Current knowledge on disease suppressive properties of composts.

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Abstract

Composts prepared from solid wastes with high concentrations of recalcitrant materials (bark, yard wastes, etc.) can be used effectively to suppress soilborne plant diseases but several factors must be controlled for optimum effects. Composts prepared from manures, especially those prepared from manure solids without bedding, are much less likely to provide these beneficial effects. The stability of the organic fraction in composts critically affects efficacy. The type of composting system used and the environment affects populations of biocontrol agents in composts. In practice, disease suppressive effects typically do not develop until after their utilization. Phytophthora, Pythium and Thielaviopsis root rots are suppressed most effectively by composts. This applies to container media as well as field soils. Inoculation of composts utilized in container media during the formulation process with specific biocontrol agents can increase the suppression spectrum to include diseases caused by sclerotium-producing pathogens such as Rhizoctonia solani. Inoculation with ISR-active biocontrol agents can further increase the suppression spectrum to include vascular wilts and foliar diseases. These diseases typically are not suppressed naturally by compost amendments. This paper presents an overview of historical perspectives and of recent findings in this field. ((codis-abstract))

Introduction

During the 1950's when chemical agriculture was in its "golden age", soils typically were tilled intensively while "organic wastes" were disposed off in landfills or applied at excessive nutrient loading rates on farmland. As a result, soil quality was poor and diseases caused by soilborne plant pathogens caused major losses even though it was understood that organic amendments could improve soil quality and plant health (Stone et al., 2004). Soils used for the production of trees and other woody ornamental plants at that time were of very low quality and suffered from erosion problems because the top soil was sold with harvested plants in root balls. Fumigants such as methyl bromide, nematocides and soil fungicides were used widely in this industry and this caused additional disruption of soil ecology and led to environmental pollution. In spite of these chemical treatments, Phytophthora root rot caused major losses on nursery crops. Breeding for resistance to these diseases was not a realistic option for woody plants even though this was a standard practice for agricultural crops (Hoitink and Fahy, 1986). Environmental problems caused by pesticides, excessive use of fertilizers and inappropriate disposal of organic wastes eventually produced legislation during 1971 that forced US agriculture to develop sustainable alternatives.

The nursery industry pioneered the return to more traditional soil management practices in two different ways. First, it began by replacing Sphagnum peat, which did not suppress Phytophthora root rots, with composted tree bark, which seemed to provide natural control of the disease. Thus, composted bark became a methyl bromide and soil fungicide alternative (Hoitink and Fahy, 1986). Unfortunately, plant growth often was variable from batch to batch in bark media. This was due to nitrogen deficiency in plants early after potting but also to imbalances of mineral nutrition and/or allelopathy problems caused by the bark from some tree species. Procedures were developed in several parts of the world for composting of bark from several different tree species that solved these plant growth issues (Hoitink and Fahy, 1986). In addition, bioassays were developed that compared the relative suppressive effects of potting mixes against diseases caused by several different types of plant pathogens. As a result of both types of efforts, compost-amended media became available that suppressed root rots caused by some *Phytophthora* and *Pythium* spp. and *Thielaviopsis basicola* (Fahy and Hoitink, 1986, Hoitink and Boehm, 1999). However, the bark-containing media did not

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consistently suppress diseases caused by *Rhizoctonia solani* or *Sclerotium rolfsii*. Vascular wilts and foliar diseases typically were not suppressed either (Stone et al., 2004).

The second move towards a return to more sustainable production practices in the nursery industry occurred during the early 1980's when composts prepared from municipal wastes and from manures became available as high quality soil amendments. Initially, leaf, bark, and sewage sludge composts were incorporated into ground beds at rates as high as 100 tons per ha. These composts were used as one time mulches or amendments to improve soil quality without causing pollution of ground or surface waters with nutrients. Follow up treatments used lower rates, based on soil type, soil quality indicators and crop requirements. These compost applications, in general, reduce the severity of Phytophthora, Pythium and Thielaviopsis root rots as long as several factors which include compost quality, soil fertility, timing of application, etc., are considered (De Ceuster and Hoitink, 1999). As observed earlier in container media, diseases caused by pathogens such as *Rhizoctonia* that produce sclerotia typically are not suppressed until several months after incorporation of the amendments into low quality, conducive to disease soils (Hoitink and Boehm, 1999, Stone et al., 2004).

