Nature of Suppression of Fusarium Wilt of Radish in a Container Medium Amended with Composted Hardwood Bark

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ABSTRACT

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The suppressive effect of a container medium amended with composted hardwood bark (CHB) to Fusarium oxysporum f. sp. conglutinans race 2 (F. o. f. sp. conglutinans) was biotic in nature. Heating destroyed the suppressive effect. Population development of F. o. f. sp. conglutinans was suppressed in the unheated but not in the heated CHB medium. A combination antagonist treatment consisting of strains of Trichoderma hamatum and an isolate of Flavobacterium balustinum consistently restored the suppressive effect in heated media. Neither antagonist type added singly was consistently effective. The CHB medium was suppressive over a wide pH range (5.4–7.4). Ammonium nitrate nitrogen did not have a significant effect on disease severity, but calcium nitrate and ammonium sulfate nitrogen did.

Fusarium wilts are important diseases of several ornamentals. Various control procedures have been developed for these diseases, including the use of resistance, fungicides, media sterilization, sanitation, and culture-indexing. Despite these measures, losses still occur, particularly

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on cylamen, chrysanthemum, and carnation. Various biological control procedures have been introduced during the past two decades, including amendment of substrates or container media with Fusarium-suppressive soils (6,23), specific antagonists (6,13,18), and composts that are suppressive to Fusarium wilts (4). One disadvantage of Fusarium-suppressive soil amendments is that they may harbor other pathogens that are not suppressed. Therefore, suppressive soils and antagonists have not been used widely on a commercial scale.

Composted hardwood bark (CHB) has been used successfully in the ornamentals industry for suppression of a variety of diseases, including those caused by *Phytophthora* spp. (9), *Pythium* spp. (5), *Rhizoctonia solani* (14,22), and *Fusarium oxysporum* f. sp. *chrysanthemi* (4). The mechanism of the suppressive effect of CHB on *Fusarium* diseases is not understood. However, media amended

with green CHB are known to be significantly less suppressive to Fusarium wilt of flax than those prepared with mature CHB (4). Media amended with fresh or aged pine bark are mildly suppressive, but those amended with Canadian peat as the sole organic component are consistently conducive (4). Because heating destroys the suppressive effect of media amended with CHB, it was proposed (4) that biotic factors were involved in suppression of Fusarium wilts (as in the suppression of R. solani in CHB media [15]).

The purpose of this research was to provide additional quantitative data on suppression of Fusarium wilt in CHB media and to examine the efficacy of selected antagonists against Fusarium wilt in CHB media.

MATERIALS AND METHODS

Production of soil inoculum. A culture of F. oxysporum f. sp. conglutinans race 2 (F. o. f. sp. conglutinans), obtained from P. H. Williams, Department of Plant Pathology, University of Wisconsin, Madison, was stored on anhydrous silica gel at -20 C (21). Sterile soil mixture (1 L of two parts Wooster silt loam to one part perlite, v/v, amended with 150 ml of water) was inoculated with F. o. f. sp. conglutinans, incubated 3 wk at 25 C, and shaken vigorously each week. After air-drying 24 hr in a laminar-flow hood and screening through a 1-mm-mesh sieve, the number of F. o. f. sp. conglutinans propagules per gram dry weight of soil inoculum was determined by dilution plating on Komada's agar (11).

Container medium and plant fertility.

The container medium consisted of CHB, Canadian sphagnum peat, and perlite (5:2:3, v/v, pH 6.5), described previously as CHB medium (15). The compost was prepared in windrows over a period of 5-7 mo (8). The pH of the CHB medium was adjusted with either elemental sulfur or a mixture of dolomitic and hydrated lime (2:1, w/w). The pH was determined before assays and after harvesting plants.

Phosphorus was added as triple super phosphate to all media during formulation (1 g of 0-46-0 per liter of CHB medium). Potash was supplied at each watering as KCl (100 mg K/L of irrigation water). Normally, nitrogen was supplied at 300 mg/L of irrigation water in ammonium nitrate form. In experiments where effects of nitrogen form and concentration on disease severity were examined, nitrogen was supplied at concentrations of 100, 200, and 300 mg/L of irrigation water, using commercial grades of ammonium nitrate, calcium nitrate, and ammonium sulfate. Micronutrients (0.6 g STEM from Peter's Fertilizer Products [W. R. Grace & Co., Allentown, PA] per liter of CHB medium) were supplied once in irrigation water after seeding.

