damping-off on almost all crops) and *Armillaria mellea* (can kill mature trees including oaks, kiwi) can grow on fresh straw and wood. These fungi cannot grow on partially decayed or composted products. Both *Pythium* and *Phytophthora* cause root rot on many plants, particularly in wet soils, and thrive on fresh green manures. For example, fresh straw applied in the fall as mulch under apple trees or red raspberry bushes increases water retention in soil and immobilizes nitrogen if it has not decayed adequately. As a result, Phytophthora collar rot is aggravated in the wet soil when trees break dormancy in the spring when the Phytophthora collar rot pathogen becomes active. Fresh ground wood can have similar negative effects in the landscape, but the effect lasts much longer because wood breaks down much more slowly than straw. In contrast, composted wood, which is more like forest litter, improves soil drainage and aeration while it also improves water retention and supports the growth of mycorrhizal fungi, all of which leads to suppression of Phytophthora root rots. Other diseases are also aggravated by shredded raw wood mulches but are controlled by composted wood. Examples include diseases caused by *Armillaria*, *Pythium*, and *Rhizoctonia*. This principle applies to many crops!

Green manures need to decompose for 10 to 14 days after they are plowed into the soil prior to crop planting to prevent a drastic increase in Pythium damping-off on many crops. A California study showed that lettuce, planted in soil one day after vetch was incorporated, suffered severe preemergence damping-off due to increased *Pythium* activity. In contrast, planting one week after incorporation provided control. Allowing green manures to degrade before planting a crop provides time for beneficial microorganisms to colonize the decaying vegetation. Colonization may take several weeks, depending upon crop species and maturity, soil temperature and moisture content.

Fresh residues generally cause problems unless they decompose to some degree before planting of the next crop. There are strategies to encourage breakdown of crop residues using nutrient-rich composts, like poultry manure-based composts. For example, application of 2.5 to 5 tonne per hectare (1.1 to 2.2 tons per acre) of fresh or composted poultry manure immediately after the harvest of corn accelerates the decomposition rate of corn stover in the field. The added nitrogen combined with minimum tillage decreases survival of plant pathogens. Thus, seed rot caused by *Pythium* and seed, stalk and ear rot of corn caused by *Fusarium graminearum* can be reduced in severity by such applications in this tillage practice. The ear rot pathogen produces mycotoxins (i.e., vomitoxin) which have serious detrimental effects on livestock.

1.5.4 Compost maturity

Plant disease suppression is the result of the activity of antagonistic microorganisms that naturally recolonize the compost during the cooling phase of the process. Composition of microbial communities starts similarly after the sanitation phase and the composition of the community changes as the temperature declines and the chemistry of the compost changes (Neher et al., 2013). These natural patterns resemble ecological succession of decomposer communities in forest litter and wood decay reported by soil ecologists. Microorganisms secrete enzymes that target portions of the decaying organic matter that provide the nutrients or energy they need. Microbial feeding on organic matter progressively alters the chemistry of compost which, in turn, promotes a microbial turnover that further changes organic carbon chemistry. This curing phase offers a substrate and environmental conditions conducive for microbial recolonization that can be expedited by inoculating post-thermophilic compost or preparing a palatable substrate that provides a competitive advantage for colonization by bacteria and fungi that offer biological control.

Immature compost corresponds with early stages in succession that favor microbial species that are most competitive when simple carbohydrates are abundant, earning them the ecological title, copiotrophs. Mature compost corresponds with later succession that favor microbial species that are most competitive with complex carbohydrates (e.g., lignin, tannins) earning them the ecological title, oligotrophs. The ratio of oligotrophic to copiotrophic organisms increases through maturation, which corresponds to enhanced disease suppression of mature compared with immature composts (Fig. 17.5).

