FUNGICIDAL TOLERANCE OF BOTRYTIS CINERA

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ABSTRACT

Numerous *Botrytis cinerea* isolates from containerized conifers within 3 Colorado nurseries exhibited levels of tolerance to commercially-used fungicides. Some isolates were tolerant to benomyl, captan, chlorothalonil, mancozeb, and zineb during in *vitro* growth tests on agar medium. Dichloran was the only fungicide that was completely inhibitory to all isolates tested. Benomyl at 50 ppm did not inhibit conidial germination on agar, although germ tube growth of sensitive isolates was restricted. These results indicate that *B.* cinerea isolates have developed tolerance to many commercial fungicides. Prescriptions for fungicide application should be based on tolerance characteristics of isolates present.

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Botrytis cinerea Fr. is an important pathogen on numerous crops grown within greenhouses 16, 19). Recent investigations at the Colorado Hydroponics Nursery (Lyons, Colorado) indicated widespread mortality of containerized lodgepole pine *(Pinus contorta)* in greenhouses caused by the pathogen. Bi-weekly benomyl application through overhead sprinkling systems did not control the disease. Significant mortality (20%) occurred in spite of fungicidal treatment.

Previous reports (7, 15, 16, 21) have identified benomyl-tolerant B. cinerea strains. Tests were conducted to determine if benomyl-tolerant strains of the fungus occurred within Colorado nurseries where the chemical was routinely used. In order to provide growers with alternative fungicide options, other commonly-used fungicides were also tested for tolerance by B. *cinerea.*

METHODS AND MATERIALS

The fungus was isolated from containerized conifer seedlings in 3 Colorado greenhouses: Colorado Hydroponics (Lyons), Colorado State Forest Service Nursery (Fort Collins), and U. S. Forest Service, Mt. Sopris Tree Nursery (Carbondale). Twenty-eight isolates were obtained from necrotic lesions on lodgepole pine, Scots pine *(Pinus sylvestris),* Engelmann spruce *(Picea engelmanii)* and blue spruce *(Picea pungens)* which were selected from locations throughout the greenhouses. Two isolates from California redwood *(Sequoia sempervirens)* seedlings, one known to be tolerant to benomyl and the other known to be benomyl-sensitive, were used for reference in each of 4 tests.

Growth tests -- Tolerance to fungicides was determined by assessing growth of B. *cinerea* isolates over the surface of potato dextrose agar (PDA) amended with fungicides. Benomyl was ground with a mortar and pestle and all fungicides dissolved in distilled water prior to incorporation into agar. Petri plates (100 mm diam.) with 25 ml of media were inoculated with an 8 mm plug of mycelium from the advancing edge of 4-day-old colonies. Each treatment was replicated 3 (Test 1) or 4 (Tests 2 & 3) times and plates incubated in the dark at about 25° C. After 6 days (14 days for isolate 78-19) fungal growth across the plates was measured. Data were analyzed using Tukey's test for multiple comparison of treatment means.

Test 1 - The following fungicides, mixed in PDA at 50 ppm active ingredient (a.i.), were used to test tolerance of 9 B. *cinerea* isolates:

	Generic Name	Trade Name	Manufacturer
1.	benomyl	Benlate ®	Dupont
2.	benomyl	Benomyl ®	Fertilome
3.	dichloran	Botran ® 75 W.P.	Tuco (Upjohn)
4.	captan	Captan ® 50 W.P.	Stauffer
5.	chlorothalonil	Daconil 2787 ®	Diamond Shamrock
6.	mancozeb	Dithane ® M-45	Rohm and Haas
7.	zineb	Dithane ® Z-78	Rohm and Haas

Isolates tested included 7 from Colorado Hydroponics and benomyl-sensitive (78-18) and tolerant (78-19) isolates from California. Benomyl was added to the media before autoclaving; the other fungicides were added to cooled media.

Test 2 - Benomyl tolerance of 30 B. *cinerea* isolates was evaluated.
Isolates tested included 18 from Colorado Hydroponics, 3 from Colorado State Forest Service, 7 from Mt. Sopris, and the 2 California reference isolates. Benomyl at 50 ppm a.i. from 2 manufacturers (Dupont and Dexol) added to PDA either before or after autoclaving was used in this test.

