Compost-Induced Systemic Acquired Resistance in Cucumber to Pythium Root Rot and Anthracnose

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This research was supported by AgriEnergy Resources, Princeton, IL, by grant US-2196-22 from BARD—The United States-Israel Binational Research and Development Fund—and by state and federal funds appropriated to the Ohio State University and the Ohio Agricultural Research and Development Center, Wooster. W. Zhang also obtained support from the National Laboratory of Grassland Ecological Engineering, Northeast Normal University, Changchun, P. R. China.

We thank J. Kuć, Department of Plant Pathology, University of Kentucky, Lexington, for supplying a culture of *Colletotrichum orbiculare*. J. Durkalski and C. A. Musselman provided valuable technical assistance.

Accepted for publication 8 July 1996.

ABSTRACT

Zhang, W., Dick, W. A., and Hoitink, H. A. J. 1996. Compost-induced systemic acquired resistance in cucumber to Pythium root rot and anthracnose. Phytopathology 86:1066-1070.

Pythium root and stem rots cause problems in production of greenhouse and nursery crops. Composts, however, can provide biological control of these diseases. We planted and germinated cucumber (*Cucumis sativus* 'Straight Eight') seeds in compost-amended (spruce or pine bark composts) or in highly decomposed sphagnum peat (H_4 on the von Post decomposition scale) mixes suppressive and conducive to Pythium root rot, respectively. Two-week-old seedlings were transplanted, using the split-root technique, into the compost-amended mixes and the peat mix. Split-root pairings were peat/compost, peat/peat, and compost/compost. Only one side of the split roots was grown in potting mix infested with *Pythium ultimum* and *P. aphanidermatum*. Root rot in the infested mix, averaged across all split-root pairings, was significantly ($P \leq 0.05$) less severe and mean root dry weights were significantly ($P \leq 0.05$) higher in plants germinated in the compost-amended mixes than in the peat mix. Also, root rot in the infested peat mix was significantly less severe on roots paired with the compost-amended mixes than those paired with the peat mix. Plants grown from seed in the compost-amended mixes or the peat mix also were tested for resistance to anthracnose. Three weeks after planting, anthracnose on the second leaf of cucumber 'Straight Eight' inoculated with *Colletotrichum orbiculare* was significantly less severe ($P \leq 0.05$) on plants grown in the compost-amended mixes than in the peat mix. Peroxidase activity, a putative marker of systemic acquired resistance (SAR) in cucumber, was significantly ($P \leq 0.05$) enhanced in plants grown in the compost-amended mixes compared to the peat mix. However, the activity of a peroxidase isozyme in the second leaf of cucumber plants was greater when plants were grown in compost as well as after prior inoculation with *C. orbiculare* than if grown in peat and with or without prior inoculation. The interaction of compost and the pathogen appeared critical for rapid activation of SAR-associated gene expression in cucumber plants.

Additional keyword: cucumber anthracnose.

Since the early 1970s, composts have been introduced as peat substitutes and used effectively for control of plant diseases caused by soilborne plant pathogens (12). In the nursery industry, disease-suppressive compost-amended container media have been effective enough to replace methyl bromide (25). Numerous reports reveal that microbiostasis and mycoparasitism can explain the disease control activity of composts (5,10,17,18,20). Foliar diseases also may be affected by composts incorporated into soil (31,36). Systemic acquired resistance (SAR) has been proposed as a mechanism underlying this activity (36), but conclusive evidence has not been presented.

Many reports show that composts suppress Pythium root rots (2,3,5–7,10,12,20,21). Microbiostasis is involved in the suppression induced by composts against *Pythium* spp. (3,5,20,21), but competition for carbon can only partially explain the suppressive effect (37). *Pseudomonas* spp. provide biological control and predominate in both rhizosphere and edaphic niches of compost-amended substrates suppressive to Pythium root rot (2,3). In contrast, gram-positive pleomorphic genera and putative oligotrophs that are incapable of inducing biological control are most abundant in consistently conducive, highly decomposed sphagnum peat substrates (3). Populations of pseudomonads and other biocontrol agents decline as organic matter decomposes, and suppressiveness to Pythium root rot is lost (37). Zhou and Paulitz (41), utilizing a split-root technique with cucumber, recently showed that plant growth-promoting pseudomonads provide Pythium root rot control of cucumber by inducing SAR. It is plausible, therefore, that SAR plays a role in suppression of Pythium root rot in compost-amended substrates.

