



## Review

## Identifying the characteristics of organic soil amendments that suppress soilborne plant diseases

Giuliano Bonanomi\*, Vincenzo Antignani, Manuela Capodilupo, Felice Scala

Dipartimento di Arboricoltura, Botanica e Patologia Vegetale, Università di Napoli Federico II, via Università 100, Portici 80055 (NA), Italy

## ARTICLE INFO

## Article history:

Received 9 March 2009

Received in revised form

12 October 2009

Accepted 15 October 2009

Available online 25 October 2009

## Keywords:

Compost

C-to-N ratio

Disease suppression

Enzymatic activities

*Fusarium*

Microbial diversity

*Phytophthora*

*Pythium*

*Rhizoctonia solani*

*Verticillium dahliae*

## ABSTRACT

Application of organic amendments has been proposed as a strategy for the management of diseases caused by soilborne pathogens. However, inconsistent results seriously hinder their practical use. In this work we use an extensive data set of 2423 studies derived from 252 papers to explore this strategy. First, we assess the capability of a specific organic amendment to control different diseases; second, we investigate the influence of organic matter (OM) decomposition on disease suppressiveness; and third, we search for physical, chemical and biological parameters able to identify suppressive OM. OM was found to be consistently suppressive to different pathogens in only a few studies where a limited number of pathogens were tested. In the majority of studies a material suppressive to a pathogen was ineffective or even conducive to other pathogens, suggesting that OM suppressiveness is often pathogen-specific. OM decomposition in many studies (73%,  $n = 426$ ) emerged as a crucial process affecting suppressiveness. During decomposition, disease suppression either increased, decreased, was unchanged or showed more complex responses, such as 'hump-shaped' dynamics. Peat suppressiveness generally decreased during decomposition, while responses of composts and crop residues were more complex. However, due to the many interactions of contributing factors (OM quality, microbial community composition, pathosystem tested and decomposition time), it was difficult to identify specific predictors of disease suppression. Among the 81 parameters analysed, only some of the 643 correlations showed a consistent relationship with disease suppression. The response of pathogen populations to OM amendments was a reliable feature only for some organic matter types (e.g. crop residues and organic wastes with C-to-N ratio lower than  $\sim 15$ ) and for pathogens with a limited saprophytic ability (e.g., *Thielaviopsis basicola* and *Verticillium dahliae*). Instead, population responses of the pathogenic fungi *Phytophthora* spp., *Rhizoctonia solani* and *Pythium* spp. appeared unrelated to disease suppression. Overall, enzymatic and microbiological parameters, rather than chemical ones, were much more informative for predicting suppressiveness. The most useful features were FDA activity, substrate respiration, microbial biomass, total culturable bacteria, fluorescent pseudomonads and *Trichoderma* populations. We conclude that the integration of different parameters (e.g. FDA hydrolysis and chemical composition by  $^{13}\text{C}$  NMR) may be a promising approach for identification of suppressive amendments.

© 2009 Elsevier Ltd. All rights reserved.

### 1. Introduction

Increasing public interest in protecting the environment and human health has prompted research on agronomic strategies with reduced requirements of fungicides, fertilizers and herbicides. Furthermore, conventional strategies, such as the use of resistant cultivars and synthetic fungicides, are not completely able to control soilborne fungal and oomycete plant pathogens, which every year cause considerable losses in crop production. In this

context, alternative control methods with high efficacy, low cost and limited environmental effects are a high priority research need for contemporary agriculture (Martin, 2003).

Organic amendments, such as animal and green manure (the incorporation of crop residues into the soil), organic wastes, composts and peats, have been proposed to control diseases caused by soilborne pathogens (Baker and Cook, 1974; Hoitink and Fahy, 1986). There are many examples of soilborne pathogens controlled effectively by the application of organic amendments: *Aphanomyces euteiches* (Lumsden et al., 1983), *Gaeumannomyces graminis* f.sp. *tritici* (Tilston et al., 2002), *Macrophomina phaseolina* (Lodha, 1995), *Rhizoctonia solani* (Papavizas and Davey, 1960), *Thielaviopsis basicola* (Papavizas, 1968), *Verticillium dahliae* (Lazarovits et al., 1999), and

\* Corresponding author. Tel.: +39 (0) 81 2539379; fax: +39 (0) 81 7760104.  
E-mail address: [giuliano.bonanomi@unina.it](mailto:giuliano.bonanomi@unina.it) (G. Bonanomi).

several species of *Fusarium* (Szczecz, 1999), *Phytophthora* (Szczecz and Smolińska, 2001), *Pythium* (McKellar and Nelson, 2003), *Sclerotinia* (Lumsden et al., 1983) and *Sclerotium* (Coventry et al., 2005).

Unfortunately, the suppressiveness of OM amendments (i.e. the ability to control plant diseases) is often inconsistent: many studies (Mazzola et al., 2001; Tilston et al., 2002) report an increase of disease incidence after amendments. In an extensive survey on compost effects, Termorshuizen et al. (2007) found disease suppression in 54% of all cases, no significant suppression in 42.7%, and disease enhancement in 3.3%. In a recent review of 1964 experimental studies, Bonanomi et al. (2007) found the effect of OM on diseases to be suppressive in 45% of the cases, no significant in 35% and conducive in 20% (increase of disease incidence).

Inconsistency and unpredictability of OM effects on plant diseases seriously hinder the practical use of these materials: OMs that are suppressive to some pathogens and conducive to others cannot be extensively applied unless their effects on diseases can be accurately predicted. Substantial effort has been made during the last decade in the search for reliable indicators of OM suppressive capability (review in Noble and Coventry, 2005; Janvier et al., 2007). The traditional approach is based on the analysis of the effects of a large number of OMs on different pathosystems, with the aim to identify characteristics correlated with disease suppression (Scheuerell et al., 2005; Termorshuizen et al., 2007). For instance, a fluorescein diacetate (FDA) hydrolysis assay has been used to measure non-specific enzyme activity (e.g. esterases, proteases, lipases, etc.) and has been correlated with organic matter decomposition (Schnurer and Rosswall, 1982), but is also positively correlated with peat (Boehm et al., 1997) and compost suppressiveness (Chen et al., 1988).

Another important indicator could be the degree of decomposition of the amendments (Hoitink and Boehm, 1999; Janvier et al., 2007). Significant changes in the correlation between suppressiveness and the level of decomposition have been reported for crop residues (Wilhelm, 1951; Papavizas and Davey, 1960), organic wastes (Croteau and Zibilske, 1998; Kotsou et al., 2004), peats (Boehm et al., 1997) and composts (Widmer et al., 1998; Diab et al., 2003). For example, Tuitert et al. (1998) reported that undecomposed and mature composts were suppressive to *R. solani* damping-off, but partially decomposed materials were conducive. A relationship between decomposition state and suppressiveness was also demonstrated by Boehm et al. on peat (1997). They showed that suppressiveness to *Pythium ultimum* decreases with peat "age" because of the progressive depletion of carbohydrates and easily degradable organic compounds, which are necessary to sustain biological control agents. An understanding of the influence of the degree of OM decomposition on the suppression of soilborne disease is essential to improve our predictive capability.

In this work we use the data set of Bonanomi et al. (2007) to 1) assess the capability of a specific organic amendment to control different diseases, 2) summarize the effects of OM decomposition on disease suppressiveness, and 3) identify factors capable of predicting the effect of OM amendments on plant diseases. We also describe trends that appear specific to different OM types and pathogen species and that might be useful for the identification of general features of suppressive amendments.