Biological control organisms can grow effectively on both immature and mature products but shift to become relatively more or less competitive against pathogens depending on the relative competitiveness on particular substrates. A classic example is for pathogens like *R. solani* that are favored in early stages of composting when concentrations of water-soluble carbon compounds are high (Chung et al., 1988). Once this carbon is depleted, as in mature compost, the efficacy of biological control fungi such as *Trichoderma harzianum* increases because it produces

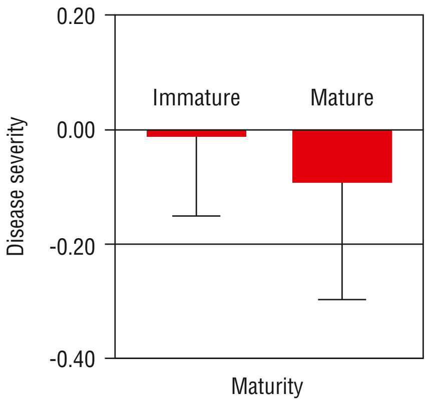

FIGURE 17.5

Relative disease severity of damping-off caused by *Rhizoctonia solani* affected by compost maturity ($F = 4.59$, $P = 0.041$). Both controls and treatments were inoculated with virulent *Rhizoctonia solani* (Illustrated are means ± 1 standard error of percent change from noncompost control.)

Source: Modified from Neher et al. (2017).

enzymes that degrade cellulose. Managing carbon quality and compost maturity are the tools that one has to manage the colonization of compost with microorganisms that will favor disease suppression.

At the other end of the spectrum, composts that are excessively stable or fully decomposed after months or years of decomposition in soil no longer have the ability to support populations of beneficial organisms. As beneficial organism populations decline, plant pathogens increase in numbers and activity and diseases increase in severity in the now "worn out" soil, even though humic acids produced from the compost are still present in the soil. For this reason, highly stabilized organic matter, such as peat or geologically old soil organic matter (as found in soils derived from prairies or in organic soils after they have been farmed for many years) are not effective in controlling plant pathogens unless new sources of stable organic matter are added.

1.5.5 Compost microorganisms and plant protection

Microorganism communities are abundant and diverse in compost. The assembly of microbial communities (consortium) are organized and influenced by recipe, choice of post-thermophilic process, and duration of curing (maturation) of composts (Neher et al., 2013). When added to soil, the nature and behavior of the consortium are modified by plant (crop) and soil type. It is only recently that scientists have the tools to solve the mysteries of how these highly coevolved relationships work so we can incorporate those insights into management practices.

Until the 1990s, the knowledge of compost microbiology was limited to organisms that would grow in Petri dish culture. Suppression was tested by exposing the pathogen to cultured organisms in vitro or measuring reduction of disease symptoms when they were inoculated in a conductive soil. This era identified the strains commonly seen on the market including species of *Pseudomonas* (γ-Proteobacteria), *Bacillus* (Firmicutes), *Streptomyces* (Actinobacteria), and *Trichoderma* (Ascomycota). Unfortunately, this approach missed 99% of the species that are now detectable by modern molecular techniques that detect microorganisms independent of their ability to grow in a Petri dish.

Molecular technology provides a new perspective on the microbial community or microbiome. A microbiome contains the genes, metabolites, proteins, and species associated with various habitats of a plant host whether it be whole plants, specific organs such as roots, or the rhizosphere (root-soil interface). Now, studies of suppressive soils can use microbiome analyses and examine the structure and complexity of interactions among microorganisms themselves and in interaction with roots and/or soil. Some generalizable patterns are emerging as the use of molecular techniques increases. For example, the assembly of bacterial and fungal communities that colonize compost during curing and maturation phases depend on whether the carbon source was hay, straw, softwood (e.g., pine), or hardwood (e.g., birch) (Neher et al., 2013). Different microbial species produce different types and diversity of enzymes that generally or very specifically target particular types of decaying organic matter. The consortium of microorganisms that can suppress disease is able to metabolize and degrade complex matrices better than the community found in conducive compost (Scotti et al., 2020). Members of this "suppression" consortium include an abundance of bacteria in the phyla Proteobacteria, Bacteroidetes, Actinobacteria, and Deinococcus-Thermus. In contrast, members of the conductive microbial consortium include an abundance of bacteria in the phyla Verrucomicrobia, Gemmatimonadetes, Acidobacteria, and Planctomycetes. Suppressive composts contain more fungi in the phylum Basidiomycota and fewer Ascomycota than the conducive compost. The Basidiomycota contain fungi that can decompose lignin associated with wood, such as the brown-rot and white-rot fungi.