Plant growth-promoting rhizobacteria and fungi also can induce SAR against foliar diseases of plants (19,22,23,34,35). A procedure has been developed to induce SAR against anthracnose of cucumber, whereby the first cucumber leaf is treated with the necrogenic pathogen *Colletotrichum orbiculare* (Berk. & Mont.) Arx (formerly *C. lagenarium* (Pass.) Ellis & Halst.) (16,34,38). Resistance to a second challenge-inoculation by *C. orbiculare* on the second leaf of the cucumber plant is then used as a test for the SAR response. An acidic peroxidase isozyme has been identified as a molecular marker of SAR in plants (1,11,24,27,28).

The objectives of this work were (i) to determine whether compost-amended potting mixes induce SAR in cucumber against Pythium root rot, utilizing a split-root procedure (41), and (ii) against anthracnose in cucumber foliage caused by *C. orbiculare* and (iii) to determine whether peroxidase activity is increased in plants grown in composts suppressive to root rot compared to plants grown in a Sphagnum peat mix conducive to root rot. A preliminary report has been published (40).

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Publication no. P-1996-0812-01R

MATERIALS AND METHODS

Potting mixes and inocula. A composted pine bark-amended potting mix was obtained from Strong-Lite, Inc., Pine Bluff, AR (experiment 1). A similar composted pine bark-amended mix and a composted spruce bark-amended mix were obtained from Earthgro, Inc., Lebanon, CT (experiments 2 through 4). These compost-amended mixes were naturally suppressive to Pythium root rot (2, 12). A dark, decomposed sphagnum peat (H_4 on the von Post decomposition scale) mix that was consistently conducive to Pythium root rot (12) was prepared as described previously (2). Soil inocula of *Pythium ultimum* Trow 211 and *P. aphanidermatum* (Edson) Fitzp. 20 were prepared as described previously (6), using Ko and Hora's chopped-potato soil medium (15). Potting mixes were infested by incorporating 0.5 g of *P. ultimum* and 0.2 g of *P. aphanidermatum* soil inocula per liter. The mixes were amended with 18 g of slow-release fertilizer (Osmocote, 14-14-14) per liter.

Pythium root rot bioassay on split-root cucumber plants. Cucumber seeds (*Cucumis sativus* L. 'Straight Eight') were germinated either in the compost-amended mixes or the peat mix as described previously (2). Roots of 2-week-old seedlings were removed from the germination mixes, washed in running tap water, divided into two approximately equal portions, and transplanted as split-root plants in 600-ml polystyrene pots (one plant per pot). Roots were split and placed in separate compartments, using a Plexiglas shield sealed with silicone to prevent direct contact or exchange of materials, including water or solution flux. The history of whether plants were germinated in the compost-amended mixes or the peat mix was recorded, and split-root pairings were prepared; they consisted of peat/compost, peat/peat, and compost/compost. One side of each pot was infested with Pythium soil inocula prepared as described above. Controls were not infested on either side of the pot containing the split roots. Root dry weight (60°C for 24 h) and root rot severity were measured 35 days after planting in the infested side of the pot. Root rot severity was rated by a scale in which 1 = symptomless, 2 = mild root rot (less than one-third of root rotted), 3 = moderate root rot (one- to two-thirds of root rotted), and 4 = severe root rot (more than two-thirds of root rotted or plant dead). Infested roots were plated on selective medium to verify the identity of the pathogen, as described previously (6).