Test 3 - This test assessed responses of B. *cinerea* to 3 fungicides at different concentrations. The fungicides and concentrations used were:

	Generic Name	Trade Name	Manufacturer	Concentration
1.	benomyl	Benlate ®	Dupont	5.0, 15.8, 50.0, 158.0, & 500.0 ppm a.i.
2.	dichloran	Botran ® 75 W	Tuco (Upjohn)	5.0, 15.8, & 50.0 ppm a.i.
3.	chlorothalonil	Daconil 2787 ®	Diamond Shamrock	5.0, 50.0, & 500.0 ppm a.i.

Three isolates chosen for their range of benomyl tolerance from each of the 3 nurseries plus the 2 California reference isolates were evaluated in this test. All fungicides were added to PDA after autoclaving.

Conidial germination tests -- Conidia were harvested from B. *cinerea* cultures growing on PDA by flooding petri plates with 10 ml distilled water and agitating spores with a sterilized camel's hair paintbrush. Cultures were either 6-days-old (Isolate group I - Table 3) or one-month-old (Isolate group II) at the time of spore harvest. Spore suspensions were passed through double layers of cheesecloth to remove mycelial fragments and 1:10 dilutions made with distilled water. Approximately 0.5 ml spore suspension was added to each test plate and spread uniformly over the agar surface with a sterilized glass rod.

Effects of benomyl on conidial germination were determined for B. *cinerea* isolates. For each isolate, one control and two benomyl plates, each with PDA amended with 50 ppm of the fungicide, were used. After 24 hours incubation at about 24^0 C, 300 randomly-chosen conidia on each plate were examined under the compound microscope. Percentage germination on PDA and benomyl-amended media was compared using a one-way analysis of variance.

RESULTS

Growth tests

Test 1 - Benomyl tolerance and susceptibility of the California reference isolates (78-19, 78-18) were confirmed in this test (Table 1). Of the 7 Colorado Hydroponics isolates tested, two (78-11, 78-12) showed high levels of tolerance to benomyl, two (78-1, 78-13) were intermediate in response,

TABLE 1 Fungicidal effects on growth of *Botrytis cinerea* (Test 1).[a]

Fungicide Treatment	*Botrytis cinerea* Isolates								
	California[b]		Colorado Hydroponics						
	78-18	78-19	78-1	78-4	78-6	78-7	78-11	78-12	78-13
Control	100 A	100 A	100 A	100 A	100 A	100 A	100 A	100 A	100 A
Benomyl (Dupont)	1 C	91 A	17 BC	6 C	9 C	8 D	90 AB	98 A	46 BC
Benomyl (Fertilome)	3 C	72 B	31 B	40 B	41 B	40 B	82 AB	122 B	74 AB
Dichloran	0 C	1 D	0 D	0 C	0 C	0 D	0 D	0 F	0 D
Captan	17 B	67 B	8 CD	6 C	12 C	10 CD	9 D	16 E	8 CD
Chlorothalonil	62 B	53 C	23 BC	5 C	19 C	22 C	31 CD	71 D	7 CD
Mancozeb	51 B	99 A	47 A	47 B	49 B	40 B	62 BC	104 A	55 B
Zineb	101 A	101 A	96 A	96 A	99 A	97 A	62 A	164 C	99 A

[a] Fungicide concentration = 50 ppm a.i.; growth expressed as percent of control. Within each isolate, means followed by the same capital letter are not significantly different (P = 0.05) using Tukey's Test for Multiple Comparisons.

[b] California reference isolates: 78-18 = benomyl sensitive
78-19 = benomyl tolerant

and three (78-4, 78-6, 78-7) were sensitive as evidenced by little growth over the benomyl-amended agar. Response to the two types of benomyl used (Dupont and Fertilome) was significantly different in 5 of the 7 Colorado isolates tested. One isolate (78-19) was more tolerant of Dupont benomyl; whereas, others (78-4, 78-6, 78-7, 78-12) showed greater tolerance to Fertilome benomyl.

