Journal of Plant Pathology (2007), **89** (3), 311-324 *Edizioni ETS Pisa, 2007*

### INVITED REVIEW

# SUPPRESSION OF SOILBORNE FUNGAL DISEASES WITH ORGANIC AMENDMENTS

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## SUMMARY

The use of organic matter (OM) has been proposed, for both conventional and biological agriculture systems, to decrease the incidence of plant diseases caused by soilborne pathogens. In this work we review reports on the application of OM amendments, focusing on the suppressive capacity of different OM materials and the response of different soilborne pathogens. A total of 250 articles were analysed, with 2423 experimental case studies. The effect of OM amendments was found to be suppressive in 45% and non-significant in 35% of the cases. In 20% of the cases, a significant increase of disease incidence was observed. Compost was the most suppressive material, with more than 50% of cases showing effective disease control. The effect of crop residues was more variable: it was suppressive in 45% of the cases, but enhanced disease in 28%. Finally, significant disease suppression with peat was recorded only in 4% of the experiments. The ability of OM to suppress disease varied largely with different pathogens: it was observed in more than 50% of the cases for *Verticillium*, *Thielaviopsis*, *Fusarium* and *Phytophthora*. In contrast, effective control of *Rhizoctonia solani* was achieved only in 26% of the cases. From this review it emerged that OM amendments have great potential but, at the same time, present some inconsistencies in their application. More investigation on the mechanisms by which OM acts on disease suppression is needed to make the use of these materials more predictable.

*Key words*: Composts, crop residues, *Fusarium* spp., organic wastes, pathogen suppression, peats, *Phytophthora* spp., phytotoxicity, *Pythium* spp., *Rhizoctonia solani*, *Thielaviopsis basicola*, *Verticillium dahliae*.

## INTRODUCTION

Soilborne fungal and oomycete plant pathogens, among the major factors limiting the productivity of agro-ecosystems, are often difficult to control with conventional strategies such as the use of resistant host cultivars and synthetic fungicides. The lack of reliable chemical controls, the occurrence of fungicide resistance in pathogens, and the breakdown or circumvention of host resistance by pathogen populations (McDonald and Linde, 2002) are some of the reasons underlying efforts to develop new disease control measures. The ban of methyl bromide, the most effective fumigant used worldwide for soil disinfestation, has further increased the need for alternative control methods (Martin, 2003). In this context, the search for alternatives with high efficiency, low cost and limited environmental impact is a challenge for eco-sustainable modern agriculture.

The use of organic amendments such as animal manure, green manure (the incorporation of crop residues into the soil), composts and peats has been proposed, both for conventional and biological systems of agriculture, to improve soil structure and fertility (Magid *et al.*, 2001; Conklin *et al.* 2002; Cavigelli and Thien, 2003), and decrease the incidence of disease caused by soilborne pathogens (Litterick *et al.* 2004; Noble and Coventry, 2005). In the past century, the introduction of synthetic inorganic fertilizers, disease-resistant varieties and fungicides has allowed farmers to break the link between organic amendments and soil fertility (Hoitink and Boehm, 1999). As a result, organic materials such as crop residues and manure from essential resources became solid wastes. After the reduction of the organic input, soil organic matter decreased over time, soil fertility declined, and a large number of diseases caused by soilborne plant pathogens spread in agro-ecosystems (Zucconi, 1996; Hoitink and Boehm, 1999; Bailey and Lazarovits, 2003). Similar problems emerged for container-produced plants such as in nurseries of horticultural and ornamental species and soil-less systems (Hoitink and Boehm, 1999). However, a renewed interest in application of organic matter (OM) to soil, for control of soilborne pathogens, has been stimulated by public concern about the adverse effects of soil fumigants and fungicides on the environment, and the need for healthier agricultural products (Lazarovits, 2001).

Several studies have shown that organic amendments can be very effective in controlling diseases caused by

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pathogens such as *Fusarium* spp. (Lewis and Papavizas, 1977; Szczech, 1999), *Phytophthora* spp. (Gilpatrick, 1969; Szczech and Smolińska, 2001), *Pythium* spp. (McKellar and Nelson, 2003; Veeken *et al.*, 2005), *Rhizoctonia solani* (Papavizas and Davey, 1960; Diab *et al.*, 2003), *Sclerotinia* spp. (Lumsden *et al.*, 1983; Boulter *et al.*, 2002), *Sclerotium* spp. (Coventry *et al.*, 2005), *Thielaviopsis basicola* (Papavizas, 1968) and *Verticillium dahliae* (Lazarovits *et al.*, 1999). Different complementary mechanisms have been proposed to explain the suppressive capacity of organic amendments: enhanced activities of antagonistic microbes (Hoitink and Boehm, 1999), increased competition against pathogens for resources that cause fungistasis (Lockwood, 1990), release of fungitoxic compounds during organic matter decomposition (Smolińska, 2000; Tenuta and Lazarovits, 2002), or induction of systemic resistance in the host plants (Zhang *et al.*, 1996; Pharand *et al.*, 2002). However, despite the potential value of organic soil amendment, there are several concerns about its efficacy and potential side-effects that limit practical applications. For instance, some reports indicate that the effectiveness of OM amendment is variable and, in some cases, can enhance disease severity (Mazzola *et al.*, 2001; Tilston *et al.*, 2002; Pérez-Piqueres *et al.*, 2006). These negative effects of OM amendment were often associated either with increased inoculum of pathogenic fungi and oomycetes because OM provided the substrate for their saprophytic growth (Croteau and Zibilske, 1998; Manici *et al.*, 2004; Bonanomi *et al.*, 2006a), or with release of phytotoxic compounds (Cochrane, 1948, Patrick, 1971; Bonanomi *et al.*, 2006b) that may could damage plant roots and predispose them to pathogen attack (Patrick and Toussoun, 1965; Ye *et al.*, 2004). The inconsistent disease control results obtained with OM amendments, with both suppressive (disease reduction) and conducive (disease increase) effects, produced scepticism in farmers about the use of these materials. In addition, despite extensive research, no reliable methods are currently available to predict the effect of different OM amendments on soilborne pathogens (Erhart *et al.*, 1999; Scheuerell *et al.*, 2005; Termorshuizen *et al.*, 2007).

