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Benomyl Tolerance of Ten Fungi Antagonistic to Plant-parasitic Nematodes[1]

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Abstract: Ten strains of fungi were tested for tolerance to the fungicide benomyl. *Verticillium chlamydosporium* strain 2 did not grow in the presence of benomyl; *Drechmeria coniospora* strains 1 and 2 and *Chaetomium* sp. tolerated only 0.1 μg benomyl/ml medium; *Acremonium bacillisporum*, an unidentified fungus, and *Phoma chrysanthemicola* uniformly grew at 1 μg/ml, but some hyphae grew at higher benomyl concentrations; *Fusarium* sp. tolerated 475 μg/ml, but some hyphae grew on medium amended with 1,000 μg/ml; *Verticillium lecanii* and *V. chlamydosporium* strain 1 routinely tolerated 1,000 μg/ml. Fungi generally grew more slowly at higher than at lower benomyl concentrations. Strains with elevated tolerance to benomyl were selected from *Acremonium bacillisporum, Drechmeria coniospora, Fusarium* sp., and an unidentified fungus. These strains retained the increased tolerance after repeated transfers on unamended medium.

Key words: benomyl, biological control, fungicide effect, fungus, *Heterodera glycines*, nematode, nontarget organism, soybean cyst nematode.

Fungicides applied to crops may inhibit the growth of beneficial nontarget fungi (20,24). For example, application of benomyl to peanuts resulted in an increase in the severity of southern stem blight due to adverse effects on *Trichoderma* (2). Fungi expressing fungicide tolerance as well as antagonism to plant parasites therefore are useful for integrated pest management systems involving chemical control.

To aid in selecting fungi with ability to act against *Heterodera glycines*, the soybean cyst nematode, 10 fungal strains were studied for tolerance to the fungicide benomyl. These fungi were screened in laboratory bioassays and identified as antagonists to *H. glycines* (18), or they are members of taxa known to affect nematodes. Benomyl was selected for this investigation for several reasons. It is registered for use on soybeans, and so might inhibit growth of a biocontrol fungus antagonistic to soybean pests. It is also applied to many other crops and might therefore come in contact with a biocontrol fungus used with various cropping situations. Furthermore, it is known that strains of a number of fungi express tolerance or resistance to benomyl (6). Fungi with increased benomyl tolerance may be more successful biocontrol agents than less tolerant strains, even in the absence of benomyl (1,3,21,22).

The objectives of this study were to 1) determine the level of benomyl required to inhibit growth of each fungus strain, 2) subculture strains found to tolerate elevated levels of benomyl, and 3) test for persistence of elevated benomyl tolerance after repeated transfers on medium not amended with benomyl. After determination of benomyl tolerance levels, studies can be done to compare strains for ability to control nematodes in the soil.

MATERIALS AND METHODS

Ten fungi (Table 1) were tested for tolerance to benomyl (50% wettable powder or 50% dispersible granules, E. I. du Pont de Nemours & Co., Wilmington, DE). Beltsville Nematology Lab Designations and ATCC numbers (where applicable) for each fungus studied are in Table 1 of Meyer et al. (18). The *Verticillium lecanii* (A. Zimmermann) Viégas strain tested is listed as strain 2 in that table. To make benomyl-amended agar, benomyl stock solutions were prepared in cooled sterilized distilled water and added to potato dextrose agar (PDA) just before pouring plates. Plugs (ca.

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TABLE 1. Benomyl tolerances of 10 strains of fungi incubated for 3 weeks on benomyl-amended agar.