Of all the fungicides tested, dichloran was the only one for which no tolerance was shown (Table 1). At least some degree of tolerance to all other fungicides was evident. Tolerance of individual isolates to more than one fungicide was common. The least effective fungicides were zineb and mancozeb; chlorothalonil was effective against only two isolates (78-4, 78-13). Next to dichloran, captan was the most effective fungicide in limiting growth of B. cinerea.

Test 2 - Of the 30 B. cinerea isolates tested, only 12 were sensitive to 50 ppm a.i. benomyl. Sensitivity was based on growth of less than 25 percent of controls for those isolates tested on Dupont benomyl. Isolates grown on the Dexol product were considered sensitive if growth was less than 50 percent of controls since this benomyl was generally less restrictive. Two of these sensitive isolates, the California reference isolate (78-18) and one from the Colorado State Forest Service Nursery (78-29), displayed no growth on benomyl-amended agar. Subsequent tests indicated that these two isolates were killed by the fungicide. The most tolerant isolates were those from Mt. Sopris Nursery, all of which grew rapidly and were not inhibited by benomyl.

There was no difference in growth response to benomyl added before or after autoclaving.

Test 3 - Results of this test (Table 2) re-confirmed benomyl tolerance and susceptibility of the California reference isolates (78-18, 78-19). Increasing benomyl concentration resulted in greater sensitivity in all isolates tested. Isolates sensitive at low concentrations (78-18, 78-29) remained sensitive throughout the range of concentration. Most significant differences in growth among treatments occurred at the higher benomyl concentrations (158.0 and 500.0 ppm a.i.).

All isolates were sensitive to dichloran at all concentrations tested. Increasing fungicide concentrations usually did not significantly alter growth responses.

Sensitivity to chlorothalonil generally increased with greater fungicide concentration. Ten of the 11 isolates tested were tolerant to the fungicide at 5.0 ppm a.i. Significant increases in growth sensitivity usually occurred between fungicide treatments of 5.0 ppm and the higher concentrations (50.0 and 500.0 ppm a.i.). Most isolates displayed tolerance to both benomyl and chlorothalonil. Some (78-18, 78-29) were sensitive to benomyl and tolerant to chlorothalonil, whereas, another isolate (78-27) was tolerant to benomyl and sensitive to chlorothalonil.

Conidial germination tests -- Benomyl did not restrict initial conidial germination of the B. cinerea isolates tested (Table 3). In fact, 6 of the isolates showed significantly greater germination in the benomyl-amended agar.

TABLE 2 Effects of benomyl, dichloran and chlorothalonil on growth of *Botrytis cinerea* (Test 3).[a]

		Botrytis cinerea Isolates										
		California[b]		Colorado Hydroponics			Colo. St. For. Serv.			Mt. Sopris		
Fungicide Treatment	Conc. (ppm)	78-18	78-19	78-1	78-4	78-11	78-20	78-27	78-29	78-36	78-38	78-39
Control	-	100 A	100 A	100 A	100 A	100 A	100 AB	100 A	100 A	100 AB	100 A	100 AB
	5.0	3 EF	63 BC	98 A	76 B	96 A	107 A	104 A	2 E	102 A	101 A	103 A
	15.8	2 EF	69 AB	48 C	13 D	110 A	97 AB	102 A	1 EF	82 C	100 A	99 AB
	50.0	3 EF	83 AB	9 F	4 D	92 A	98 AB	96 A	2 EF	86 BC	93 B	96 B
	158.0	1 EF	59 BCD	3 F	4 D	65 B	77 BC	81 B	1 EF	64 D	63 C	62 C
	500.0	0 F	26 DE	3 F	1 D	33 CD	61 C	48 C	0 F	47 EF	43 E	45 E
Dichloran	5.0	7 E	6 E	11 EF	10 D	7 E	11 E	7 DE	6 E	10 G	2 F	7 G
	15.8	1 EF	2 E	0 F	0 D	0 E	0 E	0 E	1 EF	0 G	0 F	1 H
	50.0	2 EF	2 E	3 F	3 D	1 E	1 E	13 D	2 EF	1 G	6 F	1 H
Chlorothalonil	5.0	54 D	46 CD	73 B	77 B	43 C	44 D	11 DE	50 B	60 DE	58 C	61 C
	50.0	30 C	53 BCD	42 CD	44 C	16 DE	9 E	9 DE	30 C	41 F	57 D	52 D
	500.0	18 B	31 DE	28 DE	35 C	12 E	11 E	6 DE	22 D	38 F	41 E	39 F

