SUPPRESSION OF PLANT DISEASES BY COMPOSTS

H. A. J. Hoitink, A. G. Stone and D. Y. Han
Professor and Graduate Research Associates, Department of Plant Pathology, Ohio Agricultural Research and Development Center, The Ohio State University, Wooster, OH 44691

1. ABSTRACT

Composts offer unique opportunities to examine fundamental interactions between plant pathogens, biocontrol agents, soil organic matter, and plant roots. These organic amendments have the potential to provide consistent biological control of many plant diseases. Foliar, vascular as well as root pathogens may be affected by composts. Many factors influence these beneficial effects. For example, the composition of the feedstock used in the preparation of composts affects the potential for biological control as well as the microflora active in control. Heat generated during composting kills or inactivates pathogens if the process is monitored properly. Unfortunately, biocontrol agents with the exception of *Bacillus* spp. are also killed. Therefore this beneficial microflora must largely recolonize composts after peak heating. The composting environment and conditions during curing and utilization also affect the potential for recolonization of composts by biocontrol agents and the induction of disease suppression. In practice, controlled inoculation of compost with biocontrol agents has proved necessary to induce consistent levels of disease suppression.

Stability of composts must be considered in biological control. Immature composts serve as food for pathogens. Their populations increase in fresh organic matter and cause disease even if colonized by biocontrol agents. On the other hand, biocontrol agents inhibit or kill pathogens in mature composts and thereby induce disease suppression. Biocontrol agents in composts may induce systemic acquired resistance to foliar plant pathogens. Finally, excessively stabilized organic matter does not support the activity of biocontrol agents. Microorganisms incapable of providing biological control predominate here. Disease develops on plants produced in such highly mineralized organic matter.

Physical and chemical properties of composts affect biological control. Salinity and the rate of release of plant nutrients, particularly the amount of nitrogen released, affect suppressiveness. Compost pH and timing of compost application relative to planting of crops are other factors to be considered. In summary, the field is very complex.

2. INTRODUCTION

During the 1960's, nurserymen across the United States explored the possibility of using composted tree bark as peat substitutes to reduce potting mix costs. Early during the utilization of bark composts, improved plant growth and decreased losses caused by *Phytophthora* root rots were observed as side benefits in the nursery industry. Today it is recognized that control of such root rots with composts can be as effective as that obtained with fungicides (Hardy and Sivasithamparam, 1991; Hoitink *et al.*, 1991; Ownley and Benson, 1991). Therefore, the ornamental plant industry relies heavily on compost products for control of diseases caused by these soilborne plant pathogens. Composts have replaced methyl bromide in this industry (Quarles and Grossman, 1995). In field applications of composts similar results have been obtained (Hoitink and Fahy, 1986; Lumsden et al., 1983, Schüler *et al.*, 1993). Examples of diseases controlled by composts are reviewed in Hoitink and Fahy, 1986.

Composts must be of consistent quality to be used successfully in biological control of diseases of horticultural crops, particularly if used in container media (Inbar *et al.*, 1993). The rate of respiration is one of several procedures that can be used to monitor stability of composts (Iannotti *et al.*, 1994). Variability in compost stability is one of the principal factors limiting its widespread utilization. Maturity is less important in ground bed or field agriculture as long as the compost is applied sufficiently ahead of planting to allow for additional stabilization; however, lack of maturity frequently causes problems here as well.

Effects of chemical properties of composts on soilborne disease severity often are overlooked (reviewed in Hoitink *et al.*, 1991). Highly saline composts enhance *Pythium* and *Phytophthora* diseases unless they are applied months ahead of planting to allow for leaching. Compost prepared from municipal sewage sludge have a low carbon to nitrogen ratio. They release considerable amounts of nitrogen and enhance *Fusarium* wilt (Hoitink *et al.*, 1987). On the other hand, composts from high C/N materials, such as tree barks, immobilize nitrogen and suppress *Fusarium* diseases if colonized by an appropriate microflora (Trillas-Gay *et al.*, 1986). High amonium and low nitrate nutrition increases

COMBATE BIOLOGICO

Fusarium wilts (Schneider, 1985). Perhaps the low in C/N predominantly ammonium-nitrogen-releasing sludge compost enhances *Fusarium* diseases for this reason.

