

# Chapter 2

## Enhancing Soil Suppressiveness Using Compost and Compost Tea

Chaney C.G. St. Martin

### 2.1 Introduction

Enhancing soil suppressiveness using compost and compost tea represents an alternative biocontrol approach to the conventional paradigm of plant disease control, one that is based on the use of several microorganisms at the same time to control one or many pathogens rather than the conventional use of one active ingredient or microbial agent to target one or multiple pathogens. Inclusive in this paradigm shift in disease control are (1) mixing of several known types of biocontrol agents (BCAs) with diverse modes of action or that colonise different ecological niches (Siddiqui and Shaukat 2002), (2) the enhancement of resident populations existing on or around the plant (Mazzola 2007), and (3) the introduction of partially or uncharacterised microbial communities usually with no known activity (Litterick et al. 2004). Compost and compost tea used as biocontrol agents fall under the latter group of strategies in this paradigm shift.

Although research on compost and compost tea has been conducted for decades, there is now increasing interest in their possible role in developing suppressive soils and managing plant diseases. This interest has primarily arisen due to increasing demand for organically produced foods (Dimitri and Greene 2000) and concerns by the public over the use and potential negative impacts of synthetic pesticides on human health and environment.

St. Martin (2013) argued that the theoretical basis for the effectiveness of compost and compost tea in suppressing phytopathogens is their ability to alter the microbial profile and activity of the rhizosphere and/or soil as a whole. However, it is highly debatable whether compost tea alters the microbiota of the

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C.C.G. St. Martin (✉)

Department of Life Sciences, The University of the West Indies, St. Augustine, Republic of Trinidad and Tobago

e-mail: [cstmartin@hotmail.com](mailto:cstmartin@hotmail.com)

rhizosphere and/or soil as a whole (Scheuerell and Mahaffee 2006; Larkin 2008). More so, there is no consensus on whether the suppressive effects of compost and compost tea satisfy the demonstration and measurement criteria of classic soil suppressiveness (Baker and Chet 1982). That is, a “natural reduction” in pathogen population levels and plant disease incidence, which is distinct from the decrease that occurs in monoculture of certain susceptible crops, and is often presumed to be long-standing (Hornby 1983).

Nonetheless, several field studies have shown that the compost and liquid preparations such as compost tea made from compost can suppress various phytopathogens and plant diseases (Pera and Filippi 1987; Joshi et al. 2009; Van Schoor et al. 2009; Zaccardelli et al. 2011). This means that at least one member of the microbial community of the soil, i.e. the pathogen, was affected by the application of compost or compost tea. Therefore, the application of compost or compost tea to soils either (1) made conditions more favourable for the development of resident antagonists, in which case the resulting effects can be categorised as induced suppression (Baker and Cook 1974), or (2) did not stimulate resident antagonists but added antagonists to the soil, in which case the resulting positive effects can be categorised as introduced suppression (Hornby 1983). In this context, the positive effects of compost and compost tea satisfy the more inclusive criteria of suppressive soils, that is, soils in which disease severity or incidence remains low, in spite of the presence of a pathogen, a susceptible host plant and climatic conditions favourable for disease development (Baker and Cook 1974). More so, because compost and compost tea have the potential to directly and indirectly affect the physico-chemical and biological properties of soils, they can be viewed as tools, which can be used to enhance or develop disease-suppressive soils (Trankner 1992; Stone et al. 2004). In this regard, the major impediments to the use of compost and compost tea have been the less than desirable and inconsistent levels of plant disease suppression in various cropping systems. Despite the plethora of studies done to date, our understanding of, and research into, compost and compost tea is at an early evolutionary stage, particularly as it relates to predicting disease suppression levels under field conditions.

The objectives of this chapter are to summarise current knowledge on enhancing soil suppressiveness using compost and compost tea. Predictors and mechanisms of disease suppression are discussed and factors affecting the efficacy of compost and compost tea are highlighted. Furthermore, the potential application of molecular tools for better understanding the relationship between microbial properties of compost and compost tea and soil suppressiveness is highlighted, and core areas for research are identified.

## 2.2 Definitions and Standards

Composting is the controlled, microbial aerobic decomposition and stabilisation of organic substrates, under conditions that allow the generation of high temperatures by thermophilic microbes, to obtain an end product that is stable and free of

pathogens and viable weed seeds and can be used in plant culture (St. Martin and Brathwaite 2012). The end product, which is a solid particulate extracted during the maturation and curing phase, is termed compost (Litterick and Wood 2009). Compost tea is defined as filtered products of compost brewed in water (Litterick et al. 2004) and brewing, a steeping process of compost in any solvent (usually water), which lasts for more than one hour (NOSB 2004). Various other definitions have been provided for compost and compost tea in the literature. However, the definitions used in this chapter seem more succinctly technical and representative of attempts made to standardise meanings to facilitate greater clarity of research progress on disease suppression using compost and compost tea. In this light, terms such as compost-water extracts (CWE), which are used in many studies, have been recategorised as either aerated compost tea (ACT) or non-aerated compost tea (NCT) in accordance with definitions presented in the Compost Tea Task Force Report (NOSB 2004). ACTs refer to products where the compost-water extract is actively aerated during the brewing process, and NCTs are products where the compost-water extract is not aerated or receives minimal aeration only at the initial mixing stage of the brewing process (Litterick and Wood 2009). Compost-water extracts are filtered products of compost mixed primarily with water (or any solvent) but not brewed or held for more than one hour before use (Scheuerell and Mahaffee 2002; NOSB 2004). Scheuerell and Mahaffee (2002) and NOSB (2004) can be consulted for a more thorough review of these terms and others and, likewise, St. Martin and Brathwaite (2012) and Scheuerell and Mahaffee (2002) for detailed reviews on compost and compost tea production methods, practices and technologies.