A number of sound reviews focus on different aspects such as the capacity of OM types to control a range of plant pathogens (Abawi and Widmer 2000; Akhtar and Malik, 2000; Litterick *et al.*, 2004; Noble and Coventry, 2005), and sustain the activity of beneficial microbes (Hoitink and Boehm, 1999); the application of compost "tea" and extracts (Scheuerell and Mahafee, 2002); the eradication of pathogens during composting (Noble and Roberts, 2004), and the properties of suppressive soils (Janvier *et al.*, 2007). However, some of these reviews focus on specific and selected aspects, and do not provide a quantitative and bias-free evaluation (Gurevitch and Hedges, 1993). The aim of this work is to provide a quantitative review of the available studies on the impact of OM application for control of diseases caused by soilborne fungal and oomycete pathogens. Analysis of the mechanisms underling OM suppressiveness and identification of parameters able to predict the effects of OM application are beyond the scope of this work, and are only cursorily discussed. Here we will focus on three main aspects: (i) the suppressive capacity of different OM materials, (ii) the response of different soilborne pathogens to OM amendment, and (iii) the relationship between OM disease suppressive ability and phytotoxicity.

## LITERATURE SEARCH, DATA COLLECTION AND ANALYSIS

**Literature search and data collection**. We searched for articles published between 1940 and 2006 concerning the effect of OM amendment on disease incidence and/or population response of fungal soilborne pathogens. The search was carried out in all international journals using online versions of the Biological Abstract, Blackwell Synergy, Science Citation Index, Science Direct, and within the APS*net* site. Key words used were "amendment", "compost", "crop residues", "damping-off", "green manure", "organic matter", "peat", "root rot", "soilborne pathogens", "suppression", "waste" and "wilt". Many articles were gathered from the literature of previously collected papers.

Criteria for article selection were decided a priori to avoid personal bias. Only articles containing quantitative data on disease incidence and/or severity and population response of pathogens were included.

The different types of OM utilized for amendment were classified in four broad groups: composts, crop residues, peats and organic wastes. Compost is organic material subjected to aerobic biological decomposition, during which temperatures of 40-70°C are reached as a result of microbial activity. This process allows both the sanitization of the material (from human and plant pathogens and weed seeds) and its stabilization. Detail about composting processes can be found in Zucconi and de Bertoldi (1987). Crop residues include non-decomposed materials such as green manure and non-harvestable plant remains (stems, roots, leaves, etc.). Peat is a natural product derived from the progressive accumulation of partially decayed vegetation (mosses and higher plants). Peats harvested in the superficial layers of bogs (light) and in the deeper layers (dark) were included. In this review, organic waste was the most heterogeneous category: it comprises all the organic materials not included in the previous three classes, such as undecomposed animal manure and by-products of different industrial processes such as fish, meat and bone meal (Tenuta and Lazarovits, 2004), paper mill (Croteau and Zibilske, 1998) and olive mill residues (Kotsou *et al.*, 2004).

**Data analysis.** The impact of OM amendments on disease incidence and severity caused by soilborne pathogens, compared to the non-amended control, was classified as: 1. suppressive, (significant disease reduction); 2. null, (no significant effect), and 3. conducive, (significant disease increase). Additionally, for each study we evaluated the percentage of suppressive experimental cases resulting in disease reduction >80% compared to the non-amendment control. This is the minimum disease control level considered adequate for farmers to use OM in conventional agricultural systems (Scheuerell *et al.*, 2005).

The impact of OM amendments on population densities of soilborne pathogens, compared to the non-amended control, was analyzed in three categories taking into account the following effects: 1. significant population reduction; 2. non-significant changes, and 3. significant population increase.

The OM application rate influences suppressive ability of different amendments. For each OM type, we calculated the average application rate in the experiments carried out either in controlled conditions (pot trials), or in open fields. Finally, we evaluated how OM application rate influenced disease suppression.

The phytotoxicity of each type of OM was assessed in two ways. First, we evaluated the frequency of occurrence of studies where phytotoxicity was recorded; second, we calculated the average, across all study cases, of the minimum application rate of OM at which phytotoxicity was noted. We considered that OM was phytotoxic when it reduced plant growth in treatments not inoculated with pathogens, and when the effect was not due to nutrient deficit. In a large number of studies, distinctive phytotoxicity symptoms (root browning, root tip dieback, etc.) were also reported.

## RESEARCH OVER THE LAST 70 YEARS

From all the studies examined, a total of 250 articles were chosen for analysis, with 1964 and 459 experimental studies assessing the effect of OM amendment on disease incidence and pathogen populations, respectively (Annex 1). Compost was the most studied OM type (n=1016; 51.7% of studies), with a continuous increase of published papers from the 1970s until today (Fig. 1a). Soil amendment with crop residues was also frequently investigated (n=586; 29.8% of the studies), with two peaks of research, in the 1960s and in the last 20 years (Fig. 1a). Less studied were peat and organic waste. However, the number of studies for these materials increased in the last two decades (Fig. 1a). The continuous increase of papers published in the last 30 years indicates the growing interest in this subject.

*Rhizoctonia solani*, with a large number of cases, was the most studied pathogen followed by *Pythium* spp. (Fig. 1b). For *Fusarium* spp. and *Phytophthora* spp. we recorded more than 150 studies, while for *Verticillium* spp., *Sclerotinia* spp., *Thielaviopsis basicola*, *Aphanomyces* spp., *Sclerotium* spp. and *Macrophomina phaseolina* the number of experiments studies ranged between 84 and 20 (Fig. 1b). The pathogens that were featured in fewer than 20 reports (data not shown) were not further analysed.