The rhizosphere provides the frontline defense for plant roots against attack by soilborne pathogens. As Fig. 17.6 illustrates, plants are able to influence the composition and activation of their rhizosphere microbiome through exudation of compounds that stimulate (green arrows) or inhibit (red blocked arrows). Vice versa, a wide range of soilborne pathogens is able to affect plant health. Prior to infection, these deleterious microbes are in competition with many other microbes in the rhizosphere for nutrients and space. In this battle for resources, beneficial microbes limit the success of the pathogen through production of biostatic compounds, consumption of (micro)nutrients, or by stimulating the immune system of the plant. Most microbes neither affect the plant nor the pathogen directly

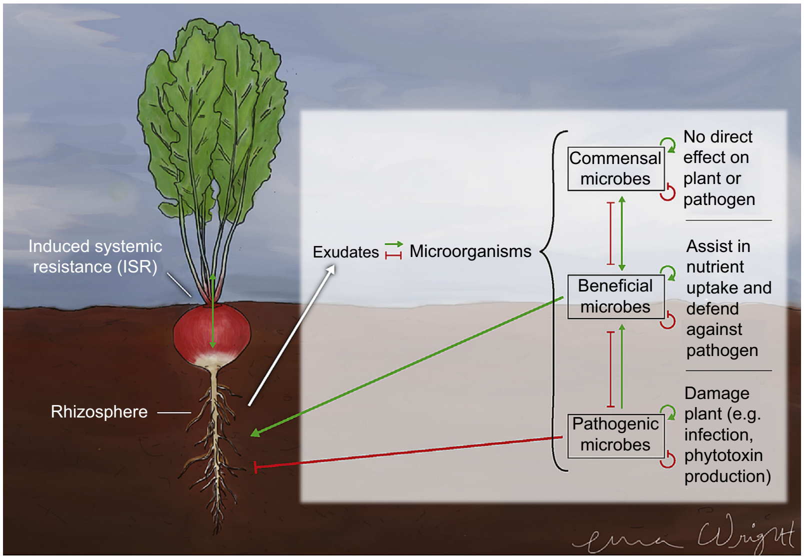

FIGURE 17.6

Interactions in the rhizosphere.

Source: Emma Wright (Research Technician, University of Vermont).

because they occupy different ecological niches (commensal microbes) but are likely to affect every other organism to a certain extent through a complex network of interactions.

The action within the rhizosphere takes place at the scale of micrometers (1 μm = 0.000039370 inch), which is why molecular scale tools are necessary to study the phenomenon. Plants naturally leak sugars and a wide variety of small molecules (e.g., amino acids, organic acids, phenolics, alkaloids) through their roots as lubrication for roots to grow by extension into soil and for root defense. This leakage (exudates) is food and energy for soil organisms, attracting them to root surfaces and the volume of soil adhering to the root. Plants actively recruit beneficial soil microorganisms in their rhizospheres to counteract pathogen assault (Lakshmanan, 2015). In return, microorganisms can promote plant growth by mineralizing nutrients, producing plant hormone imitations, or secreting antibiotics to defend against other microorganisms (Bais et al., 2006).

Rhizosphere microorganisms can differentiate plant species by exudate "flavors." For example, *R. solani* is an invading pathogenic fungus that induces, directly or via the plant, a stress signal detected by the rhizosphere bacterial community (Chapelle et al., 2015). In response, the microbiome shifts in community composition and activates traits that protect roots by restricting the ability of the pathogen to infect and cause disease. For example, when *R. solani* attacks the rhizosphere of sugar beet, a consortium of bacteria response by antagonizing the pathogen, e.g., *Paraburkholderia* (β-Proteobacteria), *Pseudomonas* (γ-Proteobacteria), and *Streptomyces* (Actinobacteria) (Mendes et al., 2011). Additional known pathogen antagonist groups include bacteria (β-Proteobacteria: *Burkholderia*; γ-Proteobacteria: *Serratia*; Firmicutes *Bacillus*), and fungi (*Trichoderma*, *Penicillium*, *Gliocladium*, *Sporidesmium*, nonpathogenic *Fusarium* spp.). The means or mechanism of antagonism can include production of antibiotics (against bacteria or fungi) or competition (for nutrients, trace elements, or colonization sites). For example, *Streptomyces* (Actinobacteria) and *Trichoderma* (Ascomycota) species are prolific producers of antibiotics. Antibiotics secreted in low concentrations can mediate intercellular signaling (communication), and in high concentrations can inhibit pathogen growth. Sometimes, it takes multiple species of microorganisms working together collectively to antagonize pathogens (syntropy). Root-associated bacteria can distinguish among their neighbors and fine-tune the biosynthesis of antimicrobial metabolites. These types of natural suppression are highly coordinated events influenced by the plant host and soil (Bais et al., 2006).