## 2.3 Suppression of Phytopathogens and Diseases

### 2.3.1 Soilborne Phytopathogens and Diseases

#### 2.3.1.1 Compost

An increasing body of evidence shows that soils amended with compost can partly or wholly suppress soilborne phytopathogens and plant diseases (Dickerson 1999; Fuchs 2002; Tilston et al. 2005). Most of the research efforts on enhancing soil suppressiveness using compost have focused primarily on root and soilborne pathogens including *Rhizoctonia*, *Pythium*, *Phytophthora* and *Fusarium* spp. For example, Fuchs (2002) found that after 5 years, the receptivity of soils applied annually with 10 tons/ha of compost to *Pythium ultimum* or *Rhizoctonia solani* was lower compared to soil not amended with compost. More so, the suppressive effects of compost were clearly observed 1 year after compost application, particularly in more intensively worked and cultivated fields. Similarly, Tilston et al. (2005) found that soils amended with green waste compost at a rate of 150 Mg ha<sup>-1</sup> significantly suppressed take-all (*Gaeumannomyces graminis* var. *tritici*). However, residual or

cumulative effects of compost application on the disease suppression were not detectable within the duration of the field trials. Escudra and Amemiya (2008) reported that Fusarium wilt (*Fusarium oxysporum* f. sp. *spinaciae*) suppression in spinach was not evident during the first cultivation. However, notably higher disease suppressiveness was conferred by compost mixes applied before every two croppings compared to those applied only at planting.

Notwithstanding the absence or presence of residual, cumulative or delayed suppressive effects, most studies show that where >50 % disease control was recorded, compost was applied at a rate of at least 100 tons/ha (Coventry et al. 2006; Zaccardelli et al. 2011). Such high application rates exceed the allowable limit of 30 tons/ha for most green composts and 20–30 tons of green or food-derived compost per hectare set for nitrate vulnerable zones (NVZs) (Council Directive 91/676/EEC 1991). Moreover, these rates are also potentially hazardous to the environment, particularly with reference to groundwater and surface water pollution and the conveyance of heavy metals to the soil.

Juxtaposed against the potential environmental hazard of high compost application rates is the issue of the repeatability of disease suppression. This relates to the difficulty in replicating and standardising compost quality across production batches and differences in climate, soil type, crop production practices and/or experimental protocols used in the field. To date, this has been one of the major limitations in recommending compost as an input for enhancing soil suppressiveness in commercial crop production.

In this light, composts have been shown to have neutral and negative effects on phytopathogens and disease suppression. For example, Merriman (1976) found that after 245 days, tomato compost applied to sandy clay loam soil at a rate of 17.5 tons/ha significantly increased the mean number of viable sclerotia of *Sclerotinia sclerotiorum*, the causal agent of white mould. Likewise, Pera and Filippi (1987) reported that poplar bark compost applied to field plots of carnation plants at a rate of 15 % or 30 % (w/w of 20 cm of topsoil) did not suppress Fusarium wilt (*F. oxysporum* f. sp. *dianthi*). Similar results were reported in studies which evaluated various compost types against Fusarium blight (*Microdochium nivale*) (Pratt 2003), root rot (Kim et al. 1997; Rangarajan et al. 2001) and cavity rots (Coventry et al. 2005). In contrast, Dickerson (1999) found that sewage sludge compost applied at 48 tons/ha significantly suppressed root rot (*Phytophthora capsici* L.) of chile peppers, whereas rates of 72 tons/ha or higher enhanced the severity of root rot. More complex trends of the effect of compost on soil suppressiveness have been reported. For example, Abbasi et al. (2002) observed that compost showed a significant suppressive effect only in the year with a higher disease level. Similarly, Lodha et al. (2002) reported that the incidence of dry root rot (*M. phaseolina*) of cluster bean differed significantly between years, with disease suppression with compost being greater in the year with higher disease levels.

Currently, fewer direct comparisons are being made between the level of disease suppression achieved through the use of composts and that achieved using standard fungicide treatments (Litterick and Wood 2009). However, data from such

comparisons are critical in rationalising the comparative advantages of using compost in combination with or rather than other control methods such as synthetic pesticides. In this regard, Asirifi et al. (1994) found that the application of the fungicide vinclozolin had a significant but lower suppressive efficacy than lucerne hay compost against *Sclerotinia* rot (*S. sclerotiorum*) in lettuce. In contrast, Coventry et al. (2006) reported that onion waste compost was as effective as a standard fungicide treatment (tebuconazole) in reducing onion white rot (*Sclerotinia cepivorum*).