## 2. Materials and methods

### 2.1. Literature search and data collection

The current analysis uses the data set compiled by Bonanomi et al. (2007). Data were obtained from 252 articles published between 1940 and 2006 with a total of 2423 experimental study cases concerning the effect of organic amendments on disease

incidence ( $n = 1964$ ) and population ( $n = 459$ ) of fungal and oomycete pathogens. International journals were searched using online versions of Biological Abstracts, Blackwell Synergy, ISI Web of Knowledge, Science Citation Index, Science Direct, and within the APSnet site. The search words were: "amendment," "compost," "crop residues," "damping-off," "green manure," "organic matter," "peat," "root rot," "soilborne pathogens," "suppression," "waste", and "wilt". Only articles containing quantitative data on disease incidence and/or severity and population response of pathogens were included to avoid subjective selection bias. For further details and the full list of articles utilized, see Bonanomi et al. (2007).

### 2.2. Data analysis

#### 2.2.1. Organic amendment multiple suppression

The effects of OM amendments on disease incidence and severity caused by soilborne pathogens, relative to a non-amended control, were classified as: 1. suppressive, (significant disease reduction); 2. null, (not significant effect), and 3. conducive, (significant disease increase).

The capability of a specific OM amendment to control different pathogens was evaluated by selecting studies that dealt with at least two different pathogens. To analyse the data we calculated an index of multiple suppression (MSI):

$$MSI = \frac{\text{No. Suppressive} - \text{No. Conducive Null}}{\text{No. Total cases}}$$

where: "No. Suppressive" indicates the number of cases of effective disease control; "No. Conducive & Null" indicates the number of cases in which the amendment is null or increases the disease; and, "No. Total cases" indicates the number of study cases for each type of amendment. MSI values range between +1 and -1: values between 0 and +1 indicate that an amendment is more frequently or always (+1) suppressive, while values between -1 and 0 indicate an amendment more frequently or always (-1) conducive or null. A MSI value of 0 indicates high variability, with both suppressive and conducive effects on diseases. We calculated the MSI for each OM type tested on at least two different pathosystems.

#### 2.2.2. Decomposition of organic amendments and disease suppression

The effects of the degree of decomposition of the OM on disease incidence and severity was classified into six categories, and took into account the suppressiveness trends observed during decomposition: 1. increased suppression; 2. constant suppression (with no significant changes, as reported in the original articles); 3. constant conductivity or null (with no significant changes); 4. decreased suppression; 5. decreased suppression followed by an increase (hereafter indicated as U-shaped); and 6. increased suppression followed by a decrease (indicated as  $\cap$ -shaped). Data were subjected to three types of analysis: i. the general behaviour of each organic matter type (compost, crop residues, waste and peat); ii. the response of each different pathogen to all amendments pooled, and, iii. all possible combinations between OM types and pathogen species.

#### 2.2.3. Identifying suppressive organic amendments

We followed the approach proposed by Janvier et al. (2007) for suppressive soils to evaluate parameters for the prediction of OM amendment suppressiveness. Correlations between analytical parameters and suppressiveness found in literature were classified as positive, negative or not significant, as reported in the original articles, for both abiotic and biotic characteristics. In this way, it was possible to assess the consistency of the relationships for each analytical parameter with disease suppression.

In addition, we evaluated each parameter using a literature-based approach to calculate a quantitative, bias-free index of suppression (Suppression Index, SI). First, available data were categorized by assigning a numerical value to each type of relationship: 1, 0 or –1 for positive, not significant and negative relationships, respectively. Then SI was calculated as follows:

$$SI = \frac{\text{Correlation mean} \times \text{No. studies}}{\text{No. total studies}} \times 100$$

where: “Correlation mean” indicates the mean of the numerical value assigned to the correlations with suppressiveness of each parameter; “No. studies” is the number of studies available for each parameter; and, “No. total studies” are the number of study cases. SI values range between  $+\infty$  and  $-\infty$ : positive values indicate a prevalence of positive correlations, while negative values are the results of negative relationships. This index takes into account both the consistency of the relationships with suppressiveness (positive, not significant or negative) and the number of available correlations. SI has the advantage that it gives a realistic quantification of the values of a parameter according to the knowledge available at present. However, the use of this index is limited because of a dependency on the number of study cases available. Where there are only a few study cases, the SI will be underestimated, and for parameters with a larger number of studies higher SI values are obtained. Moreover, since the SI index is based on correlations, it provides only an indirect indication of the underlying mechanisms operating during disease suppression by specific OM amendments.

A different approach was carried out to investigate the relationships between the pathogen population density and the disease suppression after OM application. We assessed the response of the pathogen population when the OM amendment has a suppressive effect on disease incidence. This analysis was carried out both for different pathogen species and OM types. Finally, we analysed the role of OM microbial community and the capability of an OM to induce resistance in plants in disease suppression. In the first case we quantified the number of studies where OM sterilization positively or negatively affects disease suppression. In the latter case, we identified the number of studies in which OM amendments induce plant resistance to pathogens by recording the cases of significant decreasing disease severity.

### 3. Organic amendment multiple suppression

In most of the studies in the data set, the suppressiveness of one type of OM was tested against one pathogen and only 122 out of 1964 experiments tested two or more pathogens. Although the number of pathogens tested for each type of OM ranged between 2 and 21 with a mean of 3.5, the majority of studies (95 out of 122) considered only two or three pathogens. Our analysis showed that in a few studies, and only when a limited number of pathogens were tested, did the organic amendment show a consistent response (Fig. 1). In many cases a variable response was shown, where a material suppressive to a pathogen was ineffective or even conducive to other pathogens. When three or more pathogens were considered (e.g. Lumsden et al., 1983) the results were inconsistent (Fig. 1). These results suggest that OM suppressiveness is often pathogen-specific and related to the mechanism(s) of disease suppression. For instance, the application of green manure with *Vicia sativa*, a nitrogen fixing species that releases ammonia during residue decomposition, was able to control *T. basicola*, but enhanced the incidence of *Pythium* spp. and *R. solani* (Rothrock and Kirkpatrick, 1995). This difference could depend on the greater sensitivity of *T. basicola* to ammonia (Candole and Rothrock, 1997). In another case, Termorshuizen et al. (2007) reported that a compost suppressive in the pathosystems

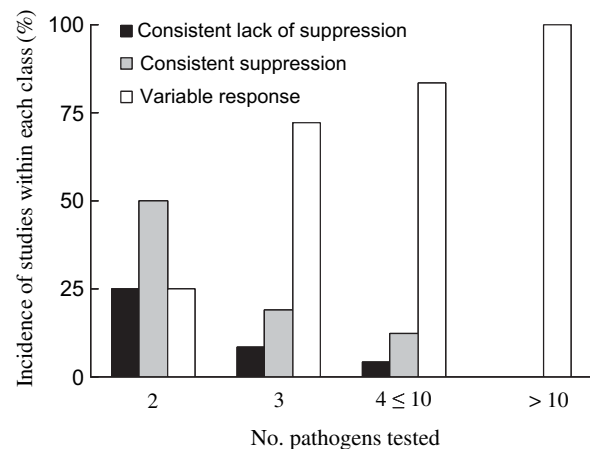


Fig. 1. Class distribution of the multiple suppression index (MSI) in relation to the number of pathogens tested on a specific organic matter type. Classes of  $MSI \geq 0.5$ , indicate consistent suppression;  $MSI \leq -0.5$ , indicate a consistent lack of suppression; MSI ranging from  $-0.5$  to  $0.5$  indicate a variable response.

