Review on Compost as an Inducer of Disease Suppression in Plants Grown in Soilless Culture

Manuel Avilés[1] • Celia Borrero[2] • Mª Isabel Trillas[3*]

[1] Departamento de Ciencias Agroforestales, Escuela Técnica Superior de Ingeniería Agronómica. Universidad de Sevilla, Ctra Utrera Km 1, 41013 Seville, Spain
[2] Biocontrol Technologies, S.L. Parc Científic de Barcelona (Edificio Satélite) C/ Baldiri Reixac, 15-21. 08028, S.L. Barcelona, Spain
[3] Departament de Biologia Vegetal, Unitat Fisiologia Vegetal, Facultat de Biologia. Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain

Corresponding author: * **mtrillas@ub.edu**

ABSTRACT

The soil/substrate that supports plant roots and provides water and nutrients to plants is often considered a hostile environment that harbours plant pathogens. Moreover, the most common strategy used to control risk of disease from the soil is the eradication or minimization of soil pathogens regardless of the presence of other organisms. Consequently, the extensive use of physical/chemical biocides generates a soil/substrate microbiological vacuum which makes it more susceptible to reinfestation by pathogens, increases disease incidence and in some cases enhances fungal resistance. In Europe, legislation on plant protection products has been re-evaluated since 1991 (Directives 1991/414 and 2009/128), leading to a drastic reduction in the use of chemical compounds. A reduction in fungicides that effectively combat disease is achieved with the use of suppressive composts in pot plants. Suppressive composts similar to suppressive soils are examples of natural biological control of disease as the result or a more or less complex three-way interaction between microorganisms in the composts, plant pathogens, and plants. The roles of the physical properties and chemical composition of composts are also important in the suppressive effect, not only because they are responsible for the type and quantity of microorganisms established, but also because of their effects on pathogens, plant root health and leaf nutrient status. The two classic modes of action of microorganisms involved in the suppression of soil-borne plant pathogens (general and specific suppression) can be defined in composts. In specific suppression, only one or a few species are involved; while in contrast, a great diversity of microorganisms working together as a nutrient sink contributes to general suppression. A third mode of action is also induced by microorganisms in composts: systemic resistance, similar to challenge inoculation with a pathogen or beneficial organism.

CONTENTS

INTRODUCTION

Since the 1950s, several authors (Bunt 1988; Handreck and Black 1991) have shown the different requirements of plants growing in soil from those growing in a container (soilless culture), and the importance of the physical (air and water relationship) and physicochemical properties (nutrient availability, E.C., pH, CIC). In Europe, the leading substrate used, due to its ease of handing, homogeneous material and favourable agronomic properties, is based on *Sphagnum* peat mixed with inert products: mostly perlite and vermiculite in different ratios. The low biological activity of peat (Waksman and Purvis 1932; Borrero *et al*. 2004, 2009; Castaño *et al*. 2011) used alone or as the sole organic component in mixtures has been shown to be generally conducive to several plant diseases (Hoitink and Fahy 1986; Cotxarrera *et al*. 2002; Noble and Coventry 2005; Borrero *et al*. 2004, 2006; Trillas *et al*. 2006; Borrero *et al*. 2009; Bonanomi *et al*. 2010). Only certain Sphagnum peats (light-coloured and classified as H_2 on the von Post decomposi-

Invited Review

tion scale) have been shown to suppress root rot in poinsettia (Inbar *et al*. 1991; Hoitink and Boehm 1999). On the other hand, the environmental problems derived from peat extraction, as non-removable soil and as an important CO_2 sink, led to a search for other sources of substrates such as coir fiber and composts made from a wide range of local organic residues. Coir fiber is a renewable product obtained from the thick mesocarp or husk of the coconut fruit, and appears to be a suitable alternative to peat for formulation of substrates due to its physical and chemical properties (Abad *et al*. 2002). However, the microbial characteristics of coir fiber are similar to those of peat and so it is also conducive to plant diseases (Borrero *et al*. 2009).

The idea of using compost instead of peat comes from Hoitink *et al*. (1975). Those authors suggest using compost made from bark in order to control root rot in ornamentals (Hoitink *et al*. 1977). As part of overall control of soil-borne plant pathogens, this strategy is widely extended for pot plants in the USA, but not in Europe (Litterick *et al*. 2004). Not all composts suppress plant diseases and also the range of pathogens and level of suppression are variable (**Table 1**). For several years, for instance, our group has been working with the same type of composts and olive and grape marc compost has proved to consistently suppress *Fusarium oxysporum* f.sp. *dianthi* and f.sp. *lycopersici* to a high degree, and to suppress moderately *Rhizoctonia solani*. In contrast, cork compost consistently suppresses *R. solani* to a high degree and only moderately suppresses Fusarium wilt diseases (Borrero *et al*. 2004; Trillas *et al*. 2006; Borrero *et al*. 2009). Disease suppression by composts is mainly attributed to the microbial populations linked to the source of the organic matter in the composts. This fact has been pointed out from the very beginning by Hoitink and colleagues, who observed that the suppression phenomenon was eliminated or reduced by heating (60°C) the compost or irradiating it with gamma radiation of (Nelson and Hoitink 1983; Trillas *et al*. 1986). As with soils, the suppressive potential of composts can be restored by reintroducing a mixture of microorganisms, a specific microorganism, or amendments of suppressive soil/composts (Hoitink *et al*. 1997; Cotxarrera *et al*. 2002; Trillas *et al*. 2006; Weller *et al*. 2002; Dukare *et al*. 2011; Noble 2011).

The parallels between suppressive soils and suppressive substrates formulated with composts are many. Suppression by soils and composts has been described for the most important soil pathogens and it is not considered a rare phenomenon (Cook and Baker 1983; Tilston *et al*. 2002; Raviv 2009). Furthermore, mechanisms that confer suppressive potential to composts are phenomena that have been studied and can be classed as general or specific suppression, as proposed for soils.

PHYSICAL CHARACTERISTICS OF COMPOSTS THAT REDUCE PLANT DISEASES (HYDRAULIC CONDUCTIVITY AND IMPROVED AIR AND WATER AVAILABILITY)

The higher air capacity of composts compared with some soils and peats not only improves plant growth but also has a positive effect on the severity of rotting diseases of the plant roots. The use of pine bark compost alone or peat amended with pine bark compost reduced root rot in rhododendrons caused by *Phytophthora cinnamomi* grown in 15-cm-tall containers in commercial conditions. Phytophthora root rot in rhododendrons is most prevalent in growth media with an air capacity lower than 15% (Hoitink 1980; Hoitink and Kuter 1985). Tree bark composts usually have an air capacity of over 25%, a percolation rate of more than 2.5 cm/min and they suppress root rots. Amendments of sand to pine bark reduce the air capacity of the medium and destroy the suppressive effect. This suggests the importance of air capacity in those diseases where free water is important in the asexual multiplication of fungi (Spencer and Benson 1982; Hoitink and Fahy 1986). Nevertheless, the physical properties *per se* are not enough to explain the ob-

served suppression of Phytophthora root rot by pine bark composts, since pine bark compost mixed with sand and peat mixed with sand (media with very similar drainage properties) showed different disease incidence in lupin seedlings at three different inoculum levels of *P. cinnamomi*. Other factors might be important in the suppression, possibly including heat-stable chemical(s) (Sang *et al*. 2010).

Due to the fact that the water potential is important in diseases caused by oomycetes, as a control strategy, the possibility of producing adverse conditions for as long as possible during zoospore formation presents itself (Hoitink and Kutter 1986; Hardy and Sivasithamparam 1991b). A negative water potential inhibits zoospore release from the sporangia of several *Phytophthora* spp. (Duniway 1979; Wilcox and Mircetich 1985). In order to reduce the incidence of disease due to these root rot pathogens, the necessary components of the growth media should be chosen in the proper amounts together with the correct irrigation system and watering strategy (Filmer *et al*. 1986; Hoitink and Kuter 1986; Hoitink and Powell 1990; Ownley *et al*. 1990).

THE EFFECTS OF pH AND ELECTRIC CONDUCTIVITY IN INTERFERING NUTRIENTS AVAILABILITY TO THE PATHOGENS

Blaker and MacDonald (1983) showed that the majority of Phytophthora root rot diseases are inhibited by a low pH. The low pH reduced sporangium formation, zoospore release and motility, for this reason the low pH of *Shagnum* peats and pine bark compost might have beneficial secondary effects to plants. In this sense root rots caused by *P. cinnamomi* or *Phytophthora citricola* in *Aucuba japonica* was reduced in a pine bark compost with a pH of 4.4 – 4.5 even in waterlogging conditions (Spencer and Benson 1981). However the pH of pine bark increase after few weeks of crop, reaching values of about 6, making impractical this approach for disease control. Moreover, there are few plants with an optimal growth condition of low pH and for this reason it is difficult to use it in the control of the root rot diseases (Hoitink and Kuter 1985).

Nevertheless, high pH values justify the suppressive effect of certain composts made from agricultural and industrial wastes, compared with peat, on Fusarium wilt in tomato and carnation (Borrero *et al*. 2004, 2009). The pH of the plant growth medium, as a determinant of Fusarium wilt severity, is associated with the availability of macro- and micro-nutrients, important for growth, sporulation and the virulence of *F. oxysporum* (Jones *et al*. 1991). The pH reduces the availability of nutrients such P, Mg, Mn, Cu, Zn and Fe in organic growth media (Handreck and Black 1991), as the pathogen is more vulnerable than the host plant (Woltz and Jones 1981). Borrero *et al*. (2004) show a significant positive correlation between Fusarium wilts severity and final availability in the growth media of Cu on the one hand, and the final nutrient status in the plants of Fe, Cu and P on the other. These results are consistent with the importance of pH as a chemical environmental index for Fusarium wilt in tomato (Woltz and Jones 1981; Jones *et al*. 1991; Alabouvette *et al*. 1996; Cotxarrera *et al*. 2002).