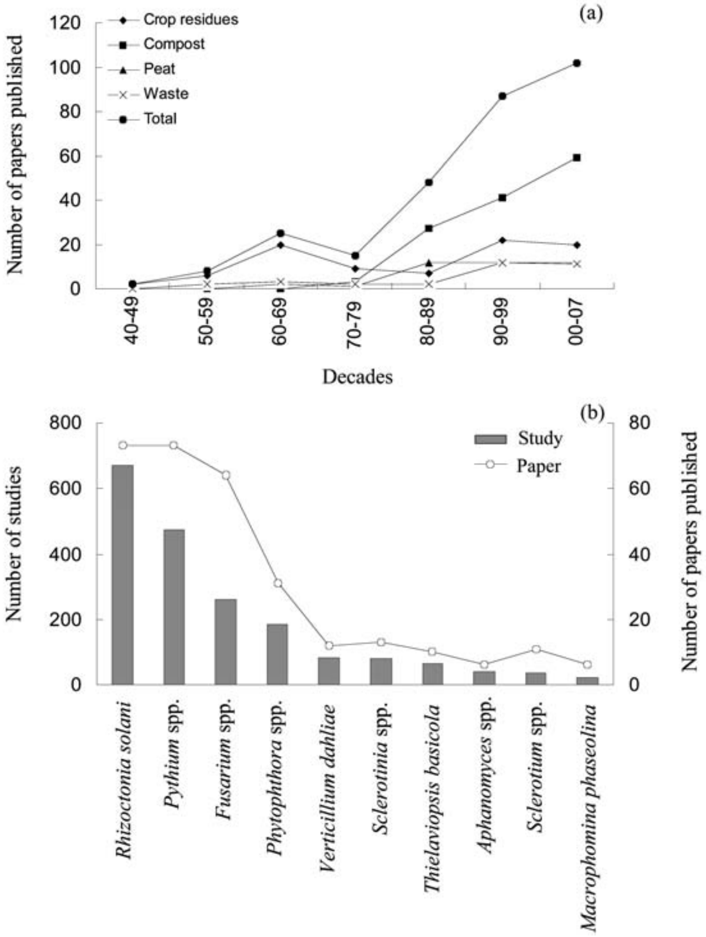

**Fig. 1.** Number of papers published in the last 70 years for different OM types (a), and for different species of pathogens (b). In the latter case the number of studies is also reported.

## EFFECT OF OM AMENDMENT ON DISEASE SUPPRESSION

Considering the effect of all OM types on all pathogens, OM was suppressive in 45% and non-significant in 35% of the cases, while in 20% a significant increase of disease incidence was found. OM amendment resulted was highly suppressive (disease reduction >80%) only in 12% of the cases.

**Disease suppression by OM amendment: a general comparison**. Suppressive capacity varied dramatically among different OM types (Fig. 2a). Composts and organic wastes were the most suppressive (>50%), and only in a few cases did these materials increase disease incidence (<12%). The effect of amendment with crop residues was more variable, and although they were often suppressive (45%), they could also be conducive (28%). Disease suppression with peat was rarely significant, and was recorded only in 4% of cases.

The suppressive capacity of the amendment, considering all OM types together, varied largely towards different pathogens (Fig. 2b). Suppression was very high for both *V. dahliae* and *T. basicola* (>65%), above 50% of cases for *Fusarium* spp., *Sclerotinia* spp. and *Phytophthora* spp. and slightly below 50% for *Pythium* spp. In contrast, effective control of *R. solani* was achieved only in 26% of cases (Fig. 2b). An increase of disease incidence was relatively rare (<15%) for *Verticillium* spp., *T. basicola*, *Fusarium* spp. and *Phytophthora* spp., but rose to 20% of cases for *Sclerotinia* spp. and *Pythium* spp.. *R. solani* was a remarkable exception, because the cases of conductivity enhancement (38%) exceeded those of suppression (26%). Control of *R. solani* with OM amendment is notoriously difficult (Krause *et al.*, 2001; Scheuerell *et al.*, 2005; Termorshuizen *et al.*, 2007). Some authors (Hoitink and Boehm, 1999) report that *R. solani* can be controlled only in the presence of specific antagonistic microbes (e.g. *Trichoderma* spp.) Obviously, this specific microflora is not consistently present in all OM types. The control of pathogens such as *Pythium*, *Fusarium* and *Phytophthora*, instead, has often been related to general suppression due to OM amendments (Baker and Cook, 1974; Weller *et al.*, 2002). In this case, a broad variety of microbial species create a competitive environment which is suppressive for pathogens (Serra-Whittling et al., 1996; Stone et al., 2001).

**Disease suppression: interaction between OM type and pathogen species**. In Table 1 we report the effect of different OM types on the six most studied pathogens. Compost application gave effective control in more than 55% of cases for all species studied, with the exception of *R. solani* (32%). The best result was for *Fusarium* spp. with successful control in 74% of cases. Organic waste was very effective in controlling V. dahliae, with not a single case of disease increase (Table 1). However, organic waste had rather variable effects on *R. solani*, *Fusarium* spp. and *Phytophthora* spp. Crop residues had variable effects towards different pathogens. *V. dahliae*, *T. basicola*, *Fusarium* spp. and *Phytophthora* spp. were predominantly suppressed, while *Pythium* spp. and *R. solani* were prevalently increased (Table 1). In this context, several studies showed that organic waste (Gilpatrick, 1969; Tenuta and Lazarovits, 2002) and crop residues (Wilhelm, 1951; Candole and Rothrock, 1997) with a low C/N ratio was very effective in the control of *Verticillium* spp., *T. basicola* and *Phytophthora* spp.

Finally, the use of peat showed similar results for all pathogens, with a large prevalence of non-significant or conducive effects, although some reports indicated significant suppression for *Pythium* spp. (Boehm *et al.*, 1997). Hoitink and Boehm (1999) suggested that the

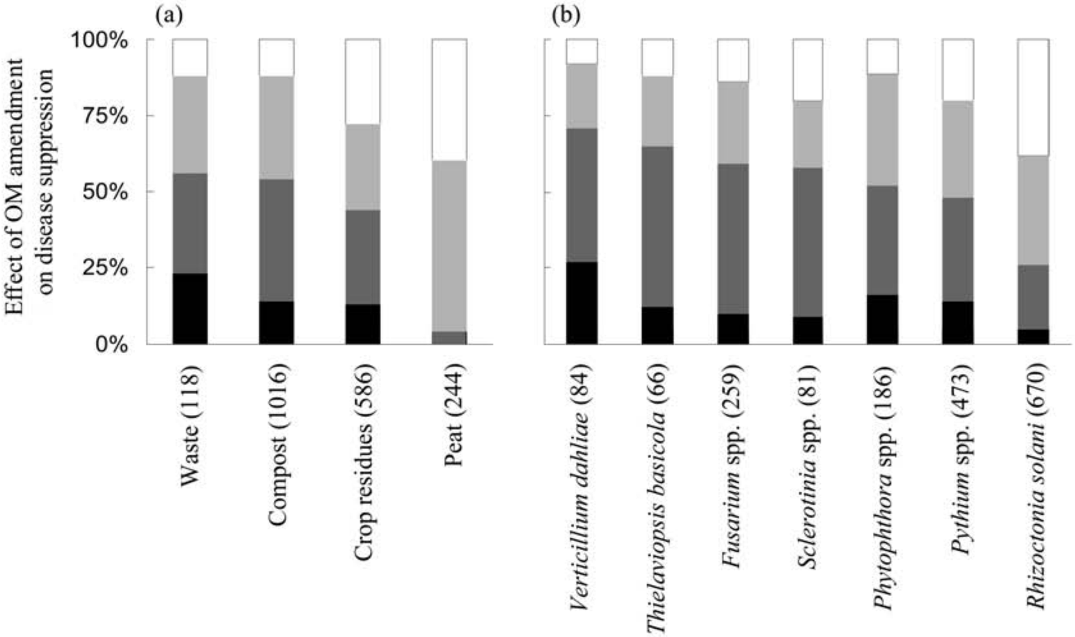

**Fig. 2.** Effect of OM amendments on disease suppression (black = highly suppressive, dark grey = suppressive, grey = null, white= conducive) in relation to different OM types (a) and soilborne fungal pathogens (b). Total percentage of suppressive cases is the sum of highly suppressive and suppressive. Only pathogens with more than 50 study cases (numbers in brackets) are shown.