To allow successful utilization, control must be exerted with respect to the raw materials used as feedstock, the composting process itself, the degree to which the compost has been stabilized during curing (i.e. maturity / stability), particle size, and finally, biological, chemical and physical properties of the product (De Ceuster and Hoitink 1999, Hoitink and Boehm, 1999). Composts that are most effective are those prepared from bark and woody residues, or created from animal wastes bulked with high in carbon material or straw. Least effective, and possibly problematic, are those prepared from post consumer food wastes, farm manures devoid of bedding (i.e. sawdust, stover or straw), both of which tend to be low in recalcitrant carbon. These less effective products also need to be applied in the fall to allow for leaching of salts if crops sensitive to Phytophthora or Pythium root rot are planted on the amended soil (De Ceuster, et al, 1998; De Clercq, et al., 2003; Stone et al, 2004). Thus, it is not surprising that composts do not consistently provided control of diseases caused by soilborne plant pathogens (Fuchs and Larby, 2005; Scheuerell et al., 2005; Termorshuizen et al., 2006).

Organic matter mediated biocontrol

The decomposition level (also refered to as maturity or stability) of the organic fraction in composts critically affects biological control (Hoitink and Boehm, 1999; Stone et al, 2004; Wang et al., 2006). Most vegetative and woody materials release glucose and/or other sugars early during their decomposition. These and other soluble nutrients support the growth of resident microbes, especially that of mycelium-producing plant pathogens. Although biocontrol agents such as *Trichoderma* reach high populations in such substrates, they initially do not suppress the pathogen due to glucose-induced repression of enzyme synthesis required for parasitism (Hoitink and Boehm, 1999). Antibiotics produced by some bacterial biocontrol agents also are affected in this manner (Duffy and Defago, 1999). To avoid problems associated with net pathogen stimulation by readily assimilable carbon, composts must be stabilized to a rate of respiration of no more than 1.0 mg CO_2-C g^{-1} dw d^{-1} (Wang et al., 2004) or they must be applied to field soil in the fall to decompose further in soil before planting of the crop in the spring.

The other end of the decomposition scale, which implies excessively stabilized or humified organic matter, typically does not support control either. For example, charred or pyrolyzed particles in composts do not support the levels of microbial biomass required to generally suppress root rots (Hoitink and Boehm, 1999). Charred particles are produced during composting when temperatures exceed 70°C for long periods of time, particularly when composts are dry. Maintenance of a moisture content > 45% and adjustment of windrow height (which affects the process temperature) during composting helps to prevent charring. Excessively humified organic matter, the other end of the decomposition spectrum, such as that in highly decomposed Sphagnum peat or as in composts after their mineralization in potting mixes for more than their "useful life time", does not support control either (Boehm and Hoitink, 1999; Stone et al, 2004). Thus, substrate chemistry matters and the microbial properties that lead to suppressiveness cannot be maintained indefinitely!

The longevity of the suppressive effect of composts depends on many factors. Stabilized lignocellulosic substances in composts, the chemistry of which resembles particulate organic matter (POM) in soil, seem to form the basis for long-term control (Stone et al., 2004). Generally, compost-amended container media become conducive to root rot within 12-24 month after potting, but this varies with the materials used and the climate. The rate of hydrolysis of fluorescein diacetate seems to best reflect this suppressive effect against root rots (Hoitink and Boehm, 1999; Stone et al, 2004).

Fate of biocontrol agents in composts

The microflora associated with the composting process includes organisms originating in the source material as well as those colonizing the piles during the composting process. Some of these can act directly as biocontrol agents, but it is thought that only heat-tolerant species, such as some *Bacillus* spp., will represent substrate-borne biocontrol inoculum (Hoitink and Boehm, 1999). The fate of this microflora in high temperature composts seems similar to that of pathogens (Termorshuizen et al, 2005). While it is possible for other colonists to survive in the outer layers of stabilized piles, the moisture content in this layer often is too dry (< 45 % (w/w) for significant levels of growth. Thus, opportunities for colonization of such composts by biocontrol agents can be minimal. Biocontrol agents, mycorrhizae and nitrifying bacteria often do not colonize compost-amended substrates until days or weeks after the compost has been utilized (Hoitink and Boehm, 1999). This in practice means that potted crops highly sensitive to Pythium damping-off (e.g. poinsettia) must be drenched once with an effective Pythium fungicide immediately after planting to ensure damping-off control. Thereafter, natural suppression provides control (Hoitink, and Lewandowski, 2006).