Fungus	Highest benomyl concentration with fungus growth from one or more inoculum plugs	Highest benomyl concentration with fungus growth from 100% of inoculum plugs
Verticillium chlamydosporium Strain 2	0.1 (1 plug of 12)	0 (12 plugs)
Drechmeria coniospora Strain 1	0.1 (12 plugs of 12)	0.1 (12 plugs)
Drechmeria coniospora Strain 2	0.1 (6 plugs of 6)	0.1 (6 plugs)
Chaetomium sp.	0.1 (6 plugs of 6)	0.1 (6 plugs)
Acremonium bacillisporum	10 (2 plugs of 12)	1 (12 plugs)
Unidentified fungus	10 (1 plug of 17)	1 (15 plugs)
Phoma chrysanthemicola	13 (2 plugs of 6)	1 (12 plugs)
Fusarium sp.	1,000 (1 plug of 11)	475 (6 plugs)
Verticillium lecanii	1,000 (6 plugs of 6)	1,000 (6 plugs)
Verticillium chlamydosporium Strain 1	1,000 (6 plugs of 6)	1,000 (6 plugs)

Benomyl concentrations are μg benomyl/ml potato dextrose agar.

9 mm d) were cut from the peripheries of fungal colonies with a cork borer. Each plug was placed colony side down in the center of a petri dish containing either PDA or PDA + benomyl. The plugs were incubated at 25 C. Colony diameters, including the widths of the plugs, were measured 1, 2, and 3 weeks after inoculation. Each fungus was inoculated onto medium in three petri dishes at each benomyl concentration (0, 0.1, 1.0, 10, and 100 μg benomyl/ml medium), and the experiments were repeated at least once. An unidentified fungus and *Phoma chrysanthemicola* Hollós were also tested at 25, 50, and 75 μg/ml; *P. chrysanthemicola* at 13 μg/ml; *Verticillium chlamydosporium* Goddard strain 1, *Verticillium lecanii,* and *Fusarium* sp. at 125–500 μg/ml in increments of 25 μg/ml, and at 1,000 μg/ml; *Fusarium* sp. was also tested at 600–800 μg/ml in increments of 25μg/ml.

Strains that grew on elevated benomyl levels (referred to herein as "EBS"—elevated benomyl strains) were isolated. These EBS were obtained by selecting hyphae that grew at abnormally high benomyl concentrations. Single spore isolates were then made from *Drechmeria coniospora* (Drechsler) W. Gams and Jansson; the other EBS were made from mass transfers. To determine whether elevated benomyl tolerance would be retained in the absence of benomyl, the EBS were transferred at least five times on PDA over a period of 16 months or longer and were then tested for growth on benomyl-amended agar.

RESULTS

Benomyl tolerance varied among the fungi (Tables 1, 2). *Verticillium chlamydosporium* strain 2 did not grow even at the lowest concentration of benomyl. There was one exception; a small amount of mycelium developed from 1 of the 12 plugs inoculated onto 0.1 μg benomyl/ml PDA. *Chaetomium* sp. and both strains of *D. coniospora* tolerated only 0.1 μg/ml. The *Chaetomium* strain had a much smaller diameter at 1 week on PDA + benomyl than on PDA without benomyl, but colony diameters 3 weeks after inoculation were similar on the two media (Table 2).

All *Acremonium bacillisporum* (Onions & Barron) W. Gams colonies grew at 1.0 μg/ml, but only ⅙ of the colonies inoculated onto 10 μg/ml grew (Table 1). Although hyphae grew from all plugs at 1.0 μg/ml, the colony diameters did not increase as quickly on this medium as they did on 0 or 0.1 μg/ml (Table 2).

Hyphae grew from one plug of the unidentified fungus at 10.0 μg/ml, but not from the other 16 plugs at that concentration (Table 1). The diameter of the growing colony after 3 weeks on 10 μg/ml was only 10 mm. Hyphae of *P. chrysanthemicola* grew at concentrations up to 13 μg/ml, but the highest concentration at which mycelium grew from 100% of the plugs was 1.0

TABLE 2. Diameters (mm) of fungal colonies at weeks 1 and 3 as affected by benomyl at concentrations of 0 to 1,000 μg/ml potato dextrose agar.