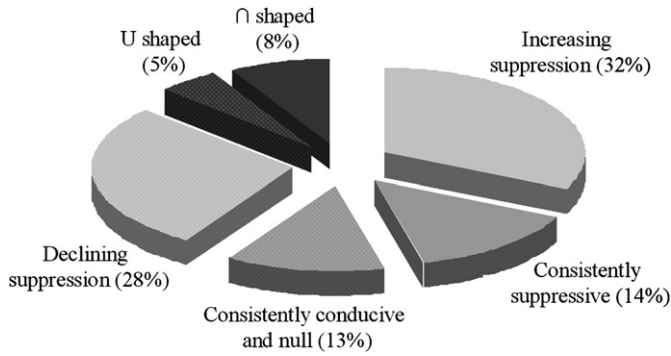
*Cylindrocladium spathiphylli* – *Spathiphyllum*, *R. solani* – cauliflower, *Fusarium oxysporum* – flax and *Phytophthora nicotianae* – tomato was otherwise conducive in the *V. dahliae* – eggplant combination. However, some notable exceptions exist: Nelson and Boehm (2002) reported that the application of sewage sludge was significantly suppressive to five different pathogens (*Laetisaria fuciformis*, *Pythium graminicola*, *R. solani*, *Sclerotinia homoeocarpa* and *Typhula incarnate*). Cases of consistently suppressive (e.g. Darby et al., 2006) or conducive (e.g. Tilston et al., 2002) organic amendments are relatively rare in our data set.

### 4. Decomposition of organic amendments and disease suppression

Organic amendments introduced into soil or horticultural substrates are subject to decomposition processes dependent on organic matter quality, water availability and temperature (Berg and McClaugherty, 2003). The effect of OM decomposition on soilborne diseases was detailed in 36 of the 252 papers examined and covered 426 studies. The duration of the decomposition process was quite variable among the studies, ranging between a few days to a maximum of about three years.

Our analysis indicates that decomposition is a crucial process for pathogen suppressiveness. OM decomposition significantly affected the degree of disease suppression in 73% of studies, either at short (days or weeks; Phillips et al., 1971) or long time scales (months or years; Widmer et al., 1998; Stone et al., 2001). The response to decomposition was variable with a prevalence of studies reporting an increase (32%) or a reduction (28%) of disease suppression (Fig. 2). The U- and  $\cap$ -shaped responses were less frequent, but evident in 13% of cases (Fig. 2). The large variability observed for pathogen species and OM types makes any attempt to make generalizations very difficult. However, some consistent results emerged when pathogen species and OM types were analysed separately.

Peat is a natural product derived from the progressive accumulation of plant and moss residues decomposed under waterlogged conditions. During decomposition, peat generally loses its suppressiveness (Fig. 3a). This result has been attributed to the progressive reduction of cellulose, carbohydrates and easily degradable organic compounds (Hoitink and Boehm, 1999). These chemical changes may drive a progressive shift in the microbial community composition from Gram negative bacteria, which have



**Fig. 2.** Effect of organic matter decomposition on disease suppression. Data are expressed as percentage of the total number of studies ( $n = 426$ ).

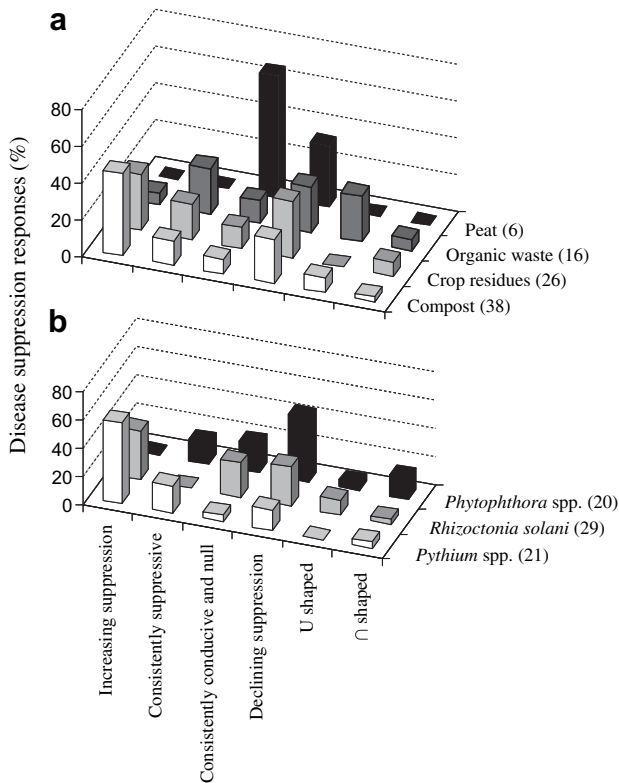
antagonistic ability, to Gram positive bacteria, which are less able to antagonize soilborne pathogens (Boehm et al., 1997). Accordingly, light peats which are richer in carbohydrates support more microbial activity as measured by the rate of hydrolysis of fluorescein diacetate (FDA), compared to dark peats which are often conducive (Boehm et al., 1997).

In contrast to peat, the relationship between compost maturity and suppressiveness is complex. Compost is obtained by the biological decomposition of organic materials which causes their chemical stabilization and the sanitization from human and plant pathogens and weed seeds (Noble and Roberts, 2004). Composts are very heterogeneous materials due to the diversity of composting methodologies, feedstock origin (e.g. municipal waste, animal manure, plant pruning, etc.) and especially the stage of maturity (Tuitert et al., 1998). The many interactions of these factors means that it is difficult to predict the suppressive efficacy of

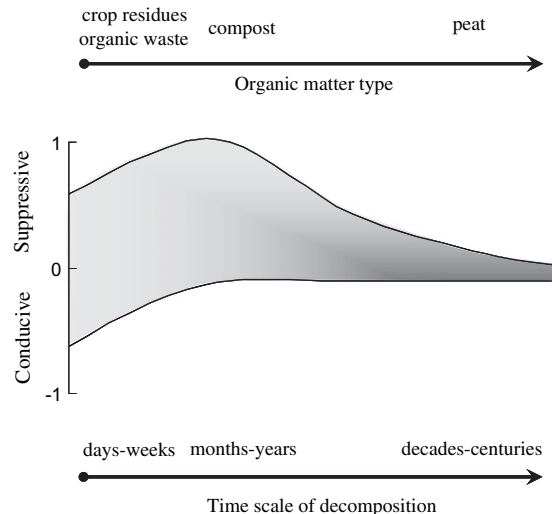
a compost. Disease suppression often increased during decomposition (44%), but also showed a significant decline (23%) in many experiments. U- and ∩-shaped responses were reported only in a few cases for composts (Fig. 3a). Increasing compost suppressiveness with decomposition could be related to the incomplete microbial colonization of undecomposed OM (Scheuerell and Mahaffee, 2005). OM not completely colonized by microbes still contains organic carbon resources and nutrients available for utilization by saprophytic pathogens for inoculum production. As decomposition proceeds, the availability of easily degradable carbon sources progressively diminishes, creating microbiostatic conditions that may produce an increase of suppressiveness by favouring competitive saprophytes. In the late stage of decomposition, the microbial community has completely exhausted carbon-based resources, which as already described for peats (Boehm et al., 1997), may cause a reduction of suppressiveness. However, until the maturation status of composts has a better chemical and microbiological definition (Mondini et al., 2003), the search for general principles that relate decomposition to suppressiveness will be difficult to attain.

