

Impact of Azoxystrobin, Dimethomorph, Fluazinam, Fosetyl-AI, and Metalaxyl on Growth, Sporulation, and Zoospore Cyst Germination of Three *Phytophthora* spp.

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ABSTRACT

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In vitro activity of azoxystrobin, dimethomorph, and fluazinam on growth, sporulation, and zoospore cyst germination of *Phytophthora capsici*, *P. citrophthora*, and *P. parasitica* was compared to that of fosetyl-AI and metalaxyl. The 50% effective concentration (EC₅₀) values for inhibition of mycelial growth of the three pathogens usually were lowest for dimethomorph and metalaxyl, ranging from <0.1 to 0.38 µg/ml. However, the 90% effective concentration (EC₉₀) levels for dimethomorph always were lower than the other four tested compounds, with values ranging from 0.32 to 1.6 µg/ml. Mycelial growth of *P. capsici*, *P. citrophthora*, and *P. parasitica* was least affected by azoxystrobin and fluazinam, with estimated EC₉₀ values >3,000 µg/ml. Reduction of sporangium formation by *P. capsici*, *P. citrophthora*, and *P. parasitica* in the presence of dimethomorph at 1 µg/ml was significantly greater than that recorded for the same concentration of azoxystrobin, fluazinam, and fosetyl-AI. For the three species of *Phytophthora*, zoospore motility was most sensitive to fluazinam (EC₅₀ and EC₉₀ values of <0.001 µg/ml) and least sensitive to fosetyl-AI, with EC₅₀ and EC₉₀ values ranging from 299 to 334 and 518 to 680 µg/ml, respectively. Germination of encysted zoospores of *P. capsici*, *P. citrophthora*, and *P. parasitica* was most sensitive to dimethomorph (EC₅₀ and EC₉₀ values ranging from 3.3 to 7.2 and 5.6 to 21 µg/ml, respectively), intermediate in sensitivity to fluazinam (EC₅₀ and EC₉₀ from 18 to 108 and 67 to >1,000 µg/ml, respectively) and metalaxyl (EC₅₀ and EC₉₀ from 32 to 280 and 49 to 529 µg/ml, respectively), and lowest in sensitivity to azoxystrobin and fosetyl-AI (EC₅₀ and EC₉₀ from 256 to >1,000 µg/ml). The activity of azoxystrobin, dimethomorph, and fluazinam on one or more stages of the life cycle of *P. capsici*, *P. citrophthora*, and *P. parasitica* suggests that these compounds potentially could provide *Phytophthora* spp. disease control comparable to that of the established fungicides fosetyl-AI and metalaxyl.

Diseases caused by species of the genus *Phytophthora* continue to inflict significant losses on numerous important crops worldwide (11). Among these diseases are gummosis and root rot of citrus caused by *P. citrophthora* and *P. parasitica* and crown and root rot of pepper (*Capsicum annuum*) caused by *P. capsici*, diseases of importance in Arizona (22,25) as well as other regions where these crops are grown. The impact of *Phytophthora* spp. on food and fiber production is revealed by the large number of publications from throughout the world that deal with every aspect of this genus of plant pathogenic organisms (29). Losses attributable to *Phytophthora* spp. diseases of some tree fruit and vegetable crops in the United States have been reduced through the use of the systemic fungicides fosetyl-AI (Aliette, Rhone-Poulenc Ag Co., Research Triangle Park,

NC) or metalaxyl (Ridomil, Novartis Crop Protection, Greensboro, NC) (25,28,30,31). Recently, some other chemistries have been reported to have activity on some species of *Phytophthora*, including azoxystrobin (Abound, Zeneca Ag Products, Wilmington, DE; 15), dimethomorph (Acrobat, American Cyanamid Co., Princeton, NJ; 7,21), and fluazinam (Zeneca Ag Products; 9,33).

The objective of the following study was to evaluate and compare the in vitro impact of azoxystrobin, dimethomorph, fosetyl-AI, fluazinam, and metalaxyl on growth, sporulation, and zoospore cyst germination of *P. capsici*, *P. citrophthora*, and *P. parasitica*. Preliminary accounts of this research were reported earlier (23,24).

MATERIALS AND METHODS

Fungi and fungicides. One isolate each of *P. capsici*, *P. citrophthora*, and *P. parasitica* was used in these investigations. The isolate of *P. capsici* was recovered from a chile-pepper plant in a commercial field in southeastern Arizona, whereas isolates of *P. citrophthora* and *P. parasitica* originated from infected citrus trees in western and central commercial orchards of the state. The following formulations of tested fungicides were used in all experiments:

azoxystrobin (Abound 80WG), dimethomorph (Acrobat 50WP), fluazinam (Fluazinam 50WP), fosetyl-AI (Aliette 80WDG), and metalaxyl (Ridomil 2E).