### 2.3.1.2 Compost Tea

Research on enhancing soil suppressiveness against soilborne diseases using compost tea in open-field system is limited. Even rarer are studies on the residual, cumulative effects and comparative field evaluations of NCT and ACT against soilborne diseases. From this standpoint, the argument for compost tea as an input for enhancing soil suppressiveness is weaker than that of compost, particularly as compost tea has a lower capacity than compost to serve as a substantial carbon or nutrient source for introduced or resident soil microorganisms. Nonetheless, compost teas have been shown to suppress soilborne diseases in various crops and field conditions (Manandhar and Yami 2008; Joshi et al. 2009; Islam et al. 2014). For example, Manandhar and Yami (2008) found that aerated and non-aerated compost and vermicompost teas significantly suppressed foot rot (*F. moniliforme*) in rice. Similar results were reported in studies, which evaluated various compost tea types against bacterial wilt (*Ralstonia solanacearum*) (Islam et al. 2014), stem canker (*Rhizoctonia solani*) (Islam et al. 2013b), apple replant disease (Van Schoor et al. 2009) and dollar spot (*Sclerotinia homoeocarpa*) (Hsiang and Tian 2007). In contrast, Kelloway (2012) reported that the efficacy of the mink compost tea in controlling dollar spot disease was site specific and variable, with only one location showing significant control. In one of the few field studies to investigate the combinatory effects of compost tea and compost, Joshi et al. (2009) found that poultry manure, *Lantana camara* and *Urtica* spp. composts and fermented extracts made using these composts, significantly suppressed root rot (*R. solani*) in French bean (*Phaseolus vulgaris* L.) over two growing seasons. More so, the suppression levels of these treatments were similar with seeds treated with the chemical fungicide, carbendazim. Similarly, Larkin (2008) investigated the relative effects of biological amendments and crop rotations on soilborne diseases and found that soil applied with ACT and the combination of ACT with a mixture of beneficial microorganisms reduced stem canker (*R. solani*) and common scab (*Streptomyces scabiei*) on Irish potato tubers in the 2-year barley/ryegrass but not in the barley/clover rotations.

## 2.3.2 Foliar and Fruit Phytopathogens and Diseases

### 2.3.2.1 Compost

Field studies on the use of compost to enhance soil suppressiveness against foliar and fruit (aerial) phytopathogens and diseases are limited. However, the majority of published works show that composts suppress foliar diseases under field conditions, mainly by inducing plant defences (Zhang et al. 1996; Stone et al. 2003; Vallad et al. 2003). For example, Stone et al. (2003) found that the amendment of soil with paper mill residue compost (PMRC) at a rate of 78.4 Mg/ha resulted in the suppression of brown spot (*Pseudomonas syringae* pv. *syringae*) and anthracnose (*Colletotrichum lindemuthianum*) in snap bean and angular leaf spot (*P. syringae* pv. *lachrymans*) in cucumber. Similarly, Vallad et al. (2003) reported that bacterial speck (*P. syringae* pv. *tomato*) in tomato was suppressed with the application of PMRC or PMRC + bark composts to the soil at a rate of 78.4 Mg/ha. In contrast, Abbasi et al. (2002) found that the application of yard waste compost to soil at a rate of 12–15 tons/ha did not result in the suppression of anthracnose in tomato. However, applied at 24–30 tons/ha, yard waste compost significantly reduced the severity of anthracnose in tomato. Conversely, Stone et al. (2003) reported that soil amended with PMRC + bark composts at a rate of 38.1 or 78.4 Mg/ha had no effect on the severity of anthracnose or angular leaf spot of cucumber.

### 2.3.2.2 Compost Tea

Unlike compost, the majority of field studies conducted with compost tea have focused on suppressing aerial phytopathogens and diseases. Though the majority of these field studies show that compost tea can suppress aerial phytopathogens and diseases, the suppressive effect is often attributed to changes in the phyllosphere rather than the rhizosphere. The work done by Islam et al. (2013a) is one of the only published field study, which has evaluated the suppressive effects of compost tea applied as a soil drench against a foliar disease. Islam et al. (2013a) found that compost tea significantly suppressed the severity of late blight (*Phytophthora infestans*) in tomato and potato. They suggested that suppression was associated with the positive effects of compost tea on soil microbial communities as it relates to increasing the diversity and populations of beneficial microorganisms on root surfaces and the activation of plant defence pathways in host plants. Similar claims have been reported in controlled studies; however, further studies with similar objectives are needed to corroborate such findings.

## 2.4 Predictors of the Suppressive Capacity of Compost and Compost Tea

Although not fully understood, the predictors of the suppressive capacity of compost and compost tea have generally been linked to live microorganisms, since soil suppressiveness against various pathogens has been reduced or lost with the application of sterilised compost or compost tea (Serra-Wittling et al. 1996; Bonanomi et al. 2010). To this end, the presence, population density, diversity, activity, composition and function of microbes in compost and compost tea have been discussed as single or interrelated biological factors associated with the development of disease-suppressive soils.

Pal and Gardener (2006) noted that the microbes that contribute most to disease control are most likely competitive saprophytes and facultative hyperparasites and plant symbionts. Generally, these microbes, which are at low trophic levels, can survive on dead plant matter and are able to colonise and express biological control activities while growing on plant tissues (van Bruggen and Termorskuizen 2003; Pal and Gardener 2006). Avirulent species such as strains of *F. oxysporum* binucleate *Rhizoctonia*-like fungi, which are phylogenetically very similar to phytopathogens, also contribute significantly to disease control. In this light, though other genera are involved, bacteria in the genera *Bacillus*, fluorescent *Pseudomonas*, *Serratia* and *Streptomyces* and fungi in the genera *Penicillium*, *Trichoderma* and *Gliocladium* are generally regarded as the main microbes responsible for the suppressive effects of compost and compost tea (Phae et al. 1990; Hoitink and Fahy 1986; Litterick et al. 2004). As such, most studies have focused almost exclusively on bacterial and fungal consortia with little focus on specific fungal types such as yeasts or other microbes including protozoa and beneficial nematodes, as live agents responsible for the disease-suppressive effects of compost and compost tea. However, a recent study by St. Martin et al. (2012) highlighted the possible role of yeast present in ACTs in suppressing the growth of *P. ultimum*. Viruses have not generally been considered as agents responsible or related to the disease suppression resulting from compost and compost tea application. However, a study by Heringa et al. (2010), which found that five-strain bacteriophage mixture isolated from sewage effluent and applied to dairy manure compost reduced the population of *Salmonella enterica*, may illustrate the potential role of viruses in disease suppression with compost and compost tea. Though important, Hoitink and Fahy (1986) noted that the mere presence of known or suspected antagonists in the compost or compost tea does not ensure disease suppression.