The relationship between the decomposition state of crop residues and disease suppression is very variable (Fig. 3a). In nine studies crop residues had been subjected to decomposition periods of comparable duration and suppression of *Pythium* spp. consistently increased during decomposition, while for *R. solani* it often decreased. The contradictory behaviour of the two pathogens (Fig. 3b) could be partially related to their different saprophytic capability. *Pythium* spp. are aggressive saprophytes on fresh materials such as undecomposed plant residues (Rothrock and Kirkpatrick, 1995; Sumner et al., 1995). Rapid spore germination and high growth rate (Nelson, 2004), together with the ability to colonize senescent tissues confers to *Pythium* spp. an advantage over specialized saprophytic microbes. However, since *Pythium* spp. are not good competitors in soil, a general suppressiveness would rapidly arise a few days after amendment addition (Grünwald et al., 2000). *R. solani*, in contrast, is a slower colonist of OM, but more competitive than *Pythium* spp. on complex substrates rich in cellulose (Papavizas, 1970). This competitive advantage is in part due to the enzymes that it possesses (Sneh et al., 1996) that allow *R. solani* to utilize a wide array of crop residues with different C-to-N ratios (Croteau and Zibilske, 1998; Yulianti et al., 2006).

In Fig. 4 we propose a synthesis of the relationship between OM decomposition and disease suppression. Crop residues, composts



**Fig. 3.** Effect of organic matter decomposition on disease suppression in relation to the organic matter type (a) and pathogen species (b). Data are expressed as percentage values calculated from the total number of studies within each OM type (a) and pathogen species (b). The number of studies is reported in brackets.



**Fig. 4.** Schematic representation of disease suppression dynamics during organic matter decomposition.



and peats represent three points along a continuum of decomposition state in which the sign (suppressive vs. conducive) and the magnitude of suppressiveness dramatically change. Bonanomi et al. (2007) reported that undecomposed materials, represented by crop residues and wastes, span all the possible outcomes being either very suppressive or conducive. More decomposed materials, such as mature composts, are on an average more suppressive with fewer cases of disease increase (Bonanomi et al., 2007). Finally, extremely decomposed materials, such as peats, are much less variable: they are slightly suppressive or moderately conducive.

## 5. Identifying suppressive organic amendments

Among all the variables assessed (81 for 643 correlations), only some of them were consistently correlated with disease suppression. We therefore restrict the discussion below to the pathogens most commonly studied.

### 5.1. Pathogen population and disease suppression

By comparing different OM types with all pooled pathogens, we found that disease suppression correlated with a decrease of pathogen population in more than 50% of the cases for crop residues and organic waste (Fig. 5a). Pathogen populations either increased or decreased with a similar frequency when disease suppressive composts were applied (Fig. 5a). A consistent positive correlation between disease suppression and decrease of pathogen populations was recorded for *T. basicola*, *V. dahliae* (~80%) and *Fusarium* spp. These results indicate that population decline is one of the mechanisms underlying the control of these microbes with organic amendments (mainly wastes and crop residues). *Fusarium* spp. and *T. basicola* propagules commonly germinate after amendment with crop residues (Patrick and Toussoun, 1965; Adams and Papavizas, 1969) and consequently, in absence of the host, germinating propagules are often lysed resulting in a drastic reduction of the pathogen population. *V. dahliae* control is commonly due to a direct killing of microsclerotia by toxic compounds as ammonia and nitrous acid produced by decaying OM (Tenuta and Lazarovits, 2002).

In contrast, only in few cases could a decline of pathogen population be correlated with disease suppression for *Phytophthora* spp.,

*R. solani* and especially for *Pythium* spp. (Fig. 5b). Interestingly, for these pathogens a large number of studies reported significant disease suppression with increased pathogen populations. This result has been recorded for *Fusarium* spp. (Ros et al., 2005), *Phytophthora* spp. (Widmer et al., 1998; Szczech and Smolińska, 2001), *R. solani* (Sumner et al., 1995; Croteau and Zibilske, 1998) and especially for *Pythium* spp. (Lewis et al., 1992). The induction of disease resistance in plants and/or soil fungistasis is the mechanism proposed, but rarely tested, to explain the observed disease suppression. The hypothesis of induced resistance merits further investigation considering the low number of studies available ( $n = 17$  in four papers) and the high percentage of cases where this mechanism has been found positively correlated with suppressiveness (59%). In conclusion, the response of pathogen populations to OM amendments may be a reliable indicator only for some organic matter types (e.g. crop residues and wastes with low C-to-N ratio) and for pathogens with limited saprophytic capability. This evidence is consistent with the observation that crop residues can be used to control weak saprophytic phytopathogens such as *T. basicola* (Hood and Shew, 1997) and *V. dahliae*, but are often ineffective or conducive to microbes with high saprophytic capability such as *Pythium* spp. and *R. solani* (Bonanomi et al., 2007).

### 5.2. Chemical and physical variables

Chemical and physical variables ( $n = 40$ ) were less informative predictors of suppressiveness than enzymatic and microbiological ones (18% and 9% of positive and negative correlations,  $n = 299$ ). Despite a large number of relevant studies, many chemical characteristics (e.g. nutrients and metals) were apparently not correlated with disease suppression (Figs. 6 and 7).

The C-to-N ratio is considered a key index to assess the litter decay rate and the pattern of nitrogen release during decomposition of OM (Berg and McClaugherty, 2003). Unfortunately, the same does not seem to be true for disease suppression because the C-to-N ratio of OM was poorly correlated with OM suppressiveness (Figs. 6 and 7). This probably is attributable to the suppressive capability of materials with either a high or low C-to-N ratio. Materials with a high C-to-N ratio stimulate microbial activity that, by reducing the N availability, impairs pathogen saprophytic

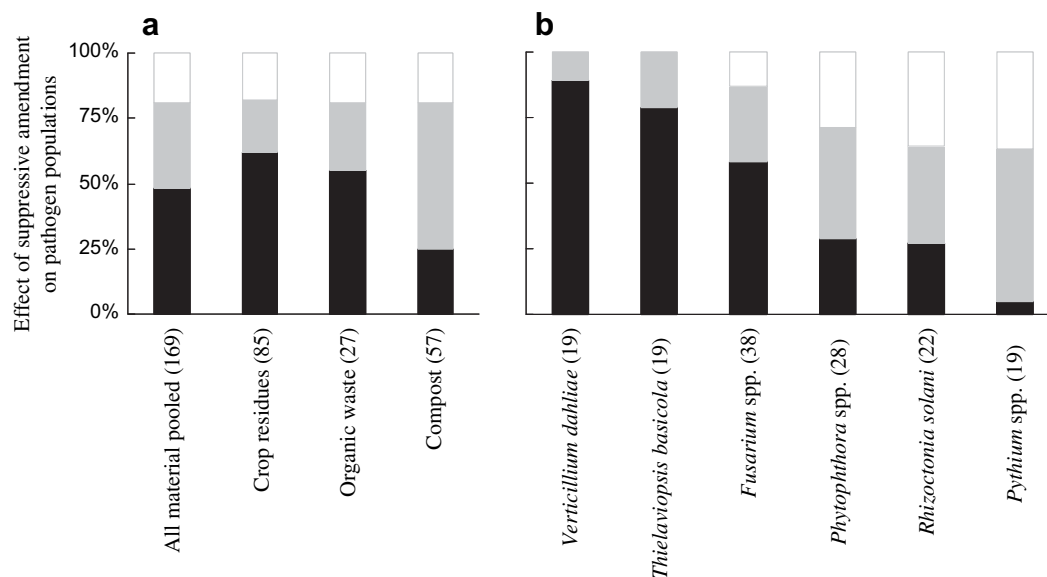
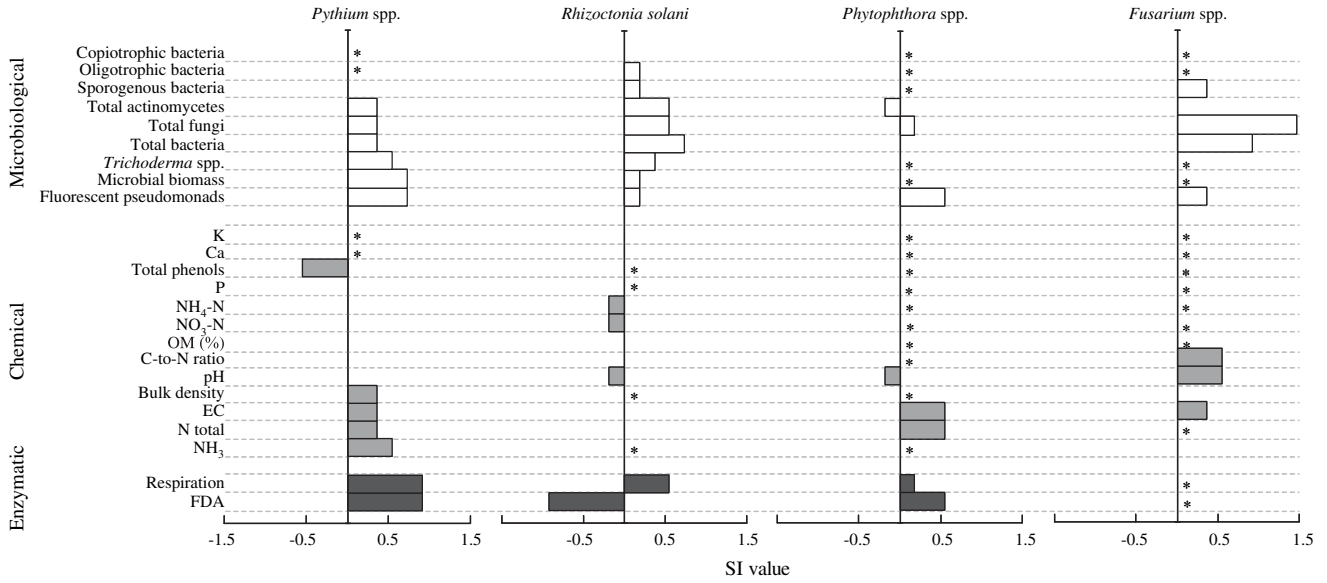