3. FATE OF BIOCONTROL AGENTS DURING COMPOSTING

The composting process is often divided into three phases. The initial phase occurs during the first 24-48 hr as temperatures gradually rise to 40-50 C, and sugars and other easily biodegradable substances are destroyed. During the second phase, when high temperatures of 55- 70 C prevail, less biodegradable cellulosic substances are destroyed. Thermophilic microorgansims predominate during this part of the process. Plant pathogens and seeds are killed by the heat generated during this high phase (Bollen 1993; Farrell 1993). Compost piles must be turned frequently to expose all parts to high temperature to produce a homogeneous product free of pathogens and weed seeds. Unfortunately, most beneficial microorganisms also are killed during the high temperature phase of composting.

Curing begins as the concentration of readily biodegradable components in wastes declines. As a result, rates of decomposition, heat output and temperatures decrease. At this time, mesophilic microorganisms that grow at temperatures <40 C recolonize the compost from the outer low temperature layer into the compost windrow or pile. Therefore, suppression of pathogens and/or disease is largely induced during curing, because most biocontrol agents recolonize composts after peak heating also.

Bacillus spp., *Enterobacter* spp., *Flavobacterium balustinum*, *Pseudomonas* spp., other bacterial genera and *Streptomyces* spp., as well as *Penicillium* spp., several *Trichoderma* spp., *Gliocladium virens* and other fungi have been identified as biocontrol agents in compost-amended sustrates (Chung and Hoitink 1990; Hadar and Gorodecki, 1991; Hardy and Sivasithamparam 1991; Hoitink and Fahy 1986; Nelson *et al.*, 1983; Phae *et al.*, 1990). The moisture content of compost critically affects the potential for bacterial mesophiles to colonize the substrate after peak heating. Dry composts (<34% moisture, w/w) become colonized by fungi and are conducive to *Pythium* diseases. In order to induce suppression, the moisture content must be high enough (at least 40-50%, w/w) so that bacteria as well as fungi colonize the substrate after peak heating. Water must often be added to composts during composting and curing to avoid the dry condition. Compost pH also affects the potential for beneficial bacteria to colonize composts. A pH <5.0 inhibits bacterial biocontrol agents (Hoitink *et al.*, 1991).

Variability in suppression of *Rhizoctonia* damping-off and *Fusarium* wilt encountered in substrates amended with mature composts is due in part to random recolonization of compost by effective biocontrol agents after peak heating. Field compost more consistently suppresses *Rhizoctonia* diseases than the same compost produced in a partially enclosed facility where few microbial species survive heat treatment (Kuter *et al.*, 1983). Compost produced in the open near a forest (field compost), an environment that is high in microbial species diversity, is colonized by a greater variety of biocontrol agents than the same produced in an in-vessel system (Kuter *et al.*, 1983). Frequently, however, *Rhizoctonia* and other diseases are observed for some time after composts are first applied (Kuter *et al.*, 1988; Lumsden *et al.*, 1983). Three approaches can be used to solve this problem: Curing of composts for four months or more renders composts more consistently suppressive (Kuter *et al.*, 1988). The second approach is to incorporate composts ino field soils for several months before planting (Lumsden *et al.*, 1983). The third approach is to inoculate composts with specific biocontrol agents (Kwok *et al.*, 1987).

A specific strain of *Flavobacterium balustinum* and an isolate of *Trichoderma hamatum* have been identified that induce consistent levels of suppression to diseases caused by a broad spectrum of plant pathogens, if inoculated into compost after peak heating, but before significant levels of recolonization have occurred. Patents have been issued to The Ohio State University for this process (Hoitink, 1990). In Japan, Phae et al. (1990), isolated a *Bacillus* strain that induces predictable biological control in composts. It has been recognized for decades that single strains are not as effective in biological control in field applications as mixtures of microorganisms, (Garrett, 1955). The same applies to container media (Kwok *et al.*, 1987).