Cucumber anthracnose bioassay. An isolate of *C. orbiculare* was obtained from J. Kuć, Department of Plant Pathology, University of Kentucky, Lexington. Classic SAR was induced 14 days after seeding by prior inoculation on the abaxial side of the first leaf with a conidial suspension of *C. orbiculare* (30 10-µl drops, 8.6×10^4 CFU ml^{-1}) (16). Inoculated plants were placed in a growth chamber (25°C, 75% relative humidity, 14 h of light per 10 h of dark). Resistance was detected via challenge-inoculation 7 days later by placing 30 10-µl drops of a conidial suspension (10^4 to 10^5 CFU ml^{-1}) on the second leaf of the same plants and incubating in a moisture chamber (25°C, 24 h of dark). Anthracnose severity on the second leaf was rated 7 days later by a rating system that involved counting the number and diameter of lesions (experiment 3) and overlaying the leaves with a transparent sheet containing a lined grid (5 × 5 mm square) followed by photographing of the leaves (experiment 4). The necrotic lesion area and total leaf area were measured by counting the number of squares (5 × 5 mm) represented by each. Disease severity was expressed as the percentage of total leaf area affected by necrosis.

Peroxidase activity. For the split-root experiments, the second leaf of the cucumber plant was removed 21 days after planting and was frozen in liquid nitrogen until further analyses. Peroxidase activity, assayed using guaiacol as the hydrogen donor, as described previously (11), was expressed as change in absorbance at 470 nm min^{-1} mg^{-1} of protein.

Electrophoretic analysis for peroxidase. The second leaf of the cucumber plant was removed 7 days after challenge-inoculation on the same leaf and was frozen in liquid nitrogen. Previously frozen leaves were placed in a porcelain mortar with additional liquid nitrogen and ground using a pestle cooled in the refrigerator (4°C). Equal amounts of protein were loaded for each treatment, and peroxidase isozymes were separated and detected as previously described (4). Gels were stained at room temperature with a solution containing 5 ml of 3% hydrogen peroxide (H_2O_2) and 10 ml of *O*-dianisidine solution until bands were detected (about 1 h) (11). Destaining was accomplished with a 50% glycerol solution, and the stained gel was photographed. Analysis was performed for plants grown in the peat, composted pine bark-amended (experiment 2), and composted spruce bark-amended mixes (experiment 3).

Experimental designs and statistical analysis. All treatments were blocked (six replications) with treatments randomized within each block. Each experiment was performed at least twice. Data were subjected to analysis of variance. When a significant ($P \leq 0.05$) F test was obtained for treatments, separation of means was accomplished by the least significant different test ($LSD_{0.05}$).

RESULTS

Pythium root rot. Pythium root rot on cucumber seedlings germinated in compost-amended mixes was significantly ($P \leq 0.05$) less severe than on seedlings germinated in peat mix, regardless of whether both sides of the split roots were transplanted into compost or peat mixes (Table 1, top). The overall treatment mean for root rot severity of plants germinated in the composted pine bark-amended mix was 1.5 versus 1.8 in the peat mix. The overall treatment mean was 1.6 for plants germinated in the composted spruce park-amended mix versus 2.0 in the peat mix. Dry weight of cucumber roots also was significantly ($P \leq 0.05$) greater for plants germinated in the two compost-amended mixes than in the peat mix (Table 1, top). Root dry weights of plants germinated in the compost-amended mixes was 0.12 g per plant compared to 0.09 g per plant germinated in the peat mix.

Mean root rot severity was significantly ($P \leq 0.05$) less for split roots in the infested peat mix paired with the compost-amended

TABLE 1. Pythium root rot severity (mean of six replicates) in cucumber plants (*Cucumis sativus* 'Straight Eight') grown in infested compost-amended mixes versus a peat mix

Treatment	Exps. 1 and 2		Exps. 3 and 4	
	Root rot severity[x]	Root dry wt (g)	Root rot severity[x]	Root dry wt (g)
Germination mix[y]				
Composted pine bark	1.5	0.12		
Composted spruce bark			1.6	0.12
Peat	1.8	0.09	2.0	0.09
$LSD_{0.05}$	0.1	0.02	0.3	0.01
Paired split root[z]				
P_i/C (pine bark)	1.5	0.12		
P_i/P	2.2	0.07		
$LSD_{0.05}$	0.3	0.03		
P_i/C (spruce bark)			1.6	0.11
P_i/P			2.4	0.07
$LSD_{0.05}$			0.4	0.02

[x] Rating value: 1 = symptomless; 2 = mild root rot (less than one-third of root rotted); 3 = moderate root rot (one- to two-thirds of root rotted); and 4 = severe root rot (more than two-thirds of root rotted or plant dead).