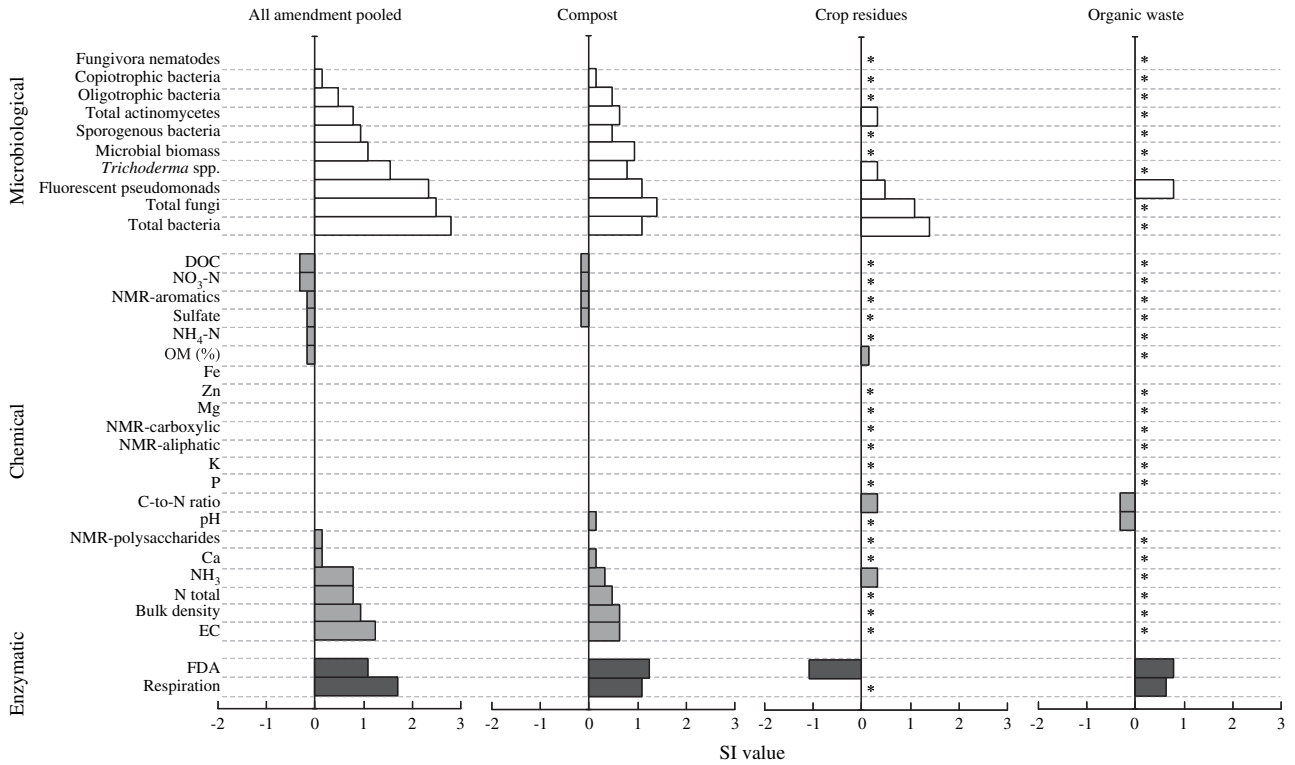
Fig. 5. Effect of suppressive organic matter on pathogen population dynamics (black = decrease, grey = null, white = increase). Analysis was carried out for different organic matter types (a) and soilborne pathogens (b). Only OM types and pathogens with at least 15 study cases are reported (number of studies in brackets).



**Fig. 6.** Suppression indices (SI) for different soilborne pathogens, irrespective of organic matter type. Positive SI values indicate a prevalence of positive correlations with disease suppression, a value of 0 indicates no correlation with disease suppression, and negative values a prevalence of negative correlations with disease suppression. Asterisks indicate data not available.

capability, and thus the infection process (Snyder et al., 1959). However, it should also be noted that N starvation immediately after OM application can impair plant growth (Hodge, 2004). On the other hand, there is evidence that the temporary accumulation of ammonia or nitrous acid (in acidic soils), following the application of OM with high N contents (C-to-N ratio below 15–10), is

responsible for the eradication of *V. dahliae* (Tenuta and Lazarovits, 2002). These suppressive effects were reported to be variable among different soil types, being more effective in sandy OM-poor soils (Tenuta and Lazarovits, 2004). Even so, in this case a low C-to-N ratio is not a reliable indicator of the decomposing substrates that are releasing either ammonia or nitrous acid.



**Fig. 7.** Suppression indices (SI) for all organic matter types and different organic matter types. Positive SI values indicate a prevalence of positive correlations with disease suppression, a value of 0 indicate no correlation with disease suppression, and negative values a prevalence of negative correlations with disease suppression. Asterisks indicate data not available.

Decomposed materials, such as mature composts or humus-like OM, usually have low C-to-N ratios, but are stable and mineralize nitrogen very slowly. The C-to-N ratio was not informative in terms of suppressiveness to other pathogens, such as *Pythium* spp., *Phytophthora* spp. and *R. solani*. For composts, which usually have C-to-N ratios with a more limited range compared to that of crop residues (from ~10 to 40–50 and ~10 to >100, respectively), we did not find significant correlations. Accordingly, the integration of the C-to-N ratio with the other factors involved in the N cycle (N total,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NH}_3$ ,  $\text{HNO}_2$ ) could be a useful approach.

Amendment pH showed a prevalence of not significant relationships with both different OM types and all pathogens, except for *Fusarium* species (Fig. 6). In this case we found positive correlations in 43% of cases. This is in agreement with previous studies which established the beneficial effects of high soil pH on the reduction of soilborne diseases caused by *Fusarium* species (Jones et al., 1993; Borrero et al., 2004).