In this regard, microbial population metrics of compost and compost tea have been evaluated as predictors of disease suppression. However, it is difficult to draw meaningful conclusions from the results of these studies. For example, Craft and Nelson (1996) reported that recoverable microbial populations, particularly of fungi and actinomycetes, were generally higher in suppressive than non-suppressive composts. However, Stockwell et al. (1994) reported that though no clear statistical relationships between bacterial populations and disease suppression were observed

in their study, other reports indicate many of the bacteria and actinomycetes recovered from suppressive composts were suppressive to *P. graminicola* in laboratory bioassays. In a similar context, a review paper by Scheuerell and Mahaffee (2002) indicated that disease-suppressive compost teas had total bacterial populations ranging from  $10^7$  to  $10^{10}$  CFU/ml. In contrast, Pane et al. (2012) found that compost tea with total bacterial count of lower than  $10^{-3}$  CFU/ml inhibited *Alternaria alternata*, *B. cinerea* and *Pyrenochaeta lycopersici*.

In view of these seemingly contrasting findings, St. Martin et al. (2012) suggested that an examination of the population metrics of specific microorganisms rather than total microbial populations or types may prove to be more reliable in rationalising the efficacy between aerated and non-aerated compost teas. Borrero et al. (2004) found that the microbes in composts that were involved in suppression of Fusarium wilt in tomato were cellulolytic and oligotrophic actinomycetes and fungi. They also reported a strong negative correlation between Fusarium wilt severity and the ratios of cellulolytic actinomycetes/cellulolytic bacteria, oligotrophic bacteria/copiotrophic bacteria and oligotrophic actinomycetes/oligotrophic bacteria. To this end, in a meta-analytical review article, Bonanomi et al. (2010) reported that total culturable bacteria, fluorescent pseudomonads and *Trichoderma* populations were most useful in predicting disease suppressiveness of organic soil amendments against soilborne plant diseases. However, the authors cautioned that though total cultural bacteria is an important characteristic, it should not be considered in isolation to be a reliable predictor of disease suppression, either in relation to organic matter types or different pathogen species. With the exception of *Fusarium* spp., total cultural fungi were considered a poor predictor of disease suppression. Bonanomi et al. (2010) also reported that in some cases, the negative effects of composts and crop residues on disease suppression could be explained by the application of partially colonised organic materials that enhance the microbial population but also pathogen saprophytic activity.

Owing to the lack of a significant relationship between the level of pathogen inhibition and the abundance of culturable bacteria or fungi (after 24-h incubation) in ACT, Palmer et al. (2010) concluded that microbial diversity, more than abundance of culturable bacteria and fungi, was a main factor contributing to the suppression of disease by compost tea. Similarly, Nitta (1991) and Postma et al. (2008) all reported positive relationships between microbial diversity of compost and general disease suppression for various pathogens. In contrast, Borrero et al. (2004) reported that higher microbial diversity could not explain the suppression of Fusarium wilt (*F. oxysporum* f. sp. *lycopersici*) of tomato in plant growth media containing or not containing compost. More so, unlike the results of Nitta (1991), Borrero et al. (2004) found that lower diversity was not associated with conduciveness to Fusarium wilt. Though important, Borrero et al. (2004) cautioned that microbial diversity should not be regarded as a reliable predictor of disease suppression unless examined in the context of corresponding microbial activity and biomass.

In this light, Chen et al. (1988) reported a high positive correlation between microbial activity in a compost-amended medium and induction of damping-off



(*P. ultimum*) suppression. Conversely, Erhart et al. (1999) found that microbial activity was positively correlated to damping-off incidence. To this end, Bonanomi et al. (2010) and Chen et al. (1988) concluded that microbial activity is indicative of suppressiveness only when the plant growth substrate itself is not stimulatory to population development of the pathogen. Investigations on the effect of compost tea application on the enzymatic (e.g. microbial activity and substrate respiration) and microbiological (fluorescent pseudomonads and *Trichoderma* populations) properties of soil and their relationship to disease suppression are lacking and therefore needed.

With regard to microbial community and functions, Boehm et al. (1997) concluded that a shift in the microbial community composition from Gram-negative bacteria, which generally have antagonistic ability, to Gram-positive bacteria, which are less able to antagonise soilborne pathogens, reduces the suppressive capacity of compost. McKellar and Nelson (2003) found that bacteria and *Actinobacteria* capable of metabolising fatty acids (linoleic acid) reduced sporangium germination of *P. ultimum*, which resulted in induced suppression of *Pythium* damping off in cotton. Fuchs (2002) noted that the significant negative correlation between more intensively worked and cultivated fields and disease receptivity was likely due to a greater disturbance of the biological equilibrium in these fields compared to fields that were not as intensively worked or cultivated. However, the term “biological equilibrium”, which can imply functional relationships among microorganisms, was not clearly defined by Fuchs (2002). It is not uncommon to find the use of such ambiguously defined terms, which implies some microbial functional relationship offered as an explanation for the success or failure of disease control using compost or compost tea. This highlights the need for further research on the quantitative relationships between microbial abundance, diversity, functions and disease-suppressive efficacy of compost and compost tea. More so, a better understanding of mechanism of suppression will serve as an important proxy for developing more accurate predictors of the suppressive capacity of compost and compost tea under field conditions.