[y] Data were combined from plants for which both sides of the split-root system were grown in the same mixture (i.e., composts or peat), but prior to transplanting, seeds were germinated in either the compost-amended mixes or the peat mix.

[z] Treatment means presented are for root rot severity ratings of plants grown in infested peat (P_i) paired with either compost-amended mixes (not infested) or the peat mix (not infested).

mixes than in the infested peat mix paired with the noninfested peat mix (Table 1, bottom). Roots grown in the infested peat mix paired with the composted pine bark-amended mix (not infested) had a root rot severity rating of 1.5 versus a rating of 2.2 when the infested peat mix was paired with the noninfested peat mix. A similar comparison of roots in the infested peat mix paired with the composted spruce bark-amended mix (not infested) yielded root rot severity values of 1.6 versus 2.4. However, root rot severity of plants grown in infested compost-amended mixes paired with compost (not infested) and plants grown in infested peat mix paired with the same compost (not infested) were not statistically different (data not shown). *P. ultimum* and *P. aphanidermatum* were recovered from infested plants on selective medium. Control plants were free of root rot.

After split-root transplanting, dry weight of cucumber roots grown in the infested peat mix paired with either compost-amended mix (not infested) was significantly greater ($P \leq 0.05$) than that of roots grown in the infested peat mix paired with the noninfested peat mix (Table 1, bottom). Root dry weight was significantly correlated with root rot severity ($r = 0.64$, $n = 36$, $P \leq 0.05$).

TABLE 2. Severity of anthracnose caused by *Colletotrichum orbiculare* on the second leaf of cucumber plants (*Cucumis sativus* 'Straight Eight') in compost-amended mixes versus a peat mix

Potting mix	First leaf inoculation[y]	Anthracnose severity (%)[z]
Composted pine bark	–	63.3 ab
Composted spruce bark	–	42.7 bc
Peat	–	85.7 a
Overall mean		63.9
Composted pine bark	+	28.0 c
Composted spruce bark	+	35.7 c
Peat	+	35.7 c
Overall mean		33.5

[y] + = systemic resistance induced by prior inoculation of the first leaf with *C. orbiculare*;– = mimic inoculation with distilled water only on the first leaf.

[z] Anthracnose severity was measured on the second leaf for all treatments and is expressed as the percentage of total leaf area exhibiting necrosis. Measurements were made by overlaying a transparent sheet containing a lined grid (5 × 5 mm square) on leaves and counting the necrotic lesion area and total leaf area. Experiments were performed four times with six replicates for each experiment. Means with different letters are significantly different at $P \leq 0.05$. $LSD_{0.05} = 24.0$.

TABLE 3. Peroxidase activity in leaves (mean of six replicates) of cucumber plants (*Cucumis sativus* 'Straight Eight') grown in compost-amended mixes versus a peat mix

Treatment	Peroxidase activity[x]	
	Exps. 1 and 2	Exps. 3 and 4
Germination mix[y]		
Composted pine bark	4.3	
Composted spruce bark		4.6
Peat	3.5	3.4
$LSD_{0.05}$	0.6	0.9
Paired split root[z]		
P_i/C (pine bark)	4.7	
P_i/P	3.7	
$LSD_{0.05}$	0.8	
P_i/C (spruce bark)		5.0
P_i/P		3.9
$LSD_{0.05}$		1.2

[x] Peroxidase activity is expressed as the change in absorbance at 470 nm min^{-1} mg^{-1} of protein.

[y] Data were combined from plants in which both sides of the split-root system were grown in the same mixture (i.e., composts or peat), but prior to transplanting, seeds were germinated in either the compost-amended mixes or the peat mix.

[z] Treatment means presented are for root rot severity ratings of plants grown in infested peat (P_i) paired with either the compost-amended mixes (not infested) or the peat mix (not infested).