Fungus	0		0.1		1		10		100		1,000	
	1	3	1	3	1	3	1	3	1	3	1	3
Verticillium chlamydosporium Strain 2	30 ± 3.1 12	71 ± 6.5 12	NG 12	+ 12	NG 6	NG 6	NG 6	NG 6	NG 6	NG 6	—	—
Drechmeria coniospora Strain 1	13 ± 1.5 12	25 ± 3.0 12	13 ± 1.5 12	25 ± 2.8 12	NG 12	NG 12	NG 12	NG 12	NG 6	NG 6	—	—
Drechmeria coniospora Strain 2	12 ± 0.6 6	22 ± 4.2 6	12 ± 1.0 6	23 ± 2.3 6	NG 6	NG 6	NG 6	NG 6	NG 6	NG 6	—	—
Chaetomium sp.	81 ± 4.2 6	85 ± 0.0† 6	39 ± 6.0 6	85 ± 0.0† 6	NG 6	NG 6	NG 6	NG 6	NG 6	NG 6	—	—
Acremonium bacillisporum	29 ± 3.4 12	57 ± 14.5 12	30 ± 4.1 12	68 ± 9.2 12	12 ± 2.5 12	30 ± 4.8 12	NG 12	+ 12	NG 6	NG 6	—	—
Unidentified fungus	36 ± 3.1 18	78 ± 7.4 18	33 ± 2.6 12	73 ± 11.4 12	26 ± 4.0 15	65 ± 7.0 15	NG 18	+ 17	NG 12	NG 12	—	—
Phoma chrysanthemicola	32 ± 2.5 24	79 ± 6.1 24	30 ± 2.0 12	78 ± 6.6 11	31 ± 2.3 12	81 ± 4.3 12	+ 24	12 ± 4.1 24	NG 12	NG 12	—	—
Fusarium sp.	63 ± 7.2 24	84 ± 3.0 24	63 ± 9.1 12	83 ± 3.8 12	41 ± 5.2 6	85 ± 0.0† 6	17 ± 2.0 12	38 ± 3.8 12	12 ± 0.9 18	22 ± 2.3 18	NG 12	+ 11
Verticillium lecanii	28 ± 1.3 12	67 ± 7.8 9	48 ± 25 6	76 ± 10.2 6	21 ± 1.2 6	65 ± 18.5 6	15 ± 1.0 9	39 ± 4.7 6	13 ± 1.4 15	29 ± 6.0 12	12 ± 0.7 6	30 ± 5.0 6
Verticillium chlamydosporium Strain 1	31 ± 2.1 12	73 ± 10.2 12	31 ± 1.1 6	74 ± 5.7 6	30 ± 1.0 6	71 ± 2.8 6	20 ± 0.8 6	42 ± 2.2 6	17 ± 1.7 12	33 ± 4.2 12	14 ± 0.7 6	27 ± 5.8 6

Mean ± standard deviation over number of colonies measured.
NG = no growth; + = some growth on at least one plug; — = not tested.
† 85 mm = diameter of petri dishes.

μg/ml. Colony diameters at 0, 0.1, and 1.0 μg/ml were similar (Table 2).

Fusarium sp. tolerated high levels of benomyl. Mycelium grew from 100% of the plugs inoculated onto medium containing 475 μg/ml (Table 1). At the next highest concentration measured—500 μg/ml—hyphae grew from 11 of 12 plugs. Of the 11 plugs on agar containing 1,000 μg/ml, hyphae grew from only one plug. The colony diameters were smaller at 10 μg/ml and the higher concentrations than at 0.1 and 1.0 μg/ml (Table 2). Colony diameters at 1 week on 1.0 μg/ml were smaller than on 0 and 0.1 μg/ml, but diameters were similar after 3 weeks.

Verticillium lecanii and *V. chlamydosporium* strain 1 tolerated 1,000 μg benomyl/ml PDA, which was the highest level of fungicide tested. Hyphae grew from 100% of the plugs inoculated onto medium at this concentration of benomyl (Table 1). Neither fungus was completely unaffected by the fungicide; the colony diameters were substantially smaller at a concentration as low as 10 μg/ml (Table 2).