Suppressiveness bioassay. A radish (Raphanus sativus L. 'White Icicle') bioassay developed by Scher and Baker (19) for soil systems was modified for the CHB medium. To determine the effects of heating on suppressiveness of CHB media, 2-L samples (about 400 g dry wt) were incubated in polyethylene bags at 60 C for 5 days (15). Control samples were

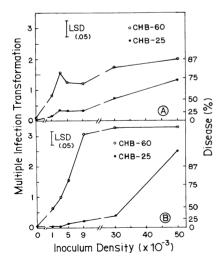


Fig. 1. Effect of inoculum density (cfu/g dry wt of container medium) on Fusarium wilt severity of radish, expressed as MITR (multiple infection transformation, number of infections per plant) and as percentage of diseased plants. CHB-25 and CHB-60 are unheated and heated composted hardwood bark container media, respectively. Mean MITR value of 0.00 = 100% healthy plants and $3.26 \cong 100\%$ diseased plants. (A) Data obtained in first planting. (B) Data obtained after replanting of the bioassay.

incubated at 25 C. The CHB medium was infested by adding F.o. f. sp. conglutinans soil inoculum to 2-L volumes in polyethylene bags and shaking vigorously (30 sec) to distribute inoculum evenly. Actual inoculum concentration was determined by dilution plating of CHB medium samples on Komada's agar (two replicates per treatment). The infested container medium (2 L) was then distributed evenly in five 10-cm-tall pots per treatment. Pots were seeded with 15 radish seeds and incubated 14 days at 22 C with a 16-hr photoperiod (225 μ E m⁻² s⁻¹).

Symptoms of disease were evident after 9 days. Plants were harvested and rated for disease severity (healthy, diseased, or dead) after 14 days. F. o. f. sp. conglutinans was isolated routinely from wilted and dead plants to verify the presence of the pathogen. Population development of F. o. f. sp. conglutinans in the container medium during the bioassay was followed by dilution plating of duplicate samples on Komada's agar.

Disease data were transformed with the multiple-infection transformation (MITR), which theoretically is based on the Poisson distribution (2,19). The number of infections per plant (MITR) can be estimated from ln[1/(1-x)], where x = proportion of diseased plants. An MITR value of 0.0 represents 100% healthy plants and an MITR value of 0.69 represents 50% healthy plants. An MITR value of 3.26 represents approximately 100% diseased plants. MITR is most accurate at low levels of infection. We used the transformation for all data, however, to produce an additive scale and correct for unequal variances of the percentages.

After transformation to MITR, data were analyzed by one-way or two-way analysis of variance, according to the design of the experiment. Treatment means were based on five pots per treatment and separated using least significant difference (LSD) tests when experimental factors were significant (P = 0.05).

Antagonists effective in suppression of Rhizoctonia and Pythium damping-off in CHB media (5,16) that were tested for efficacy against radish Fusarium wilt were Trichoderma hamatum (Bonord.) Bain. Aggr. isolates 559 (ATCC 20764) and 382 (ATCC 20765) and Flavobacaterium balustinum isolate 299 (ATCC 53199). Flavobacterium inoculum was produced in nutrient broth (72 hr, 25 C), washed by centrifugation, and added to heated CHB medium to a population level of about 10⁶ cfu/g dry wt. Trichoderma inoculum was produced on Difco PDA agar (1 wk, 25 C). Conidial suspensions were washed by centrifugation in distilled water and added to heated CHB medium to a population level of about 10⁵ cfu/g dry wt. The CHB medium was then infested with F. o. f. sp.

conglutinans inoculum and bioassayed for suppressiveness as described. Actual F. o. f. sp. conglutinans inoculum densities were determined thereafter by dilution plating on Komada agar.

The fate of F. o. f. sp. conglutinans propagules in the CHB medium was followed with a membrane sandwich technique. Mycelium produced on an 8μm pore, 25-mm-diameter Nucleopore filter and incubated 4 days at 25 C on Difco PDA was rinsed twice with sterilized distilled water and sandwiched between two 47-mm-diameter filters. After the perimeter of the sandwich was sealed, it was stapled between two layers of nylon screen and buried vertically 1 cm below seeds in the container medium. Filters were recovered after 3, 7, 10, and 14 days and stained 30 min with Europium Chelate and Calcofluor white ST, then rinsed twice in 50% ethanol and distilled water separately (10). Thereafter, filters were mounted on a slide and examined with epifluorescensce (405-, 460-, and 495-nm filters, respectively).