**Table 1.** Effect of amendments with different OM types on diseases caused by the six most studied soilborne pathogens. Data are the percentage of cases with highly suppressive (HS), suppressive (S), null (N) or conducive (C) effects. The total suppressive cases are the sum of HS and S. Only combinations with at least 10 studies are shown.

| | *Rhizoctonia solani* | | | | *Pythium* spp. | | | | *Fusarium* spp. | | | | *Phytophthora* spp. | | | | *Verticillium dahliae* | | | | *Thielaviopsis basicola* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | HS | S | N | C | HS | S | N | C | HS | S | N | C | HS | S | N | C | HS | S | N | C | HS | S | N | C |
| Compost | 5 | 27 | 48 | 20 | 19 | 44 | 30 | 7 | 14 | 60 | 23 | 3 | 18 | 40 | 33 | 9 | 6 | 55 | 21 | 18 | - | - | - | - |
| Waste | 18 | 23 | 36 | 23 | - | - | - | - | 21 | 25 | 46 | 8 | 10 | 28 | 45 | 17 | 63 | 18 | 19 | 0 | - | - | - | - |
| Crop residues | 9 | 32 | 16 | 43 | 1 | 28 | 23 | 48 | 5 | 51 | 25 | 19 | 21 | 29 | 41 | 9 | 31 | 43 | 23 | 3 | 14 | 54 | 11 | 21 |
| Peat | 1 | 3 | 36 | 60 | 4 | 7 | 11 | 78 | 0 | 0 | 42 | 58 | 0 | 12 | 50 | 38 | - | - | - | - | - | - | - | - |

limited suppressive ability of peat was related to its low content of carbohydrates and easily degradable organic compounds that cannot sustain the activity of biocontrol agents. This hypothesis is corroborated by the observation that light peat, richer in carbohydrates, supports more microbial activity as measured by the rate of hydrolysis of fluorescein diacetate (FDA), compared to dark peat which is consistently conducive (Boehm et al., 1997).

In general negative or non-significant results are less likely to be published, and this could affect the data reported above. However, this caveat appears less important for recent studies which compare a very large number of OM materials and plant-pathogen systems (Erhart et al., 1999; Scheuerell et al., 2005; Termorshuizen et al., 2007), where the authors are more likely to have included non-significant and negative results.

**Application rate of OM amendments.** We found that the application rate considerably varied for different OM types, especially for studies carried out under controlled conditions (Fig. 4a). Average values were well below 5% (v/v) for organic wastes and especially for crop residues (1.3%). A large increase in application rate was recorded for composts, although variability was large (values from 1% to 100%), and for peats where the highest application rate was reported (Fig. 4a). Possible explanations for this pattern are discussed after the section on OM phytotoxicity. Application rates were less variable in field experiments (Fig. 4b), but the same trend was found (composts > wastes > residues).

In more than 50% of studies, increased application rate corresponded to increased disease suppression for crop residues, wastes and composts, but this was not found for peats, for which only two studies were avail-

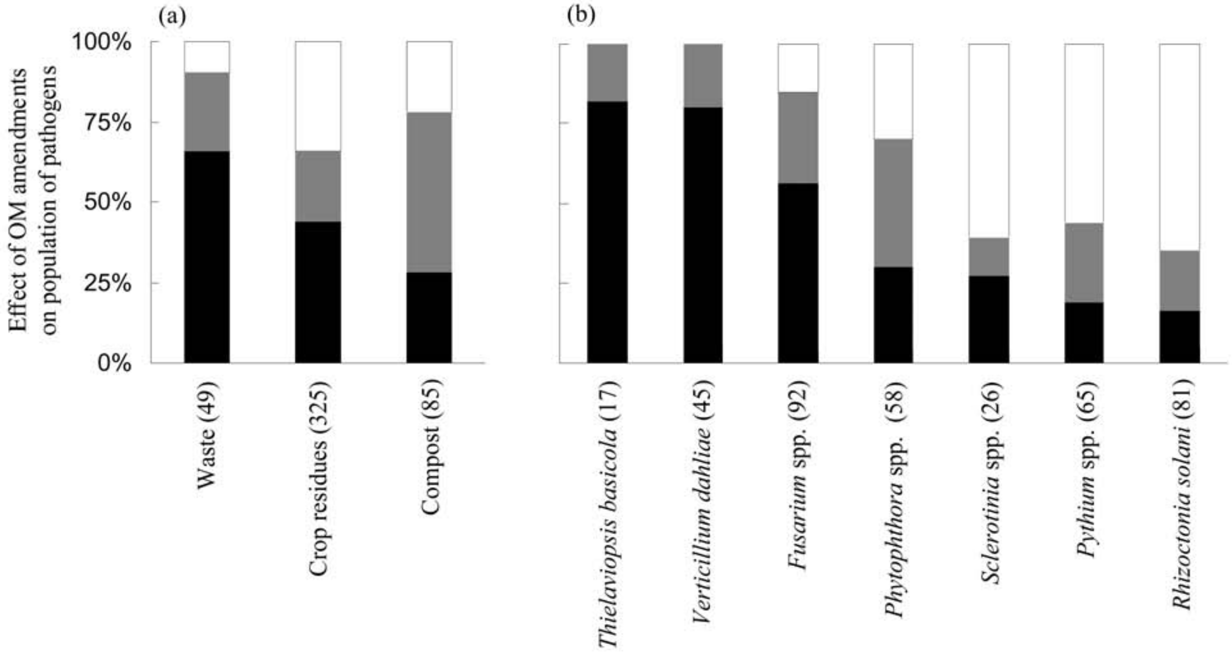

**Fig. 3.** Effect of OM amendments on population density of fungal and oomycetes pathogens (black = decrease, grey = null, white = increase) in relation to different OM types (a) and soilborne fungal pathogens (b). Only pathogens with more than 15 cases (numbers in brackets) are shown.

able (Fig. 4c). However, increased application rates resulted in significantly less disease suppression, for crop residues and organic wastes in about 30% of the cases. This effect was less frequent for compost (Fig. 4c). Several studies (Serra-Whittling *et al.*, 1996; Tuitert *et al.*, 1998; Diab *et al.*, 2003) reported that for compost an application rate of at least 20% (v/v) is necessary to achieve significant disease suppression. This contrasts with experiments where significant disease suppression was found with application of only 1% (van Os and van Ginkel, 2001; Pascual *et al.*, 2002).