When no fungicide was present, *Chaetomium* sp. and *Fusarium* sp. had the largest colony diameters at the end of 3 weeks. The unidentified fungus and *P. chrysanthemicola* also had wide diameters at that time. The two strains of *Drechmeria* had the smallest diameters.

The EBS from *D. coniospora* was originally isolated from strain 1 hyphae growing on agar amended with 10 μg benomyl/ml medium. At this concentration, strain 1 required more than 3 weeks to show growth. Several single spore isolates were made from the EBS and were tested separately. At 0 and 0.1 μg/ml, the three single spore isolates had approximately the same colony diameters as the original mixed population (Tables 2, 3). Unlike the original strain 1, however, all three single spore isolates grew at 1.0 and 10.0 μg/ml within the time limit of the experiment. Furthermore, the colonies were as wide on these concentrations as on 0 μg/ml (Table 3).

Colony diameters of the *A. bacillisporum* EBS were roughly similar to diameters of

TABLE 3. Diameters (mm) of EBS† colonies at weeks 1 and 3 as affected by benomyl at concentrations of 0 to 1,000 μg/ml potato dextrose agar.

Fungus	0		0.1		1		10		100		1,000	
	1	3	1	3	1	3	1	3	1	3	1	3
Drechmeria coniospora Strain 1, single spore isolate 1	14 ± 0.9	28 ± 1.4	14 ± 1.5	28 ± 2.2	15 ± 1.7	27 ± 2.3	13 ± 1.0	26 ± 1.2	—	—	—	—
Drechmeria coniospora Strain 1, single spore isolate 2	12 ± 0.4	22 ± 1.2	13 ± 2.9	24 ± 2.9	12 ± 1.5	23 ± 1.7	11 ± 1.3	23 ± 1.1	—	—	—	—
Drechmeria coniospora Strain 1, single spore isolate 3	14 ± 1.7	28 ± 2.8	14 ± 1.2	28 ± 0.9	15 ± 1.9	28 ± 2.2	12 ± 0.7	25 ± 1.2	—	—	—	—
Acremonium bacillisporum	23 ± 1.6	55 ± 15.2	25 ± 5.8	58 ± 6.5	22 ± 2.9	50 ± 8.6	12 ± 1.7	24 ± 4.3	—	—	—	—
Unidentified fungus	24 ± 1.7	61 ± 2.7	23 ± 0.7	60 ± 2.0‡	22 ± 1.9	57 ± 2.2‡	16 ± 1.0	36 ± 2.9	—	—	—	—
Fusarium sp.	19 ± 1.4	55 ± 9.4	17 ± 1.0	47 ± 4.2	—	—	17 ± 2.2	41 ± 4.8	16 ± 1.0	34 ± 1.8	13 ± 1.0	27 ± 2.0

Mean ± standard deviation.
— = not tested.
† EBS = elevated benomyl strains; i.e., strains with elevated tolerance to benomyl.
‡ Number of colonies measured (n) = 5. For all other treatments, n = 6.

the original strain at 0 and 0.1 μg/ml, but were much wider at 1.0 (Tables 2, 3). The EBS was initially isolated from agar amended with 10 μg benomyl/ml PDA. Hyphae grew from all six EBS plugs at 10.0 μg/ml, and growth was extensive enough to be measured.

The EBS of the unidentified fungus was isolated from a colony growing at 10 μg/ml. Colony diameters of the EBS were smaller than those of the original strain at 0 and 0.1 μg/ml, somewhat similar at 1 μg/ml, and wider at 10 μg/ml (Tables 2, 3). Colonies grew from all six EBS plugs at 10 μg/ml.