4. MECHANISMS OF SUPPRESSION IN COMPOSTS

Two classes of biological control mechanisms known as "general" and "specific" suppression have been described for compost-amended substrates. The mechanisms involved are based on competition, antibiosis, hyperparasitism and the induction of systemic acquired resistance in the host plant. Propagules of plant pathogens such as *Pythium* and *Phytophthora* spp., are suppressed through the "general suppression" phenomenon (Boehm *et al.*, 1993; Chen *et al.*, 1988a; Chen *et al.*, 1988b; Cook and Baker 1983; Hardy and Sivasithamparam 1991; Mandelbaum and Hadar 1990). Many types of microorganisms present in compost-amended container media function as biocontrol agents against diseases caused by *Phytophthora* and *Pythium* spp. (Boehm *et al.*, 1993; Hardy and Sivasithamparam 1991). Propagules of these pathogens, if inadvertently introduced into compost-amended substrates, do not germinate in response to nutrients released in the form of seed or root exudates. The high microbial activity and biomass caused by the "general soil microflora" in such substrates prevents germination of spores of these pathogens and infection of the host, (Chen *et al.*, 1988a; Mandelbaum and Hadar 1990). Propagules of these pathogens remain dormant and are typically not killed if introduced in compost-amended soil (Chen *et al.*, 1988a; Mandelbaum and Hadar, 1990). An enzyme assay, that determines microbial activity based on the rate of hydrolysis of fluorescein diacetate (FDA), predicts suppressiveness of potting mixes to *Pythium* diseases (Boehm and Hoitink 1992; Chen *et al.*, 1988a; Mandelbaum and Hadar 1990; You and Sivasithamparam, 1994). Similar information has been developed for soils on "organic farms" where soilborne diseases are less prevalent (Workneh *et al.*, 1993). The length of time that the suppressive effect lasts also may be determined with FDA activity (Boehm and Hoitink, 1992). This is known as the "carrying capacity" of the substrate relative to biological control.

The mechanism of biological control for *Rhizoctonia solani* in compost-amended substrates is different from that of *Pythium* and *Phytophthora* spp. because only a narrow group of microorganisms is capable of eradicating *R. solani*. This type of suppression is referred to as "specific suppression" (Hoitink *et al.*, 1991). *Trichoderma* spp, including *T. hamatum* and *T. harzianum*, are the predominant hyperparasites recovered from composts prepared of lignocellulosic wastes (Kuter *et al.*, 1983; Nelson *et al.*, 1983). Hyperparasites are microorganisms capable of colonizing plant pathogens resulting in lysis or death. These fungi interact with various bacterial strains in the biological control of *Rhizoctonia* damping-off (Kwok *et al.*, 1987). It is of interest that *Penicillium* spp. are the predominant hyperparasites recovered from sclerotia of *Sclerotium rolfsii* in composted grape pomace, a high sugar and low cellulose content waste (Hadar and Gorodecki, 1991). *Trichoderma* spp. were not recovered from this compost and were not effective when introduced. The composition of the feed stock, as expected, appears to have an impact on the microflora in composts active in biological control.

5. BIOLOGICAL ENERGY AVAILABILITY VERSUS SUPPRESSIVENESS

The decomposition level of organic matter in compost-amended substrates has a major impact on disease suppression. For example, *R. solani* is highly competitive as a saprophyte (Garrett, 1962). It can utilize cellulose and colonize fresh wastes but not low cellulose mature compost (Chung *et al.*, 1988). Trichoderma, an effective biocontrol agent of *R.solani*, is capable of colonizing fresh as well as mature compost but it grows better in fresh compost (Chung *et al.*, 1988; Nelson *et al.*, 1983). In fresh, undecomposed organic matter, biological control does not occur because both the pathogen and the biocontrol agent grow as saprophytes. Therefore, *R. solani* (the pathogen) remains capable of causing disease here. Presumably, synthesis of lytic enzymes involved in hyperparasitism of pathogens by *Trichoderma* is repressed in fresh organic matter due to high glucose concentrations in such waste (de la Cruz *et al.*, 1993). The same processes may occur in antibiotic production, which also plays an important role in biocontrol.