[a] Growth expressed as percent of control. Within each isolate for all fungicide treatments, means followed by the same capital letter are not significantly different (P = 0.05) using Tukey's Test for Multiple Comparisons.

[b] California reference isolates:
78-18 = benomyl sensitive
78-19 = benomyl tolerant

TABLE 3 Effects of benomyl on germination of *Botrytis cinerea* conidia.

Isolate Group[a]	Isolate	Percentage Germination		F values[d]		Benomyl Tolerance Class[e]
		Control[b]	Benomyl (500 ppm)[c]			
I	78-1	87.7	87.0	0.12	NS	
	78-11	95.2	95.2	0.00	NS	T
	78-18	91.6	96.8	58.43	***	S
	78-20	93.6	95.6	5.18	*	T
	78-27	95.8	96.9	1.77	NS	T
	78-29	93.5	93.7	0.30	NS	S
	78-36	93.3	94.8	0.56	NS	T
	78-38	93.2	95.6	9.83	**	T
	78-39	79.5	80.4	0.12	NS	T
Average (Isolate Group I)		91.5	92.9			
II	78-2	58.4	57.5	0.08	NS	T
	78-3	84.2	92.3	10.46	**	S
	78-4	85.1	94.0	43.04	***	S
	78-7	77.3	96.3	107.89	***	S
	78-16	54.1	54.9	0.48	NS	T
Average (Isolate Group II)		71.8	79.0			

[a] Isolate Groups: I = from six-day-old cultures
II = from one-month-old cultures

[b] Average values from 300 examined spores

[c] Average values from 600 examined spores

[d] Based on one-way analysis of variance comparing control and benomyl treatments.

NS = Not statistically significant
* = Statistically significant (P = 0.10)
** = Statistically significant (P = 0.05)
*** = Statistically significant (P = 0.01)

[e] T = benomyl tolerant based on growth of germ tubes over agar surface
S = benomyl susceptible based on germ tube lysis and restricted growth

Response of germ tubes after initial emergence provided additional evidence for fungicide tolerance. Germ tubes from spores of benomyl-susceptible isolates (Table 3) often lysed or wrapped around the spore, whereas, germ tubes from benomyl-tolerant isolates grew over the agar surface with no apparent inhibition.

One-way analysis of variance indicated that significantly greater percentage of spores from six-day-old cultures germinated than spores from one-month old cultures. Isolates varied in germinability.

DISCUSSION

Production of forest tree seedlings in containers within greenhouses has resulted in the development of problems from facultative pathogens such as B. *cinerea* (16, 19). Trees grown under these conditions are often crowded. Overhead irrigation increases the problem by maintaining high humidity necessary for development of B. *cinerea.* The fungus usually is a saprophyte on necrotic tissue (6, 13, 141; however, under greenhouse conditions the fungus may become parasitic and attack live plant tissues (16).

Regular application of fungicides, usually incorporated into overhead irrigation, have been used to control *B. cinerea* in greenhouses (19). In spite of these preventative measures, there are an increasing number of reports indicating fungicidal tolerance of the fungus. For example, B. *cinerea* isolates have been reported tolerant to benomyl (15, 16, 21) and dichloran (22). This tolerance may be due in part to the intense selection pressure exerted on resident populations of the pathogen by heavy application of a single fungicide.

Isolates of B. *cinerea* obtained from conifer seedlings at three Colorado nurseries were tolerant to benomyl, captan, chlorothalonil, mancozeb, and zineb when exposed on PDA-amended media. Only a small percentage of the isolates tested were sensitive to benomyl which was the most commonly used fungicide by the nurseries.