Anthracnose severity. Anthracnose on the second leaf of cucumber plants was significantly ($P \leq 0.05$) less severe on plants grown in the composted spruce bark-amended mix versus the peat mix (Table 2). Anthracnose severity on plants grown in the composted pine bark-amended mix also was less severe than on plants grown in the peat mix, but the difference was significant at $P \leq 0.10$. Disease severity in the peat and composted pine bark-amended mixes was significantly ($P \leq 0.05$) less on plants after prior inoculation of the first leaf with *C. orbiculare* (induced) compared to plants without prior inoculation. The necrotic lesion areas on the second leaves of noninduced plants ranged from 85.7% for plants grown in the peat mix to 42.7% for plants grown in the composted spruce bark-amended mix and 63.3% for plants grown in the composted pine bark-amended mix. There was no significant difference in disease severity between plants grown in the composted spruce bark-amended mix versus those in which SAR was induced (regardless of mix treatment) through prior inoculation of first leaves with *C. orbiculare* (percentage of lesion area [35.7%], Table 2). Disease severity on plants grown in the composted pine bark-amended mix (percentage of lesion area [63.3%]) was significantly ($P \leq 0.05$) greater than on plants with prior inoculation of first leaves with *C. orbiculare*, but it was significantly less ($P \leq 0.10$) on plants grown in the peat mix.

Peroxidase activity. Peroxidase activity in leaves of cucumber plants was significantly ($P \leq 0.05$) increased in plants germinated in the compost-amended mixes versus those germinated in the peat mix (Table 3, top). After split-root transplanting, peroxidase activities also were greater when roots were paired with the composted spruce bark or pine bark mixes than when roots were paired with the peat mix (Table 3, bottom). The highest peroxidase activity was observed when the peat mix was paired with the composted

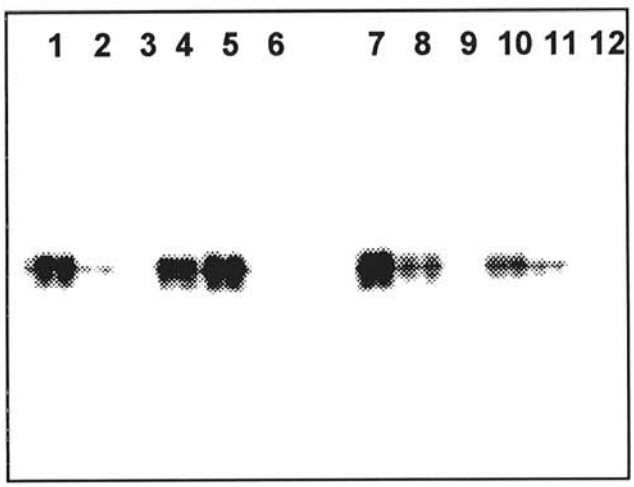

Fig. 1. Peroxidase isozyme expression in the second leaf of cucumber plants (*Cucumis sativus* 'Straight Eight') grown in compost-amended mixes or a peat mix. Some plants were induced to express systemic resistance by prior inoculation of the first leaf with *Colletotrichum orbiculare*. Challenge-inoculation on the second leaf was with *C. orbiculare* 7 days after prior inoculation of the first leaf. Lanes 1 and 10, plants grown in peat that were induced and challenged with *C. orbiculare*. Lanes 2 and 11, plants grown in peat that were not induced but were challenged with *C. orbiculare*. Lanes 3 and 12, plants grown in peat and not induced or challenged. Lane 4, plants grown in compost spruce bark-amended mix that were not induced but were challenged with *C. orbiculare*. Lane 5, plants grown in composted spruce bark-amended mix that were induced and challenged with *C. orbiculare*. Lane 6, plants grown in composted spruce bark-amended mix that were not induced or challenged. Lane 7, plants grown in composted pine bark-amended mix that were induced and challenged with *C. orbiculare*. Lane 8, plants grown in composted pine park-amended mix that were not induced but were challenged with *C. orbiculare*. Lane 9, plants grown in composted pine park-amended mix that were not induced or challenged.

spruce bark-amended mix, and the activity was significantly ($P \leq 0.05$) higher than in plants grown in the peat mix paired with itself. Similar results were obtained when the peat mix was paired with the composted pine bark mix.