In mature compost, where concentrations of free nutrients are low (Chen *et al.*, 1988a), sclerotia of *R. solani* are killed by the hyperparasite, and biological control prevails (Nelson et al., 1983). The foregoing reveals that composts must be adequately stabilized to reach that decomposition level where biological control is feasible. In practice, this occurs in composts (tree barks, yard wastes, etc.) that have been (1) stabilized far enough to avoid phytotoxicity and (2) colonized by the appropriate specific microflora. Practical guidelines that define this critical stage of decomposition in terms of biological control are not yet available. Industry presently controls decomposition level by maintaining constant conditions during the entire process and adhering to a given time schedule. Composted pine bark produced by such a process has been utilized with great success in floriculture indicating that this approach to quality control is quite acceptable (Hoitink et al., 1991).

Excessively stabilized organic matter, the opposite end of the decomposition scale, does not support adequate activity of biocontrol agents. As a result, suppression is lacking and soilborne diseases are severe, as in highly mineralized soils where humic substances are the predominant forms of organic matter (Workneh *et al.*, 1993). The length of time that soil-incorporated composts support adequate levels of biocontrol activity has not yet been determined. Presumably, it varies with soil temperature, soil characteristics and the type of organic matter from which the compost was prepared. Loading rates and farming practices of course also play a role.

We have studied the "carrying capacity" of soil organic matter in potting mixes prepared with sphagnum peat to bring a partial solution to this problem (Boehm and Hoitink 1992; Boehm et al., 1993). Sphagnum peat typically competes with compost as a source of organic matter in horticulture. Both the microflora and the organic matter in peat itself can affect suppression of soilborne diseases. The literature on that effect is reviewed briefly here.

Dark, more decomposed sphagnum peat, harvested from a four foot or greater depth in most peat bogs, is low in microbial activity and consistently conducive to *Pythium* and *Phytophthora* root rots (Hoitink *et al.*, 1991; Boehm and Hoitink, 1992). On the other hand, light, less decomposed sources of sphagnum peat, harvested from near the surface of peat bogs, have a higher microbial activity (FDA activity) and suppress root rot. Unfortunately, the suppressive effect of light peat to *Pythium* root rots is of short duration. (Boehm and Hoitink, 1992; Tahvonen, 1982; Wolffhechel 1988). Light peats are used most effectively for short production cycles (6-10 week crops), such as in plug and flat mixes used in the ornamentals industry. Composts have longer lasting effects (Boehm and Hoitink, 1992; Boehm et al, 1993; You and Sivasithamparam, 1994).

As mentioned above, the rate of hydrolysis of FDA predicts suppressiveness of peat mixes and of compost-amended substrates to *Pythium* root rot (Boehm and Hoitink, 1992). As FDA activity in suppressive substrates declines to < 3.2 =B5g FDA hydrolyzed min-1 g-1 dry weight mix, the population of *Pythium ultimum* increases, infection takes place and root rot develops. During this collapse in suppressiveness, the composition of bacterial species also changes (Boehm *et al.*, 1993). A microflora typical of suppressive soils, which includes *Pseudomonas* spp. and other rod-shaped Gram negative bacteria as the predominant rhizosphere colonizers, is replaced by pleomorphic Gram-positive bacteria (e.g., Arthrobacter) and putative oligotrophs (Wu *et al.*, 1993). The microflora of the conducive substrate resembles that of highly mineralized niches in soil (Kanazawa and Filip, 1986).