The lignin/cellulose ratio of wastes affects the duration of the composting process and also further use and handling of fertilisation as container media (Hoitink and Fahy 1986). Pine bark, for instance, has a high lignin and low cellulose content, and frequently is not composted or is composted for only a short period before its use as a container medium. Under these circumstances, the pine bark does not immobilize large amounts of nitrogen, but it can be amended with essential micronutrients such as calcium and magnesium in order to improve the potential for growth of the majority of crops (Brown and Pokorny 1975; Cobb and Keever 1984). On the other hand, hardwood bark and sewage sludge, which experience important levels of decomposition during the composting process, do not require the addition of micronutrients. However, high levels of chloride, in the form of ions or as salt, can neutralize the suppressive

Table 1 Summary of the main composts studied, soil pathogens, main effects and reference groups studying composts as an inducer of plant disease suppression.

Compost materials	Disease suppression	Observed effects	References
Hard wood bark – sand compost	*Phytopthora cinnamomi* in lupine seedlings	Suppressiveness of compost was not related to drainage. Suppression was link to chemical and biological factors.	Hoitink *et al.* 1977
Hard wood bark and pine bark	*Phytophtora. Pythium. Thielaviopsis* root rots, *Rhizoctonia* damping off and *Fusarium* wilt	Hardwood bark suppressed all 5 diseases; however, pine bark suppressed *Phytopthora* and *Pythium* but not *Rhizoctonia*.	Hoitink 1980
Hardwood bark (HBC) and pine bark (PB)	*Phytophthora citricola* and *P. cinnamomi* in lupine	HBC was more effective than PB with and without added sand. Sand and lime amendments to PB reduced the suppressive capacity to values similar than peat.	Spencer and Benson 1981
Composted liquorice roots	*Pythium aphanidermatum*	This compost is proposed as substitute to peat substrate.	Hadar and Mandelbaum 1986
Hardwood bark	*Pythium ultimum* in cucumber plants	Hardwood bark centre pile (high temperature, >60ºC) was conducive and after 3-4 days at 25ºC became suppressive. Suppression was due to mesophilic organisms, great microbial activity and low levels of nutrients. Importance of microbiostasis.	Chen *et al.* 1988
Pine bark: sand (3: 1), pine bark : peat (3: 1) and peat: sand: soil (1: 1: 1)	*Phytophthora cinnamonmi* in rhododendron plants	Best control with pine bark : sand, intermediate with pine bark and peat and greatest disease with peat : sand : soil. Importance of the physical properties in the disease development.	Ownley *et al.* 1990
Leachates extracted from pine bark (NM) and *Eucalyptus* bark medium (CEB)	Five *Phytophthora* spp.	In non sterile CEB, sporangia of all five *Phytophthora* spp. were suppressed.	Hardy and Sivasithamparan 1991
Peat with different levels of decomposition and bark	*Pythium ultimum* in cucumber plants	Microbial activity predicted suppressiveness to this disease.	Inbar *et al.* 1991
Peats mixtures (peat : perlite, 1:1, v/v) with different levels of decomposition	*Pythium ultimum* root rot of cucumber and *Poinsetia*	Less decomposed light peat (H2) mixed (1: 1, v/v) with perlite) was more suppressive than the most decomposed dark (H4) peat. Suppression is biological in origin.	Boehm and Hoitink 1992
Organic mulch (oat straw + mature chicken manure) applied in soil	*Phytophthora cinnamomi* in avocado plantation mulch	Control was related with proportion of fungi and actinomycetes which were affected by temperature and moisture of the mulch.	You and Sivasithamparam 1995
Composts from a variety of feedstocks of different ages	*Pythium graminicola* damping off and root rot of *creeping bentgras*	The best compost was from brewery sludge, biosolids and some animal manures. The microbial properties are the major factors influencing suppression. Microbial activity is also related to suppression. Disease suppressiveness was reduced or eliminated in heated composts.	Craft and Nelson 1996
Composted municipal waste (CMW) amendment of citrus soils	*Phytophthora nicotianae* in citrus seedlings	Disease decreased increasing proportions of one CMW (20% v/v).	Widmer *et al.* 1998
Animal manures	*Phytophthora cinnamomi* in lupine and two cut-flower species	Chicken manure compost better control than cow, horse and sheep manure. Suppression was biological in nature and populations of fluorescent *Pseudomonas* were involved in the effect.	Aryantha *et al.* 2000
Peat moss amended with a range of 4 to 20% composted swine wastes at different weeks of maturity	*Pythium ultimum* and cucumber bioassay. Rhizoctonia pre-emergence damping-off of impatiens	Potting mixes amended at a rate of 20% with composts after 35 weeks or more of curing was more suppressive to Rhizoctonia and Pythium damping-off. Compost maturity and cellulose content have direct effects over *Rhizoctonia*.	Diab *et al.* 2003
Compost from viticulture (1), organic fraction differentiated (2) or undifferentiated (3) municipal bio waste, cow manure (4) and peat and differentiated municipal biowaste (1: 1, v/v)	*Pythium ultimum*, *Rhizoctonia solani* and *Sclerotinia minor*	All composts performed better than peats. The best composts against *P. ultimum* were: 2, 4 and 5. The best composts against *R. solani* were 1 and 4. The best compost against S. *minor* was 2.	Pane *et al.* 2011
Hardwood bark	*Rhizoctonia solani* on Celosia and radish plants	Importance of antagonisms and compost age (degree of decomposition) on disease suppression.	Nelson and Hoitink 1983; Nelson *et al.* 1983
Hardwood bark suppressive and conducive	*Rhizoctonia solani* in radish plants	High populations of *Trichoderma* spp. were isolated from suppressive compost while the most abundant taxa from conducive were *Penicillium* and *Geomyces*.	Kutter *et al.* 1983
Cattle manure compost and grape marc compost	*Rhizoctonia solani* and *Sclerotium rolfsii* in radish plants, pothos, beans and chickpeas	Importance of antagonistic microorganisms since gamma irradiation eliminated suppressive effect.	Gorodecki and Hadar 1990
Vegetable fruit and garden (VFG) waste	*Rhizoctonia solani* in cucumber plants	Long matured (5 – 7 months) 20% VFG amending peat perlite mixtures was more suppressive than short (1 month) matured compost. Origen and age of compost is important in this disease suppression.	Tuitert *et al.* 1998
Cork compost (CC) Olive marc compost (OC) Grape marc compost (GMC) Spent mushroom compost (SMC)	*Rhizoctonia solani* (Rhizoctonia damping-off)	Disease incidence reduction in CC (0.5 – 1year age) and in OC, GMC and SMC (1.5 – 3 year age). Effect of T34 in disease incidence reduction. Importance of nature of materials and age of compost.	Trillas *et al.* 2006

Table 1 (Cont.)

Compost materials	Disease suppression	Observed effects	References
Hardwood bark	*Fusarium oxysporum* f.sp. *conglutinans*	Suppressiveness was biotic, since heat destroyed the suppressive effect. A combination of *Trichoderma* and *Flavobacterium* restored suppressive heat effect, but not added singly.	Trillas *et al.* 1986
Organic fraction of the municipal solid wastes	*Fusarium oxysporum* f.sp. *lini* 2×10^4 cfu/g^{-1}, in flax plants	Soil moderately suppressive. Heat treated soil amended with compost at 10, 20 and 30% made the soil suppressive. Heat treated compost was as effective as untreated compost.	Serra-Wittling *et al.* 1996
Vegetable+ animal market wastes + sewage sludge and yard wastes	*Fusarium oxysporum* f.sp. *lycopersici* (Fusarium wilt of tomato) Two dose of pathogen 5×10^4 cfu/ml and 5×10^5 cfu/cm^3	Compost suppressiveness is compared with peat: vermiculite mix (1: 1), natural Fusarium Chateaurenard suppressive soil, sterilized natural soil amended with 10% compost, or with *Trichoderma* spp. or Fo47, BCAs.	Cotxarrera *et al.* 2002
Grape marc compost (GMC), Cork compost (CC).	*Fusarium oxysporum* f.sp. *lycopersici* (Fusarium wilt of tomato) 10^5 conidia/cm^3	GMC was the most suppressive, CC was intermediate and peat and vermiculite were conducive media. Heated GMC was still moderately suppressive. Importance of pH, β-glucosidase activity and microbial populations.	Borrero *et al.* 2004
Grape marc compost, cork compost, olive oil husk+ cotton gin trash + rice husk, Spent mushroom and peat.	*Fusarium oxysporum* f.sp. *dianthus* (Fusarium wilt of carnation) 6.5×10^4 conidia/ml	Compost data is compared to peat, coir fiber and vermiculite. Grape marc was the most effective. pH and β-glucosidase activity are confirmed as good predictive factors of suppressiveness.	Borrero *et al.* 2009
Grape marc and extracted olive press cake (GM + EPC), olive tree leaves and olive mill waste water (OL + OMW), and spent mushroom compost (SMC)	*Fusarium oxysporum* f.sp. *radicis lycopersici* in tomato plants	The three composts were highly suppressive and suppression is related to the presence of specific microorganism.	Ntougias *et al.* 2008; Kavroulakis *et al.* 2010
Pulp and paper mill	*Fusarium oxysporum* f.sp. *radicis lycopersici* in tomato plants	*Pythium oligandrum* enriched composts induced histological and cytological changes near the pathogen ingress.	Pharand *et al.* 2002
Compost from tomato plants and cow manure	*Fusarium oxysporum* f.sp. *melonis*	These composts were very suppressive to this disease and in this study it is evaluated the effect of storage (different temperature and moisture) on suppression. The suppressiveness is maintained but not improved.	Saadi *et al.* 2010
Mature biosolids compost (sewage sludge and yard waste)	*Sclerotinia rolfsii* in bean plants	Prolonged compost curing negates suppressiveness. Combination of microbial populations and the chemical environment were responsible for pathogen suppression.	Danon *et al.* 2007
Cork compost and light peat	Verticillium wilt of tomato	Cork compost was suppressive in comparison with peat. This compost had higher microbial activity and biomass. The two plant growth media differed in their carbon metabolic profiles.	Borrero *et al.* 2002
18 composts from different countries	*Verticillium dahliae* (eggplants), *Rhizoctonia solani* (cauliflower and pinus), *Phytophthora nicotianae* (tomato) *Phytophthora cinamomi* (lupin), *Cylindrocladium spathiphylli* (spathiphyllum); *Fusarium oxysporum* f.sp. *lini* (flax)	Among studied composts, the most consistent disease suppression (64 – 71%) was found against *F. oxysporum* and the most infrequent (4.7 – 6.5%) was against *P. cinnamomi* and *R. solani*.	Termorshuizen *et al.* 2006

effects of the compost against Phytophthora root rot, unless there are washed previous to use as growth media (Hoitink *et al*. 1993). In contrast, Pane *et al*. (2011) report a negative correlation between the damping-off induced by *Sclerotinia minor* and the salinity of compost-amended plant growth media. Phytotoxicity due to the manganese available in certain bark composts is also documented, which must be amended with calcium carbonate before use (Solbraa 1986).