If the pathogen breaks through this first line of defense, it encounters the basal and induced defense mechanisms of the plant. Plants communicate with microorganisms in the rhizosphere through root exudates. A direct attack by pathogens stimulates the plant to release chemical signals consisting of phenolic compounds (e.g., coumaric, cinnamic, salicylic acids) or saponins (glycosides with triterpene or steroid backbones). Phenolic compounds stimulate germination of fungal conidia in low concentrations and inhibit fungal growth in high concentrations.

Mal-timed chemical signals can trick fungal pathogens into germination in unfavorable conditions disarming them from a successful infection. Saponins form complexes with sterols and damage the cell membranes of plant pathogens. Indirectly, root exudates stimulate microorganisms to produce small water-soluble molecules, called volatile organic compounds (VOCs). The type and temporal dynamics of VOC production are extremely species-specific, at least for *Trichoderma* that produces a diversity of sesquiterpene emission patterns (Guo et al., 2020). VOCs evaporate easily at room temperature and distribute into the surrounding air, enabling them to act as communication signals within and among organisms. When the density of these molecules exceeds a certain threshold (measured as parts per trillion with modern instrumentation), it triggers a coordinated community response (quorum sensing) that activate various plant defense-related genes that either suppresses disease symptoms or stimulate plant growth. VOC-producing organisms in the rhizosphere suppress symptoms include *Pseudomonas trivialis* (γ-Proteobacteria), *Pseudomonas fluorescens* (γ-Proteobacteria), *Bacillus subtilis* (Firmicutes), *Burkholderia cepacia* (γ-Proteobacteria), and *Trichoderma* (Ascomycota). Those that promote plant growth are produced by *Flavobacterium* (Bacteroidetes), *Streptomyces* (Actinobacteria), and *Trichoderma*. Microbial species promote plant growth by production of antibiotics to combat pathogens, manufacturing plant growth mimics, and/or induced systemic resistance (ISR) that protects noninfected tissues throughout the plant. ISR in plants by compost occurs in cucumber Pythium root rot (i.e., *Pythium ultimum* and *Pythium aphanidermatum*). Traditionally, the role of VOCs was overlooked partly due to analytical limitations. With modern tools, we are likely to gain knowledge about how they operate ecologically and are modified by soil type, neighboring species, and plants.

By intentionally designing recipes and curing methods, compost can become a tool to manipulate or deliver a natural consortium of microorganisms in soil, onto seeds, and planting materials. The advantage of assembling microorganisms with complementary or synergistic traits provides a more effective and consistent effect. For example, a consortium containing both *Flavobacterium* and *Chitinophaga* conferred significant and more consistent protection against fungal root infection than individual consortium members (Scotti et al., 2020). However, the next scientific challenge is to find or select the right players of a consortium. Rather than single species, consortia are communities that mimic general disease suppression in soil. One may argue that control of different pathogens on different crops requires a different combination of microorganisms and/or mechanisms (Termorshuizen et al., 2006; Bonanomi et al., 2010). This is probably true for different groups of soilborne plant pathogens, that is, bacteria, fungi, oomycetes, and nematodes. However, studies on natural disease-suppressive soils have pointed to common players and identical mechanisms and genes in the suppressiveness of soils to different fungal pathogens. Furthermore, the onset of natural disease suppressiveness of soils follows a similar pattern for various fungal pathogens suggesting that similar processes, mechanisms, and microorganisms may be required for the transition of a soil from a conducive to a suppressive state.