The situation can be quite different for composting plants that use small windrows with low process temperatures, especially when a cover is used to mitigate drying during curing. After several years of operation on a site, composts produced in this manner can be expected to support higher populations of biocontrol agents in the cured product (Hoitink and Boehm 1999), including inoculants that can induce suppression to foliar diseases of plants (Horst et al, 2005). The turning machines used in these small windrow systems continually facilitate dissemination of microorganisms among windrows. Turning of mature compost first, followed by turning of fresh materials last, and a clean up operation before the next turning operation, is the best strategy. However, even with composts prepared by this method, formulated media do not naturally suppress Pythium diseases adequately until several days after planting. Thus, highly sensitive crops such as begonias must be drenched at planting with a Pythium fungicide for complete control (Horst et al, 2005, Hoitink and Lewandowski, 2006). Subsequent fungicide applications typically are not required until the medium loses suppressiveness towards the end of its useful lifespan. Another approach is to incubate biocontrol agent-fortified potting mixes for several days in storage so as to allow biocontrol agents to proliferate. This approach to disease control poses fewer risks for potted crops. In the large plant container industry, this approach typically is not practical due to the size of operations.

General disease suppression induced by composts

Compost effects on suppression have been related to amendment characteristics and soil type (Hoitink and Boehm, 1999).. Consistent and effective suppression of Phytophthora root rots provided by composts versus partial or lack of suppression of diseases caused by pathogens such as *Rhizoctonia solani* can be explained on the basis of the differences between the mechanisms that underly their suppression. Suppression of root infections by *Phytophthora* and *Pythium* is supported by microbiostasis which implies competition and antibiotic production by competing microorganisms (Baker and Paulitz, 1996). Numerous soil microorganisms contribute to this effect in soils. The general suppression phenomenon *sensu* Gerlach, which is soil carbon dependent, best explains this type of disease control provided by composts (Hoitink and Boehm, 1999). Other plant pathogens that produce small propagules (<200 U in diameter) seem to be suppressed by the same mechanism.

Recently, nucleic acid based techniques have been used to gain a better understanding of the microbial community structure and function in disease suppressive substrates (Kowalchuck et al., 2003; Mazzola, 2004; Benitez et al., 2007; Borneman and Becker, 2007). Using such approaches, very subtle shifts in community structure related to soilborne disease suppression can be observed in response to cropping history and rotation (Benitez et al 2007, Baysal et al 2008). Still, compost applications in the field have been shown to promote dramatic transient shifts in abundance, but not in the overall structure of native microbial communities (McSpadden Gardener et al 2002). This indicates that stimulation of general suppression is mediated by enhanced growth of the microflora present in the field. Such studies generally support conclusions from earlier work based on culturing of microorganisms but also reveal that an even greater abundance of microorganisms seems to play a role in disease suppression than realized previously.

Specific disease suppression induced by composts

Specific suppression refers to control of particular pathogens. It can be mediated by biocontrol inoculants. These specific biocontrol agents often act through multiple mechanisms, but it is becoming clear that those that induce plant host resistance can be particularly effective. This is because induced resistance in plants can be effective against several root, vascular and foliar diseases. Effective suppression of diseases caused by pathogens that produce sclerotia (e.g. *R. solani*) typically requires that biocontrol agents kill their infective propagules (Baker and Paulitz, 1996). This implies antibiosis and/or parasitism. Lack of consistent colonization of composts by such specific microorganisms explains the inconsistent control of diseases caused by these pathogens (Hoitink and Boehm, 1999). Specific inoculants of biocontrol agents such as strains of *Trichoderma* spp. can be inoculated into compost-amended substrates to provide a more consistent degree of control (Hoitink and Boehm, 1999; Khan et al., 2003; Horst et al, 2005; Cotxarrera et al., 2002). For crops highly susceptible to Rhizoctonia damping-off such as New Guinea impatiens, a single fungicide sprench (heavy spray) must be applied at planting to avoid losses. Introduced biocontrol agents do not provide adequate control on such crops unless the biocontrol agents can fully established themselves in the substrate (Hoitink and Lewandowski, 2006). Later in the cropping cycle, the biocontrol agent-fortified substrate can be more suppressive to Rhizoctonia root rot than the most effective fungicides.