The *Fusarium* EBS was isolated from agar containing 900 μg benomyl/ml PDA. Colony diameters were much smaller than those of the original strain at 0 and 0.1 μg/ml (Tables 2, 3). At 10 μg/ml, however, the EBS colonies had the same diameters as the original strain, and at 100 μg/ml, the EBS colony diameters were wider than those of the original strain. All EBS colonies grew on 1,000 μg benomyl/ml PDA.

Discussion

Effects of pesticides on beneficial organisms have been investigated for a number of chemicals and biocontrol agents. This area is of such importance in biocontrol work that it is studied both by independent researchers and by groups that organize tests and report jointly on the results (13). Fungicides have been shown to affect nematophagous fungi. Benomyl can inhibit growth and (or) nematode-antagonistic activity of various fungi, including *Arthrobotrys conoides* Drechsler (7), *A. irregularis* (Matruchot) Mekht. (4), *A. oligospora* Fresenius (7), *Cylindrocarpon destructans* (Zins.) Scholten (5), *Glomus fasciculatum* (Thaxter *sensu* Gerdemann) Gerdemann & Trappe (26), *Hirsutella rhossiliensis* Minter & Brady (23), and *Verticillium chlamydosporium* (5). Kapur et al. (15) found deleterious effects of benomyl and other fungicides on various soil-inhabiting fungi, but fungi generally resumed growth after benomyl treatment. Strains of nematode-antagonistic fungi have been genetically manipulated to decrease benomyl sensitivity. Mutants of *Paecilomyces lilacinus* (Thom) Samson and *V. chlamydosporium* with resistance or tolerance to benomyl have been induced (9,10).

Tolerances to benomyl were variable among the fungal strains tested in the current study. Difference in tolerance levels occurred even within one species; one strain of *V. chlamydosporium* could not tolerate benomyl, whereas the other grew at high concentrations of the fungicide. The strain of *V. chlamydosporium* that exhibited no tolerance to benomyl in the current study reduced viability of *H. glycines* eggs in a laboratory bioassay (18). The strain with high tolerance to benomyl did not affect egg viability in that study. A strain of *V. chlamydosporium* studied by Gaspard (9) for control of *Meloidogyne incognita* also exhibited tolerance or resistance to benomyl. The selective medium used to isolate this fungus contained 25 μg benomyl/ml medium (9). The fungus caused some reduction in egg and juvenile numbers, but not enough to result in significant nematode control (9).

Drechmeria coniospora was included in the current study because it has been found to control *Meloidogyne* spp. in the greenhouse (14) and because one strain was observed infecting live *H. glycines* eggs (18). Unlike the two strains of *V. chlamydosporium* studied for benomyl tolerance, the two strains of *D. coniospora* placed on benomyl-amended agar responded similarly. Both *D. coniospora* strains exhibited almost no tolerance to benomyl. However, some hyphae did grow in the presence of benomyl, so strains with increased benomyl tolerance were subcultured. The EBS retained elevated tolerance even after repeated transfers on unamended agar. All cultures of *D. coniospora* grew slowly, even on unamended agar.

Phoma chrysanthemicola decreased viability of SCN eggs in a laboratory bioassay (18). This strain did not exhibit tolerance to high levels of benomyl. *Verticillium lecanii* is a nematode antagonist (18,25) and an insect biocontrol agent (12,27). Because

this fungus has been applied to control insects on greenhouse plants, researchers have determined benomyl tolerance of various strains (8,11,13,16,17,19,28). Differing results reflect strain differences and variations in testing methods. The strain of *V. lecanii* tested in the current study was selected because it adversely affected *H. glycines* eggs (18). This strain exhibited high tolerance to benomyl, but colony diameters were smaller at 10 μg/ml and higher concentrations than at lower benomyl concentrations.

Fungicide tolerance can vary greatly among different strains of a fungus species, so each strain of interest should be tested individually. Levels of benomyl tolerated by nematode antagonists have been reported in this study, including levels tolerated by fungus strains that reduced viability of *H. glycines* eggs in culture and (or) infected eggs (18).

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