CONTROL OF POWDERY MILDEW (*ERYSIPHE POLYGONI*) IN TOMATO BY FOLIAR APPLICATIONS OF COMPOST TEA

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SUMMARY

The use of compost tea extracts to control leaf diseases is an alternative that enables the use of chemicals in agriculture to be reduced. However, little is known about the mechanisms responsible. We examined an aerated compost tea prepared from composted market and garden wastes and tested its effect on naturally occurring powdery mildew disease produced by the foliar pathogen *Erysiphe polygoni* in tomato plants (*Lycopersicon esculentum* cv. Roma) grown in perlite in an unheated greenhouse. Untreated plants showed whitish patches of powdery mildew, while in the treated plants the mycelium could hardly be seen and leaves only showed localized yellow spots corresponding to former sites of infection. Tea compost reduced disease incidence by 19% when used as a preventive treatment and eradicated the pathogen on the leaves when applied as a curative treatment. Treatment was not associated with increased peroxidase or chitinase activity in the leaves and induction of local resistance is unlikely to have been responsible. Instead, the effects of the compost could be due to the presence of bacteria and fungi, which may act as antagonists to the pathogen. The compost was rich in inorganic salts, organic carbon and phenols, which can affect pathogen growth and phyllosphere microorganisms.

Key words: biological control, compost tea, powdery mildew, tomato.

INTRODUCTION

Powdery mildew is a widespread leaf disease that affects several vegetable crops, in the field and in the greenhouse (Bourbos *et al*., 1999; Matsuda *et al*., 2001). Commercial cultivars have shown different degrees of susceptibility to powdery mildew (Olalla and Tores, 1998; Kiss *et al*., 2001; Matsuda *et al*., 2001, Utkhede *et al*., 2001). The increasing public outcry against pesticides and growing legislative pressure to reduce their use in agriculture has generated an interest in the use of compost and compost extracts (compost tea) to prevent and control diseases in warm regions of intensive horticulture such as the Iberian Peninsula (http://ec.europa.eu/food/plant/protection/evaluation/exist_subs_rep_en.htm; UNEP, 2002). An increasing number of studies have described the use of compost extracts in controlling leaf diseases. In those studies, compost extracts prepared from various organic materials were assayed either *in vitro,* on detached leaves, or in the field. Such extracts have been used successfully to control leaf diseases caused by *Botrytis cinerea, Venturia inaequalis,* and powdery and downy mildew, sometimes with an effectiveness similar to conventional fungicides (Weltzien and Ketterer, 1986; Weltzien, 1991; Ketterer *et al*., 1992; McQuilken *et al*., 1994; Cronin *et al*., 1996; Hoitink *et al*., 1997; Litterick *et al*., 2004). Compost tea drench applied to the substrate also reduced soil diseases (Scheuerell and Mahaffee, 2004; Litterick *et al*., 2004). However, to date, extracts from compost tea have been poorly characterised (Scheuerell and Mahaffee, 2004, 2006). Moreover, their role in activating plant defence mechanisms has hardly been studied (Haggag and Saber, 2007; Siddiqui *et al*., 2009), although chitinase and peroxidise activities are simple and reliable parameters of plant disease resistance (Yedidia *et al*., 1999; Segarra *et al*., 2007b).

In this study we tested the effect of an aerated compost tea on a naturally-occurring disease produced by the leaf pathogen *Erysiphe polygoni* in tomato plants in an unheated greenhouse. We also characterised the compost tea chemically, physicochemically and microbiologically and the tomato leaf environment microbiologically and ultrastructurally, in order to explore the mechanisms of action. A growth chamber experiment was used to study the induction of plant defence mechanisms by compost tea.

MATERIALS AND METHODS

Greenhouse cultivation of tomato plants. *E. polygoni*

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disease was evaluated in tomato plants grown in an unheated greenhouse. Tomato (*Lycopersicon esculentum* cv. Roma) seeds (Semillas Fitó, Spain) were sown on vermiculite seedling trays, and 25 days later two seedlings per pot were planted in perlite in 10 l pots. The greenhouse had been severely infected by *E. polygoni* in the previous season. Plant density was 5.44 plants m^{-2}, about double the usual tomato density (Serrano, 1999).