RESULTS

The percentage of diseased plants increased with increasing levels of F. o. f. sp. conglutinans inoculum in both the heated and unheated CHB media (Fig. 1A). Significantly (P = 0.05) higher levels of disease were present in the heated medium than in the CHB medium incubated at 25 C. Equations for simple linear regression lines for the unheated and heated CHB media were y = 0.142 +0.077I and y = 0.875 + 0.085I, respectively, where I = initial inoculum level and <math>y =MITR. Both equations were significant at P < 0.01. The intercept values differed significantly (P = 0.01); however, slope values did not differ. The difference in the intercepts indicated that the overall level of infection for heated CHB was higher than for the unheated medium. Because there were not many low inoculum levels in the study, it was not possible to derive regression equations that had zero intercepts. The model presented represents a best fit for the data but does not give a precise estimate of inoculum efficiency. ED₅₀ values for F. o. f. sp. conglutinans inoculum in the unheated and heated media were about 3×10^4 and $< 10^3$ cfu/g dry wt of container medium, respectively.

Replanting increased the percentage of diseased plants in the heated medium at all but the lowest inoculum levels (Fig. 1B). In the unheated medium, a significant increase (P = 0.05) was observed with the highest inoculum level only. MITR values for the unheated medium again were significantly (P = 0.05) lower for all inoculum levels tested. Equations for MITR as a function of I in the unheated and heated CHB were $y = 0.11 - 0.12I + 0.02I^2$ and $y = 0.04 + 1.29I - 0.10I^2$, respectively (P < 0.01). All coefficients were significantly different (P = 0.01).

F. o. f. sp. conglutinans population development. Propagule levels of F. o. f. sp. conglutinans, determined by dilution plating, did not change significantly (P = 0.05) in the unheated CHB medium during the first bioassay or after replanting (Table 1). In the heated medium, however, propagule levels increased significantly from 3.2×10^2 cfu/g dry wt of container medium at the time of the first planting to a level of 1.4×10^4 cfu after 4 wk (at harvest of the second planting).

Chlamydospores and macroconidia as well as microconidia germinated within 3 days in sandwiches incubated in both heated and unheated container media. F. o. f. sp. conglutinans propagules incubated 3 days in the heated medium stained bright red, whereas propagules in the unheated medium were mostly green. Much more hyphal development was observed in the unheated than in heated CHB medium. On the other hand, chlamydospores were more evident at all times after incubation in the heated than in the unheated medium. Differences in development of propagules in unheated and heated media were most pronounced after 15 days.

Effect of pH on suppressiveness. With the exception of the lowest pH treatment, pH of container media did not change appreciably during the 2-wk bioassay (Table 2). The percentage of diseased plants was significantly lower (P = 0.05) in the unheated than in the heated medium regardless of pH. A significantly higher percentage of diseased plants occurred in the unheated medium with a pH of 6.4 than in those with a pH of 5.4, 6.0, or 7.5, but all were suppressive compared with the heated container media. In the heated media, highest percentages of diseased plants occurred at the lowest pH treatment (pH 5.4) but were conducive. The experiment was repeated twice, and similar results were obtained.

Effect of nitrogen on disease severity. Increasing concentrations of nitrogen supplied as ammonium nitrate or ammonium sulfate did not result in significant changes in disease (Table 3). However, the highest concentration of calcium nitrate treatment significantly (P = 0.05) reduced disease levels. Ammonium sulfate applied at concentrations higher than 100 μ g N/ml of irrigation water induced yellowing in radish leaves. High MITR values in the uninoculated ammonium sulfate treatments were not due to disease caused by F. o. f. sp. conglutinans because it was not recovered on PDA from affected plants. Finally, the pH of the CHB medium did not change during the 2-wk bioassay period in any of the fertility treatments. The experiment was repeated, and similar results were obtained.