1.5.6 Compost salinity

Many plants experience stress by excessively high concentrations of salts in the root environment (EC readings >10 dS/m). In turn, stressed plants are more susceptible to diseases, particularly root diseases caused by *Pythium* and *Phytophthora*. Even when the salinity levels are not stressful to plants, elevated concentrations of salts can negate the disease suppression benefits supplied by the organic and biological components of the compost. Composted livestock manure tends to have relatively high levels of soluble salts and may not produce the expected disease benefits in container-grown plants.

It is often impractical to adjust feedstock recipes to lower compost salinity levels. Instead, one can blend high-salinity composts with low-salinity compost (e.g., most yard trimmings composts). It is advisable to apply compost to fields well ahead of planting to allow salts to leach below the root zone if there is adequate rain (or snow). However, an unintended side effect could be the loss of mineral nutrients to leaching too. For mulches, the best approach is to blend composted materials high in salinity with woody or bark mulches which typically are low in salinity to dilute the negative factors and provide long-lasting beneficial effects for value added markets. These blends can be applied as mulches at any time of year and provide beneficial effects more consistently.

1.5.7 Compost nutrient content

A growing body of research shows a link between soil fertility and plant disease incidence/severity. Generally, plants are more susceptible to disease if they are either nutrient stressed (limited) or their roots are surrounded by a nutrient surplus. Nitrogen (N) is the primary nutrient to consider for two reasons. First, availability of mineral N (ammonium and nitrate) from composts or mulches varies more than that of any other nutrient. Composts made from biosolids or animal manures typically contain between about 1.5% and 2.5% total N (dry weight) but values may exceed 4%, particularly for composted poultry manure. Most N, usually above 90%, in compost is organically bound, with only a small proportion being immediately plant available (i.e., ammonium, nitrate). Typically, only a small part (0% to 10%) of the total N in these composts is converted to mineral N forms (ammonium and nitrate) within the first three months after their amendment to soil in spring/early summer. A much higher proportion would be mineralized from raw, high N manures. The remaining organically bound N may be released in as little as two to five years or as long as 30 years or more. If very mature composts with high nitrate concentrations are used, or if mineralization supplies high concentrations of nitrate during the growing season, certain plant diseases may be exacerbated unless care is taken to avoid N overloading of the soil. Nutrient budgets that account for mineral soil N levels and inputs from both organic soil amendments and mineral fertilizers can prevent this. Composted cow manure contains mostly nitrate whereas poultry manure composts are high in ammonia.

Mineral N availability has a major effect on plant disease. Bacterial leaf spots (e.g., *Pseudomonas syringae*, *Xanthomonas campestris*), fire blight on apples and pears (*Erwinia amylovora*), and Pythium root rots and Fusarium wilts are more severe with immature composts that are high in ammonium and low in nitrate, even in hydroponic systems. Thus, great care should be taken in selecting composts for use on crops susceptible to these *Fusarium* diseases (e.g., celery, basil, cyclamen). Low N composts such as those prepared from bark or yard trimmings are best for control of these diseases and then particularly so in greenhouse crops if inoculated with *Trichoderma* strains capable of suppressing Fusarium wilts.

A lack of available N can also aggravate plant disease incidence/severity, especially when immature compost with a high C:N ratio is used. N-poor composts that are relatively young with a high degree of biological activity can tie up and immobilize N when applied to the soil. Because N release or mineralization from these composts is dependent on soil microorganisms, they may create a temporary N deficiency for plants and favorable conditions for plant pathogens to establish.

1.5.8 Timing of compost applications

Compost analysis, soil test results, and crop requirements together should form the basis for determining compost application rates. Nutrient release from composts in the field, particularly that of N must be balanced against what is in the soil, the requirements of the crop, and what is applied with mineral fertilizers. Once growers have applied compost to soil, it becomes more important to properly estimate the quantity of nutrients released from compost before any additional nutrients (organic or mineral) are applied. Fruit growers who do not address this issue will increase fire blight on apple due to excessive N supply even though they will maintain control of Phytophthora collar rot (Fig. 17.7). Grape producers would decrease wine quality. This problem was identified in Italian field studies during the 1990s as the only possible negative aspect associated with 30 years of compost use in vineyards when soil fertility and nutrient supply were not addressed adequately.