## 2.5 Mechanisms of Suppression of Compost and Compost Tea

Six mechanisms of suppression, which are related to the biotic or abiotic characteristics of compost and compost tea, have been identified: (1) competition for carbon and nutrients (such as Fe) by beneficial microorganisms, (2) production of antibiotics or other compounds that is toxic to phytopathogens, (3) hyperparasitism or predation of phytopathogens by lytic bacteria and fungi, (4) activation of disease-resistance genes in plants by the compost and compost tea microflora, (5) improved plant nutrition and vigour due to microbes and (6) physico-chemical properties of compost and compost tea that are directly toxic to phytopathogens, improve

nutritional status of crops or induce disease resistance (Hoitink and Boehm 1999; Mehta et al. 2014). According to Hadar and Papadopolou (2012), the first three mechanisms target the pathogen directly and reduce its survival and capacity to invade the plant, whereas the subsequent two act indirectly via the plant and affect disease progression in the host plant. The last mechanism shows features of both direct and indirect pathogen and disease suppression. Most researchers have explored each mechanism separately. However, it is likely that several mechanisms may be functioning simultaneously in the suppression of diseases. To date, microbiostasis (competition for growth resources and/or antibiosis) and hyperparasitism/predation have been identified as the principal mechanisms by which phytopathogens are suppressed (St. Martin and Brathwaite 2012; Scheuerell and Mahaffee 2002).

### 2.5.1 *Microbiostasis*

In the context of soil suppressiveness, microbiostasis refers to the process of inhibiting the growth, reproduction and multiplication of pathogens but not killing them (Ko 1982). It is mainly caused by nutrient deprivation imposed by microbial activity (Ko 1982), i.e. competition, or by antibiosis, which refers to the release of specific and/or non-toxic specific metabolites or antibiotics by one organism that directly suppresses the activity of pathogens (Litterick and Wood 2009). Suppression by microbiostasis seems to be more effective against pathogens with propagules <200 µm diam. including coliforms, *Phytophthora* and *Pythium* spp. (Hoitink and Ramos 2008).

### 2.5.2 *Competition*

Chen et al. (1987) noted that disease suppression based on competition could be related to microbial metabolic activities and is controlled by the availability and rate of utilisation of nutrients and energy sources. In this light, Sivan and Chet (1989) reported that some microorganisms reduce the disease incidence by limiting iron availability for pathogens through the production of low-molecular-weight ferric-specific ligands (siderophores) under iron-limiting conditions. Pantelides et al. (2009) reported that the main mechanism of action of the nonpathogenic *F. oxysporum* against *V. dahliae* was the competition for space or nutrients on the root surface of host plants. Likewise, Serra-Wittling et al. (1996) concluded that the suppression of Fusarium wilt was due to microbial nutrient competition, involving the total microflora of the soil and compost.

### 2.5.3 Antibiosis

Strains of *Bacillus subtilis* and other *Bacillus* spp., *Gliocladium virens*, *Enterobacter*, *Trichoderma harzianum* and *Pseudomonas* spp., which have been found in compost and compost tea, are known to produce antibiotics or enzymes that can inhibit growth germination and multiplication of many phytopathogens (Brinton and Droffner 1995). For example, Vinale et al. (2009) found that harzianic acid, a metabolite produced by a *T. harzianum* strain, displayed antibiotic activity against *Pythium irregulare*, *Sclerotia sclerotiorum* and *R. solani*. Chitinolytic enzymes produced by *Enterobacter* strains were also reported to be antagonistic to *R. solani* (Chernin et al. 1995), as was “gliotoxin” isolated from *Gliocladium virens* to *P. ultimum* (Lumsden et al. 1992).

### 2.5.4 Hyperparasitism/Predation

Microbial hyperparasitism refers to the phenomena in which pathogens are colonised by specific phylogenetically unrelated microorganisms resulting in lysis or death (Hoitink et al. 1997). In contrast, microbial predation refers to interactions in which pathogens are killed usually through phagocytosis (Matz et al. 2007). Microbial predation is pathogen non-specific, and disease suppression levels are usually less predictable than with microbial hyperparasitism (Pal and Gardener 2006).

In contrast to microbiostasis, hyperparasitism has generally been observed with phytopathogens with propagules of >200 µm diam. and in 20 % of uninoculated composts (Hoitink et al. 1996; Hoitink and Ramos 2008). According to Hoitink et al. (1996), parasitism is affected by the organic matter decomposition level and the presence of glucose and other soluble nutrients, which repress the production and effect of lytic enzymes used to kill pathogens. Hoitink et al. (1997) postulated that a similar relationship between organic matter decomposition levels and the production of antibiotics might exist. For example, in compost consisting of fresh bark, *Trichoderma* spp. including *T. hamatum* and *T. harzianum*, which produce many lytic enzymes, do not directly attack the phytopathogen, *R. solani*. However, as composting progresses, lower concentrations of readily available cellulose and glucose activate the chitinase genes of *Trichoderma* spp., producing chitinase to parasitise *R. solani* (Kwok et al. 1987; Benítez et al. 2004). Conversely, *Penicillium* spp. were the predominant hyperparasites recovered from sclerotia of *Sclerotium rolfsii*, in a high-sugar and low-cellulose-composted grape pomace (Hadar and Gorodecki 1991). It is possible for a pathogen to be hyperparasitised by several fungal species. For example, Kiss (2003) reported that together, *Acremonium alternate*, *Acrodontium crateriforme*, *Ampelomyces quisqualis*, *Cladosporium oxysporum* and *G. virens* have the capacity to parasitise powdery mildew pathogens.

With regard to liquid extract of compost, El-Masry et al. (2002) concluded that the presence of clear inhibition zones between compost-water extracts (CWE) from several composts and pathogenic fungi, the absence of antibiotics or siderophores in CWE and the presence of protease, chitinase, lipase and  $\beta$ -1,3-glucanase (cell wall-degrading enzymes) in the CW indicated a possible role for mycoparasitism. Similarly, Benhamou and Chet (1997) concluded that the marked alteration of the (beta)-1,3-glucan component of the *Pythium* cell wall suggested that (beta)-1,3-glucanases played a key role in the interaction between *T. harzianum* and *P. ultimum*.