## EFFECT OF OM AMENDMENTS ON PATHOGEN POPULATIONS

**Effect of different OM types.** The ability of different OM types to reduce pathogen populations was highest for organic waste, intermediate for crop residues and lowest for composts (Fig. 3a). However, it is interesting to notice that crop residues increased pathogen populations more frequently (34% of cases), compared to organic wastes and composts.

For crop residues, a key factor that affects the fate of pathogen populations is oxygen availability in amended soil. In aerobic conditions the effect of amendment on pathogen populations was very variable, and a decrease, no effect, and an increase of the population were observed, respectively in 36, 25 and 39% of the cases. One may argue that "crop residues" is a very broad category. In fact, this includes N rich tissue with a low C/N ratio (nitrogen fixer species such as *Trifolium* spp., *Medicago* spp., *Vicia* spp., etc.), cruciferous species rich in glucosinolates that are known for their antimicrobial activity after hydrolysis to isothiocyanates (Sarwar *et al.*, 1998), and N-poor residues with high C/N ratio (grasses, straw, wood chips, etc.). However, when the above categories were analyzed separately, either on the basis of their taxonomic classification (legumes *vs.* grasses *vs.* cruciferous) or C/N ratio, no consistent pattern emerged (data not shown). In contrast, in anaerobic conditions we found a significant reduction of the pathogen population density in all studies (n=41), irrespective of the type of residue utilized. Examples include *Verticillium* spp. (Menzies, 1962; Blok *et al.*, 2001; López-Escudero *et al.*, 2007), *R. solani* (Blok *et al.*, 2001), *Pyrenochaeta terrestris* (Watson, 1965) and several species of *Fusarium* (Blok *et al.*, 2001; Bonanomi et al., 2007).

This effect was not related to direct oxygen deficit, but to production of fungitoxic compounds such as methane, short-chain organic acids, aldehydes, alcohols and sulfur which are typical products of anaerobic OM decomposition (Ponnamperuma, 1972). Interestingly, this phenomenon has been observed with very different plant materials (e.g. broccoli, wheat straw, *Medicago sativa* residues, leaves of many wild species, etc.), thus suggesting that microbial anaerobic decomposition produces non-specific rather than crop-specific fungitoxic compounds.

**Pathogen population responses**. *V. dahliae* and *T. basicola* were the most sensitive species, with a significant population reduction in more than 80% of cases, and no report of population increase (Fig. 3b). In contrast, *Sclerotinia* spp., *Pythium* spp. and, especially, *R. solani* showed population increase in over 50% of the cases,

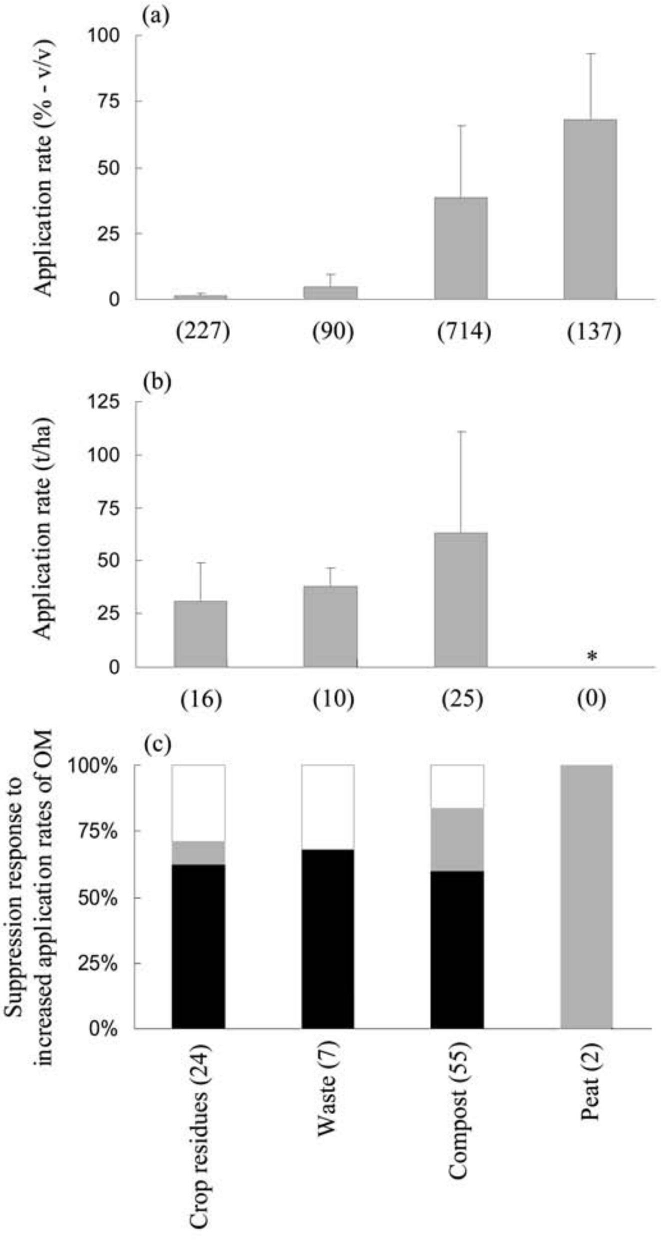

**Fig. 4.** Application rate of different OMs in controlled conditions (a), open field (b). In (a) and (b) values are average +1 SD; the number of study cases for each type of OM is indicated in brackets. Suppressive responses to increasing doses of OM (black = suppression increase, grey = no effect, white = suppression decrease) is shown in (c).

and a decrease only in a few experiments (Fig. 3b). *Fusarium* spp. and *Phytophthora* spp. showed intermediate behaviour (Fig. 3b).