NITROGEN SOURCES AND C/N RATIO IN DISEASE SUPPRESSION

High nitrogen levels and high ammonium to nitrate ratios increase Fusarium wilt incidence and severity (Woltz and Jones 1981; Jones *et al*. 1993, Borrero *et al*. 2012). In this sense, nitrate amendments may help to subdue Fusarium wilt diseases in ornamentals (carnation, chrysanthemum) and horticultural crops (cucumber, tomato, asparagus, pea, radish, etc.) (Huber and Thompson 2007). Plants grown in bark compost immobilize nitrogen; mainly as ammonium since nitrates contain the nitrogen available for plant growth. However, sewage sludge compost (with a low C/N ratio) might release ammonium and consequently increase Fusarium wilt, even under colonization by biological control

agents capable of inducing suppression under other conditions (Hoitink *et al*. 1987). Cotxarrera *et al*. (2002) used compost from vegetable and animal wastes, sewage sludge and yard wastes and it suppressed Fusarium wilt in tomato to a high degree. This compost had low available ammonia, which might be a direct effect of the high C/N ratio of other materials also included in the composts, beside the negative effect on the pathogen of high pH and the reduced availability of Fe, Cu and Zn.

Nitrogen fertility also affects the severity of diseases like Phytopthora dieback, a minor disease of rhododendrons, was related to different types of bark compost that differ in wood (cellulose) content and fertility levels. A positive correlation was established between nitrogen concentration in the juvenile tissue of rhododendrons and dieback susceptibility (Hoitink and Fahy 1986).

LEVELS OF MATURITY OF COMPOSTS AND REDUCTION OF PLANT DISEASES

Hadar and Mandelbaum (1986) found that the degree of decomposition of compost has a strong effect on the rate of disease suppression. They showed that immature compost could not suppress damping-off (*Pythium aphanidermatum*)

in cucumber seedlings, while mature compost could. Another example can be found in *R. solani* (a pathogen which is highly competitive as a saprophyte) and *Trichoderma* (an effective biocontrol agent of *R. solani*). Fresh undecomposed organic matter does not exert biological control over *R. solani* because both organisms grow as saprophytes and *R. solani* remains capable of causing disease. The synthesis of lytic enzymes involved in the parasitism of pathogens by *Trichoderma* is repressed in fresh organic matter due to the high glucose concentrations. In mature compost, where concentrations of nutrients such as glucose are low, the sclerotia of *R. solani* are killed by the parasite and biological control prevails (Hoitink *et al.* 2001). In this sense, the suppressive potential of composts with regard to Rhizoctonia damping-off increases with the maturity of the composts (Trillas *et al.* 2006). Saadi *et al.* (2010) demonstrate that compost suppressive potential against Fusarium wilt in melon can be maintained for at least one year under a wide range of storage conditions, without any loss.

On the other hand, when composts are excessively stabilized, they will not support microbiological activity, so disease suppression potential is lost (Widmer *et al.* 1998). Similarly, Tahvonen (1993) found lightly decomposed peats (H2-H3) to suppress soil-borne diseases. Darker and more decomposed peats are lower in microbial activity and are conducive to Pythium and Phytophthora root rots (Boehm and Hoitink 1992). Similarly, Danon *et al.* (2007) demonstrates that compost suppressive potential towards *S. rolfsii* is lost over curing time.

THE ROLE OF MICROBIAL COMMUNITIES IN THE SUPPRESSIVE POTENTIAL OF COMPOSTS

Composts are usually free from plant pathogens because, during the high temperatures reached during the thermophillic phase of the composting process, pathogens as well as beneficial microorganisms are either killed or inactivated (Noble and Roberts 2004). During composting, the beneficial microflora may survive in the outer most layers, at lower temperature. After temperatures fall below 40°C, mesophilic microorganisms colonize the semi-pasteurized compost, this is reinforced during the curing phase when there is also recolonization by surrounding antagonists/ beneficial microorganisms which develops the natural disease suppression capacity of the compost (Hoitink and Fahy 1986; Hoitink and Boehm 1999). The environment surrounding the composting plant, the system of composting used, and the composition of the raw material, all affect the species richness and therefore the degree and spectrum of the suppressive effect (Hoitink *et al.* 1993; Castaño *et al.* 2011).

The amendment of specific microorganisms to composts is sometimes necessary, since the potential of composts to suppress plant disease is a highly variable phenomenon and also because of the dilution of the suppressive effect due to the fact that most compost must be formulated in order to improve its physical and physicochemical properties. The inoculation of mature composts with efficient biological control agents improves the efficiency of those composts (Hoitink *et al.* 1997; Cotxarrera *et al.* 2002; Trillas *et al.* 2006; Dukare *et al.* 2011; Noble 2011).

The composition of the microorganisms in composts is affected by the chemistry of the materials from which the compost is prepared (Castaño *et al.* 2011). Composts with high lignocellulosic substances (tree barks) are mostly colonized by *Trichoderma* spp. In contrast, grape pomace, with low cellulosic substances and high sugars, becomes colonized by *Penicillium* spp. and *Aspergillus* spp. (Kutter *et al.* 1983; Gorodecki and Hadar 1990). Borrero *et al.* (2006) show that in composts that suppress tomato Fusarium wilt, peat conducive microbial communities use mostly sugars (carbohydrates and acids derived from carbohydrates) while the very suppressive grape marc compost and the moderately suppressive cork compost communities use mostly carboxylic acids, amino acids, amines, phenolic compounds and polymers. The microbial populations involved in composts that suppress Fusarium wilt in tomato were cellulolytic and oligotrophic actinomycetes, fungi and the ratios of cellulolytic actinomycetes/cellulolytic bacteria, oligotrophic bacteria/copiotrophic bacteria and oligotrophic actynomycetes/oligotrophic bacteria (Borrero *et al.* 2004). The microbial community that induced suppression of Pythium damping-off in cotton were populations of bacteria and actinobacteria capable of metabolizing fatty acids (linoleic acid) and thereby reducing the sporangium germination of *Pythium ultimum* (McKellar and Nelson 2003). Rhizospheric and root-associated/endophytic bacteria isolated from suppressive compost-based plant growth media showed protection of tomato plants against *F. oxysporum* f.sp. *radicis-lycopersici* (Kavroulakis *et al.* 2010).

Bonanomi *et al.* (2010) concluded that fluorescein diacetate hydrolysis, basal respiration, microbial biomass, total culturable bacteria, fluorescent pseudomonad counts and *Trichoderma* populations gave the best predictions of disease suppression. This suggests that both total microbial activity and that of specific groups are associated with disease suppressing effects. Various mechanisms are hypothesized to drive the phenomenon of disease suppression. Most of them are the result of interactions between the antagonistic microorganisms and the pathogens either by competition, antibiosis or hyperparasitism (Hoitink *et al.* 1993). However, in certain studies an additional biocontrol mechanism was also suggested, which is the activation in the plants of the induction of disease resistance in a way similar to/ different from the induction of SAR or ISR (Zhang *et al.* 1996, 1998; Yogev *et al.* 2010; Sang *et al.* 2010). According to Hoitink and Boehm (1999), the majority of composts naturally suppress Pythium and Phytophthora root rot, while only 20% of composts naturally suppress Rhizoctonia damping-off and very few (< 10%) induce resistance in plants.

MECHANISMS OF COMPOST SUPPRESSIVE POTENTIAL

There are two kinds of suppressive potential (general and specific) according to the spectrum of microorganisms involved in the phenomenon. In specific suppressive potential, suppression is related to the action of one or a few organisms in the substrate, while general suppressive potential is linked to abiotic and biotic substrate characteristics that are not related to a microorganism or group of antagonistic microorganisms in particular (Baker and Cook 1974; Cook and Baker 1983; Termorshuizen and Jeger 2008). The two types of suppressive potential are not mutually exclusive.

General suppressive potential

General suppressive potential, in the case of it being due to the biological characteristics of the substrate or soil, is directly related to total microbial activity in the medium at critical times for pathogenesis, particularly during germination of plant pathogen propagules and their growth during host rhizosphere colonization (Baker and Cook 1974; Cook and Baker 1983; Hoitink *et al.* 1991, 1993). General suppressive potential in composts is explained by the ability of these materials to sustain sufficient microbial activity over time, fed by slow degradation of complex carbon compounds, particularly polymeric carbohydrates (Baker and Cook 1974; Cook and Baker 1983; Hoitink *et al.* 1991, *et al.* 1993, 1996). Thus, the whole microbial community increases nutrient withdrawal, resulting in fungistasis of fungal pathogen propagules, or competition for colonization of rhizosphere zones which are rich in radical exudates.