The positive correlation between suppressiveness and substrate electrical conductivity (EC) (Fig. 7) is probably spurious and results from an increased substrate EC after amendment addition that is difficult to related with specific mechanisms of disease suppression. The weak negative correlation between bulk density that usually decreases after the amendment with disease suppression, may also be a spurious correlation. Finally, analysis of OM by  $^{13}\text{C}$  NMR (nuclear magnetic resonance) spectroscopy gave rise to low SI values indicating a prevalence of no significant relationships (Figs. 6 and 7), with the exception of the already described study on peats by Boehm et al. (1997). However, we suggest that  $^{13}\text{C}$  NMR spectroscopy could be more useful if it is associated with analysis of the activities and structure of microbial communities.

### 5.3. Enzymatic and functional variables

Correlations of disease suppression with enzymatic and functional variables had larger correlation coefficients than those for disease suppression or microbiological and chemical variables (57% positive correlations,  $n = 85$ ). The rate of FDA hydrolysis was one of the most studied ( $n = 37$ ) and has been proposed as a promising measure for predicting organic matter suppressiveness (Hoitink and Boehm, 1999). Chen et al. (1988) provided the first compelling evidence that FDA hydrolysis is consistently related to suppressiveness of composts on *Pythium*. However, subsequent studies (e.g. Erhart et al., 1999; Yulianti et al., 2006) and the present paper report contrasting relationships for disease suppression in relation to both OM type and pathogen species. For peats, organic wastes and especially composts, we found a consistent prevalence of positive correlations, while negative relations prevailed for crop residues (Figs. 6 and 7). Moreover, contrasting trends between FDA hydrolysis and suppressiveness for different pathogens (*Pythium* spp. and *R. solani*) were found (Fig. 6). In fact, *Pythium* spp. and *R. solani* showed the same response to crop residues (negative) and to composts (positive), but, because of the differential research effort (more studies were done for *R. solani* on crop residues) the SI was strongly negative for *R. solani* and positive for *Pythium* spp. Other enzyme assays ( $\beta$ -glucosidase, dehydrogenase, phosphatase, urease, ATP and NGA-glucosaminase) also gave rise to consistent positive correlations. However, in order to be considered reliable factors, further studies are needed to extend the scanty data set currently available.

For substrate respiration, which is another indicator of microbial activity, we propose considerations similar to those reported for FDA hydrolysis to explain the correlation with disease suppression. Substrate respiration had high SI values for composts; and among pathogens *Pythium* spp. recorded a SI value more than twice that of *R. solani* (Figs. 6 and 7). This difference is consistent with the

hypothesis that control of *Pythium* spp. may be explained by the model of general suppression (Weller et al., 2002).

Finally, a low SI value indicates that the application of Biolog<sup>TM</sup> profile is not an easily feasible and reliable method for assessing disease suppression in relation to both OM types and pathogen species. This is in agreement with the observation that this method is more useful for relative comparison among samples, rather than for community characterization (Preston-Mafham et al., 2002).

### 5.4. Microbiological parameters

Microbiological parameters showed a prevalence of positive correlations (46%) compared with 5% of negative correlations ( $n = 243$ ), and some of them (e.g. culturable bacteria, fungi, fluorescent pseudomonads and *Trichoderma*) attained the highest SI values (Figs. 6 and 7). These results, together with the evidence that OM sterilization generally (95% of the cases) reduced disease suppression, confirm the crucial role of the biotic component in this process.

Total culturable bacteria appears to be the best parameter (highest SI) when all OM types and pooled pathogens were considered ( $n = 46$ ; Figs. 6 and 7). The occurrence of some negative correlations for composts and crop residues (12 and 11%, respectively) could be explained by the application of partially colonized organic materials that enhance the microbial population, but also pathogen saprophytic activity. Total cultural bacteria is an important characteristic, but should not be considered in isolation to be a reliable predictor of disease suppression either in relation to OM types or different pathogen species. A similar pattern, but with fewer cases of positive and negative correlations, has been found for total culturable fungi in relation to OM types (Fig. 7). However, overall we consider measurements of total cultural fungi to be a poor predictor of disease suppression, with the exception of *Fusarium* spp. for which we recorded a prevalence of positive correlations (Fig. 6). This is indirectly supported by the evidence that non-pathogenic *Fusaria*, common components of soil microbial communities, are strongly antagonistic to pathogenic *Fusaria* (Fravel et al., 2003). Moreover, deuteromycetes such as *Penicillium* species are very common soilborne saprophyte fungi and are known to be potent antagonists of pathogenic *Fusaria* (Sabuquillo et al., 2005).

Actinomycetes attain low SI values, in spite of the relevant number of study cases ( $n = 34$ ), both in relation to OM types and pathogen species (Figs. 6 and 7). This is surprising because these microbes are known to be strong producers of antibiotic compounds (Cross, 1982) that can have a direct influence on disease suppression (Tuitert et al., 1998; Mazzola et al., 2001). However, in a more general context the prevalence of no significant correlations indicates that actinomycetes are directly involved in disease suppression in only a limited number of experimental cases.

Based on the general suppressiveness model, microbial biomass surprisingly attained low SI values for all OM types and pathogen species (Figs. 6 and 7). The only exception was for *Pythium* species that accounted for a prevalence of positive correlations between disease control and microbial biomass. This result is supported by the positive correlations also found with FDA hydrolytic activity and substrate respiration (Figs. 6 and 7). Although *Phytophthora* species such as *P. nicotianae* and *Phytophthora cinnamomi* are often considered highly sensitive to microbial competition (You and Sivasinghthamparam, 1995), this hypothesis is not supported by our analysis because we found a prevalence of no significant correlations with microbial biomass, FDA activity and substrate respiration.

Fluorescent pseudomonads attained the highest percentage of positive correlation (73%), followed by sporogenous bacteria (60%) and *Trichoderma* spp. (56%) (Figs. 6 and 7), with no cases of negative correlation with suppressiveness. These microbes are well-known

to be effective antagonists of soilborne pathogens, and several species have been developed as biocontrol agents, with modes of action such as antibiotic production (Whipps, 1997) and mycoparasitism (Harman et al., 2004). The occurrences of both positive and no significant correlations suggest that these microbes are often involved in disease suppression, but that they are not necessarily the key factor in disease control. Undoubtedly, these are excellent parameters for the prediction of OM disease suppression, but integration with other measures is required to identify situations where other factors are involved in disease suppression. Despite the large number of published studies (total  $n = 670$ ;  $n = 272$  for composts), our analysis supported the conclusions of Scheuerell et al. (2005) and Termorshuizen et al. (2007) that suppression of disease caused by *R. solani* is erratic and difficult to predict. While microbes like *Trichoderma hamatum* (Krause et al., 1997) and *Trichoderma harzianum* (Harman et al., 2004) have been identified as specific antagonists of *R. solani*, our analysis does not support the specific suppressiveness model proposed for control of *R. solani* (Weller et al., 2002), because low SI values were recorded also when only antagonistic microbes like *Trichoderma* were considered.

## 6. Conclusions

Amendments with OM can improve soil fertility and plant health, but application can result in coincidental negative effects such as increasing disease incidence and severity. In spite of the considerable research effort of recent decades, we are still far from being able to predict the suppressive capabilities of OM amendments. However, significant progress has been made in identifying parameters suitable for predicting OM suppressiveness and the most useful are FDA activity, substrate respiration, microbial biomass, total culturable bacteria, fluorescent pseudomonads and *Trichoderma* populations. However, it is evident that no one variable in isolation can be considered to be a reliable and consistent feature for predicting the suppressiveness of all different OM amendments versus all soilborne pathogens. It is likely this occurs because the mechanisms of disease suppression are different and there are many variables that need to be simultaneously monitored. Although it is important to identify specific characteristics associated with suppressive organic amendments, it is equally relevant to recognize variables consistently unrelated to suppressiveness. To date, results summarized in this work demonstrate that many parameters are consistently unrelated to disease suppression.