Compost amendments had similar effects on *Pythium* spp. and *Pythophthora* spp. populations (Table 2), with a few negative cases and a majority of non-significant responses. Differently, *Fusarium* spp. showed population depression in many cases (Table 2). Organic waste was especially effective in reducing the populations of *V. dahliae* and *T. basicola*, but was less effective towards *Fusarium* species. *R. solani* also emerged in this case as an exception, with no cases of population decrease (Table 2). The population response to crop residues allowed the most complete comparison among pathogens, because of the largest number of studies available (n=312; 69% of total cases). Populations of *V. dahliae* and *T. basicola* were consistently reduced by amendment with crop residues, as previously reported for organic waste (Table 2). An intermediate behaviour, with either positive or negative responses, was observed for *Fusarium* spp. and *Phytophthora* spp. Finally, *Pythium* spp. and *R. solani* increased their population in the majority of the studies, and only rarely were negatively affected by the amendment (Table 2).

To explain the differential responses of the pathogens analyzed is not easy: we suggest that a significant amount of the observed variability could be related to the saprophytic capacity of the pathogens. Several *Pythium* species are aggressive saprophytes, especially on fresh plant residues such as green manure (Rothrock and Kirkpatrick, 1995; Sumner et al., 1995; Manici et al., 2004). The rapid spore germination and high growth rate of *Pythium* (Nelson, 2004) together with its ability to colonize senescent tissues, seems to confer on this fungus an advantage versus pure saprophyte species. However, since *Pythium* spp. are not good competitors in the soil, a general suppression could rapidly arise after amendment (Watson, 1970; Grünwald et al., 2000). Also *R. solani* is a strong and polyphagous saprophyte, but it is more competitive than *Pythium* spp. in presence of complex substrates rich in cellulose (Papavizas, 1970). This capacity is in part determined by its enzymatic arsenal (Sneh et. al., 1996), that allows *R. solani* to utilize materials with a broad range of C/N ratios (Papavizas and Davey, 1960), such as various crop residues (Sumner et al., 1995; Yulianti et al., 2006) and materials very poor in N (Croteau and Zibilske, 1998). In contrast, *V. dahliae* and, especially, *T. basicola* are known as poor saprophytes (Hood and Shew, 1997). This is consistent with the results summarized in Fig. 3 and Table 3. For instance, soil amendments with nitrogen-fixer species significantly reduced population density and disease incidence of *T. basicola*, but not that of *Pythium* spp. and *R. solani* (Rothrock et al., 1995). The different responses were related to the high sensitivity of *T. basicola* to ammonia released during the early stage of residue decomposition (Candole and Rothrock, 1997).

**Correlation between disease suppression and pathogen populations**. Comparison of data on the impact of amendments on disease suppression and pathogen population density showed that control of different soilborne pathogens is achieved in two different ways: eradicating the pathogens and inducing fungistasis in the soil, or inducing resistance in the host. Thus for *T. basicola* and *V. dahliae*, we found that disease control was almost always (>80% of cases) correlated with a significant reduction of the pathogen population. A similar, but less pronounced pattern was observed for *Fusarium* spp. Pathogen propagules of *T. basicola* and *Fusarium* spp. such as chlamydopores and macroconidia are often subject, after OM amendment, to rapid germination and subsequent lysis (Patrick and Toussoun, 1965; Papavizas, 1968) that in the absence of the host reduce the pathogen population. Bacterial colonization of germinating propagules is thought to be involved in the phenomenon, which remains poorly understood. A similar process has been reported for *Phytophthora cinnamomi* (Hoitink et al., 1977).

In contrast, for *R. solani*, but especially for *Pythium* spp., we found that disease control was only rarely (<30% and <10% of cases, respectively) correlated with significant reduction of pathogen populations. A large number of studies reported significant disease suppression with a corresponding increase, in some cases quite remarkable, of the pathogen population. Examples of this unexpected result have been reported by Croteau

**Table 2.** Effect of amendments with different OM types on population size of the six most studied soilborne pathogens. Data are the percentage of cases with decreased (D), not affected (N) or increased (I) populations. Only combinations with at least 5 studies represented are shown. Sufficient data were not available for peat.

| | *Rhizoctonia solani* | | | *Pythium* spp. | | | *Fusarium* spp. | | | *Phytophthora* spp. | | | *Verticillium dahliae* | | | *Thielaviopsis basicola* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | D | N | I | D | N | I | D | N | I | D | N | I | D | N | I | D | N | I |
| Compost | - | - | - | 6 | 72 | 22 | 67 | 20 | 13 | 18 | 50 | 32 | - | - | - | - | - | - |
| Waste | 0 | 67 | 33 | - | - | - | 54 | 31 | 15 | 100 | 0 | 0 | 82 | 18 | 0 | - | - | - |
| Crop residues | 10 | 15 | 75 | 25 | 7 | 68 | 50 | 25 | 25 | 31 | 38 | 31 | 78 | 22 | 0 | 82 | 18 | 0 |

and Zibilske (1998) for *R. solani* and by Schüler *et al.* (1989) for *P. ultimum*, among many others. Disease suppression in these cases has been related, often without clear experimental proof, to the induction of disease resistance in the host plants and/or to the induction of soil fungistasis.

The above examples clearly indicate how our current knowledge is still inadequate about the ecology of the saprophytic phase of soilborne pathogens and its role in pathogenesis. Further studies on the saprophytic capacity of different pathogens, also in comparison with other saprophytes which inhabit the soil, should greatly improve our ability to predict the impact of OM amendments.

## ORGANIC MATTER PHYTOTOXICITY AND DISEASE SUPPRESSION

OM phytotoxicity has often been considered an idiosyncratic phenomenon and consequently, an unpredictable side-effect of OM amendments. The present review, and recent studies on decaying litter in natural ecosystems, indicates that occurrence and intensity of phytotoxicity are measurable and predictable depending on the environmental conditions where decomposition occurs.

Our analysis shows that phytotoxicity largely varied among different OM types, according to the following rank: crop residues ≥ organic wastes > composts > peats (Fig. 5). In detail, the occurrence of OM phytotoxicity was high, above 10% of cases, for wastes and crop residues, much lower for composts, and null for peats (Fig. 5a). If the application rate of the amendment was also taken into account, the differences among organic materials became even more evident. The minimum application rate at which the phytotoxicity was detected, was very low for organic waste (4.7%) and especially for crop residues (1.9%), but this limit sharply increased for compost, until 50% v/v (Fig. 5b).