Plants were irrigated using 2 litres/h^{-1} drippers, with a half-concentrated, modified Hoagland solution controlled by an irrigation controller (AMI 5000, DGT Volmatic, Denmark). Air temperature and environmental humidity were recorded with a datalogger (SDL 5250, UK). Drainage was kept between 20 and 40%. During the experiment, the greenhouse mean air temperature was 15.7ºC (8.5 to 27.0ºC). Mean air relative humidity was 60.1% (18 to 85%).

Compost tea treatment. Aerated compost tea was prepared weekly in a 10 l bucket, with 0.4 l of compost and 2 l of tap water (1:5, v:v), adapted from Weltzien (1991). Initially the mix was manually agitated and then aerated with a small air compressor (Rena Air 200, France) for 7 days. Before application, the compost tea was filtered through filter paper to remove large solid particles. The compost was obtained from market, urban and garden wastes composted in a tunnel system (Metrocompost S.A., Barcelona, Spain). This compost has been reported to be suppressive against *Fusarium oxysporum* f. sp. *lycopersici*, in tomato plants (Cotxarrera *et al*., 2002). When the first *E. polygoni* infected leaves were observed (two months after sowing), plants were separated into 10 plots of 12 plants each, using curtains of clear 100 µm polyethylene. Applications of compost tea were then made in five of these plots alternately situated in the greenhouse, using a manual low pressure sprayer; this was omitted in the other five plots, which were treated with the same amount of tap water (1.5 l for the five plots). Compost tea was sprayed five times (once per week), until the end of the experiment. No other materials were applied during the experiment.

Disease evaluation. At the end of the experiment the percentage of leaves affected by powdery mildew was determined in each plant by counting diseased leaves out of the total number of leaves.

Characterisation of compost tea. pH and electrical conductivity of the compost tea were measured for each batch in a water extract (2:1, vol/vol), as described by Gabriëls *et al*., (1991). Total carbohydrate, phenol and organic carbon content of the compost was determined in the first batch according to the methods by Whistler *et al.* (1965), Horwitz (1960), and Nelson and Sommers (1996). Elemental analysis (K, Ca, S, Mg, P, Fe, B, Zn, Mo, Ni and Mn) of the compost tea was made on 10 ml of the first batch. Nitric acid was added to the compost tea (1% final concentration), and the elements were detected by inductively coupled plasma optical emission spectrometry (ICP-OES), using a Perkin Elmer Optima-3200 RL apparatus (Segarra *et al*., 2007a).

Ultrastructural characterisation of tomato leaves. At the end of the experiment, five leaf tissue samples from each treatment were taken for electron microscope examination. Leaf fragments were fixed in 2% paraformaldehyde and 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.2), post-fixed in 1% osmium tetroxide and 0.8% potassium ferrocyanide in the same buffer, dehydrated in a graded acetone series and embedded in Spurr's resin. Thin sections (0.5 µm) were used to select zones to explore under the electron microscope. Ultrathin (50-80 nm) sections were cut with an ultramicrotome (Leica Ultracut UCT, Germany) using a diamond knife. They were then mounted on Cu grids and post-stained, first with 2% uranyl acetate for 10 min, then with lead citrate for 20 min. Observations were made with a Jeol EM 1010 transmission electron microscope, operated at 80 kV.

Microbiological characterisation of compost tea and tomato leaves. At the end of the experiment, leaf tissue samples from treated and untreated plants were collected from healthy and diseased/yellowed zones for microbe population determination. From each treatment 10 discs 12.56 mm^2 in size were collected and agitated in 9 ml of water-agar (0.6 g l^{-1}). Samples from the compost itself were also included. The samples were serially diluted in water-agar and plated onto selective media to quantify the populations of filamentous fungi (water-agar, with 18 g l^{-1} agar and 50 µg ml^{-1} rifampicin) and cultivable bacteria (4% Scharlab tryptone soy agar with 100 µg ml^{-1} cycloheximide), adapted from Scheuerell and Mahaffee (2004).