Effects of antagonists. Infestation of the heated CHB medium with F.

balustinum 299 or T. hamatum 382 or T. hamatum 559 alone did not consistently reduce percentages of diseased plants in bioassays. An example is presented in Table 4. Infestation of the heated CHB medium with a combination treatment of F. balustinum 299 and either isolate of T. hamatum significantly reduced the percentage of disease in four of five experiments during the first bioassay.

Replanting significantly (P = 0.05) decreased the percentage of diseased plants induced by the combination antagonist treatment in the one assay where the treatment was not effective at first

DISCUSSION

Comparative studies on suppressive effects of container media (soilless

Table 1. Population densities of *Fusarium oxysporum* f. sp. *conglutinans* race 2 in unheated (CHB-25) and heated (CHB-60) composted hardwood bark media during a bioassay and after replanting^a

	Fusarium population level (cfu/g dry wt container medium)					
Container medium	At planting	After first bioassay	After replanting			
CHB-25						
Uninfested	0	0	0			
Infested	6.3×10^{2}	1.5×10^{3}	3.7×10^2			
CHB-60						
Uninfested	0	0	0			
Infested	3.2×10^{2}	4.1×10^{3}	1.1×10^4			

 $^{^{}a}$ LSD (0.05) = 3.6 × 10 3 .

Table 2. Effect of container medium pH on percentage of diseased radish plants (MITR)^a

	pH value					
Container medium ^b	Before	After assay	Mean MI	TR value ^c	Mean percentage	
	assay		Uninfested	Infested d	Uninfested	Infested
CHB-25	5.4	4.4	0.00	1.09	0.0	66.4
CHB-60	5.4	5.0	0.00	3.26	0.0	100.0
CHB-25	6.0	5.5	0.00	1.00	0.0	63.2
CHB-60	6.0	6.0	0.00	2.59	0.0	92.5
CHB-25	6.4	6.0	0.00	1.81	0.0	83.6
CHB-60	6.4	6.5	0.00	2.52	0.0	92.0
CHB-25	7.4	7.1	0.00	0.89	0.0	58.9
CHB-60	7.4	7.2	0.00	2.72	0.0	93.4

^a The interaction of container medium, pH value, and inoculum was significant (P = 0.05), LSD (0.05) = 0.57.

Table 3. Effect of nitrogen (N) form and concentration on radish Fusarium wilt severity (MITR) in a heated composted hardwood bark medium^a

	Concentration ^a	Mean MI	TR value ^b	Mean percentage	
N form		Uninfested	Infested ^c	Uninfested	Infested
Ammonium					
nitrate	100	0.12	2.00	11.3	86.5
	200	0.09	2.12	8.6	88.0
	300	0.05	2.42	4.9	91.1
Ammonium					
sulfate	100	0.12	3.26	11.3	100.0
	200	1.53	3.26	78.4	100.0
	300	2.78	3.26	93.8	100.0
Calcium					
nitrate	100	0.06	2.95	5.8	94.8
	200	0.38	3.26	31.6	100.0
	300	0.07	1.58	6.8	79.4

^aThe interaction of N source, N concentration, and inoculum was significant (P = 0.05), LSD (0.05) = 0.54

^bCHB-25 and CHB-60 are unheated and heated composted hardwood bark media, respectively. ^cA mean MITR (multiple-infection transformation) value of 0.00 = 100% healthy and $3.26 \cong 100\%$

^dInfested with 1×10^4 cfu Fusarium oxysporum f. sp. conglutinans race 2 per gram dry weight of container medium.

^bRepresents mg N/L of irrigation water.

^c A mean MITR (multiple-infection transformation) value of 0.00 = 100% healthy and $3.26 \approx 100\%$ diseased plants.

^dInfested with 3×10^4 cfu/g dry wt of container medium.

systems) require that bioassays used to measure such effects be quantitative. The chrysanthemum and flax bioassays used for *Fusarium* diseases in the past (4) were lacking in this aspect. Not only does the choice of host, pathogen, and antagonist influence interactions but factors associated with mineral nutrition and pH may affect disease severity caused by *Fusarium* spp. (7,20) and, therefore, quantitative aspects of bioassays.