Relative activity of a peroxidase isozyme in the second leaves of cucumber plants grown in the peat mix was low (Fig. 1, lanes 3 and 12). Activity in the leaves from plants produced in the composted spruce bark- and pine bark-amended mixes also was very low (Fig. 1, lanes 6 and 9, respectively), although some very faint bands, which do not show in the figure, were evident. Inoculation with *C. orbiculare* on the second leaf dramatically increased the activity of this peroxidase isozyme in plants grown in the peat-amended mixes (Fig. 1, lanes 2 and 11), but this increase was even greater in plants grown in the compost-amended mixes (Fig. 1, lanes 4 and 8). The highest activity occurred when plants were both grown in compost-amended mixes that were prior inoculated as well as challenge-inoculated with *C. orbiculare* (Fig. 1, lanes 5 and 7). Even here, peroxidase levels were higher in the two compost-amended mixes than in the peat mix.

DISCUSSION

The significantly ($P \leq 0.05$) reduced root rot severity observed in split roots of plants produced in the Pythium-infested conducive peat mix paired with the suppressive compost-amended mixes (Table 1) suggests that compost-induced SAR played a role in control of Pythium root rot. The significantly ($P \leq 0.05$) lower anthracnose severity (Table 2) observed on the second leaves of cucumber plants in compost-amended mixes strengthens this argument. Finally, increased peroxidase activity (Table 3) and enhanced peroxidase isozyme level (Fig. 1) in plants produced in the compost-amended mixes over that in the conducive peat mix are further evidence of the role of compost-induced SAR in control of these diseases.

The mechanisms by which these composts induced SAR remain unknown. Chemical as well as biological factors can induce this effect in plants (14,19,22,23,26,33–35,41). The high populations of biocontrol agents in the compost-amended mixes versus low populations in the conducive peat mix (3) suggest they play a role in SAR, because many of the bacterial strains present in the compost-amended mixes that induce suppression to Pythium root rot also induce SAR in plants (19,22,23,33–35,39,41). Furthermore, autoclaving destroys the suppressive effect of compost-amended mixes against Pythium root rot (6). Finally, the conducive peat mix, as mentioned above, is colonized predominantly by obligate oligotrophs and pleomorphic gram-positive bacteria that are unable to induce biological control (3,30) and, thus apparently, also are unable to induce SAR.

Many phytotoxic chemicals, including salicylic acid, can induce SAR (14,26,32). Alcohols and organic acids can occur in phytotoxic concentrations in immature composts (9) and, possibly, also in compost steepages (8,31,36). The composts used in this work, however, were cured well beyond the stability level that produces phytotoxic concentrations of such compounds (12). Allelopathic substances also may be present in composts prepared from tree barks (12,29). These products, however, are readily destroyed during composting (29) and, therefore, are thought to not have had a role in SAR induced by composts in cucumber in this work.

Nutritional factors affect the severity of many plant diseases (13). The concentration of plant nutrients used in the peat and compost mixes used in this work were adjusted to within optimum ranges for cucumber (6). Plants in both peat and compost-amended mixes developed at similar rates, and availability of essential plant nutrients was discounted as having a role in the disease control observed in this work.

The systemic protection of split-roots from Pythium root rot (Table 1) induced by compost was accompanied by increased peroxidase activity (Table 3) in leaf tissue. Acidic peroxidase is a putative molecular marker of SAR in cucumber (11,24,27,28). Based on peroxidase isozyme activity in electrophoretic analysis (Fig. 1), however, the composts by themselves were weak inducers of SAR relative to SAR induced by prior inoculation with *C. orbiculare*. The obviously higher peroxidase isozyme activity in leaves of cucumber plants that were prior inoculated, as well as challenge-inoculated, and grown in compost compared to peat (Fig. 1) suggests that as yet unidentified factors in composts complemented the activity of *C. orbiculare* in induction of SAR. The interaction of compost and the pathogen appeared critical for rapid activation of SAR-associated gene expression in cucumber plants.

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