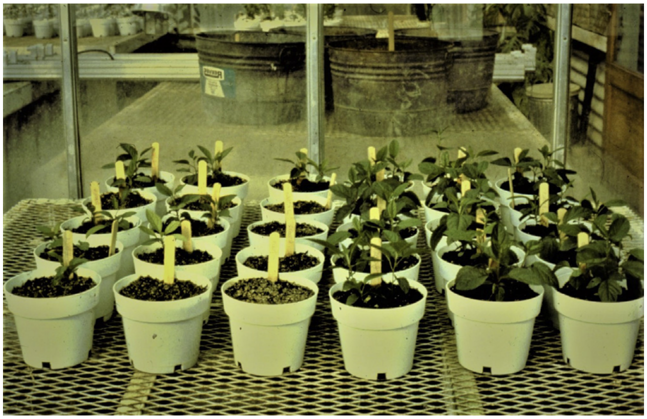

FIGURE 17.7

Suppression of Phytophthora collar rot on apple in a bark mix versus a conducive peat mix with three *Phytophthora cactorum* inoculum density levels in each (Spring et al., 1980).

Source: Courtesy of Harry A. Hoitink.

Application of bark or leaf-derived composts with boosted N content (up to between 1.7% and 2.2%) at high rates (5.0–7.5 cm; 2–3 inches; equivalent to approximately 500–750 m^3/ha) followed by incorporation into the topsoil (15–20 cm; 6–8 inches) has been used to control soilborne diseases in ornamental nursery crops. This approach eliminated the need for methyl bromide fumigation in these crops since the 1970s. Moderate to high application rates of composts can replace methyl bromide for control of the strawberry black root rot complex caused by several pathogens.

Application of N-rich composted biosolids or manure to a depth of 2.5 cm (1 inch; equivalent to approximately 250 m^3/ha) and incorporation into the topsoil (10 cm; 4 inches) prepares an ideal seed bed for most woody plants and for seeding new lawns. As mentioned above, only highly stabilized composts in which mineral N is present primarily as nitrate-N should be used to amend soils growing crops that are sensitive to ammonium-N and Fusarium wilt. Especially on sandy soils and in potting mixes, care must be taken to avoid ammonium toxicity.

Composts with high ammonia or salinity are best applied several weeks before planting so that salts disperse and much of the ammonium is adsorbed and converted to nitrate. This is especially critical for manure-based composts applied to crops highly susceptible to Phytophthora root rots and salinity (e.g., soybeans). Crops such as small grains are much less sensitive to these diseases than many vegetables, but they may suffer from Rhizoctonia damping-off. For these crops also, it is better to apply the compost a month or more ahead of planting to minimize this problem. This also avoids ammonium toxicity induced by composted manures that still are high in ammonium content. In regions where crops are planted immediately after another has been harvested, it would be best to apply compost to a disease resistant crop (e.g., corn) that is grown before a susceptible crop is planted.

1.6 Indicators of suppression

Based on a simple understanding of ecological succession and compost maturity, one might anticipate that a simple fungal to bacterial ratio would suffice as a measure of mature and suppressive compost. However, this is oversimplified as illustrated above. The resolution of identification of both bacteria and fungi must include information about their ecological role and lifestyle, e.g., parasitic, saprophytic, oligotrophic, copiotrophic. That said, it is neither practical nor affordable for farmers to run DNA tests to look at specific bacterial and fungal species. Nonetheless, there is an unfulfilled need for reliable indicators to detect composts that suppress soilborne pathogens. Furthermore, these tools are likely to have tweaks and modifications tailored to specific diseases or pathogens.

Disease suppression is best tested by plant bioassays (Wichuk and McCartney, 2010). Effective plant bioassays are standardized by plant cultivar and environmental conditions but are time-consuming (2–4 weeks) to complete which may be longer than desired. Comparably robust, but quicker (1–2 days) assays would be ideal for quality control and quarantine programs.

Microbial biomass and activity: Simple measures of microbial activity or biomass predict *Pythium ultimum* and *Pythium irregulare* but not *R. solani* (Scheuerell et al., 2005). Compost analytical labs have a variety of measures to reflect microbial activity by respiration (CO_2 evolution) by dehydrogenase, Solvita test, and/or hydrolysis of fluorescein diacetate (FDA) (Green et al., 2006). Advantages of these methods are their simplicity and rapid response. However, the methods are criticized for imprecision and weak associations with populations of known biological control agents such as fluorescent *Pseudomonas* and *Trichoderma* spp. (Pane et al., 2013; Scotti et al., 2020). FDA has been a tool that works to predict suppression of Oomycota pathogens (e.g., *Pythium* and *Phytophthora*) but not necessarily fungal soilborne pathogens (Hadar and Papadopoulou, 2012).