### 2.5.5 Induced Resistance

Plant disease suppression with compost and compost tea through the induction of plant host defences was believed to be a fairly rare and variable phenomenon (Hadar and Papadopolou 2012). However, it has been shown that this phenomenon is more common than previously thought (Zhang et al. 1998; Khan et al. 2004; Ntougias et al. 2008; Sang et al. 2010). Microbes present in compost and compost tea or extracts have been reported to induce plant host defences in the presence of soilborne and foliar pathogens (Zhang et al. 1998; Wei et al. 1991). Such inductions, which are described as being local and/or systemic in nature, are dependent on the type, source and amount of stimuli (Keen 1990). In this regard, two forms of induced plant resistance have been identified: systemic acquired resistance (SAR) and induced systemic resistance (ISR). In both SAR and ISR, plant defences are preconditioned by prior infection or treatment that results in resistance (or tolerance) against subsequent challenge by a pathogen or parasite (Vallad and Goodman 2004). However, SAR and ISR can be differentiated based on the nature of the elicitor and the regulatory pathways involved. SAR is induced by the exposure of root or foliar tissues to biotic or abiotic elicitors, is associated with the accumulation of pathogenesis-related (PR) proteins and is dependent on the phytohormone salicylate (Vallad and Goodman 2004), whereas ISR is induced by the exposure of roots to specific strains of plant growth-promoting *Rhizobacteria* (PGPR), is not associated with the accumulation of PR proteins and is independent of salicylate but dependent on the phytohormones ethylene and jasmonate (Vallad and Goodman 2004). Moreover, as demonstrated by their reliance on a functional version of the gene NPR1 in *Arabidopsis thaliana*, SAR and ISR are intertwined molecularly (Vallad and Goodman 2004).

Kavroulakis et al. (2006) found that the expression of certain PR genes in the roots of tomato plants grown in suppressive compost increased, even in the absence of any pathogen. They therefore concluded that the expression of PR genes may be triggered by the microflora of the compost or could be associated with abiotic characteristics of the compost. Using the split-root technique, Zhang et al. (1996) found that peroxidase activity, a putative marker of SAR in cucumber, was significantly enhanced in plants grown in the compost-amended mixes. They concluded

that the interaction between compost and the pathogen appears to be a critical factor for rapid activation of SAR-associated gene expression in cucumber plants grown in compost mix. Similar findings have been reported for compost tea or extracts and microorganisms isolated from compost. For example, based on the increased concentration of inducible resistance-related compounds including peroxidase, phenol oxidase and phenylalanine ammonia lyase activities, Siddiqui et al. (2008) concluded that induced host resistance was stimulated in okra plants treated with non-sterilised and filter-sterilised compost teas. Likewise, Sang and Kim (2011) attributed the suppressive-effect compost-water extract against anthracnose in cucumber and pepper to a compost mediated ISR property. Hoitink et al. (2006) and Horst et al. (2005) reported that *Trichoderma* spp. isolated from compost triggered system resistance effect in host plants against *Phytophthora* spp. and *Botrytis cinerea*, respectively. *Trichoderma* spp., which are also known for their mycoparasitic and antibiosis effects, are also widely studied their ISR effects (Hoitink et al. 2006; Khan et al. 2004).

## 2.6 Improved Plant Nutrition and Vigour Due to Microbes

Compost and compost tea have been reported to contain plant growth-promoting *Rhizobacteria* (PGPR) and endophytes, which are known to improve plant growth and vigour (Scheuerell and Mahaffee 2002; Insam et al. 2002; Castaño et al. 2011). As such, even when the composts are not directly suppressive to phytopathogens, plant growth and vigour may be stimulated or induced by increased nutrient uptake. The resulting effect may be plants that are more resistant or tolerant to pathogen attack. Some Gram-negative bacteria species from the genera such as *Pseudomonas*; Gram-positive bacteria species from the genera *Bacillus*, *Paenibacillus* and actinomycetes; as well as arbuscular mycorrhizal fungi (AMF) species have been reported to be involved in such indirect mechanisms of phytopathogen and disease control. *Pseudomonas fluorescens*, which is the most studied species within the genus *Pseudomonas*, stimulate plant growth by suppressing deleterious rhizosphere microorganisms (Bouizgarne 2013), facilitating nutrient uptake from soil (De Weger et al. 1986) or by producing plant growth-promoting substances (Ryu et al. 2005). In contrast, species of *Paenibacillus* have been shown to induce plant growth by fixing atmospheric nitrogen (von der Weid et al. 2002) and producing auxins (Da Mota et al. 2008) and cytokinin (Timmusk et al. 1999). Moreover, certain *Bacillus*, actinomycetes and AMF species are reported to stimulate plant growth by increasing the uptake of soluble phosphorus (El-Tarabily 2008; Deepa et al. 2010).

Microorganisms including AMF and strains of *Pythium oligandrum* have also been shown to induce anatomical and morphological changes in root systems (Pharand et al. 2002; Atkinson et al. 1994), alter rhizosphere profiles (Meyer and Linderman 1986) and increase host tolerance to pathogen attack by compensating for the loss of root biomass or function caused by pathogens (Cordier et al. 1996).