Mycelial growth. Each species of *Phytophthora* was grown on V-8 juice agar (V8A; commercial V-8 juice, 200 ml; CaCO₃, 2 g; agar, 17 g; and distilled water, 800 ml) plates at 24°C for 5 days. Individual agar disks (6 mm in diameter) were removed from the edge of an actively growing culture of each pathogen and placed at the edge of a plastic Petri dish (9 cm in diameter) containing corn meal agar (CMA; 17 g of Difco corn meal agar in 1 liter of distilled water) amended with a test fungicide at concentrations of 0.1, 1, 10, 100, 1,000, and 3,000 µg a.i./ml. Fungicides were added to CMA after autoclaving when the agar had cooled to approximately 55°C. Control Petri dishes contained only CMA. Five replicate plates of each fungicide concentration as well as controls were prepared for each species of *Phytophthora*. After a 4-day incubation period at 24°C in darkness, the radial growth of mycelia was measured.

Sporangium formation. Sporangia were produced by growing the *Phytophthora* spp. on V8A plates as described earlier. Four agar disks (6 mm in diameter) were removed from the edge of an actively growing culture of each isolate and placed in a series of plastic Petri dishes (60 mm in diameter) containing 7 ml of 1.5% non-sterile soil extract amended with one of the test fungicides to give a final concentration of 1, 10, 100, or 1,000 µg a.i./ml. Nonsterile soil extract was prepared by mixing 15 g of a sandy loam orchard soil in 1 liter of distilled water with a magnetic stirrer for 8 h at 25 ± 2°C. After an additional 16-h incubation period without stirring, the coarse soil particles settled to the bottom of the container and the remaining suspension was decanted and used as the soil extract. Five replicate plates of each fungicide concentration, in addition to control plates containing nonsterile soil extract without fungicides, were prepared for each species of *Phytophthora*. Following a 4-day incubation period at 24°C in darkness, the liquid was decanted from each Petri dish and the agar disks were stained and fixed with acid fuchsin in 85% lactic acid. The number of sporangia along the margins of each agar disk was counted.

Zoospore motility, encystment, and germination. Sporangia were produced as

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described above by placing four V8A disks (6 mm in diameter) from the edge of an actively growing culture of each species of *Phytophthora* into a series of plastic Petri dishes (60 mm in diameter) containing 7 ml of 1.5% nonsterile soil extract, then incubating these dishes in darkness at 24°C for 4 days. Sporangia were induced to release zoospores by chilling at 4°C for 20 min. After rewarming at 25°C for 20 min, agar disks and attached mycelia were removed from each Petri dish and the volume of the remaining zoospore suspension was determined. Aqueous mixtures of each fungicide at a concentration of 0.002, 0.02, 0.2, 2, 20, 200, and 2,000 µg a.i./ml were added to equal volumes of the zoospore suspensions, giving final concentrations of 0.001, 0.01, 0.1, 1, 10, 100, and 1,000 µg a.i./ml. Control zoospore suspensions received an equal volume of water only. Zoospore suspensions were maintained at 25°C and observed microscopically at 75× to determine the maximum elapsed time for complete cessation of motility. Observations were made at 1-min intervals for the first 15 min, then at 15-min intervals for the next 45 min, and finally at 1-h intervals until no zoospore movement was detected.

The majority of zoospore cysts were adhering to the bottom of each plastic Petri dish. To determine the viability of these encysted zoospores, the aqueous treatment mixture was decanted and replaced with 5 ml of 5% clarified sterile V-8 juice broth (V-8 juice centrifuged for 10 min at 1,000 × g, after which the supernatant is diluted with sterile water). Petri dishes containing encysted zoospores were incubated at 24°C and examined after 24 and 48 h for the appearance of mycelial growth arising from germinating cysts. The number of colonies appearing on each plate were recorded.

Analysis of data. Each experiment in this study was conducted twice. Data from repeated experiments were combined for analysis, because variances between experiments were homogeneous. All data were processed with the SigmaStat statistical software package (SPSS Science, Chicago). Error bars represent 95% confidence intervals (Fig. 1). Means with nonoverlapping 95% confidence intervals were considered significantly different (16). For each species of *Phytophthora*, the concentration of each fungicide causing 50% (EC₅₀) or 90% (EC₉₀) reduction in mycelial growth, sporulation, duration of zoospore motility, and zoospore cyst germination compared to the absence of the fungicide was estimated from the fitted regression line of the logit-transformed percent inhibition plotted against the log-transformed fungicide concentration (4).

RESULTS

Mycelial growth. EC₅₀ values for inhibition of mycelial growth of *P. capsici*, *P.*

citrophthora, and *P. parasitica* usually were lowest for dimethomorph and metalaxyl, ranging from <0.1 to 0.38 µg/ml (Table 1). However, the EC₉₀ levels for dimethomorph always were lower than the other four tested compounds, with values ranging from 0.32 to 1.6 µg/ml. Mycelial growth of *P. capsici*, *P. citrophthora*, and *P. parasitica* was least affected by azoxystrobin and fluazinam, with estimated EC₉₀ values >3,000 µg/ml (Table 1). Reduction of mycelial growth of *P. capsici*, *P. citrophthora*, and *P. parasitica* by dimethomorph at a concentration of 1 µg/ml was significantly greater than that recorded for the same concentration of azoxystrobin, fluazinam, fosetyl-Al, and metalaxyl (Fig. 1). At a concentration of 1,000 µg/ml, inhibition of mycelial growth for the three pathogens was significantly greater in the presence of dimethomorph, fosetyl-Al, and metalaxyl compared to azoxystrobin and fluazinam. In the absence of a fungicide, the average mycelial growth for *P. capsici*, *P. citrophthora*, and *P. parasitica* on CMA after 4 days at 24°C was 33, 44, and 24 mm, respectively.