Compost maturity: Mature composts have greater C:N and lignin, cellulose ratios, and slow-release of nutrients than immature composts. Mature composts are promoted as suppressive to *R. solani* (Scheuerell et al., 2005; Coventry et al., 2006).

Ideally, methods should reflect a composite of species and mechanisms and do not require a specialist and expensive analytical equipment. Promising candidates are (1) competition plate assays (Pane et al., 2013; Neher and Weicht, 2018), (2) ecoenzymes (Neher et al., 2017), and/or (3) physiological profiles using Biolog EcoPlates that screen for utilization of 31 carbon types (Scotti et al., 2020; Wright, 2020). Antibiosis activity on plate assays are effective tests for *R. solani* (Neher et al., 2017), *Streptomyces scabies* (Bakker et al., 2013), *Sclerotinia minor* (Pane et al., 2013), and *Fusarium* (Borrero et al., 2006). Suppressive colonies create a visible zone of inhibition around the pathogen colony. Microbial ecoenzymes active on chitin and cellulose are better predictors of disease suppressiveness by fungal pathogens than microbial respiration (Neher et al., 2017). The enzymes might damage cell walls of fungal pathogens such as *Rhizoctonia*, *Fusarium*, and *Verticillium*. However, Oomycota *Phytophthora* and *Pythium* have cellulose in their cell walls instead of chitin.

1.7 Conclusions

Everyone wants shelf-ready products that are inexpensive and easy to use. Unfortunately, the science is lagging to provide these immediately for composts, especially composts that allege disease-suppression benefits. As living entities, composts require more care than synthetic fertilizers and pesticides. For example, the effectiveness changes with age. Disease suppression may be negligible or even harmful in young composts; it may diminish in old material. Compost biology may be altered by high moisture, extreme heat, direct sunlight or, less likely, freezing temperatures.

Still, composts applied to soils can provide biological control of root diseases and occasionally also of foliar diseases of plants. Many factors must be considered to obtain consistent disease-suppressive effects with composts. First, the compost must have met temperature and time requirements for sanitation. In addition, it must have been adequately cured and matured, sufficiently enough for beneficial biocontrol organisms to colonize and proliferate. Compost that performs consistently must be prepared by a consistent process and from a relatively consistent feedstock recipe. Compost is at a point in history where organic farming was 20 to 25 years ago. The landscaping and road construction industries have widely adopted compost standards, but similar standards are scarce for field crops production.

Compost must be applied at a time of year and an application rate that meets, but does not overwhelm, the fertility needs of the crop. Soil fertility and nutrient supply must be included in these decisions. The quantity of essential plant nutrients such as N and phosphorus in the soil accumulates with each compost application. Soil fertility and mineral fertilizer application must be considered when subsequent compost application rates are determined to avoid increasing the severity of disease or cause other negative side effects due to excessive soil nutrient levels. Fall application is required for crops sensitive to Phytophthora root rot if composts high in salinity are used. In general, it is safest to apply compost weeks to months in advance of planting to avoid possible problems with ammonia, salts and immaturity.

Concerning disease-suppressive composts, the curing stage remains underappreciated. Commercial composting guidelines require a high-temperature phase designed to facilitate the removal of human and plant pathogens. However, these requirements stop short of guidelines for compost curing (cooling) in the post-thermophilic phase. The curing phase offers favorable conditions for microbial recolonization, accomplished by either inoculating post-thermophilic compost or creating a palatable substrate that offers a competitive advantage for colonization by bacteria and fungi capable of suppressing soilborne pathogens. With a better understanding of the microbiology of composting, the pivotal conditions can be managed to enhance disease suppressiveness either by regulating the microbe-to-microbe interactions or microbe-to-plant interactions in soil. This knowledge will elucidate which recipe and post-thermophilic practices are best to develop compost for more reliable strategies to manage ubiquitous and difficult to manage soil pathogens.

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