The future challenge is the identification of specific parameters for predicting the suppressiveness of each OM type in combination with each different pathogen species. The approach used by Bloem et al. (2006) to quantify the concept of soil quality and identification of a minimum data set could be an effective tool for predicting the suppressiveness of organic amendments. This approach is recommended as a promising way forward for the integrative use of different parameters to produce reliable indicators capable of characterizing suppressive amendments.

## Acknowledgements

We are grateful to Prof. Astolfo Zoina, Franco Zucconi and Stefano Mazzoleni for their useful discussions on the subject of OM suppressiveness and soil organic matter cycle. Comments of two anonymous reviewers greatly improved the manuscript.

## References

Adams, P.B., Papavizas, G.C., 1969. Survival of root-infecting fungi in soil. X. Sensitivity of propagules of *Thielaviopsis basicola* to soil fungistasis in natural and alfalfa-amended soil. *Phytopathology* 59, 135–138.

- Baker, K.F., Cook, R.J., 1974. *Biological Control of Plant Pathogens*. Freeman, San Francisco.
- Berg, B., McLaugherty, C., 2003. *Plant Litter. Decomposition, Humus Formation, Carbon Sequestration*, second ed. Springer, Berlin.
- Bloem, J., Hopkins, D.W., Benedetti, A., 2006. *Microbiological Methods for Assessing Soil Quality*. CABI Publishing, Oxfordshire, UK.
- Boehm, M.J., Wu, T., Stone, A.G., Kraakman, B., Iannotti, D.A., Wilson, G.E., Madden, L.V., Hoitink, H.A.J., 1997. Cross-polarized magic-angle spinning (sup13)C nuclear magnetic resonance spectroscopic characterization of soil organic matter relative to culturable bacterial species composition and sustained biological control of *Pythium* root rot. *Applied and Environmental Microbiology* 63, 162–168.
- Bonanomi, G., Antignani, V., Pane, C., Scala, F., 2007. Suppression of soilborne fungal diseases with organic amendments. *Journal of Plant Pathology* 89, 311–340.
- Borrero, C., Trillas, M.I., 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.
- Candole, B.L., Rothrock, C.S., 1997. Characterization of the suppressiveness of hairy vetch-amended soils to *Thielaviopsis basicola*. *Phytopathology* 87, 197–202.
- Chen, W., Hoitink, H.A.J., Madden, L.V., 1988. Microbial activity and biomass in container media for predicting suppressiveness to damping-off caused by *Pythium ultimum*. *Phytopathology* 78, 1447–1450.
- Coventry, E., Noble, R., Mead, A., Whipps, J.M., 2005. Suppression of *Allium* white rot (*Sclerotium cepivorum*) in different soils using vegetable wastes. *European Journal of Plant Pathology* 111, 101–112.
- Cross, T., 1982. Actinomycetes: a continuing source of new metabolites. *Developments in Industrial Microbiology* 23, 1–18.
- Croteau, G.A., Zibilske, L.M., 1998. Influence of papermill processing residuals on saprophytic growth and disease caused by *Rhizoctonia solani*. *Applied Soil Ecology* 10, 103–115.
- Darby, H.M., Stone, A.G., Dick, R.P., 2006. Compost and manure mediated impacts on soilborne pathogens and soil quality. *Soil Science Society American Journal* 70, 347–358.
- Diab, H., Hu, S., Benson, D.M., 2003. Suppression of *Rhizoctonia solani* on impatiens by enhanced microbial activity in composted swine waste amended potting mixes. *Phytopathology* 93, 1115–1123.
- Erhart, E., Burian, K., Hartl, W., Stich, K., 1999. Suppression of *Pythium ultimum* by biowaste composts in relation to compost microbial biomass, activity and content of phenolic compounds. *Journal of Phytopathology* 147, 299–305.
- Fravel, D., Olivain, C., Alabouvette, C., 2003. *Fusarium oxysporum* and its biocontrol. *New Phytologist* 157, 493–502.
- Grünwald, N.J., Hu, S., van Bruggen, A.H.C., 2000. Short-term cover crop decomposition in organic and conventional soils: soil microbial and nutrient cycling indicator variables associated with different levels of soil suppressiveness to *Pythium aphanidermatum*. *European Journal of Plant Pathology* 106, 51–60.
- Harman, E., Howell, R., Viterbo, A., Chet, I., Lorito, M., 2004. *Trichoderma* species – opportunistic, avirulent plant symbionts. *Nature Reviews* 2, 43–56.
- Hodge, H., 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* 162, 9–24.
- Hoitink, H.A.J., Fahy, P.C., 1986. Basis for the control of soilborne plant pathogens with composts. *Annual Review of Phytopathology* 24, 93–114.
- Hoitink, H.A.J., Boehm, M.J., 1999. Biocontrol within the context of soil microbial communities: a substrate-dependent phenomenon. *Annual Review of Phytopathology* 37, 427–446.
- Hood, M.E., Shew, H.D., 1997. Reassessment of the role of saprophytic activity in the ecology of *Thielaviopsis basicola*. *Phytopathology* 87, 1214–1219.
- Janvier, C., Villeneuve, F., Alabouvette, C., Edel-Hermann, V., MATEILLE, T., Steinberg, C., 2007. Soil health through soil disease suppression: which strategy from descriptors to indicators? *Soil Biology and Biochemistry* 39, 1–23.
- Jones, J.P., Engelhard, A.W., Woltz, S.S., 1993. Management of *Fusarium* wilt of vegetables and ornamentals by macro- and micro- element nutrition. In: Engelhard, A.W. (Ed.), *Soilborne Plant Pathogen: Management of Disease with Macro- and Microelement*. The American Phytopathological Society Press, St Paul, Minnesota.
- Kotsou, M., Mari, I., Lasaridi, K., Chatzipavlidis, I., Balis, C., Kyriacou, A., 2004. The effect of olive oil mill wastewater (OMW) on soil microbial communities and suppressiveness against *Rhizoctonia solani*. *Applied Soil Ecology* 26, 113–121.
- Krause, M.S., Musselman, C.A., Hoitink, H.A.J., 1997. Impact of Sphagnum peat decomposition level on biological control of *Rhizoctonia solani* damping-off of radish by *Flavobacterium balustinum* 299 and *Trichoderma hamatum* 382. *Phytopathology* 87, 555.
- Lazarovits, G., Conn, K.L., Potter, J.W., 1999. Reduction of potato scab, *Verticillium* wilt, and nematodes by soy meal and meat and bone meal in two Ontario potato fields. *Canadian Journal of Plant Pathology* 21, 345–353.
- Lewis, J.A., Lumsden, R.D., Millner, P.D., Keinath, A.P., 1992. Suppression of damping-off of peas and cotton in the field with composted sewage sludge. *Crop Protection* 11, 260–266.
- Lodha, S., 1995. Soil solarization, summer irrigation and amendments for the control of *Fusarium oxysporum* f. sp. *Cumini* and *Macrophomina phaseolina* in arid soils. *Crop Protection* 14, 215–219.
- Lumsden, R.D., Lewis, J.A., Millner, P.D., 1983. Effect of composted sewage sludge on several soilborne pathogens and diseases. *Phytopathology* 73, 1543–1548.
- Martin, F.N., 2003. Development of alternative strategies for management of soilborne pathogens currently controlled with methyl bromide. *Annual Review of Phytopathology* 41, 325–350.