Growth chamber cultivation of tomato plants. Enzymatic activity related to plant defence mechanisms (peroxidase and chitinase) of tomato leaves treated with compost tea was measured in plants cultivated in a growth chamber. Temperature was kept at 25±2ºC and photoperiod was 16 h light/8 h darkness. Seeds were germinated on vermiculite and fertilized with half-concentrated modified Hoagland nutrient solution. Two weeks later, tomato plantlets were transplanted to 400 ml pots containing perlite as a substrate, four plants per pot and 5 pots per treatment. The pots were arranged in a fully randomized design.

There were three treatments: (i) plants sprayed with tap water; (ii) plants sprayed with unfiltered compost tea; (iii) plants sprayed with compost tea filtered through 0.2 µm Nalgene syringe filters to eliminate mi-

croorganisms. The treatments were applied on the day of planting and after 3, 7, 10, 14, 17 and 21 days.

Measurement of enzymatic activities. Three samples (each consisting of the whole aerial part of the plant) from three different pots per treatment were used to measure enzymatic activities at four different time points: 10, 14, 17 and 21 days after planting, just before the corresponding compost tea application. Samples were ground under liquid N_2 and peroxidase and chitinase activities were measured according to Yedidia *et al.* (1999). Briefly, the homogenate was suspended in phosphate buffer, centrifuged (10,000*g* for 5 min) and the supernatant was assayed. Peroxidase was determined spectrophotometrically with phenol red as a substrate. The chitinase assay was based on colorimetric determination of p-nitrophenyl cleaved from a chitin-analogous substrate (Yedidia *et al.*, 1999).

Statistical analyses. The percentage of infected leaves per plant (the data followed a normal distribution and had homogeneous variances) and the total number of leaves per plant were analyzed with a paired t-test. Fungal and bacterial populations were analysed with one-way ANOVA. Chitinase and peroxidise activities from growth chamber plants within each sampling day were analysed with one-way ANOVA. Statistical analyses were performed with SPSS 14.0 (SPSS Inc., USA).

RESULTS

Despite the favourable atmospheric conditions and the high plant density, no disease or pest other than *E. polygoni* were observed during the experiment

Leaves of *E. polygoni*-infected tomato plants showed whitish powdery mildew patches (Fig. 1a), mainly present on the upper surface and sometimes on the stems. By contrast, leaves of compost-treated plants showed localized yellow spots (Fig. 1b), some of them with necrotic centre. When disease incidence was scored at the end of the assay, yellow spots in compost tea-treated plants were considered to be former points of fungal infection and were taken into account for disease incidence scoring. Compost tea treatment (41% infected leaves) reduced the incidence of the disease by 19% compared to untreated plants (51% infected leaves) (Table 1). Application of compost did not significantly affect the number of leaves per plant (Table 1). However, plants treated with compost tea appeared to be greener than untreated plants.