Only specific suppressive potential can be transferred to another soil by adding a small amount of the suppressive soil. Moreover, general suppressive potential is reduced but not eliminated by soil fumigation, and usually remains after treatment at up to 70°C with moist heat. In contrast, specific suppression is often eliminated by pasteurization (Weller *et al.* 2002).

Fungistasis, due to nutritional competition in substrates,

involves many species involved as agents of biocontrol against fungal diseases (Lockwood 1988), especially those with rapid growing at high and low nutrient concentrations (facultative oligotrophs) (Sugimoto *et al*. 1990). Fungistasis intensity depends on physical and chemical soil properties, both determine its microbial activity (Qian and Johnson 1987; Mondal and Hyakumachi 1998; Alabouvette 1999). Hyphae are lysed in inhibited fungi (Lockwood 1988; Mandelbaum and Hadar 1990; Hadar and Mandelbaum 1992) but fungi resistance structures are not eradicated, only inhibited for germination. Fungistasis that is maintained over time debilitates the inhibited propagules (Lockwood and Filonow 1981; Filonow and Lockwood 1983), and reduces plant pathogen inocula (Lockwood 1977). Therefore, the intensity of fungistasis and general suppression of soil-borne plant-pathogenic fungal diseases are strongly linked (Termorshuizen and Jeger 2008). This intensity is directly proportional to the microbial population densities in substrates and their activity, which is lasts for as long as the specific density it is maintained (Chen *et al*. 1988a, 1988b; Mandelbaum and Hadar 1990; Inbar *et al*. 1991; Craft and Nelson 1996; Hoitink *et al*. 1996). Thus, microbial biomass and activity are greater in suppressive than in conducive substrates (Hoitink and Boehm 1999; Borrero *et al*. 2004, 2009). Several studies suggest that fungistasis can also be due to the presence of antifungal compounds or fungi inhibitors of a microbiological origin (Liebman and Epstein 1992, 1994). In this sense, Rousk *et al*. (2010) showed that selective inhibition of bacteria in certain soils was a prerequisite for the stimulation of fungal growth, even when carbon resources for fungi were not limiting.

Not all microorganisms produce antifungal compounds and the spectrum of these compounds varies depending on the species (de Boer *et al*. 2003). This explains the positive relationships between microbial diversity and general disease suppression reported for various pathogens (Nitta 1991; Garveba *et al*. 2006; Benitez *et al*. 2007; Postma *et al*. 2008). This observation may be due to synergistic interactions between microbial populations producing toxic secondary metabolites, or to greater collective efficiency in the removal of nutrients (de Boer *et al*. 2007; Garbeva *et al*. 2011). In the same way, Garbeva and de Boer (2009) indicate that interspecific rather than intraspecific competitive interactions triggered the production of broad-spectrum antibiotics with inhibitory effects on fungi. Thus, the production of inhibitory secondary metabolites during interspecific interactions of known antibiotic-producing bacteria can also be enhanced (Dubuis and Haas 2007; Dubuis *et al*. 2007; Mazurier *et al*. 2009). There are also non-microbial inhibiting compounds that can affect pathogens, such as high ammonia concentration from N-rich organic matter decomposition (Lazarovits *et al*. 2005).

Lockwood (1977) argued that the most likely explanation for fungistasis is a combination of the nutrient-deficiency and inhibition theories. However, nutrient availability may reduce fungi sensitivity to fungistatic volatiles and toxic secondary metabolites. So, a combination of both the nutrient-deficiency and inhibition theory may also offer the best explanation for fungistasis (Garbeva *et al*. 2011).

Increased fungistasis can be the result of changing agronomic management, which can alter the soil microbial community diversity (de Boer *et al*. 2003). Measures to bring about strengthened fungistasis should stimulate the saprotrophic community, but not the pathogenic community. This usually happens in compost substrates where, in the presence of microbial competition, nutrients are not available for most plant pathogens (Weller *et al*. 2002; Noble and Coventry 2005; Termorshuizen *et al*. 2006; Bonanomi *et al*. 2010). Another approach is to manage root exudation rate through plant breeding (Ryan *et al*. 2009).

Each pathogen is usually preferably associated with a type of suppressive potential. *Pythium* spp. and *Phytophthora* spp. have propagules with small amounts of nutrients and depend on exogenous carbon sources for germination to infect host plants. They are described as highly sensitive to microbial nutrient competition and antibiosis (fungistasis) and related to general suppression (Chen *et al*. 1988a; Mandelbaum and Hadar 1990; Hardy and Sivasithamparam 1991a, 1991b; You and Sivasithamparam 1995; Craft and Nelson 1996; Hoitink *et al*. 1996; Hoitink and Boehm 1999; Aryantha *et al*. 2000).

Specific suppressive potential

In specific suppressive potential, one or more groups of organisms are responsible for biocontrol, but interactions with other members of the rhizosphere community can significantly modulate the degree of suppressive potential observed. Thus, biotic and abiotic variables can influence the structure and activity of microbial populations including pathogens and their antagonists (Weller *et al*. 2002). Specific suppressive potential in composts depends on the microorganisms that operate as biological control agents being installed after the thermophilic phase. Greater consistency in specific suppressive potential expression is possible if suitable biocontrol agents are introduced during the composting process or during cultivation, thus ensuring their presence (Hoitink and Boehm 1999). In this vein, it has been suggested that a combination of general and specific suppressive potential is active against *P. ultimum* in substrates formulated with composts, but specific suppressive potential can be guaranteed only when the compost is colonized by a specific antagonist during composting (Hoitink *et al*. 2001). Several studies have examined the relationship between the soil microbial community composition and the suppression of diseases caused by specific soil-borne pathogens (Mazzola and Gu 2002; Borneman and Becker 2007). Representatives of a range of bacterial (*Pseudomonas*, *Burkholderia*, *Bacillus*, *Serratia*, *Streptomyces*) and fungal (*Trichoderma*, *Penicillium*, *Gliocladium*, *Sporidesmium*, non-pathogenic *Fusarium* spp.) genera have been identified as antagonists of one or more soil-borne plant pathogens (Rothrock and Gottlieb 1984; Berg *et al*. 2002; Cotxarrera *et al*. 2002; Garbeva *et al*. 2004). Specific disease suppression has also been linked to the production of antibiotics that act against the pathogen or the overlap of niches between antagonists and pathogens with respect to similar substrate preferences or micro-habitats (e.g., infection sites on roots) (Raaijmakers and Weller 1998; Thomashow *et al*. 2000; Mazurier *et al*. 2009; Raaijmakers *et al*. 2010). Specific antagonistic interactions are not considered as a component of fungistasis. However, a number of recent papers have indicated that there may be differences between members of the soil microbial community with respect to their contribution to fungistasis and general soil suppression (Garbeva *et al*. 2011).

A combination of biological control agents can increase levels of suppressive potential in substrates, adding different mechanisms of suppressive potential (Pharand *et al*. 2002; de Boer *et al*. 2003). Mechanisms of suppression vary depending on the compost and the pathogen, and it is not always clear which factors are more relevant.

The biological control mechanism for plant pathogens such as *R. solani*, *Sclerotium rolfsii* and *Sclerotinia sclerotiorum* is totally different from that for Oomycetes (Hoitink *et al*. 1991; Rabeendran *et al*. 2006). The latter species produce large propagules known as sclerotia that are not nutrient dependent and therefore, less vulnerable to fungistasis (Lockwood 1988).

Substrates formulated with composted bark that suppresses *R. solani* are usually associated with the presence of a small group of microorganisms (fungi or bacteria). Important fungus genera in this sense, due to their abundance and effectiveness, are *Trichoderma* spp. and *Gliocladium virens* (Kuter *et al*. 1983; Nelson *et al*. 1983; Hoitink and Boehm 1999; Cotxarrera *et al*. 2002). Their mechanisms of action can be mycoparasitism, antibiosis, or the competition and promotion of plant growth and development (Ghisalberti and Sivasithamparam 1991). Some bacteria cited as biocontrol agents are strains of *Flavobacterium balustinum* and

Xanthomonas maltophilia (Hoitink and Fahy 1986). In some mature composts, the capacity to suppress *R. solani* is related to the presence of cellulolytic actinomycetes, oligotrophic microorganisms and fluorescent *Pseudomonas*, amongst others (Tuitert *et al.* 1998; Diab and Benson 2003), although their mechanisms of action are not well established. The natural suppressive potential of composts to *R. solani* is also conditioned by their maturity level (Trillas *et al.* 2006). This is partly explained by the fact that *R. solani* is highly competitive as a saprophyte in plant debris, utilizing cellulose and colonizing fresh bark compost but not barks with a low cellulose content (Hoitink *et al.* 1991). Thus, older composts, with a lower cellulose content, are more effective in controlling this disease.

During organic matter decomposition in soil, the ecosystem is subjected to oligotrophization and the relationship between oligotrophic organisms (K strategists) and copiotrophic (r strategists) changes during microbial succession (Van Bruggen and Semenov 1999). The range of this relationship has been associated with general suppressive potential depending on the pathogen and its position on the scale of r strategists (*P. ultimum*) to K strategists (*R. solani*) (Van Bruggen and Semenov 2000). The succession during decomposition of organic matter in compost is similar. Thus, Tuitert *et al.* (1998) found larger populations of oligotrophic populations in mature substrates that suppress *R. solani* than in less mature and conductive composts.

The overwinter structures of *F. oxysporum* and *Verticillium dahliae* (chlamydospores and microsclerotia, respectively) are highly persistent and become active only by the influence of root exudates (Ocamb and Kommedahl 1994). *F. oxysporum*, through the resistance of its chamydospores, is sensitive to competition (Alabouvette *et al.* 1986; Serra-Wittling *et al.* 1996; Alabouvette *et al.* 2001; Borrero *et al.* 2004, 2006; Termorshuizen *et al.* 2006; Borrero *et al.* 2009) and also to the activity of specific microorganisms (Alabouvette *et al.* 1996; Cotxarrera *et al.* 2002). The natural Verticillium suppressive potential in cork compost is due to the

high activity and microbial biomass (Borrero *et al.* 2002). However, different growth media amended with compost show a negative correlation between respiration and suppression to disease caused by this pathogen (Termorshuizen *et al.* 2006) showing that microbial activity was not the key factor. At the same time, fluorescent *Pseudomonas* and *Talaromyces flavus* are described as biological control agents that reduce Verticillium disease (Engelkes *et al.* 1997; Mercado-Blanco *et al.* 2004). For these reasons, natural suppressive soils and substrates have both general and specific suppressive potential (Weller *et al.* 2002) for these two pathogens; however, the mechanisms that drive suppression to *V. dahliae* are not clear or well studied.