Non-destructive analysis of soil organic matter, utilizing Fourier Transform Infra Red spectroscopy (FT-IR) and Cross Polarization Magic Angle Spinning -13Carbon Nuclear Magnetic Resonance Spectroscopy (CPMAS - 13C NMR), allows characterization of biodegradable components of soil organic fractions (Inbar et al., 1989; Chen and Inbar, 1993). CPMAS - 13CNMR allows quantitative analysis of concentrations of readily biodegradable substances such as "carbohydrates" (hemicellulose, cellulose, etc.) versus lignins and humic substances in soil organic matter [reviewed in Chen and Inbar, 1993]. In a preliminary report, Wu *et al.* (1993) reported that the "carbohydrates" decline as suppressiveness is lost. During the same time period, bacterial genera capable of causing biological control are replaced by those that cannot provide control. Biocontrol agents inoculated into the more decomposed substrate are not able to induce sustained biological control of *Pythium* root rot. The same phenomenon has been observed for *Phytophthora* root rot in the field (You and Sivasithamparam, 1994). Therefore, biocontrol of these diseases is determined by the "carrying capacity" of the substrate which regulates species composition and activity and, in turn, the potential for sustenance of biological control.

6. COMPOST FOR CONTROL OF FOLIAR DISEASES

During the past decade, a series of projects have been published on the control of plant diseases of above ground plant parts with water extracts, also known as steepages, prepared from composts (Weltzhien, 1992; Yohalem *et al.*, 1994). Steepages often are prepared by soaking mature composts in water (still culture; 1:1, w/w) for 7-10 days. The steepage is filtered and then sprayed on plants. Unfortunately, efficacy varies with the compost, batches of steepages produced, crops and the disease under question. Sackenheim (1993), utilizing plate counting procedures, has reported that aerobic microorganisms predominate in steepages. The microflora includes strains of bacteria and isolates of fungi already known as biocontrol agents. He developed a number of enrichment strategies, that include nutrients as well as microorganisms, to improve efficacy of the steepages.

Control induced by compost steepages has also been attributed to systemic acquired resistance (SAR) induced in plants by microbes present in the extracts (Weltzhien, 1992). The recent work by Sackenheim (1993) on grape, however, does not support this assumption. A factor that has not been evaluated but could play a role in efficacy of steepages is the condition of soil organic matter and the associated microflora in the soil in which treated plants are produced. Soils naturally suppressive to soilborne plant pathogens (e.g., compost-amended soils) harbor active populations of biocontrol agents (Boehm *et al.*, 1993). Several of these rhizobacteria and fungi can induce protection to foliar pathogens in the leaves of plants (Maurhofer *et al.*, 1994; Wei *et al.*, 1991). Zhang *et al.*, (1994) reported that pathogenesis - related proteins were activated in roots and shoots of cucumber plants produced in compost. Further work may reveal that composts affect resistance of the roots and foliage to diseases. Presently, control of foliar diseases with composts or steepages is highly variable.

7. DISEASE SUPPRESSION - FUTURE OUTLOOK

Success in biological control of diseases with composts is possible only if all factors involved in the production and utilization of composts are defined and kept consistent. Most composts are variable in quality. Therefore, composted pine bark remains the principal compost used for the preparation of potting mixes or soils naturally suppressive to soilborne plant pathogens. Composted manures, yard and food wastes are steadily gaining in popularity, and offer the same potential (Gorodecki and Hadar, 1990; Grebus *et al.*, 1994; Inbar *et al.*, 1993; Marugg *et al.*, 1993; Schüler *et al.*, 1993).

Controlled inoculation of composts with biocontrol agents is a procedure that must be developed on a commercial scale to induce consistent levels of suppression to pathogens such as *R. solani* (Hoitink *et al.*, 1991; Phae *et al.*, 1990; Grebus *et al.*, 1993). Recently, tree bark was proposed as a food base for the culture of biocontrol agents and as a carrier of such agents for use in agricultural applications (Steinmetz and Schönbeck, 1994). However, this new field of biotechnology, is still in its infancy. Major research and development efforts will need to be directed toward this approach for disease control. Recycling through composting is being chosen as the preferred strategy for waste treatment. This also applies to farm manures. For this reason, composts are becoming available in greater quantities. Peat, on the other hand, is a limited resource that cannot be recycled. Future opportunities for both natural and controlled-induced suppression of soilborne plant pathogens appear bright.