- Mazzola, M., Granatstein, D.M., Elfving, D.C., Mullinix, K., 2001. Suppression of specific apple root pathogens by *Brassica napus* seed meal amendment regardless of glucosinolate content. *Phytopathology* 91, 673–679.
- McKellar, M.E., Nelson, E.B., 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.
- Mondini, C., Dell'Abate, M.T., Leita, L., Benedetti, A., 2003. An integrated chemical, thermal, and microbiological approach to compost stability evaluation. *Journal of Environmental Quality* 32, 2379–2386.
- Nelson, E.B., 2004. Microbial dynamics and interactions in the spermosphere. *Annual Review of Phytopathology* 42, 271–309.
- Nelson, E.B., Boehm, M.J., 2002. Compost-induced suppression of turf grass diseases. *BioCycle* 43, 51–55.
- Noble, R., Coventry, E., 2005. Suppression of soil-borne plant diseases with composts: a review. *Biocontrol Science and Technology* 15, 3–20.
- Noble, R., Roberts, S.J., 2004. Eradication of plant pathogens and nematodes during composting: a review. *Plant Pathology* 53, 548–568.
- Papavizas, G.C., 1970. Colonization and growth of *Rhizoctonia solani* in soil. In: Parmeter, J.R. (Ed.), *Rhizoctonia solani*, Biology and Pathology. University of California Press, Berkeley, CA, USA, pp. 108–122.
- Papavizas, G.C., 1968. Survival of root-infecting fungi in soil. IV. Effect of amendments on bean root rot caused by *Thielaviopsis basicola* and on inoculum density of the causal organism. *Phytopathology* 58, 421–428.
- Papavizas, G.C., Davey, C.B., 1960. *Rhizoctonia* disease of bean as affected by decomposing green plant materials and associated microfloras. *Phytopathology* 50, 516–522.
- Patrick, Z.A., Tousoun, T.A., 1965. Plant residues and organic amendments in relation to biological control. In: Baker, F.K., Snyder, W.C. (Eds.), *Ecology of Soil-borne Pathogens: Prelude to Biological Control*. John Murray Press, London, p. 571.
- Phillips, D.J., Watson, A.G., Weinhold, A.R., Snyder, W.C., 1971. Damage of lettuce seedlings related to crop residue decomposition. *Plant Disease Reporter* 55, 837–841.
- Preston-Mafham, J., Boddy, L., Randerson, P.F., 2002. Analysis of microbial community functional diversity using sole-carbon-source utilization profiles – a critique. *FEMS Microbiology Ecology* 42, 1–14.
- Ros, M., Hernandez, M.T., Garcia, C., Bernal, A., Pascual, J.A., 2005. Biopesticide effect of green compost against *Fusarium* wilt on melon plants. *Journal of Applied Microbiology* 98, 845–854.
- Rothrock, C.S., Kirkpatrick, T.L., 1995. The influence of winter legume cover crops on soilborne plant pathogens and cotton seedling diseases. *Plant Disease* 79, 167–171.
- Sabuquillo, P., De Cal, A., Melgarejo, P., 2005. Dispersal improvement of a powder formulation of *Penicillium oxalicum*, a biocontrol agent of tomato wilt. *Plant Disease* 89, 1317–1323.
- Scheuerell, S.J., Mahaffee, W.F., 2005. Microbial recolonization of compost after peak heating needed for the rapid development of damping-off suppression. *Compost Science & Utilization* 13, 65–71.
- Scheuerell, S.J., Sullivan, D.M., Mahaffee, W.F., 2005. Suppression of seedling damping-off caused by *Pythium ultimum*, *P. irregulare*, and *Rhizoctonia solani* in container media amended with a diverse range of Pacific Northwest compost sources. *Phytopathology* 95, 306–315.
- Schnurer, J., Rosswall, T., 1982. Fluorescein diacetate hydrolysis as a measure of total microbial activity in soil and litter. *Applied and Environmental Microbiology* 43, 1256–1261.
- Sneh, B., Jabaji-Hare, S., Neate, S., Dijst, G., 1996. *Rhizoctonia* Species: Taxonomy, Molecular Biology, Ecology, Pathology and Disease Control. Kluwer Academic Publishers, Netherlands.
- Snyder, W.C., Schroth, M.N., Christou, T., 1959. Effect of plant residues on root rot of beans. *Phytopathology* 49, 755–756.
- Stone, A.G., Traina, S.J., Hoitink, H.A.J., 2001. Particulate organic matter composition and *Pythium* damping-off of cucumber. *Soil Science Society American Journal* 65, 761–770.
- Sumner, D.R., Phatak, S.C., Gay, J.D., Chalfant, R.B., Brunson, K.E., Bugg, R.L., 1995. Soilborne pathogens in a vegetable double-crop with conservation tillage following winter cover crops. *Crop Protection* 14, 495–500.
- Szczec, M.M., 1999. Suppressiveness of vermicompost against *Fusarium* wilt of tomato. *Journal of Phytopathology* 147, 155–161.
- Szczec, M.M., Smolińska, U., 2001. Comparison of suppressiveness of vermicomposts produced from animal manures and sewage sludge against *Phytophthora nicotianae* Breda de Haan var. *nicotianae*. *Journal of Phytopathology* 149, 77–82.
- Tenuta, M., Lazarovits, G., 2002. Ammonia and nitrous acid from nitrogenous amendments kill the microsclerotia of *Verticillium dahliae*. *Phytopathology* 92, 255–264.
- Tenuta, M., Lazarovits, G., 2004. Soil properties associated with the variable effectiveness of meat and bone meal to kill microsclerotia of *Verticillium dahliae*. *Applied Soil Ecology* 25, 219–236.
- Termorshuizen, A.J., van Rijn, E., van der Gaag, D.J., Alabouvette, C., Chen, Y., Lagerlöf, J., Malandrakis, A.A., Paplomatas, E.J., Rämert, B., Ryckeboer, J., Steinberg, C., Zmora-Nahum, S., 2007. Suppressiveness of 18 composts against 7 pathosystems: variability in pathogen response. *Soil Biology and Biochemistry* 38, 2461–2477.
- Tilston, E.L., Pitt, D., Groenhof, A.C., 2002. Composted recycled organic matter suppresses soil-borne diseases of field crops. *New Phytologist* 154, 731–740.
- Tuitert, G., Szczec, M., Bollen, G.J., 1998. Suppression of *Rhizoctonia solani* in potting mixtures amended with compost made from organic household waste. *Phytopathology* 88, 764–773.
- Weller, D.M., Raaijmakers, J.M., Gardener, B.B.M., Thomashow, L.S., 2002. Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annual Review of Phytopathology* 40, 309–348.
- Whipps, J.M., 1997. Development in the biological control of soil-borne plant pathogens. *Advances in Botanical Research* 26, 1–84.
- Widmer, T.L., Graham, J.H., Mitchell, D.J., 1998. Composted municipal waste reduces infection of citrus seedlings by *Phytophthora nicotianae*. *Plant Disease* 82, 683–688.
- Wilhelm, S., 1951. Effect of various soil amendments on the inoculum potential of *Verticillium* wilt fungus. *Phytopathology* 41, 684–690.
- You, M.P., Sivasithamparam, K., 1995. Changes in microbial populations of an avocado plantation mulch suppressive of *Phytophthora cinnamomi*. *Applied Soil Ecology* 2, 33–43.
- Yulianti, T., Sivasithamparam, K., Turner, D.W., 2006. Saprophytic growth of *Rhizoctonia solani* Kühn AG2-1 (ZG5) in soil amended with fresh green manures affects the severity of damping-off in canola. *Soil Biology and Biochemistry* 38, 923–930.