The pH of container media used for production of ornamentals typically is maintained within a range of 5.0–6.0 because it is optimal for availability of micronutrients in these organic plant substrates (17). Increasing the pH of the CHB medium from 5.5 to 7.4 did not have a significant effect on suppressiveness (Table 2). California *Fusarium*-suppressive soils are suppressive at pH 8.0 but conducive at pH 6.0 (18). This suggests that the mechanism of suppression of Fusarium wilt in the CHB medium differs from that in California soils.

The form of nitrogen (ammonium or nitrate) (Table 3) and liming procedures (Table 2) affect severity of tomato Fusarium diseases (3,7,20). Data obtained with various concentrations and forms of nitrogen in this work support this observation. High levels of calcium nitrate nitrogen (300 μ g N/ml of irrigation water) reduced severity of radish Fusarium wilt, even though pH of the container medium was not affected. Ammonium nitrate had no significant effect during the short bioassay period and therefore was chosen as the form of nitrogen to reduce variability in bioassays.

Destruction of the suppressive effect of CHB media by heating, followed by restoration after reintroduction of antagonists isolated originally from CHB, suggests that the suppressive effect on Fusarium wilt is due to biotic factors.

It was shown previously that heated CHB media are as conducive to Fusarium wilts of flax and chrysanthemum as media prepared with Canadian sphagnum peat (4). Therefore, heat-stabile inhibitors of Phytophthora spp. present in CHB (8) apparently do not have a significant effect on the Fusarium diseases evaluated in this system so far. A considerable effort has been made to determine the relative contributions of various fungal antagonists involved in suppression of Rhizoctonia and Pythium damping-off in suppressive CHB media (12,16). Antagonistic bacteria also have been identified, although their relative contributions to the suppressive effects of CHB media on these diseases has not been determined. Combination antagonist treatments, i.e., T. hamatum isolates with Xanthomonas maltophilia or F. balustinum, are more effective than single antagonists for control of Rhizoctonia and Pythium damping-off (G. A. Kuter, P. C. Fahy, and H. A. J. Hoitink, unpublished). Our results show that a mixture of T. hamatum with F. balustinum also was more effective in suppressing Fusarium wilt of radish than any of the antagonists added singly. To our knowledge, this is the first report of these antagonists having an effect against these three types of diseases.

Population development of F. o. f. sp. conglutinans was suppressed in the CHB medium that was incubated at 25 C but increased significantly in the heated (and therefore conducive) medium. Fusarium spp. that play a role in suppression of some Fusarium wilts in the Chateaurenard soils (1) were not isolated from suppressive CHB media (M. I. Trillas-Gay and H. A. J. Hoitink, unpublished). Based on available evidence, therefore, the mechanism of suppression of Fusarium wilt in CHB media appears to differ from those

Table 4. Induction of suppression in a heated composted hardwood bark medium (CHB) to radish Fusarium wilt by isolates T382 and T559 of *Trichoderma hamatum* and F299 of *Flavobacterium balustinum*

Container medium ^a			Mean MITR values ^b		Mean percentage	
	Inoculum treatments		First	After	First	After
	Foc-2c	Antagonists ^d	bioassay	replanting	bioassay	planting
CHB-25	_	_	0.00	0.00	0.0	0.0
CHB-60	_	_	0.00	0.00	0.0	0.0
CHB-25	+		0.39	0.86	32.3	57.7
CHB-60	+		1.76	2.88	82.8	94.4
CHB-60	+	T559 + F299	0.75	1.87	52.8	84.6
CHB-60	+	T382 + F299	1.45	1.95	76.5	85.8
CHB-60	+	T559	2.32	3.26	90.2	100.0
CHB-60	+	F299	1.99	3.26	86.3	100.0
CHB-60	+	T382	1.55	3.26	78.8	100.0
LSD $(P = 0.05)$			1.09	0.65		

a CHB-25 and CHB-60 represent unheated and heated CHB media, respectively.

in Chateaurenard and California suppressive soils.

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^bA mean MITR (multiple-infection transformation) value of 0.00 = 100% healthy and $3.26 \cong 100\%$ diseased plants.

^c Infested with 1×10^4 cfu *Fusarium oxysporum* f. sp. *conglutinans* race 2 per gram dry weight of container medium.

 $^{^{\}rm d}$ T559 and T382 were added at initial population levels of 10^5 cfu/g dry wt; F299 was added at an initial population level of 10^6 cfu/g dry wt.

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