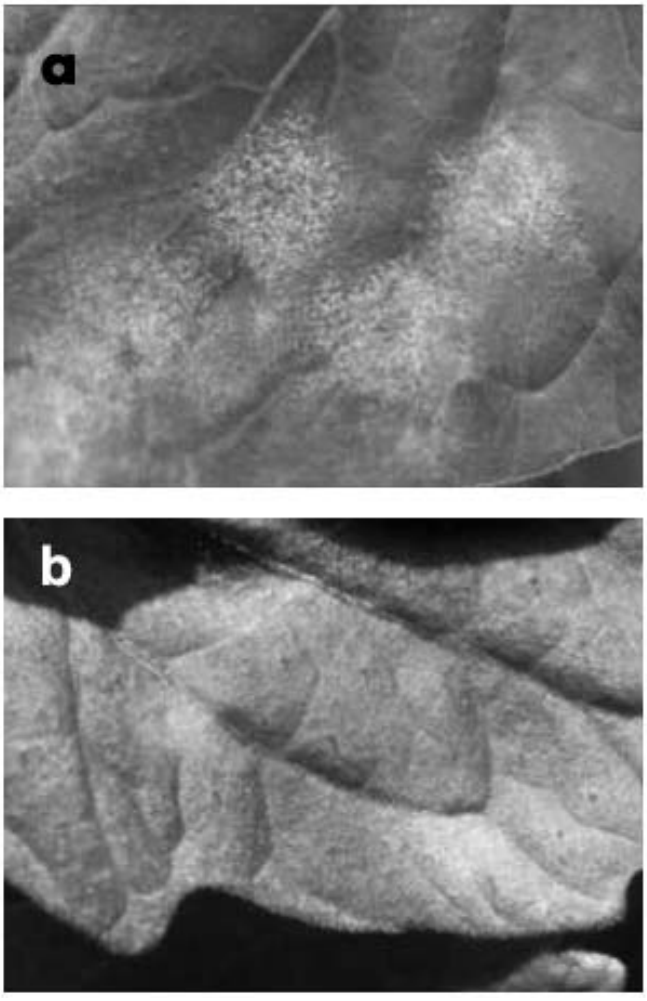

Fig. 1. General aspect of affected tomato leaves from (a) untreated control plants and (b) compost tea-treated plants. (a) Whitish spots with presence of pustules of powdery mildew on untreated leaves. (b) Yellow areas on compost tea treated leaves.

The results of the chemical and physicochemical characterization of the compost tea are shown in Table 2.

Compost tea treatment significantly increased the total number of fungi in the phyllosphere compared to control (Table 3). In healthy areas, compost treatment also increased the total counts of bacteria compared to untreated leaves (Table 3).

Transmission electron micrographs showed that yellow areas (compost-treated) had some adaxial epidermal cells from the first layer with a non-functional cyto-

Table 1. Incidence of powdery mildew disease and total number of leaves per plant.

Treatment	Percentage of infected leaves per plant[a]	Total number of leaves per plant[a]
Compost tea-treated	41.6±2.5 a	14.7±0.6 a
Control	51.4±3.3 b	13.4±0.6 a

[a]Different letters represent significant differences between treatments (paired t-test, $P < 0.05$).

plasm and the presence of the fungi outside but not inside the plant cells (Fig. 2a). In other cases, adaxial epidermal cells showed a well-functioning cytoplasm with normal organelles (mitochondria) and endoplasmic reticulum). The mesophyll cells showed an abundance of endoplasmic reticulum, mitochondria and well developed and functional chloroplasts with plastoglobuli and thylakoid membranes. When samples from white patches (untreated) were observed, host cytoplasm destruction and the haustorial body of *E. polygoni* inside the adaxial epidermal cells could be detected (Fig. 2b). The haustorial neck and suspected entry point of the fungi could be observed in various samples (Fig. 2b). The fungus present outside the epidermal cell wall in untreated infected leaves was abundant (Fig. 2b). When green healthy areas were observed from both treated and untreated plants, normal functional epidermal and mesophyll cells were seen.

Peroxidase and chitinase activity of tomato plants grown in a growth chamber, both untreated and treated with compost tea (filtered or not), showed no significant differences between treatments (Fig. 3a and 3b) during the study period.