INDUCTION OF PLANT DISEASE RESISTANCE RESPONSE BY MICROORGANISMS IN COMPOSTS

Enhancement of basal resistance levels is a common reaction of plants to biotic and abiotic stresses and is commonly referred to as induced resistance. The classic example is that of systemic acquired resistance (SAR) in which an initial attack by a pathogen triggers local defence responses and also the generation of a systemic signal throughout the plant (Van Loon *et al.* 1998; Durrant and Dong 2004). Upon reception of this signal, distal plant parts become more resistant to subsequent attack by a broad range of pathogens. SAR depends on the production of, and responsiveness to, salicylic acid, and it is associated with the induction of novel PR proteins (pathogenesis-related proteins) (Delaney *et al.* 1994; Mauch-Mani and Metraux 1998; Van Loon *et al.* 2006). Beneficial organisms such as mycorrhizal fungi, plant growth promoting rhizobacteria and biological control agents (different strains of *Trichoderma* spp.) can induce two different plant response patterns: the standard ISR (induced systemic resistance) where no direct effects of biological control agent colonization are observed and later, challenges from the pathogen are counteracted by enhanced

Table 2 Summary of the main composts studied, aerial pathogens, main effects and reference groups studying composts as an inducer of plant disease suppression.

Compost materials	Disease suppression	Observed effects	References
Spruce and Pine Bark	*Colletotrichum orbiculare* *Pythium ultimum* and *Pythium aphanidermatum*	Reduced root rot severity was observed in split roots plants produced in compost than those produced in peat. Anthracnose was less severe on plants grown in compost. Increased peroxidase activity and enhanced peroxidase isozyme levels in plants produced in compost over that in peat.	Zhang *et al.* 1996
Pine bark fortified with *Trichoderma hamatum* 382 and *Pantoea* agglomerans E278As, and water extract with tap water (1:1 v/v)	*Colletotrichum orbiculare* (cucumber plants) and *Pseudomonas maculicola* (*Arabidopsis*)	The effect of compost, compost water extract and *T. hamatum* but not *P. agglomerans* induced SAR. The effect on peroxidase activity, β-1,3-glucanase and GUS was higher after the pathogens infect plants. The induced SAR might be different from the induced by pathogens or salicylic acid.	Zhang *et al.* 1998
79 different batches of mature composts prepared from six types of wastes	*Xanthomonas campestris pv. armoraciae* 704b in radish plants	Only 1 of 79 composts suppressed bacterial leaf spot. ISR is a rare phenomena and the frequency increased with the use of fortified composts (*Trichoderma* T382).	Krause *et al.* 2003
9 composts prepared from olive oil, grape marc (GM) and spent mushroom (SMC) mixed with peat at different ratios	*Septoria lycopersici* in tomato plants	Only three composts mixed 1:3 (compost: peat, v/v) conferred ISR. SMC, GM and olive trees leafs + olive mill wastewaters.	Ntougias *et al.* 2003
Grape marc + extracted olive press cake	*Septoria lycopersici* in tomato plants	Induction of plant resistance and PR gene expression was done with tomato plants grown in this composts and also using sterilized compost extract.	Kavroulakis *et al.* 2005
Grape marc , olive marc + gin trash, cork, spent mushrooms, municipal organic and yard wastes	*Botrytis cinerea* in cucumber plants	Importance of the nutrient status (Mo, Ca, Si), electrical conductivity and microbial activity.	Segarra *et al.* 2007
Tomato-plant residues mixed with a coarse fraction of separated cattle manure	*Fusarium oxysporum* f.sp. *melonis*, *Botrytis cinerea* in cucumber and melon plants	Side-grafter split root system is a good system to study induced resistance of soil pathogens. Induction of plant resistance could be an additional mechanism involved in natural suppression of composts.	Yogev *et al.* 2010
Compost water extract	*Colletotrichum coccodes* in pepper plants and *C. orbiculare* in cucumber plants	Enhanced PR gene expression, defence-related enzyme production and hydrogen peroxide generation after pathogen infection.	Sang *et al.* 2011

defences (priming); and the hybrid pattern, where transitory direct effects of biological control agent colonization are observed and later challenges from the pathogen are counteracted mainly by the priming of defence mechanisms. ISR requires responsiveness to jasmonic acid and ethylene (Pieterse *et al*. 1996, 1998; Van Loon 2000; Van Loon *et al*. 2006; Segarra *et al*. 2009; Trillas and Segarra 2009).

In composts, in addition to the well-documented effects of microbial populations against several soil-borne diseases, induction of resistance has also been reported as an additional biocontrol mechanism against both foliar and root diseases (Zhang *et al*. 1996, 1998; Kavroulakis *et al*. 2005; Ntougias *et al*. 2008) (**Table 2**). Reduction in disease severity was demonstrated against *Septoria lycopersici* in tomato (Kavroulakis *et al*. 2005), bacterial leaf spot in radish caused by *Xanthomonas camperstris* pv. *armoraciae* (Krause *et al*. 2003), anthracnose in cucumber caused by *Colletotrichum orbiculare* (Zhang *et al*. 1996) and *Botrytis cinerea* in cucumber and melon (Segarra *et al*. 2007; Yogev *et al*. 2010). Moreover compost water extract root treatment induce systemic resistance to anthracnose caused by *C. orbiculare* in cucumber and *C. coccodes* in pepper (Sang and Kim 2011).

The way to study the involvement of specific microorganism or the whole microbial biomass of composts in the induction of plant defences is by means of temporal and spatial separation. The latter is very easy in the case of studies of foliar diseases, but for soil-borne disease the method used is a split-root system where the two halves of the roots are grown in different media. Disease suppression is compared for those plants where one half of the root is inoculated with peat (conducive substrate) and the other part with composts (putative inducer substrate) compared with the case that both parts of the roots where grown in peat.

In side-grafted melon plants (based on the split-root system) Yogev *et al*. (2010) demonstrated the involvement of plant-induced resistance against *F. oxysporum* f.sp. *melonis* and also against *B. cinerea* by compost made from tomato plant residues and cattle manure, in detached leaves of cucumber and melon and in intact plants.

However, the improvement in plant nutrition might also be responsible for the observed disease reduction in leaf pathogens, in this sense Segarra el al. (2007) found that the reduction of *B. cinerea* severity/incidence in cucumber plants grown in composts compared to those grown in peats was correlated to the supply of specific elements (Ca, Mo and Si), a certain degree of salt stress and high microbial activity. The question of whether compost microbial populations induce SAR via a signalling pathway that involves jasmonic or salicylic acid is still open.

RECOMMENDATIONS TO EVALUATE THE SUPPRESSIVE EFFECT OF COMPOSTS

Bioassays are needed to evaluate the suppressive capacity of materials. In studies of natural disease suppression by compost, the following aspects should be considered:
i) All assays should include a control plant-growth medium that is different from the compost (soil, sand, peat, coir fiber, etc). When the control medium has fewer nutrients than the compost, and sub-optimal nutrient availability, the effect of this lack of nutrients cannot be separated from the natural suppressiveness. Nutritive compensation is recommended, even if the plants are fertirrigated with complete nutrient solution during the study. It is generally accepted that the nutritive status of the plant affects the expression of disease.
ii) Several authors have speculated about the biological and/or physicochemical nature of suppression phenomena by comparing composts that had been disinfected (by autoclave, heat dry treatment, etc.) with composts that had not. It should be borne in mind that after disinfection the compost may be rapidly re-colonized by allochthonous and autochthonous thermotolerant microorganisms (Hadar and Mandelbaum 1992).

iii) In many microcosm studies the quantities of amendment applied to the soil are too high. Such amounts in the field are economically unfeasible. In any case, it should be pointed out whether the conclusions are applicable to field or pot crops.
iv) In most studies, the suppressive assays are repeated at least two or three times. In that case, a preliminary analysis should be performed to check whether the interaction (treatment × repetition) is significant. When the interaction is significant there is a large experimental error (treatments behave differently in the different assays), and the results should not be published. When there is no significant interaction, data from different studies should be pooled and an ANOVA should be performed.

Obviously, we should not accept studies in which the suppressive effect of a compost is measured by the growth inhibition of the pathogen in Petri dishes induced by adding composts to an agarized medium. The same applies to the evaluation of microbial isolates from composts by the inhibition of the pathogen in Petri dishes. Neither approach is realistic without the interaction of the plants, and other factors, with a rizospheric environment.

CONCLUDING REMARKS

In all three expressions of suppressivity, (general, specific and induction of resistance) the nature and composition of the organic matrix is determinant in selecting and maintaining the microbial community involved.

Suppression cannot be achieved for all composts produced and the factors predicted to suppress disease are different for each pathogen, and only partially identified. One important difference between suppressive soils and suppressive composts is that composts can be produced in high volumes from very different sources of waste materials whereas soils are not a renewable resource.