8. ACKNOWLEDGEMENT

Salaries and research support provided by State and federal funds appropriated to the Ohio Agricultural Research and Development Center, The Ohio State University, and by Grant no. US2196-22 from BARD, the United States-Israel Binational Research and Development Fund.

9. REFERENCES

Boehm, M. J. and H. A. J. Hoitink. 1992. Sustenance of microbial activity and severity of *Pythium* root rot of poinsettia. Phytopathology 82:259-264.

Boehm, M. J., L. V. Madden, and H. A. J. Hoitink. 1993. Effect of organic matter decomposition level on bacterial species diversity and composition in relationship to *Pythium* damping-off severity. Applied Environ. Microbiol. 59:4171-4179.

Bollen, G. J. 1993. Factors involved in inactivation of plant pathogens during composting of crop residues, p. 301-318. In: Science and Engineering of Composting: Design, Environmental, Microbiological and Utilization Aspects. H. A. J. Hoitink and H. M. Keener, eds. Renaissance Publications, Worthington, OH. 728 p.

Chen, W., H. A. J. Hoitink, A. F. Schmitthenner, and O. H. Tuovinen. 1988a. The role of microbial activity in suppression of damping-off caused by *Pythium ultimum*. Phytopathology 78:314-322.

Chen, W., H. A. J. Hoitink, and L. V. Madden. 1988b. Microbial activity and biomass in container media predicting suppressiveness to damping-off caused by *Pythium ultimum*. Phytopathology 78:1447-1450.

Chen, Y. and Y. Inbar. 1993. Chemical and spectroscopical analyses of organic matter transformations during composting in relation to compost maturity, p. 551-600. In: Science and Engineering of Composting: Design, Environmental, Microbiological and Utilization Aspects. H. A. J. Hoitink and H. M. Keener, eds. Renaissance Publications, Worthington, OH. 728 p.

Chung, Y. R., H. A. J. Hoitink, and P. E. Lipps. 1988. Interactions between organic-matter decomposition level and soilborne disease severity. Agric., Ecosys. Environ. 24:183-193.

Chung, Y. R. and H. A. J. Hoitink. 1990. Interactions between thermophilicfungi and *Trichoderma hamatum* in suppression of *Rhizoctonia* damping-off in a bark compost- amended container medium. Phytopathology 80:73-77.

Cook, R. J. and K. F. Baker. 1983. The Nature and Practice of Biological Control of Plant Pathogens. Am. Phytopathol. Soc., St. Paul, MN. 539 p.

de la Cruz, J., M. Rey, J. M. Lora, A. Hidalgo-Gallego, F. Dominguez, J. A. Pintor-Toro, A. Llobell, and T. Benitez. 1993. Carbon source control on -glucanases, chitobiase and chitinase from *Trichoderma harzianum*. Microbiol. 159:316-322.

Farrell, J. B. 1993. Fecal pathogen control during composting, p. 282-300. In: Science and Engineering of Composting: Design, Environmental, Microbiological and Utilization Aspects. H. A. J. Hoitink and H. M. Keener, eds. Renaissance Publications, Worthington, OH. 728 p. Garrett, S. D. 1955. A century of root-disease investigation. Ann. Appl. Biol. 42:211-219.

Garrett., S. D. 1962. Decomposition of cellulose in soil by *Rhizoctonia solani* Kuhn. Trans. Br. Mycol. Soc. 45:114-120.

Grebus, M. E., K. A. Feldman, C. A. Musselman, and H. A. J. Hoitink. 1993. Production of biocontrol agent-fortified compost-amended potting mixes for predictable disease suppression. Phytopathology 83:1406 (Abstr.).

Grebus, M. E., M. E. Watson, and H. A. J. Hoitink. 1994. Biological, chemical and physical properties of composted yard trimmings as indicators of maturity and plant disease suppression. Compost Sci. Util. 1:57-71.

Gorodecki, B. and Y. Hadar. 1990. Suppression of *Rhizoctonia solani* and *Sclerotium rolfsii* in container media containing composted separated cattle manure and composted grape marc. Crop Protection 9:271-274.