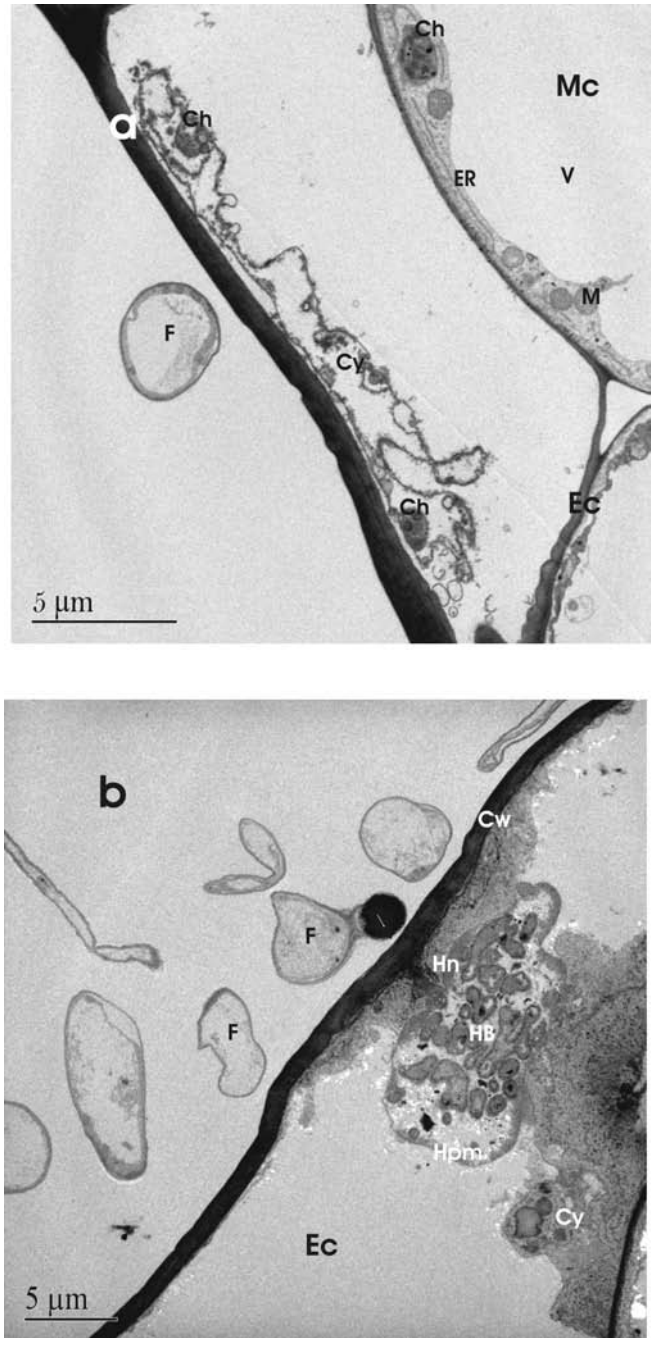

Fig. 2. Transmission electron micrograph sections of tomato leaves affected by *Erysiphe poligoni*: (a) yellowed area from a compost tea treated plant and (b) white pustule from an untreated plant. (a) Presence of the fungus outside with non-functioning cytoplasmic epidermal cell and healthy mesophyll cell. (b) Presence of fungus outside the epidermal cell wall and fungus haustorial body with accumulation of different electron-dense substances. Ch, chloroplast; Cw, host cell wall; Cy, host cytoplasm; Ec, epidermal cell; ER, endoplasmic reticulum; F, fungus; HB; fungus haustorial body; Hn, suspected haustorial neck; Hpm, host plasma membrane; M, mitochondrion; Mc, mesophyll cells; V, vacuole. Arrow close to an electron dense vesicle of fungus indicates presumed location of an appressorium on tomato epidermis.