However, the significance of these findings as it relates to plant protection or a mechanism of biocontrol has not yet been sufficiently considered or evaluated. Nonetheless, mature compost has been inoculated with some of these microbial species including *T. hamatum*, *Chryseobacterium gleum* and *B. subtilis* and non-pathogenic strains of *F. oxysporum* to improve disease-suppressive efficacy. Generally, results show small but significant increases in the suppressive effect of mature compost inoculated with suspected or known BCA or beneficial microorganisms (Coventry et al. 2006; Ryckeboer 2001). The effectiveness of microbial inocula to improve the suppressive effects of compost is dependent on the capacity of the substrate to support microbial growth and activity (Cotxarrera et al. 2002; Dukare et al. 2011; Hoitink and Fahy 1986).

## 2.7 Physico-chemical Properties of Compost and Compost Tea

While important, microbiological properties per se do not fully explain the capacity of compost and compost tea to enhance soil suppressiveness. Physico-chemical properties of compost and compost tea may protect plants against various diseases through direct toxicity, improved nutritional status or SAR. For example, Spencer and Benson (1982) and Hoitink and Fahy (1986) found that the ability of compost to suppress diseases caused by pathogens, to which free water is important for asexual multiplication, was dependent on the ability of compost to raise the air capacity of a substrate above 15 %. Cronin et al. (1996) and Sang et al. (2010) concluded that the suppressive effects of fermented compost extracts were not biological in nature since sterilising or micron filtering extracts did not significantly affect the results. They both suggested that suppression was likely due to presence or activity of heat-stable chemical compounds. However, without the identification of these specific heat-stable chemical compounds, and the use of molecular tools to elucidate the community structure and functional role of microbes in compost extracts, it is unclear whether this heat-stable chemical factor was produced by microorganisms.

Nonetheless, disease-suppressive effects have been attributed to organic and inorganic compounds present in compost or compost tea or released by microorganisms inhabiting these inputs. Humic, phenolics, bioactive compounds and volatile fatty acids (VFAs) have often been suggested as organic compounds, which play an important role in disease suppression with compost and compost tea. For example, Pascual et al. (2002) found that compost and its humic fractions significantly reduced *P. ultimum* populations in soil and the number of root lesions on pea plants. Tenuta et al. (2002) demonstrated that under acidic conditions (pH 4.75) non-ionised forms of VFAs from liquid swine manure were toxic to microsclerotia of *Verticillium dahliae* Kleb., the causal agent of *Verticillium* wilt in potato. However, the mechanism by which VFAs are toxic to *V. dahliae* is unknown.

Nonmicrobial inorganic compounds, such as aluminium and nitrogen from N-rich organic matter decomposition, can also affect pathogens (Fichtner et al. 2004; Lazarovits et al. 2005). Fichtner et al. (2004) reported an aluminium-mediated suppression of *Phytophthora parasitica* in a potting medium containing 20 % composted swine waste. Fichtner et al. (2004) noted that both abiotic and biotic suppression may have occurred, but at different times. They therefore concluded that aluminium amendments may be effective at protecting the plant before beneficial microbial populations reach a threshold necessary for suppression, if exchangeable aluminium levels of the medium are  $>2 \mu\text{M Al g}^{-1}$ . High nitrogen levels and high ammonium-to-nitrogen ratios have been reported to enhance Fusarium wilt incidence, and severity has been reported by several researchers (Woltz and Jones 1981; Hoitink et al. 1987; Borrero et al. 2012). The suppressive capacity of compost and compost tea is also affected by the pH and electrical conductivity of these inputs and of the soil (Spencer and Benson 1981; Jones et al. 1991; Hoitink et al. 1996; Cotxarrera et al. 2002). Hoitink et al. (1996) reported that highly saline compost ( $>10 \text{ dS/m}$ ) enhanced *Pythium* and *Phytophthora* diseases unless they are applied months ahead of planting to allow for leaching. In contrast, Pane et al. (2011) found a negative correlation between salinity of compost-amended substrates and damping off (*Sclerotinia minor*) in *Lepidium sativum*. MacDonald (1982) and Al-Sadi et al. (2010) reported that high salinity levels do not inhibit mycelial growth of *P. ultimum* but negatively affects plants, making them more susceptible to attack by the pathogen. Hoitink et al. (1996) noted that the pH of compost affects its potential to be colonised by beneficial bacteria. At pH values of  $<5.0$ , the growth, reproduction and multiplication of bacterial biocontrol agents are generally inhibited (Hoitink et al. 1991). Compost pH also affects the availability of macro- and micronutrients for plant uptake or pathogen use, which in turn affects disease incidence and severity. A classic example of this is the use of the pH of plant growth substrates as a chemical environmental index for Fusarium wilt in tomato (Woltz and Jones 1981; Jones et al. 1991). The unavailability of micronutrients such as Cu, Fe and Zn, at substrate pH values of  $\geq 7.5$ , can limit growth, sporulation and pathogenicity of *F. oxysporum* (Jones et al. 1993). Furthermore, the low availability of Fe can induce siderophore production and microbial competition for Fe (Alabouvette 1999). Fusarium wilt severity tends to be higher at substrate pH values of 5–7, which are most favourable for the growth and survival of pathogenic *Fusarium* species (Oritsejafor 1986). In contrast, Blaker and MacDonald (1983) showed that low pH ( $\leq 4.5$ ) reduced sporangium formation, zoospore release and motility of *Phytophthora cinnamomi*, a causal agent of root rot and dieback in many plant species. As such, pine bark compost with pH values of 4.4–4.5 has been used as a substrate or substrate component to suppress *Phytophthora*, *Rhizoctonia* and *Pythium* root rot diseases (Spring et al. 1980; Nelson et al. 1983).