Hadar, Y. and B. Gorodecki. 1991. Suppression of germination of sclerotia of *Sclerotium rolfsii* in compost. Soil. Biol. Biochem. 23:303-306.

Hardy, G. E. St. J. and K. Sivasithamparam. 1991. Suppression of *Phytophthora* Root Rot by a Composted Eucalyptus Bark Mix. Aust. J. Bot. 39:153-159.

Hoitink, H. A. J. 1990. Production of disease suppressive compost and container media, and microorganism culture for use therein. US Patent 4960348. Feb. 13, 1990.

Hoitink, H. A. J., M. Daughtery, and H. K. Tayama. 1987. Control of cyclamen *Fusarium* wilt - A preliminary report. Ohio Florist't Assoc. Bull. 693:1-3.

Hoitink, H. A. J. and P. C. Fahy. 1986. Basis for the control of soilborne plant pathogens with composts. Ann. Rev. Phytopathol. 24:93-114.

Hoitink H. A. J., Y. Inbar, and M. J. Boehm. 1991. Status of composted-amended potting mixes naturally suppressive to soilborne diseases of floricultural crops. Plant Dis. 75:869-873.

Iannotti, D. A., Grebus, M. E., Toth, B. L., Madden L. V. and Hoitink, H. A. J. 1994. Oxygen respirometry to assess stability and maturity of composted municipal solid waste. J. Env. Qual. 23:1177-1183.

Inbar, Y., Y. Chen, and Y. Hadar. 1989. Solid-state carbon-13 nuclear magnetic resonance and infrared spectroscopy of composted organic matter. Soil Sci. Soc. Am. J. 53:1695-1701.

Inbar, Y., Y. Hadar, and Y. Chen. 1993. Recycling of cattle manure: The composting process and characterization of maturity: J. Environ. Qual. 22:857-863.

Kanazawa, S. and Z. Filip. 1986. Distribution of microorganisms, total biomass, and enzyme activities in different particles of brown soils. Microb. Ecol. 12:205-215.

Kuter, G. A., H. A. J. Hoitink, and W. Chen. 1988. Effects of municipal sludge compost curing time on suppression of *Pythium* and *Rhizoctonia* diseases of ornamental plants. Plant Dis. 72:751-756.

Kuter, G. A., E. B. Nelson, H. A. J. Hoitink, and L. V. Madden. 1983. Fungal populations in container media amended with composted hardwood bark suppressive and conducive to *Rhizoctonia* damping-off. Phytopathology 73:1450-1456.

Kwok, O. C. H., P. C. Fahy, H. A. J. Hoitink, G. A. and Kuter. 1987. Interactions between bacteria and *Trichoderma hamatum* in suppression of *Rhizoctonia* damping-off in bark compost media. Phytopathology = 77:1206-1212.

Lumsden, R. D., J. A. Lewis, and P. D. Millner. 1983. Effect of composted sewage sludge on several soilborne pathogens and diseases. Phytopathology 73:1543-1548.

Mandelbaum, R. and Y. Hadar. 1990. Effects of available carbon source on microbial activity and suppression of *Pythium aphanidermatum* in compost and peat container media. Phytopathology 80:794-804.

Marugg, C., M. E. Grebus, R. C. Hansen, H. M. Keener, and H. A. J. Hoitink. 1993. A kinetic model of the yard waste composting process. Compost Sci. & Util. 1:38-51.

Maurhofer, M., C. Hase, P. Meuwly, J-P. Métraux, and G. Défago. 1994. Induction of systemic resistance of tobacco to tobacco necrosis virus by the root-colonizing *Pseudomonas fluorescens* strain CHAO: Influence of the gac, a gene and of pyoverdine production. Phytopathology 84:139-146.

Nelson, E. B., Kuter, G. A. and Hoitink, H. A. J. 1983. Effects of fungal antagonists and compost age on suppression of Rhizoctonia damping-off in container media amended with composted hardwood bark. Phytopathology 3:1457-1462.