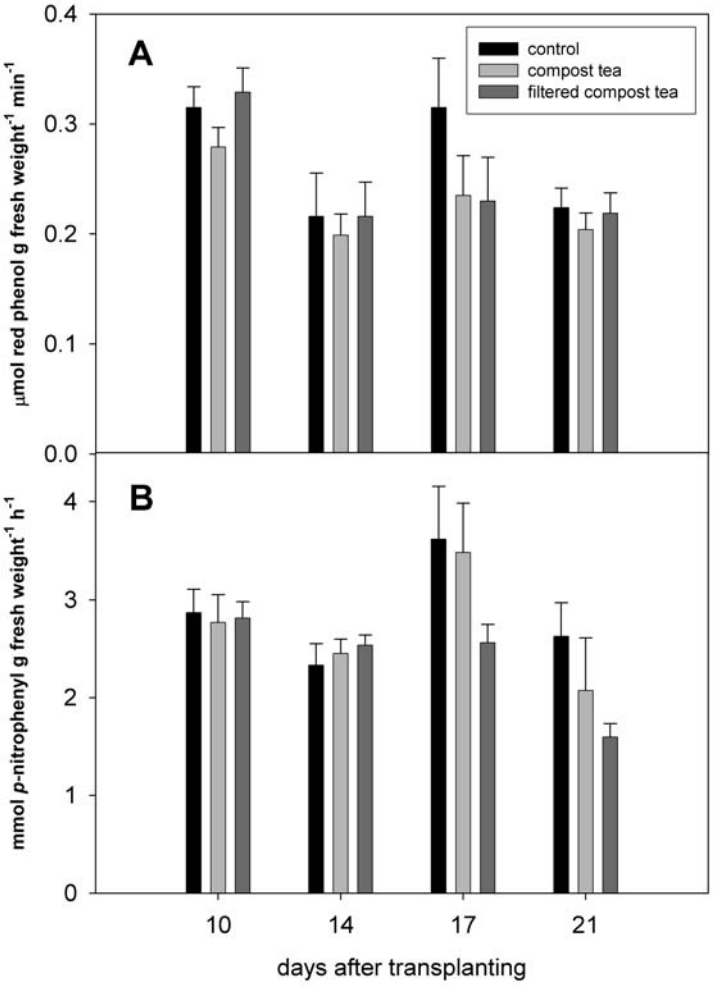

Fig. 3. Peroxidase (A) and chitinase (B) activities of tomato leaves, at different time points after transplanting that had been treated or not with filtered or unfiltered compost tea.

DISCUSSION

The application of compost tea on tomato leaves led to the disappearance of the white patches typical of powdery mildew infection caused by *E. polygoni*, and their substitution by yellow spots that appeared to be areas with little or no pathogen mycelium when observed microscopically. Most of the epidermal cells in these areas were healthy, although a few had non-functional cytoplasm. All the mesophyll cells were healthy. Thus, compost tea killed or removed the pathogen from the leaves when applied as a curative treatment. Moreover, our results show that the percentage of affected leaves was reduced by 19% in compost-treated plants, indicating that the compost acted as a preventive treatment.

When compost teas are applied to foliage, there may be direct effects on the pathogen and indirect effects through improvement in plant resistance (Weltzier and Ketterer, 1986; Diver, 1998; Ketterer *et al.*, 1992; Weltzier, 1991; Litterick *et al.*, 2004). In the present study, inducible enzymes which play a role in disease resistance (peroxidase and chitinase) were not activated by compost tea treatment. Other authors report an increase in peroxidase, polyphenol oxidase and phenylalanine ammonia lyase in okra plants (Siddiqui *et al.*, 2009) and an increase in peroxidase, β-1,3-glucanase and chitinase in tomato and onion plants (Haggag and Saber, 2007). In our system, the lack of response in the plant could be understood as a priming effect, where the plant defences would only be activated by the further presence of the pathogen. If so, the effects of compost tea could be comparable to the effect of beneficial microorganisms in the induction of plant resistance (ISR) by priming (Segarra *et al.*, 2009). Other studies have shown an initial increase in defence enzymatic activity by compost tea in okra plants, and a further increase was noted after pathogen challenge (this phenomenon is more typical of systemic/local acquired resistance) (Siddiqui *et al.*, 2009). Moreover, it has been reported that mild salt stress induced systemic resistance against another powdery mildew and grey mould in cucumber plants (Reuveni *et al.*, 2000; Segarra *et al.*, 2007a).

Interactions between microorganisms applied in the compost tea and the studied pathogen are likely to have occurred. In fact, in most composts, sterilization of the extract reduces its protective activity (Weltzien *et al.*, 1991). In contrast, the efficacy of compost tea against *Xanthomonas vesicatoria* on tomato was not affected by

Table 2. Chemical and physicochemical characterization of the compost tea.

Macronutrients (mmol l^{-1})		Micronutrients (µmol l^{-1})	
P	0.11	Fe	10.57
K	16.62	Mn	<0.46
Ca	1.43	Zn	1.38
Mg	0.59	B	51.85
S	1.38	Mo	<0.52
		Ni	<0.85
Carbohydrate content[a]			87.64
Total organic carbon[b]			40.59
Phenol content[c]			52.24
pH			8.4
Conductivity (dS m^{-1})			3.89

[a] ppm of glucose equivalents; [b]mg organic carbon 100 ml^{-1}; [c]ppm of tannic acid equivalents

Table 3. Microbial characterization of compost tea and tomato leaves where compost tea was either applied or not.