Plant-based composts are suspected to contain compounds that mimic chemical signals from the root or shoot exudates of host plants (Mehta et al. 2014). These chemical signals are suspected to be important in host identification and triggering germination of pathogens before they come in contact with host plants



(Chen et al. 1988). Mehta et al. (2014) noted that the mimicry of these chemical signals may explain why Yogeve et al. (2006) found that pathogen activity and proliferation is reduced with plant-based compost, even in the absence of a host. Mehta et al. (2014) termed this type of suppression as “ineffective pathogen proliferation” and categorised it as separate from more conventional mechanisms or factors. Further research is needed to clearly demonstrate this type of suppression and to support the need to distinguish it from more established mechanisms. This is particularly important since generally, a pathogen propagule does not significantly proliferate in the absence of a host (Lockwood 1990).

To this end, the six biological control mechanisms of compost and compost tea have been classified into two broad classes: “general” and “specific” suppression (Cook and Baker 1983). General refers to suppression that can be attributed to the activities of many different types of microorganisms, which result in the generation of a hostile environment for the development many pathogens or diseases (Hoitink and Boehm 1999). General suppression is linked to both abiotic and biotic substrate characteristics (Baker and Cook 1974). In contrast, specific suppression is attributed to the presence and/or activity of one or a few microorganisms. To this end, competition and production of antibiotics are mostly involved in general suppression effects, whereas predation, parasitism and activation of disease resistance are more often manifested by specific microorganisms (Hadar and Papadopoulou 2012; Cook and Baker 1983). It is likely that two broad classes of suppression are not mutually exclusive. In fact, Bonilla et al. (2012) hypothesised that in most cases, suppressive soils owe their activity to a combination of general and specific suppression. However, most researchers have concluded that compost and compost tea suppress phytopathogens and diseases through general rather than specific mechanisms. Unfortunately, the disease-suppressive effects resulting from general mechanisms are not easily transferable from one medium to another.

Regardless of the mechanisms, i.e. general or specific, the degree of disease suppression observed with the application of compost or compost tea to soils can vary greatly or be short lived. The duration of suppressiveness and degree of efficacy of compost and compost tea depend on many production, application and soil factors including the feedstock types composted; the composting or compost tea brewing process; the use of nutrient or microbial amendments; the rate, time and frequency of application; and the physical, chemical and biological characteristics of the soil. Some of these factors, e.g. organic matter decomposition level and compost maturity, were highlighted or briefly discussed in the previous subsections. For more comprehensive and detailed discussions of these factors, the works of St. Martin (2014), St. Martin and Ramsubhag (2014) and Scheuerell and Mahaffee (2002) can be consulted.



## 2.8 Conclusions and Future Outlook

Despite their limited use, compost and compost tea have much potential as tools for enhancing the suppressive capacity of soils. These potentially low-cost and environmentally benign alternatives to chemical fungicides have been shown to suppress many fungal and bacterial pathogens through similar mechanisms and processes ascribed to naturally suppressive soils. However, less than desirable and inconsistent levels of disease suppression achieved with compost and compost tea effectively limited their use as tools for enhancing soil suppressiveness in conventional cropping systems. Conversely, the use of compost and compost tea as tools for enhancing soil suppressiveness in organic crop production system is deemed important to producers who have limited disease control options (Mahaffee and Scheuerell 2006; St. Martin and Brathwaite 2012). This widespread use limitation appears to be related to the complexity and dynamics of microbial ecological processes involved in the production and application of compost and compost tea. As such, it appears that increasing our understanding of the microbial ecology of the compost-soil-plant interactions may assist in improving the consistency and efficacy of disease suppression for particular compost types, pathogens, crops and soil and environmental conditions. To achieve this, a systems biology approach, which addresses the complex, simultaneous and dynamic interactions of variable communities that affect plant health, is needed (Lazarovits 2014). However, thus far, there have been limited applications of these techniques in the study aimed at enhancing soil suppressiveness using composts and compost tea.

St. Martin (2014), Mehta et al. (2014) and Mazzola (2004) reviewed the potential use of molecular-based methods, including polymerase chain reaction (PCR) combined with techniques such as DNA sequencing, denaturing gradient gel electrophoresis (DGGE), temperature gradient gel electrophoresis (TGGE) and terminal restriction fragment length polymorphism (T-RFLP); real-time PCR; DNA arrays; and metagenomic libraries for assessing community structure and function as it relates to disease suppression with compost or compost tea.

Pang et al. (2009) demonstrated that metagenomic analysis could be used to identify and characterise a novel endoglucanase enzyme from compost soils. Kim et al. (2010) used metagenomic libraries to characterise a novel family VIII alkaline esterase from a pig manure-mushroom waste compost. It is expected that much more studies using the “omics” technologies such as metagenomics, metatranscriptomics and metabolomics and next-generation sequencing will be completed in the near future. Such studies will provide a tremendous opportunity for elucidating the microbial and metabolic dynamics associated with suppressiveness of compost. In turn, this will provide the basis for developing or optimising production and application protocols for consistently suppressive compost and compost tea. As with microbial biocontrol in general, research and developmental work on compost and compost tea should focus on the ecology of plant-associated microbes, the application of antagonistic microbial strains/inoculant strategies, discovering novel strains and mechanisms of action, and practical integration of these findings into

agricultural systems remain (Pal and Gardener 2006). More specifically, the long-term residual and cumulative effects of compost and compost tea soil amendments on general and specific suppression should be investigated. This research should be done on various soil types using low compost application rates.

Despite such research, inducing general or specific suppression in soils using compost or compost tea might not be sufficient or possible to achieve commercially viable disease control in many disease and cropping systems (Stone et al. 2004). In such cases, other strategies or combinations of strategies such as the use of crop rotation, cover and rotation crops, tillage and inputs including plant genetic resources and amendments will be necessary.

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