A few reports show that foliar diseases of plants can be suppressed in compost-amended substrates (Stone et al, 2003, 2004). Bioassays performed with container media prepared from 1997-2001 with 80 different types of composted products, which included conventional, organic and vermicomposts, revealed that all suppressed Pythium damping off of cucumber, 20% suppressed Rhizoctonia damping-off of radish and only one induced systemic resistance (ISR) to foliar diseases naturally. Several different biocontrol agents with ISR activity were isolated from the unique batch of compost that naturally induced systemic resistance in plants. *Trichoderma hamatum* 382 (T382) was identified as the most active inducer of resistance (Krause et al, 2003). Other active isolates were *Bacillus* strains, and less active isolates included strains of *Pseudomonas spp*. and *Pantoea agglomerans*. Thus, the types of biocontrol agents isolated from the ISR-active batch of compost-amended mix agree with the spectrum of such isolates described from soil (Pieterse, et al, 2003; Soresh et al., 2005).

The foregoing reveals that suppression of foliar diseases with natural composts is a rare phenomenon in commercial practice. Thus, growers cannot rely on this approach to foliar disease control. This may explain why compost-induced foliar disease control was not discovered by growers under commercial conditions. The question is whether this deficiency can be remedied with controlled inoculants.

The mechanisms by which beneficial rhizosphere microorganisms induce systemic resistance in plants differ (Pieterse et al, 2003). The specific strains that induce ISR do not substantially activate PR protein synthesis before the pathogen invades the plant. The ethylene and jasmonic acid pathways are involved in this resistance mechanism (Pieterse et al., 2003; Soresh et al, 2005) but just how pathogen populations are suppressed in plants was not understood until recently. The ISR-active biocontrol agent *Trichoderma hamatum* 382 (T382) alters the expression of 45 genes in tomato (Alfano et al, 2007). The induced genes have functions associated with biotic or abiotic stress as well as RNA, DNA, and protein metabolism. Four extension and extension-like proteins in addition to PR 5 were induced. Extensin proteins have long been associated with defense mechanisms in plants (Shanmugam, 2005). Upregulation of a specific extension protein in Arabidopsis induced a high degree of resistance to bacterial spot in this plant (Wei and Shirsat, 2006).Thus, further work may show that an increase in extension gene expression by ISR-active biocontrol agents may well account for much of the systemic benefits associated with composts that provide foliar disease control.

Role of substrates in compost in ISR-activity

Amendment of peat mixes with composts has enhanced the systemic effect induced by ISR-active rhizosphere microorganisms in plants. Zhang et al., (1998) showed that dark, decomposed Sphagnum peat mixes do not induce ISR naturally. Suppression of Fusarium crown and root rot of tomato induced by the biocontrol agent *Pythium oligandrum* was enhanced by amending a Sphagnum peat mix with composted papermill sludge (Pharand et al., 2002). Furthermore, suppression of Phytophthora leaf blight of cucumber induced by *T. hamatum* 382 was enhanced by amendment of a peat mix with composted dairy manure. It increased resistance of the plant to the disease (Khan et al, 2004). Finally, greenhouse tests performed with T382 in a high in microbial carrying capacity light Sphagnum peat potting mix revealed that powdery mildew and Botrytis blight of begonia were suppressed as effectively as provided by bi-weekly foliar sprays with the fungicides piperon and clorothalonil, respectively (Horst et al, 2005). In conclusion, soil organic matter quality affects the activity of biocontrol agents that induce systemic resistance in plants as observed years ago for suppression of root rots (Heyl, 1999, Stone et al, 2004).

Is the degree of resistance induced by ISR useful to growers?

To answer this question, commercial scale demonstration trials were performed with T382 in nursery container media (Hoitink et al, 2006). In a trial with rooted cuttings of *Myrica pennsylvanica*, a severe outbreak of Botryosphearia dieback caused by *Botryosphaeria dothidea* developed on the branches of this woody plant. In the control medium, 20.8% of the plants were killed and only 25.0% of the plants remained symptomless. Most were stunted in growth. In contrast, only 6.3% of the plants in the T382-inoculated medium were killed whereas 66.7% of the plants remained symptomless. In conclusion, this control batch of natural compost-amended mix did not provide control of the dieback disease whereas the mix inoculated with T382 provided effective control of Botryosphaeria dieback, a disease for which effective fungicides are not available.