			Mean values (log_{10}) ± SE[a]	
Material			Total fungi[b]	Total bacteria[c]
Compost tea[d]			3.12 ± 0.08	6.75 ± 0.06
Leaves[e]	Compost tea treated	Yellowed	2.92 ± 0.13a	3.05 ± 0.09a
		Healthy	2.89 ± 0.05a	2.86 ± 0.06a
	Control	Pustules	2.42 ± 0.03b	3.15 ± 0.27a
		Healthy	2.20 ± 0.07b	2.19 ± 0.11b

[a] n=10. For leaves, within each column, values with different letters are significantly different (ANOVA, $P<0.05$) according to Duncan's test; [b]Cultured in water agar (18 g l^{-1} agar), with 50 µg ml^{-1} rifampicin; [c]Cultured in 40 g l^{-1} tryptone soy agar with 100 µg ml^{-1} cycloheximide; [d]Microbial populations of compost tea expressed as CFU ml^{-1}; [e]Microbial populations on tomato leaves expressed as CFU cm^{-2}.

filtration or sterilization (Al-Dahmani *et al*., 2003). Moreover, in other studies, no significant relationship was found between the number of bacteria in several compost teas and disease suppression against *Pythium ultimum* (Scheuerell and Mahaffee, 2004). Compost tea may also be a source of nutrients (inorganic salts and carbon sources) both for the newly applied microorganisms and for the autochthonous microbial population. Moreover, the nutrients may have produced a shift of the autochthonous microbial populations from oligotrophy (sparse organic nutrients) to dominant or transient copiotrophy (abundance) conditions. The beneficial effects of naturally-occurring saprophytes against the pathogen should be taken into account in this case, since no fungicide had been previously applied to the leaves and microorganisms are frequently limited on the leaf surface by scarcity of either water or nutrients (Andrews and Harris, 2000). All these changes in the microorganisms might interfere with the pathogen. In addition, moderate quantities of the nutrients applied in the composted tea might affect, and even inhibit, spores of *E. polygoni*, as described for biotrophic pathogens (Blakeman and Fokkema, 1982; Dik, 1991).

Specifically, the amounts of calcium, potassium and magnesium in the compost studied were much lower than those of foliar sprays applied to reduce powdery mildew on tomato (Ehret *et al*., 2001, 2002), thus these elements might not be involved in the suppression. Considering concentration of elements and rates of application, the dose of the elements received by the leaf surface in compost-treated plants was similar to that received following application of commercial formulations for foliar fertilization, although no effect on plant growth was observed. However, improved nutritional status in treated plants can enhance their defence capacity, as described for plants grown in composts in the presence of *Botrytis cinerea* (Segarra *et al.,* 2007a).

In vitro fungal growth inhibition by soil water extracts was attributed to phenolic compounds by López-Llorca and Olivares-Bernabéu (1997). Phenolic concentrations in their extracts were approximately ten-fold lower than those found in our compost tea. Thus, a direct effect of phenols on the pathogen might be one of the mechanisms of suppression.

The compost tea used in this study had high pH and electrical conductivity, although these parameters were in the range of those described for several aerated compost teas (Scheuerell and Mahaffee, 2004, 2006). However, no relationship between these characteristics of several compost teas and disease suppression against *Botrytis cinerea* was reported (Scheuerell and Mahaffee, 2006).

Microorganisms of grape marc compost tea were reported to produce siderophores, which sequestered iron and thus prevented the development of phytopathogens *in vitro* (Diánez *et al*., 2006).

In conclusion, the chemical and/or microbial composition of the compost tea interfered with development of the powdery mildew caused by *Erysiphe polygoni* in tomato plants, with the curative effect (100%) being more efficient than the preventive effect (19%). More research should be done to characterize suppressive compost teas and study their effects on the induction of plant defences.

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