Ownley, B. H. and D. M. Benson. 1991. Relationship of matric water potential and air-filled porosity of container media to development of *Phytophthora* root rot of rhododendron. Phytopathology 81:936-941.

Phae, C. G., M. Saski, M. Shoda, and H. Kubota. 1990. Characteristics of *Bacillus subtilis* isolated from composts suppressing phytopathogenic microorganisms. Soil Sci. Plant Nutr. 36:575-586.

Quarles, W. and J. Grossmam. 1995. Alternatives to methyl bromide in nurseries - Disease suppressive media. The IPM Practitioner 17(8):1-13.

Sackenheim, R. 1993. Untersuchungen über Wirkungen von Wässerigen, mikrobiologisch aktiven Extracten aus kompostierten Substraten auf den Befall der Weinrebe (Vitis vinifera) mit *Plasmopora viticola, Uncinula necator, Botrytis cenerea* und *Pseudopezicula tracheiphila*. Ph.D. thesis. Rheinische Friedrich-Wilhelms Universität, Bonn, Germany. 157 p.

Schneider, R. W. 1985. Suppression of Fusarium yellows of celery with potassium chloride and nitrate. Phytopathology 75:40-48.

Schüler, C., J. Pikny, M. Nasir, and H. Vogtmann. 1993. Effects of composted organic kitchen and garden waste on *Mycosphaerella pinodes* (Berk, et Blox) Vestergr., Causal organism of foot rot on peas (Pisum sativum L.) Biolog. Agric. Hort. 9:353-360.

Steinmetz, J. and F. Schönbeck. 1994. Conifer bark as growth medium and carrier for *Trichoderma harzianum* and *Gliodadium roseum* to control *Pythium ultimum* on pea. J. Plant Dis. Prot. 101:200-211.

Tahvonen, R. 1982. The suppressiveness of Finnish light colored Sphagnum peat. J. Sci. Agric. Soc. Finl. 54:345-356.

Trillas -Gay, M. I., H. A. J. Hoitink, and L. V. Madden. 1986. Nature of suppression of Fusarium wilt of radish in a container medium amended with composted hardwood bark. Plant Disease: 70:1023-1027.

Wei, G., J. W. Kloepper, and Tuzun, S. 1991. Induction of systemic resistance of cucumber to Colletotrichum orbiculare by select strains of plant growth-promoting rhizobacteria. Phytopathology 81:1508-1512.

Weltzhien, H. C. 1992. Biocontrol of foliar fungal diseases with compost extracts, p. 430-450. In: Microbial Ecology of Leaves, J H Andrews and S Hirano (eds), Brock Springer Series in Contemporary Bioscience. BSBN 0387-97579-9.

Wolffhechel, H. 1988. The suppressiveness of Sphagnum peat to *Pythium* spp. Acta Hort. 221:217-222.

Workneh, F., A. H. C. Van Bruggen, L. E. Drinkwater, and C. Sherman. 1993. Variables associated with a reduction in corky root and *Phytophthora* root rot of tomatoes in organic compared to conventional farms. Phytopathology 83:581-589.

Wu, T., M. J. Boehm, L. V. Madden, and H. A. J. Hoitink. 1993. Sustained suppression of Pythium root rot: A funtion of microbial carrying capacity and bacterial species composition. Phytopathology 83:1406 (Abstr.).

Yohalem, D. S., R. F. Harris, and J. H. Andrews. 1994. Aqueous extracts of spent mushrooms substrate for foliar disease control. Compost Sci. Util. 2:67-83.

You, M. P. and Sivasithamparam. 1994. Hydrolysis of fluorescein diacetate in an avocado plantation mulch suppressive to *Phytophtora cinnamoni* and its relationship with certain biotic and abiotic factors. Soil Biol. Biochem. 26:1355-1361.

Zhang, W., W. A. Dick, and H. A. J. Hoitink. 1994. Compost induced systemic acquired resistance in cucumber to Pythium root rot and anthracnose. Phytopathology 84:1138.