ACKNOWLEDGEMENTS

REFERENCES

Abad M, Noguera P, Puchades R, Maquieira A, Noguera V (2002) Physicochemical and chemical properties of some coconut coir dust for use as a peat substitute for containerrised ornamental plants. *Bioresource Technology* **82**, 241-245

Alabouvette C, Couteaudier Y, Lemanceau P (1986) Nature of intrageneric competition between pathogenic and non-pathogenic *Fusarium* in a wilt suppressive soil. In: Swinburne TR (Ed) *Iron Siderophores and Plant Diseases*, Plenum Publishing Corporation, Nueva York, pp 165-178

Alabouvette C, Hoeper H, Lemanceau P, Steinberg C (1996) Soil suppressiveness to diseases induced by soilborne plant pathogens. In: Stotzky G, Bollag JM (Eds) *Soil Biochemistry* (Vol 9), Marcel Dekker, Inc, New York, pp 371-413

Alabouvette C (1999) Fusarium wilt suppressive soils: An example of disease-suppressive soils. *Australasian Plant Pathology* **28**, 57-64

Alabouvette C, Edel V, Lemanceau, P, Olivain C, Recorbet G, Steinberg C (2001) Diversity and interactions among strains of *Fusarium oxysporum*: application to biological control. In: Jeger JM, Spence NJ (Eds) *Biotic Interactions in Plant-Pathogen Associations*, CAB International, London, pp 131-157

Aryantha IP, Cross R, Guest DI (2000) Suppression of *Phytophthora cinnamomi* in potting mixes amended with uncomposted and composted animal manures. *Phytopathology* **90**, 775-782

Baker KF, Cook RJ (1974) *Biological Control of Plant Pathogens*, American Phytopathological Society, San Francisco, 433 pp

Benitez MS, Tustas FB, Rotenberg D, Kleinhenz MD, Cardina J, Stinner D, Miller SA, Gardener BBM (2007) Multiple statistical approaches of community fingerprint data reveal bacterial populations associated with general disease suppression arising from the application of different organic field management strategies. *Soil Biology and Biochemistry* **39**, 2289-2301

Berg G, Roskot N, Steidle A, Eberl L, Zock A, Smalla K (2002) Plant-dependent genotypic and phenotypic diversity of antagonistic rhizobacteria isolated from different *Verticillium* host plants. *Applied and Environmental Microbiol-*

ogy **68**, 3328-3338

Blaker NS, McDonald JD (1983) Influence of container medium pH on sporangium formation, zoospore release, and infection of rhododendron by *Phytophthora cinnamomi*. *Plant Disease* **67**, 259-263

Boehm MJ, Hoitink HAJ (1992) Sustenance of microbial activity and severity of Pythium root rot of *Poinsettia*. *Phytopathology* **82**, 259-264

Bonanomi G, Antignani V, Capodilupo M, Scala F (2010) Identifying the characteristics of organic soil amendments that suppress soilborne plant diseases. *Soil Biology and Biochemistry* **42**, 136-144

Borneman J, Becker JO (2007) Identifying microorganisms involved in specific pathogen suppression in soil. *Annual Review of Phytopathology* **45**, 153-172

Borrero C, Castillo C, Ordovás J, Tello JC, Avilés M (2002) Composted cork as suppressive substrate to Verticillium wilt of tomato. In: Michel Jr. FC, Rynk RF, Hoitink HAJ (Eds) *Proceedings of 2002 International Symposium Composting and Compost Utilization*, Columbus, Ohio, 6-8 May 2002, pp 1342-1352

Borrero C, Trillas MI, Ordovás J, Tello J C, Avilés M (2004) Predictive factors for the suppression of Fusarium wilt of tomato in plant growth media. *Phytopathology* **94**, 1094-1101

Borrero C, Ordovás J, Trillas MI, Avilés M (2006) Tomato Fusarium wilt suppressiveness. The relationship between the organic plant growth media and their microbial communities as characterised by Biolog®. *Soil Biology and Biochemistry* **38**, 1631-1637

Borrero C, Trillas I, Avilés M (2009) Carnation Fusarium wilt supression in four composts. *European Journal of Plant Pathology* **123**, 425-433

Borrero C, Trillas MI, Delgado A, Avilés M (2012) Effect of ammonium/nitrate ratio in nutrient solution on control of tomato Fusarium wilt by *Trichoderma asperellum* T34. *Plant Pathology* in press

Brown EF, Pokorny FA (1975) Physical and chemical properties of media composed of milled pine bark and sand. *Journal of the American Society for Horticultural Science* **100**, 119-121

Bunt AC (1988) *Media and Mixes for Container-Grown Plants*, Unwin Hyman, London, 309 pp

Castaño R, Borrero C, Avilés M (2011) Organic matter fractions by SP-MAS ^{13}C NMR and microbial communities involved in the suppression of Fusarium wilt in organic growth media. *Biological Control* **58**, 286-293

Chen W, Hoitink HAJ, Madden LV (1988a) Microbial activity and biomass in container media for predicting suppressiveness to damping-off caused by *Pythium ultimum*. *Phytopathology* **78**, 1447-1450

Chen W, Hoitink HAJ, Schmitthenner AF, Tuovinen OH (1988b) The role of microbial activity in suppression of damping-off caused by *Pythium ultimum*. *Phytopathology* **78**, 314-322

Cobb GS, Keever GJ (1984) Effects of supplemental N on plant growth in fresh and aged pine bark. *HortScience* **19**, 127-129

Cook RJ, Baker KF (1983) *The Nature and Practice of Biological Control of Plant Pathogens* (3rd Edn), American Phytopathological Society Press, St. Paul, Minnesota, 539 pp

Cotxarrera L, Trillas-Gay MI, Steinberg C, Alabouvette C (2002) Use of sewage sludge compost and *Trichoderma asperellum* isolates to suppress Fusarium wilt of tomato. *Soil Biology and Biochemistry* **34**, 467-476

Craft CM, Nelson EB (1996) Microbial properties of composts that suppress damping-off and root rot of creeping bentgrass caused by *Pythium graminicola*. *Applied and Environmental Microbiology* **62**, 1550-1557

Danon M, Zmora-Nahum S, Chen Y, Hadar Y (2007) Prolonged compost curing reduces suppression of *Sclerotium rolfsii*. *Soil Biology and Biochemistry* **39**, 1936-1946

de Boer W, Verheggen P, Klein Gunnewiek PJA, Kowalchuk GA, van Veen JA (2003) Microbial community composition affects soil fungistasis. *Applied and Environmental Microbiology* **69**, 835-844

de Boer W, Wagenaar AM, Klein Gunnewiek PJA, van Veen JA (2007) *In vitro* suppression of fungi caused by combinations of apparently non-antagonistic soil bacteria. *FEMS Microbiology Ecology* **59**, 177-185

Delaney TP, Uknes S, Vernooij B, Friedrich L, Weymann K, Negrotto D, Gaffney T, Gur-Rella M, Kessmann H, Ward E, Ryals J (1994) A central role of salicylic acid in plant disease resistance. *Science* **266**, 1247-1250

Diab HG, Hu S, Benson DM (2003) Suppression of *Rhizoctonia solani* on impatiens by enhanced microbial activity in composted swine waste-amended potting mixes. *Phytopathology* **93**, 1115-1123

Dubuis C, Haas D (2007) Cross-species GacA-controlled induction of antibiosis in Pseudomonas. *Applied and Environmental Microbiology* **73**, 650-654

Dubuis C, Keel C, Haas D (2007) Dialogues of root-colonizing biocontrol pseudomonads. *European Journal of Plant Pathology* **119**, 311-328

Dukare AS, Prasanna R, Dubey SC, Nain L, Chaudhary V, Singh R, Saxena AK (2011) Evaluating novel microbe amended composts as biocontrol agents in tomato *Crop Protection* **30**, 436-442

Duniway JM (1979) Water relations of water molds. *Annual Review of Phytopathology* **17**, 431-460

Durrant WE, Dong X (2004) Systemic acquired resistance. *Annual Review of Phytopathology* **42**, 185-209

Engelkes CA, Nuclo RL, Fravel DR (1997) Effect of carbon, nitrogen, and C:N ratio on growth, sporulation, and biocontrol eficacy of *Talaromyces flavus*. *Phytopathology* **87**, 500-505

Filmer CLR, McDonald JD, Paul JL, Leiser AT (1986) Influence of air-filled porosity of container media on *Phytophthora* root rot of toyon. *HortScience* **21**, 1010-1011

Filonow AB, Lockwood JL (1983) Loss of nutrient-independence for germination by fungal propagules incubated on soils or on a model system imposing diffusive stress. *Soil Biology and Biochemistry* **15**, 567-573

Garbeva P, van Veen JA, van Elsas JD (2004) Assessment of the diversity, and antagonism towards *Rhizoctonia solani* AG3, of Pseudomonas species in soil from different agricultural regimes. *FEMS Microbiology Ecology* **47**, 51-64

Garbeva P, Postma J, van Veen JA, van Elsas JD (2006) Effect of aboveground plant species on soil microbial community structure and its impact on suppression of *Rhizoctonia solani* AG3. *Environmental Microbiology* **8**, 233-246

Garbeva P, de Boer W (2009) Inter-specific interactions between carbon-limited soil bacteria affect behavior and gene expression. *Microbial Ecology* **58**, 36-46

Garbeva P, Hol WHG, Termorshuizen AJ, Kowalchuk GA, de Boer W (2011) Fungistasis and soil biostasis – A new synthesis. *Soil Biology and Biochemistry* **43**, 469-477

Ghisalberti EL, Sivasithamparan K (1991) Antifungal antibiotics produced by *Trichoderma* spp. *Soil Biology and Biochemistry* **23**, 1011-1022

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

Hadar Y, Mandelbaum R (1986) Suppression of *Pythium aphanidermatum* damping off in container media containing composted liquorice roots. *Crop Protection* **5**, 88-92

Hadar Y, Mandelbaum R (1992) Suppressive compost for biocontrol of soilborne plant pathogens. *Phytoparasitica* **20 (Suppl)**, 113-116

Handreck K, Black N (1991) *Growing Media for Ornamental Plants and Turf*, New South Wales University Press, Kensington, Australia, 401 pp

Hardy GESJ, Sivasithamparan K (1991a) Effect of sterile and non-sterile leachates extracted from composted *Eucalyptus* bark and pine-bark container media on *Phytophthora* spp. *Soil Biology and Biochemistry* **23**, 25-30