On Rhododendron “Roseum Elegans”, a natural dieback epidemic caused by *Phytophthora citrophthora* developed (Hoitink et al., 2006). T382 significantly (P=0.05) reduced the severity of this disease. In a test with *Pieris japonica*, the percentage plants killed by *Phytophthora parasitica* was reduced by inoculation of the mix with T382 from 26 % in the treated to 4 % in the control. The reduction in Phytophthora dieback severity occurred in these tests even though the foliage of the crops had been treated repeatedly at three week intervals with Subdue and Aliette, systemic fungicides with activity against *Phytophthora*. In vitro analysis revealed that the *Phytophthora* isolates that caused these epidemics were resistant to 100 mg ml^{-1} metalaxyl, the active ingredient in Subdue.

Recent work shows that efficacy induced by T382 against Botrytis blight of geranium is comparable to that provided by chemical fungicide under mild disease pressures which prevail under standard greenhouse conditions when growers vent houses to reduce the relative humidity. Under high moisture conditions, the fungicide was more effective and the biocontrol agent was not effective (Olson and Benson, 2007).

In conclusion, inoculation of container media which offer the potential to naturally suppress Pythium and Phytophthora root rots with ISR-active biocontrol agents such as T382 can significantly increase the spectrum of soilborne diseases suppressed and have an impact on control of foliar diseases as well. This holistic approach to disease control is particularly useful for powdery mildews and Botrytis blight under low disease pressures and for stress diseases such as those caused by *Botryospaeria dothidea* because effective fungicides are not available for the latter. For control of damping-off diseases of highly susceptible floricultural crops, an initial fungicide treatment is required. However, the degree of protection provided by ISR against foliar diseases caused by aggressive *Phytophthora* species is limited. The best strategy against these diseases apart from clean stock production is to utilize irrigation strategies that minimize pathogen dissemination and leaf wetness periods in addition to fungicide applications (Hoitink and Lewandowski, 2006).

Future Outlook

Several new technologies developed during the past decade promise to significantly increase utilization of disease suppressive composts in the United States. A novel method for production of plants, known as the “pot-in-pot system”, allows trees to be produced in containers buried in soil (Struve, 1996). In this system, the root system is protected from winter and high temperature summer impacts. Large trees can now be produced as effectively in these systems as in field soil. Furthermore, trees now can be produced in the absence of plant pathogens such as *Verticillium* spp. that survive as microsclerotia in infested soils even when treated with composts.

The pot-in-pot system is being adopted rapidly across the U.S. Therefore, the quantity of organic matter required for such systems is beginning to exceed the supply of composted bark and rice hulls. Thus, the nursery industry increasingly is testing alternatives for these basic ingredients in potting mixes. Composted yard wastes and other types of composts high in recalcitrant materials are beginning to fill this market but typically cannot be incorporated at rates that exceed 25% (v/v). Because pots used in these systems tend to be tall (30-60 cm) depending upon tree type and size, water retention and aeration requirements are different as well. Thus, larger quantities of composts that predominantly contain small particles can be utilized successfully in these media as long as nutrient levels do not exceed limits.

A second development which is a natural spin off from this new tree technology is “rapid production of nursery liners” from seed or rooted cuttings in disease suppressive systems. In this technology, liners of trees can be produced from seed into 1.5-2.0 m whips within one growing season. This avoids production of bare root field trees (whips) in pathogen or insect-infested soils and guarantees better products.

In a third development, the nursery industry incorporates composts and green manures between nursery crops into field soil on a 3-5 year production plan basis. Within three months after application of composted yard wastes or mixtures of composted bark and manures, a forest horizon develops in the treated soil. The dynamics of nutrient uptake and plant growth in such mulched systems resembles that in organic agriculture under the best conditions and in natural hardwood forest ecosystems. Root rots and feeding by leaf chewing insects are suppressed on such mulched trees relative to in the fertilized non amended control (Lloyd et al., 2002). As long as yearly fertilizer inputs take into account crop fertility needs and the quantity of nutrients available to the plant in the soil and soil type, this approach to mulching does not lead to environmental insults. This still is a controversial topic, however, because our ability to predict N release from compost still is poor unless several factors for each specific compost type are considered.

It is too early to predict the role that microbial inoculants will play in ehancing disease control. However, based on impacts of recent epidemics caused by *Phytophthora ramorum* on nursery stock in the U.S., coupled with the desire of the industry to decrease pesticide use due to increased costs, re-entry regulations, and environmental issues for some pesticides, it would seem that ISR-active inoculants will increasingly be used by growers in the future. Indeed, the biopesticide industry has been expanding during the past five years to meet this perceived need with the development and registration of over two dozen new active ingredients that target soilborne diseases.

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