At Colorado Hydroponics Nursery, the first crop of conifers within specific greenhouses had B. *cinerea* strains tolerant to benomyl. Benomyl was not applied to the previous crop (tomatoes) within these greenhouses.

Application of benomyl at the Colorado State Forest Service Nursery has been common on many conifers for a number of years. Losses due to B. cinerea have occurred at low levels. Three of the 4 isolates tested from This nursery displayed benomyl tolerance.

B. *cinerea* isolates from Mt. Sopris Nursery were obtained from the second conifer crop grown in a new greenhouse. Although no losses were noted in the first crop, benomyl was routinely applied as a precautionary measure. Mortality of scattered trees was found in the second crop in spite of continued benomyl application. All B. *cinerea* isolates tested from this nursery displayed benomyl tolerance, which indicates that either tolerant strains were present in the field or that tolerance was rapidly developed in the greenhouse within a year.

Some B. cinerea isolates were tolerant to more than one fungicide. Multiple-fungicide tolerance by this and other fungi has been previously reported (1, 22). However, other reports (2, 3, 8, 18, 20) emphasize that fungi tolerant to one fungicide are often susceptible to other chemicals.

All isolates tested were sensitive to dichloran, even at low concentrations. No field resistance to dichloran has been reported for Botrytis spp. (17); although, there is one report (10) of resistance developed by Sclerotium cepivorum on onions. This fungicide provides a possible alternative for B. cinerea control in Colorado nurseries. However, use of a single fungicide is discuraged due to the rapid development of tolerance exhibited by the pathogen (16, 9).

The performance of chlorothalonil was disappointing compared to its reported effectiveness on B. squamosa (11) and Cercospora arachidicola (9) strains tolerant to benomyl. Although this fungicide has been recommended as an alternative to benomyl for B. cinerea control on containerized conifers (15), our results indicate that tolerance in fungus populations tested may preclude its usefulness in certain Colorado nurseries.

Captan was generally effective against the isolates tested. This non-systemic organic compound has a history of good performance (17) and is often considered a viable alternative to benomyl and other systemic fungicides for which tolerance may develop (17, 18).

The stability of fungicidal tolerance exhibited by B. cinerea agrees with other reports (4, 16) and is indicative of a dominant genetic trait (5, 16).

Fungicide-tolerant strains displayed decreasing tolerance with increasing chemical concentration. This agrees with results found by other investigators (12, 16). On the other hand, sensitive isolates were restricted throughout the fungicide concentration spectrum. From a practical standpoint, heavy fungicide applications will probably have little effect in overcoming tolerance. Rather, such applications will most likely increase selection pressure and result in the development of more tolerant strains of the fungus.

Benzimidazole fungicides are believed to inhibit mycelial growth rather than fungal spore germination (23). Benomyl did not reduce conidial germination of B. cinerea isolates tested. Rather, the chemical affected germ tubes after emergence by causing lysis and abnormal growth in benomylsensitive isolates. Therefore, the fungicide probably limits infection subsequent to spore germination. Germ tube growth and development were not affected by benomyl in B. cinerea strains tolerant to the chemical.

Based on the results of this investigation, the following recommendations are made to reduce losses from B. cinerea on containerized conifer seedlings:

1. Promote cultural methods that are unfavorable to fungus buildup including greater aeration and spacing among seedlings, modification of watering schedules to reduce moisture retention on foliage, and sanitation practices to reduce potential inoculum.

2. Avoid the exclusive use of a single fungicide for extended periods and apply necessary chemicals at the lowest possible rates to achieve satisfactory control.
3. Rotate use of different fungicides and integrate chemicals with different modes of fungicidal action into schedules to avoid the possibility of multiple tolerance.
4. Establish and maintain a program to detect fungicidal tolerance by screening isolates on fungicide-amended agar. Such a program will provide necessary information for adjusting fungicide schedules.

This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed have been registered. All uses of pesticides must be registered by appropriate State and/or Federal agencies before they can be recommended.

CAUTION: Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or other wildlife -- if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

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