Hardy GESJ, Sivasithamparan K (1991b) Sporangial responses do not reflect microbial suppression of *Phytophthora drechsleri* in composted *Eucalyptus* bark mix. *Soil Biology and Biochemistry* **23**, 757-765

Hoitink HAJ, Schmitthener AF, Herr LJ (1975) Composted bark for control of root rot in ornamentals. *Ohio Report* **60**, 25-26

Hoitink HAJ, VanDoren Jr. DM, Schmitthenner AF (1977) Suppression of *Phytophthora cinnamomi* in a composted hardwood bark potting medium. *Phytopathology* **67**, 561-565

Hoitink HAJ (1980) Composted bark a lightweight growth medium with fungicidal properties. *Plant Disease* **64**, 142-147

Hoitink HAJ, Kuter GA (1985) Effect of composts in container media on diseases caused by soilborne plant pathogens. *Acta Horticulturae* **172**, 191-196

Hoitink HAJ, Fahy PC (1986) Basis for the control of soilborne plant pathogens with composts. *Annual Review of Phytopathology* **24**, 93-114

Hoitink HAJ, Kuter GA (1986) Effects of composts in growth media on soilborne pathogens with composts. *Annual Review of Phytopathology* **24**, 93-114

Hoitink HAJ, Daughtrey M, Tayama HK (1987) Control of cyclamen Fusarium wilt. A preliminary report. *Ohio Florist's Association Bulletin* **693**, 1-3

Hoitink HAJ, Powell CC (1990) Fighting *Phytophthora* – a guide to combating *Phytophthora* root rot and dieback in ericaceous crops. *American Nurseryman* **171**, 67-73

Hoitink HAJ, Inbar Y, Boehm MJ (1991) Status of compost-amended potting mixes naturally suppressive to soilborne diseases of floricultural crops. *Plant Disease* **75**, 869-873

Hoitink HAJ, Boehm MJ, Hadar Y (1993) Mechanisms of suppression of soilbome plant pathogens in compost-amended substrates. In: Hoitink HAJ, Keener HM (Eds) *Science and Engineering of Composting: Design, Environmental, Microbiological and Utilization Aspects*, Renaissance Publications, Worthington, Ohio, pp 601-621

Hoitink HAJ, Madden LV, Boehm MJ (1996) Relationships among organic matter decomposition level, microbial species diversity and soilborne disease severity. In: Hall R (Ed) *Principles and Practice of Managing Soilborne Plant Pathogens*, American Phytopathological Society Press, St. Paul, Minnesota, pp 237-249

Hoitink HAJ, Stone AG, Han DY (1997) Suppression of plant diseases by composts. *HortScience* **32**, 184-187

Hoitink HAJ, Boehm MJ (1999) Biocontrol within the context of soil microbial communities: A substrate-dependent phenomenon. *Annual Review of Phytopathology* **37**, 427-446

Hoitink HAJ, Krause MS, Han DY (2001) Spectrum and mechanisms of plant disease control with composts. In: Stoffela PJ, Kahn BA (Eds) *Compost, Utilization in Horticultural Cropping Systems*, Lewis, Boca Raton, Florida, pp 263-273

Huber DM, Thompson IA (2007) Nitrogen and plant disease. In: Datnoff LE, Elmer WH, Huber DM (Eds) *Mineral Nutrition and Plant Disease*, The American Phytopathological Society, St. Paul, Minnesota, pp 31-44

Inbar Y, Boehm MJ, Hoitink HAJ (1991) Hydrolysis of fluorescein diacetate

in sphagnum peat container media for predicting suppressiveness to damping-off caused by *Pythium ultimum*. *Soil Biology and Biochemistry* **23**, 479-483

Jones JB, Jones JP, Stall RE, Zitter TA (1991) *Compendium of Tomato Diseases*, The American Phytopathological Society, St. Paul, Minnesota, 100 pp

Jones JP, Engelhard AW, Woltz SS (1993) Management of Fusarium wilt of vegetables and ornamentals by macro-and microelement nutrition. In: Engelhard WA (Ed) *Soilborne Plant Pathogens: Management of Diseases with Macro-and Microelements*, American Phytopathological Society Press, St Paul, Minnesota, pp 18-32

Kavroulakis N, Ehaliotis C, Ntougias S, Zervakis GI, Papadopoulou KK (2005) Local and systemic resistance against fungal pathogens of tomato plants elicited by a compost derived from agricultural residues. *Physiological and Molecular Plant Pathology* **66**, 163-174

Kavroulakis N, Ntougias S, Besi MI, Katsou P, Damaskinou A, Ehaliotis C. Zervakis GI, Papadopoulou KK (2010) Antagonistic bacteria of composted agro-industrial residues exhibit antibiosis against soil-borne fungal plant pathogens and protection of tomato plants from *Fusarium oxysporum* f.sp. *radicis-lycopersici*. *Plant and Soil* **333**, 233-247

Krause MS, De Ceuster TJJ, Tiquia SM, Michel FCJR, Madden LV, Hoitink HAJ (2003) Isolation and characterization of rhizobacteria from composts that suppress the severity of bacterial leaf spot of radish. *Phytopathology* **93**, 1116-1123

Kuter GA, Nelson EB, Hoitink HAJ, Madden LV (1983) Fungal populations in container media amended with composted hardwood bark suppressive and conducive to Rhizoctonia damping-off. *Phytopathology* **73**, 1450-1456

Lazarovits G, Conn KL, Abbasi PA, Tenuta M (2005) Understanding the mode of action of organic soil amendments provides the way for improved management of soilborne plant pathogens. *Acta Horticulturae* **698**, 215-224

Liebman JA, Epstein L (1992) Activity of fungistatic compounds from soil. *Phytopathology* **82**, 442-446

Liebman JA, Epstein L (1994) Partial characterization of volatile fungistatic compound(s) from soil. *Phytopathology* **84**, 442-446

Litterick AM, Harrier L, Wallace P, Watson CA, Wood M (2004) The role of uncomposted materials, composts, manures, and composts extracts in reducing pest and disease incidence and severity in sustainable temperate agricultural and horticultural crop production – a review. *Critical Reviews in Plant Sciences* **23**, 453-479

Lockwood JL (1977) Fungistasis in soils. *Biological Reviews of the Cambridge Philosophical Society* **52**, 1-43

Lockwood JL, Filonow AB (1981) Responses of fungi to nutrient-limiting conditions and to inhibitory substances in natural habitants. *Advances in Microbial Ecology* **5**, 1-61

Lockwood JL (1988) Evolution of concepts associated with soilborne plant pathogens. *Annual Review of Phytopathology* **26**, 93-121

Lunt OR (1957) Ornamental crop production. *California Agriculture* **2 (4)**, 15-18

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

Mauch-Mani B, Métraux J-P (1998) Salicylic acid and systemic acquired resistance to pathogen attack. *Annals of Botany* **82**, 535-540

Mazurier S, Corberand T, Lemanceau P, Raaijmakers JM (2009) Phenazine antibiotics produced by fluorescent pseudomonads contribute to natural soil suppressiveness to Fusarium wilt. *ISME Journal* **3**, 977-991

Mazzola M, Gu YH (2002) Wheat genotype-specific induction of soil microbial communities suppressive to disease incited by *Rhizoctonia solani* anastomosis group (AG)-5 and AG-8. *Phytopathology* **92**, 1300-1307

McKellar ME, Nelson EB (2003) Compost-induced suppression of *Pythium* damping-off is mediated by fatty-acid-metabolizing seed-colonizing microbial communities. *Applied and Environmental Microbiology* **69**, 452-460

Mercado-Blanco J, Rodríguez-Jurado D, Hervás A, Jiménez-Díaz JM (2004) Suppression of Verticillium wilt in olive planting stocks by root associated fluorescent *Pseudomonas* spp. *Biological Control* **30**, 474-486

Mondal SN, Hyakumachi M (1998) Carbon loss and germinably, viability, and virulence of chlamydospores of *Fusarium solani* f.sp. *phaseoli* after exposure to soil at different pH levels, temperatures, and matric potentials. *Phytopathology* **88**, 148-155

Nelson EB, Hoitink HAJ (1983) The role of microorganisms in the suppression of *Rhizocotnia solani* in composted hardwook bark container media. *Phytopathology* **73**, 274-278

Nelson EB, Kuter GA, Hoitink HAJ (1983) Effects of fungal antagonists and composts age on suppression of Rhizoctonia damping-off in container media amended with composted hardwood bark. *Phytopathology* **73**, 1457-62

Nitta T (1991) Diversity of root fungal floras: Its implications for soil borne disease and crop growth. *JARQ - Japan Agricultural Research Quarterly* **25**, 6-11

Noble R, Roberts SJ (2004) Eradication of plant pathogens and nematodes during composting: A review. *Plant Pathology* **5**, 548-568

Noble R, Coventry E (2005) Suppression of soil-borne plant disease with composts: A review. *Biocontrol Science and Technology* **15**, 3-20

Noble R (2011) Risks and benefits of soil amendment with composts in relation to plant pathogens. *Australasian Plant Pathology* **40**, 157-167

Ntougias S, Papadopoulou KK, Zervakis GI, Kavroulakis N, Ehaliotis C (2008) Suppression of soil- borne pathogens of tomato by composts derived from agro-industrial wastes abundant in Mediterranean regions. *Biology and Fertility of Soils* **44**, 1081-1090

Ocamb CM, Kommedahl T (1994) Growth of rhizosphere competent and incompetent *Fusarium* species from corn on carbon substrates. *Phytopathology* **84**, 508-514

Ownley BH, Benson DM, Bilderback TE (1990) Physical properties of container media and relation to severity of *Phytophthora* root rot of rhododendron. *Journal of the American Society for Horticultural Science* **115**, 564-570