A limited number of studies (n=19) explicitly investigated the phytotoxicity dynamics of OM during the decomposition process (results are summarized in Fig. 5c). These experiments, all carried out in aerobic conditions, showed that as decomposition proceeds, phytotoxicity consistently declines. Only in a few cases was phytotoxicity constant, or an increase was followed by a decrease. Regularly increasing phytotoxicity during decomposition was never found (Fig. 5c).

Many ecological studies report the phytotoxic effects of decaying plant materials (review in Rice 1984). However, during decomposition, both the abundance and the activity of phytotoxic compounds continuously change over time because of their sorption and polymerisation on soil organic matter and clay minerals (Makino *et al.*, 1996), and because of chemical transformation by microorganisms (Blum *et al.*, 1999). Bonanomi *et al.* (2006b) showed not only a widespread presence of phytotoxicity in decaying plant litter, but also predictable dynamics in relation to both decomposition duration and environmental conditions. In detail, litter phytotoxicity was observed for different plant functional groups (nitrogen fixer > forbs = woody >> grasses–sedges), and all species tested (n=25) showed consistent patterns of phytotoxicity dynamics with a

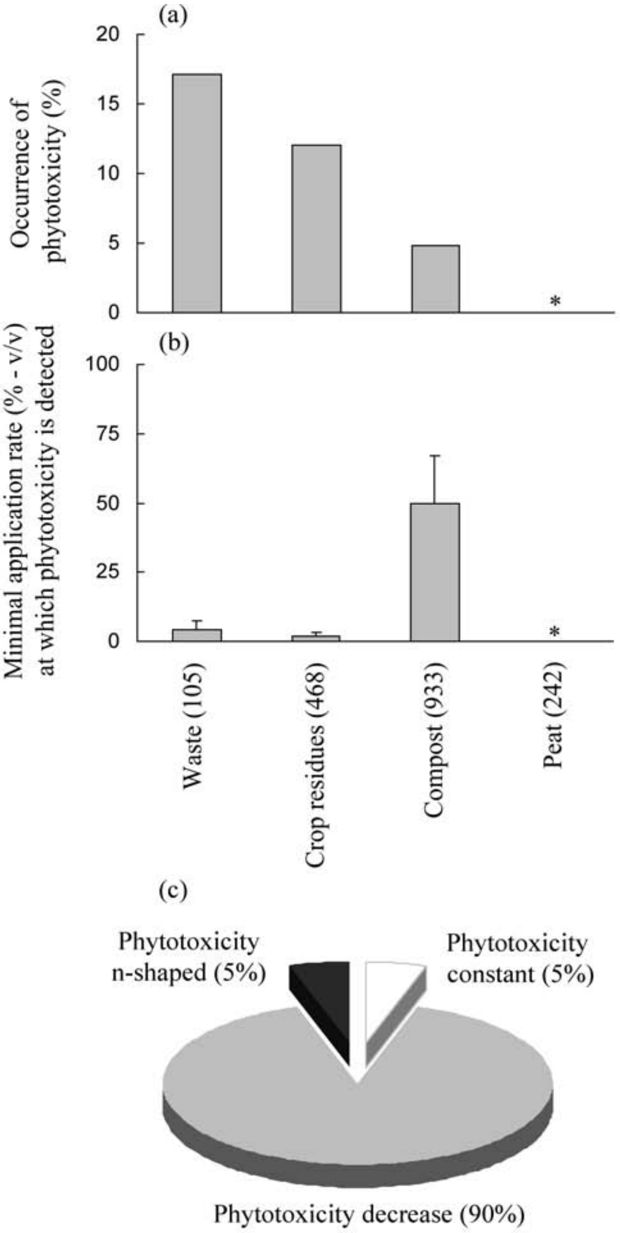

**Fig. 5.** Occurrence of phytotoxicity after amendments with different OM types (a), and minimal application rate with phytotoxic effects (b). Values are percentage +1 SD, for peat no cases of phytotoxicity were found (*). In (c) is shown the change of phytotoxicity during OM decomposition (n-shaped = phytotoxicity increase followed by a decrease during decomposition). Values are percentage (n=19).

rapid decrease, in aerobic conditions. In light of these findings, the observation that during decomposition of applied amendments, phytotoxicity rapidly decreased in aerobic conditions is coherent with the phytotoxicity rank described above. Crop residues and organic waste are undecomposed materials and showed the highest phytotoxicity. At the intermediate level, we have composts which are partially decomposed materials that have generally lost their phytotoxicity during composting (Zucconi *et al.*, 1981). Finally, peats completely lost their initial phytotoxicity during their long decomposition process. On this basis, we speculate that OM phytotoxicity is the main factor that determines the upper limit of the application rate of different OM types (compare Figs. 4a and 5b).

It should be pointed out that decomposition of OM in anaerobic or poorly aerobic conditions follows completely different pathways (Ponnamperuma, 1972), and OM phytotoxicity is clearly higher and more persistent in these conditions (Patrick, 1971; Bonanomi *et al.*, 2006b).

## TOWARDS RATIONAL MANAGEMENT OF OM AMENDMENTS FOR CONTROL OF SOILBORNE PATHOGENS

Diversity of both OM amendment types and plant-pathogen systems makes any generalization particularly difficult. Nevertheless, some suggestions about the application of OM for plant health management can be given.

**Crop residues and organic wastes.** OM amendments have multiple direct and indirect effects on the plant-pathogen-beneficial microbe system. Understanding the relative importance of these effects is important for management of crop residues and organic wastes. For these materials, the balance between negative effects (i.e. phytotoxicity and food base for pathogens) and positive effects (i.e. fungitoxic and fungistatic effects and resistance induction) is pivotal to avoid disease increase.

Promising results have been obtained with *T. basicola* and *V. dahliae*. Strong evidence indicates that the temporary accumulation of ammonia or nitrous acid (in acidic soils), following the application of crop residues or wastes with high N contents (C/N ratio below 10), are responsible for the eradication of *Verticillium* microsclerotia (Tenuta and Lazarovits, 2002). Unfortunately, these effects were very variable among different soil types, being more effective in sandy, OM-poor soils (Tenuta and Lazarovits, 2004). Detailed and quantitative knowledge of the pathways of the N cycle (ammonification, nitrification, denitrification, etc.) in different soils is necessary, for effective disease control and to avoid environmental pollution if large quantities are applied.

Positive results have also been achieved by using OM with high C/N ratios. These materials can stimulate microbial activity, which can in turn deplete N availability, and, consequently, impair the pathogen infection process (Snyder *et al.*, 1959). However, N starvation immediately after OM application can also impair plant growth (Seligman *et al.*, 1986; Michelsen *et al.*, 1995).

To avoid OM phytotoxic effects is a basic step for correct management of crop residues and wastes. This can be achieved by optimizing application rate and the timing between OM application and planting the crop. In the early stages of decomposition, and especially when the available oxygen is low as in water-logged soil, crop planting should be avoided, or at least delayed to avoid phytotoxicity. Unfortunately, it is impossible to generalize about how long planting should be delayed. If decomposition occurs anaerobically, OM generates adverse conditions for many phytopathogenic fungi, but unfortunately, also for plant growth. Applications of OM in conjunction with anaerobiosis, for example with the application of tarping, have been proposed (Blok *et al.*, 2001). Such conditions create indubitable fungitoxic effects but great care should be taken because of the intense phytotoxicity. These results emphasize the importance of studying both plant and pathogen responses to OM during decomposition. Special attention should be paid to choosing the application rate.

Finally, application of crop residues, and to a lesser extent of undecomposed organic wastes, should be avoided if the phytopathological problems are due to *Pythium* spp. or *R. solani*. These pathogens often respond positively to OMs and colonize them as nutrient substrates. *Sclerotium* spp. is another good example of such a pathogen, favoured by the presence of crop residues. Volatile compounds emanating from such residues can stimulate germination of sclerotia with a consequent overall increase of disease incidence and severity (Punja and Grogan, 1981).

**Compost.** Feedstock origin (Termorshuizen *et al.*, 2007), compost maturity (Tuitert *et al.*, 1998), and application rate (Serra-Whittling *et al.*, 1996; Tilston *et al.*, 2005) are the most important factors for predicting compost suppressivity. Phytotoxicity occurs only rarely with composts, and is limited to immature materials (Zucconi *et al.*, 1981; Widmer *et al.*, 1998) and very high application rates (Erhart *et al.*, 1999; Szczech and Smolińska, 2001).

Differently from organic wastes and crop residues, the suppression capacity of composts is only in a few cases due to eradication of pathogens. Induction of fungistasis (Serra-Whittling *et al.*, 1996) or systemic resistance (Zhang *et al.*, 1996; Pharand *et al.*, 2002) are alternative, although not mutually exclusive, explanations.

Composts are very effective for the control of several *Fusarium* spp. species (Table 3). The underlying mechanisms have been elucidated in some cases (Borrero *et al.*, 2004), but very little is known about the relationships between the chemical and microbiological characteristics of a compost and disease suppression.

Compost amendments are often suppressive for *Pythium* damping-off, but rather variable responses have been reported (Erhart *et al.*, 1999). In addition, several recent broad surveys (Craft and Nelson, 1996; Ben-Yephet and Nelson, 1999; Erhart *et al.*, 1999; Diab *et al.*, 2003; Scheuerell *et al.*, 2005) failed to identify chemical or microbiological parameters that consistently predict compost suppressivity. A promising parameter is FDA activity (Chen *et al.*, 1988), which includes several soil enzymes (non-specific esterases, proteases, lipases) related to organic matter decomposition (Nannipieri *et al.*, 2003). FDA has been found in several studies to positively correlate with soil disease suppressive capacity towards *Pythium* (Craft and Nelson, 1996; Stone *et al.*, 2001), but was unreliable in other cases (Erhart *et al.*, 1999).

Control of *R. solani* damping-off with composts was erratic and almost unpredictable based on any of the parameters that have been studied (Scheuerell *et al.*, 2005; Termorshuizen *et al.*, 2007). For example, Tuitert *et al.* (1998) found that immature and very mature composts were suppressive, but at an intermediate maturity level it was conducive. In spite of the enormous number of studies carried out (total n=670; n=272 for composts), *R. solani* is still the most problematic pathogen. Considerable research will be required to obtain acceptable control of this pathogen with these materials.

**Peat.** Peat is the most utilized material for the preparation of potting mix in nursery systems, for both horticultural and ornamental species. Constant chemical and physical properties such as high water retention capacity, optimal porosity and controlled pH are the main benefits of using peat. Unfortunately, this material is hardly ever suppressive to soilborne pathogens (Fig. 2a and Table 1). Moreover, use of peat will probably be discouraged because of its limited sustainability and negative impact on global climatic changes (it is a source of greenhouse gases). In this view, the substitution of peats with composts seems to be promising, as demonstrated by successful applications in some countries (USA, The Netherlands, etc.).

## CONCLUSIONS AND FUTURE DIRECTIONS

There is an urgent requirement to find sustainable strategies for the control of soilborne diseases, for both conventional and low-input farming systems. In the last 70 years a massive number of studies have been carried out on the subject of OM amendments for the control of plant diseases, and this technique appears to be one of the most promising for its low cost and the limited environmental impact compared to fungicides and fumigants. However, the picture that emerges from this review is that OM amendments have great potential but give inconsistent control and sometimes increased disease severity and phytotoxicity, factors which still limit their use. There is no doubt that the benefits of OM amendments far outweigh their drawbacks but while the impact of this technique on pathogen populations and disease suppression remains unpredictable, farmers may be justified in ignoring it as a tool for controlling soilborne pathogens.

Significant progress has been made towards understanding the biology of disease suppression by OM amendments in specific plant-pathogen systems, such as peat-*Pythium* (Boehm *et al.*, 1997), leaf compost-*Pythium* (McKellar and Nelson, 2003), N-rich waste-*V. dahliae* (Lazarovits, 2001), compost-*F. oxysporum* f.sp. *lycopersici* (Borrero *et al.*, 2004) etc.

However, still lacking are reliable guidelines to predict the impact of any type of OM amendment on specific soilborne diseases. In this context, we doubt that further studies with the aim of immediate application would produce a remarkable increase of in our general understanding of this subject. To attain significant progress, we suggest concentrating research on the following topics:

1. Investigating how different OM types modulate plant-pathogen-antagonist relationships;
2. Developing OM amendments able to enhance the activity of beneficial microbes, without stimulating pathogen populations and virulence;
3. Improving the effectiveness of combined applications of OM amendments and biological control agents;
4. Identifying parameters that consistently predict the suppressive ability of different OMs;
5. Developing models able to integrate all the available information.

Rapid answers to these questions are needed to predict how and when OM suppression occurs, and to avoid possible detrimental effects.

## ACKNOWLEDGEMENTS

The authors dedicate this work to the memory of Prof. Giovanni Del Sorbo, prematurely deceased in the autumn of 2004. We are grateful to the reviewers for their constructive comments.

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Received June 12, 2007
Accepted July 9, 2007