Pane C, Spaccini R, Piccolo A, Scala F, Bonanomi G (2011) Compost amendments enhace peat suppressiveness to *Pythium ultimum*, *Rhizoctonia solani* and *Sclerotinia minor*. *Biological Control* **56**, 115-124

Pharand B, Carisse O, Benhamou N (2002) Cytological aspects of compost-mediated induced resistance against Fusarium crown and root rot in tomato. *Phytopathology* **92**, 424-438

Pieterse CMJ, Van Wees SCM, Hoffland E, Van Pelt JA, Van Loon LC (1996) Systemic resistance in *Arabidopsis* induced by biocontrol bacteria is independent of salicylic acid accumulation and pathogenesis-related gene expression. *The Plant Cell* **8**, 1225-1237

Pieterse CMJ, Van Wees SCM, Van Pelt JA, Knoester M, Laan R, Gerrits H, Weisbeek PJ, Van Loon LC (1998) A novel signaling pathway controlling induced systemic resistance in *Arabidopsis*. *The Plant Cell* **10**, 1571-1580

Postma J, Schilder MT, Bloem J, van Leeumen-Haagsma WK (2008) Soil suppressiveness and functional diversity of the soil microflora in organic farming systems. *Soil Biology and Biochemistry* **40**, 2394-2406

Qian P, Johnson LF (1987) Chemical and physical soil characteristics related to lysis of oospores of *Pythium ultimum*. *Phytopathology* **77**, 1062-1066

Raaijmakers JM, Weller DM (1998) Natural plant protection by 2,4-diacetyl-phloroglucinol e producing *Pseudomonas* spp. in take-all decline soils. *Molecular Plant-Microbe Interactions* **11**, 144-152

Raaijmakers JM, de Bruijn I, Nybroe O, Ongena M (2010) Natural functions of lipopeptides from *Bacillus* and *Pseudomonas*: More than surfactants and antibiotics. *FEMS Microbiology Reviews* **34**, 1037-1062

Rabeendran N, Jones EE, Moot DJ, Stewart A (2006) Biocontrol of Sclerotinia lettuce drop by *Coniothyrium minitans* and *Trichoderma hamatum*. *Biological Control* **39**, 352-362

Raviv M (2009) Recent advances in soil-borne disease control using suppressive media. *Acta Horticulturae* **819**, 125-134

Rothrock CS, Gottlieb D (1984) Role of antibiosis in antagonism of *Streptomyces hygroscopicus* var *geldanus* to *Rhizoctonia solani* in soil. *Canadian Journal of Microbiology* **30**, 1440-1447

Rousk J, Brookes PC, Baath E (2010) Investigating the mechanisms for the opposing pH relationships of fungal and bacterial growth in soil. *Soil Biology and Biochemistry* **42**, 926-934

Ryan PR, Dessaux Y, Thomashow LS, Weller DM (2009) Rhizosphere engineering and management for sustainable agriculture. *Plant and Soil* **321**, 363-383

Saadi I, Laor Y, Medina S, Krassnovsky A, Raviv M (2010) Compost suppressiveness against *Fusarium oxysporum* was not reduced alter one-year storage under various moisture and temperature conditions. *Soil Biology and Biochemistry* **42**, 626-634

Sang MK, Kim J-G, Kim KD (2010) Biocontrol activity and induction of systemic resistance in pepper by compost water extracts against *Phytophthora capsici*. *Phytopathology* **100**, 774-783

Sang MK, Kim KD (2011) Biocontrol activity and primed systemic resistance by compost water extracts against anthracnoses of pepper and cucumber *Phytopathology* **101**, 732-740

Segarra G, Casanova E., Borrero C, Avilés M, Trillas I (2007) The suppressive effects of composts used as growth media against *Botrytis cinerea* in cucumber plants. *European Journal of Plant Pathology* **117**, 393-402

Segarra G, Van der Ent S, Trillas MI, Pieterse CMJ (2009) MYB72, a node of convergence in induced systemic resistance triggered by a fungal and a bacterial beneficial microbe. *Plant Biology* **11**, 90-96

Serra-Wittling C, Houot S, Alabouvette C (1996) Increased soil suppressiveness to Fusarium wilt of flax after addition of municipal solid waste compost. *Soil Biology and Biochemistry* **28**, 1207-1214

Solbraa K (1986) Bark as growth medium. *Acta Horticulturae* **178**, 129-135

Spencer S, Benson DM (1981) Root rot of *Aucuba japonica* caused by *Phytophthora cinnamomi* and *P. citricola* and suppressed with bark media. *Plant Disease* **65**, 918-921

Spencer S, Benson DM (1982) Pine bark, hardwood bark compost, and peat amendment effects on development of *Phytophthora* spp. and lupine root rot. *Phytopathology* **72**, 346-351

Sugimoto EE, Hoitink HAJ, Tuovinen OH (1990) Enumeration of oligotrophic rhizosphere pseudomonads with diluted and selective media formulations. *Biology and Fertility of Soils* **9**, 226-230

Tahvonen R (1993) The disease suppressiveness of light-coloured sphagnum peat and biocontrol of plant diseases with *Streptomyces* sp. *Acta Horticulturae* **342**, 37-42

Termorshuizen AJ, van Rijn E, van der Gaag DJ, Alabouvette C, Chen Y, Langerlöf J, Malandrakis AA, Paplomatas EJ, Rämert B, Ryckeboer J,

Steinberg C, Zmora-Nahum S (2006) Suppressiveness of 18 composts against 7 pathosystems: Variability in pathogen response. *Soil Biology and Biochemistry* **38**, 2461-2477

Termorshuizen AJ, Jeger MJ (2008) Strategies of soilborne plant pathogenic fungi in relation to disease suppression. *Fungal Ecology* **1**, 108-114

Thomashow LS, Mavrodi OV, Mavrodi DV, Raaijmakers JM, Bonsall RF, McSpadden-Gardener B, Lee YJ, Park MJ, Weller DM (2000) 2,4-Diacetylphloroglucinol, a major determinant in the biological control of take-all disease of wheat. In: DeWit PJGM, Bisseling T, Stiekema WJ (Eds) *Biology of Plant-Microbe Interactions* (Vol 2), International Society for Molecular Plant-Microbe Interactions, St. Paul, Minnesota, pp 331-335

Tilston EL, Pitt D, Groenhof AC (2002) Composted recycled organic matter supressess soil-borne diseases of field crops. *New Phytologist* **154**, 731-740

Trillas MI, Casanova E, Cotxarrera L, Ordovás J, Borrero C, Avilés M (2006) Composts from agricultural waste and the *Trichoderma asperellum* strain T-34 suppress *Rhizoctonia solani* in cucumber seedlings. *Biological Control* **39**, 32-38

Trillas MI, Segarra G (2009) Interactions between nonpathogenic fungi and plants. In: Van Loon LC (Ed) *Advances in Botanical Research. Plant Innate Immunity* (Vol 51), Academic Press, Burlington, pp 321-359

Trillas-Gay MI, Hoitink HAJ, Madden LV (1986) Nature of suppression of Fusarium wilt of radish in a container medium amended with composted hardwood bark. *Plant Disease* **70**, 1023-1027

Tuitert G, Szczech M, Bollen GJ (1998) Suppression of *Rhizoctonia solani* in potting mixtures amended with compost made from organic household waste. *Phytopathology* **88**, 764-773

Van Bruggen AHC, Semenov AM (1999) A new approach to the search for indicators of root disease suppression. *Australasian Plant Phatology* **28**, 4-10

Van Bruggen AHC, Semenov AM (2000) In search of biological indicators for soil health and disease suppression. *Applied soil Ecology* **15**, 13-24

Van Loon LC, Bakker PAHM, Pieterse CMJ (1998) Systemic resistance induced by rhizobacteria. *Annual Review of Phytopathology* **36**, 453-483

Van Loon LC (2000) Systemic induced resistance. In: Slusarenko AJ, Fraser RSS, Van Loon LC (Eds) *Mechanisms of Resistance to Plant Diseases*, Kluwer Academic Publishers, Dordrecht, pp 521-574

Van Loon LC, Rep M, Pieterse CMJ (2006) Significance of inducible defense-related proteins in infected plants. *Annual Review of Phytopathology* **44**, 135-162

Waksman SA, Purvis ER (1932) The microbiological population of peat. *Soil Science* **34**, 95-113

Weller DM, Raaijmakers JM, McSpadden Gardener BB, Thomashow LS (2002) Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annual Review of Phytopathology* **40**, 309-348

Widmer TL, Graham JH, Mitchell DJ (1998) Composted municipal waste reduces infection of citrus seedlings by *Phytophthora nicotianae*. *Plant Disease* **82**, 683-688

Wilcox WF, Miretich SM (1985) Influence of soil water matric potential on the development of *Phytophthora* root and crown rots of mahaleb cherry. *Phytopathology* **75**, 648-653

Woltz SS, Jones JP (1981) Nutritional requirements of *Fusarium oxysporum:* Basis for a disease control system. In: Nelson PE, Toussoun TA, Cook RJ (Eds) *Fusarium*: *Diseases, Biology, and Taxonomy*, The Pennsylvania State University Press, University Park, Pennsylvania, pp 340-349

Yogev A, Raviv M, Hadar Y, Cohen R, Wolf S, Gil L, Katan J (2010) Induced resistance as a putative component of compost suppressiveness. *Biological Control* **54**, 46-51

You MP, Sivasithamparam K (1995) Changes in microbial populations of an avocado plantation mulch suppressive to *Phytophthora cinnamomi*. *Applied Soil Ecology* **2**, 33-43

Zhang W, Dick WA, Hoitink HAJ (1996) Compost-induced systemic acquired resistance in cucumber to Pythium root rot and anthracnose. *Phytopathology* **86**, 1066-1070

Zhang W, Han DY, Dick WA, Davis KR, Hoitink HAJ (1998) Compost and compost water extract-induced systemic acquired resistance in cucumber and arabidopsis. *Phytopathology* **88**, 450-455