Sporangium formation. Estimated EC₅₀ values for inhibition of sporangium formation by *P. capsici*, *P. citrophthora*, and *P. parasitica* ranged from <1.0 to 5.0 µg/ml for azoxystrobin, dimethomorph, fluazinam, and metalaxyl. In comparison, EC₅₀ values recorded for the three pathogens in the presence of fosetyl-Al ranged from 3.1 to 12.0 µg/ml. The EC₉₀ concentration for the three tested species of *Phytophthora* ranged from <1.0 µg/ml for dimethomorph to a high of 208 µg/ml for fosetyl-Al (Table 1). Reduction of sporangium formation by *P. capsici*, *P. citrophthora*, and *P. parasitica* in the presence of dimethomorph at 1 µg/ml was significantly greater than that recorded for the same concentration of azoxystrobin, fluazinam, and fosetyl-Al (Fig 1). Formation of sporangia by *P. capsici* and *P. citrophthora* was totally suppressed by dimethomorph at 1.0 µg/ml. In comparison, a 10- to 1,000-fold higher concentration of azoxystrobin, fluazinam, fosetyl-Al, and metalaxyl was required to achieve the same result. Sporangium formation by *P. parasitica* was completely arrested by dimethomorph or metalaxyl at 10 µg/ml; whereas, a 10- to 100-fold higher concentration of the other tested chemistries was required to achieve the same result. The average number of sporangia developing in soil extract in the absence of a fungicide after 4 days at 24°C from an agar disk containing mycelia of *P. capsici*, *P. citrophthora*, and *P. parasitica* was 470, 500, and 498, respectively.

Zoospore motility, encystment, and germination. Among the five chemicals tested, the duration of motility for zoospores of *P. capsici*, *P. citrophthora*, and *P. parasitica* was most sensitive to fluazinam (EC₅₀ and EC₉₀ values of <0.001 µg/ml;

Table 1). In contrast, zoospore motility of these pathogens among tested compounds was affected least by fosetyl-Al, with respective EC₅₀ and EC₉₀ values ranging from 299 to 334 and 518 to 680 µg/ml. The percent reduction in the duration of motility for zoospores of *P. capsici*, *P. citrophthora*, and *P. parasitica* in the presence of fluazinam at concentrations ranging from 0.001 to 1 µg/ml was significantly higher than that observed for azoxystrobin, dimethomorph, fosetyl-Al, and metalaxyl at the same levels (Fig 1). On the other hand, at a concentration of 1,000 µg/ml, all tested materials reduced zoospore motility by at least 98% compared to zoospores not exposed to a fungicide. Zoospores of *P. capsici*, *P. citrophthora*, and *P. parasitica* not treated with a fungicide retained their motility for at least 187, 142, and 203 min, respectively.

Germination of encysted zoospores of *P. capsici*, *P. citrophthora*, and *P. parasitica* was most sensitive to dimethomorph among tested compounds, with EC₅₀ and EC₉₀ values ranging from 3.3 to 7.2 and 5.6 to 21 µg/ml, respectively (Table 1). Among the five chemicals tested, the highest EC₅₀ and EC₉₀ values for the three pathogens generally were recorded for azoxystrobin and fosetyl-Al, ranging from 256 to >1,000 µg/ml. Intermediate sensitivity of encysted zoospores was noted for fluazinam (EC₅₀ and EC₉₀ values ranging from 18 to 108 and 67 to >1,000 µg/ml, respectively) and metalaxyl (EC₅₀ and EC₉₀ values ranging from 32 to 280 and 49 to 529 µg/ml, respectively; Table 1). Inhibition of zoospore cyst germination for *P. capsici*, *P. citrophthora*, and *P. parasitica* in the presence of dimethomorph at 10 µg/ml was significantly higher than that recorded for azoxystrobin, fluazinam, fosetyl-Al, and metalaxyl at the same concentration (Fig 1). Inhibition of zoospore cyst germination for the three species of *Phytophthora* was achieved with at least 100 µg/ml of dimethomorph and 1,000 µg/ml of metalaxyl, but not with 1,000 µg/ml of azoxystrobin, fluazinam, or fosetyl-Al.

DISCUSSION

The ultimate value of any chemical compound as a control agent for a disease depends on the mode of action of the molecule at the physiological level on one or more components of the life cycle of the pathogen. Considering all the stages in the life cycle of soilborne *Phytophthora* spp., sporangium formation and zoospore release provide the greatest opportunity for a rapid buildup in the number of infective propagules and subsequent higher potential for host infection and disease development (10,18,32). Therefore, any chemical that significantly suppresses formation of sporangia, duration of zoospore motility, or germination of encysted zoospores should reduce the ability of *Phytophthora* spp. to

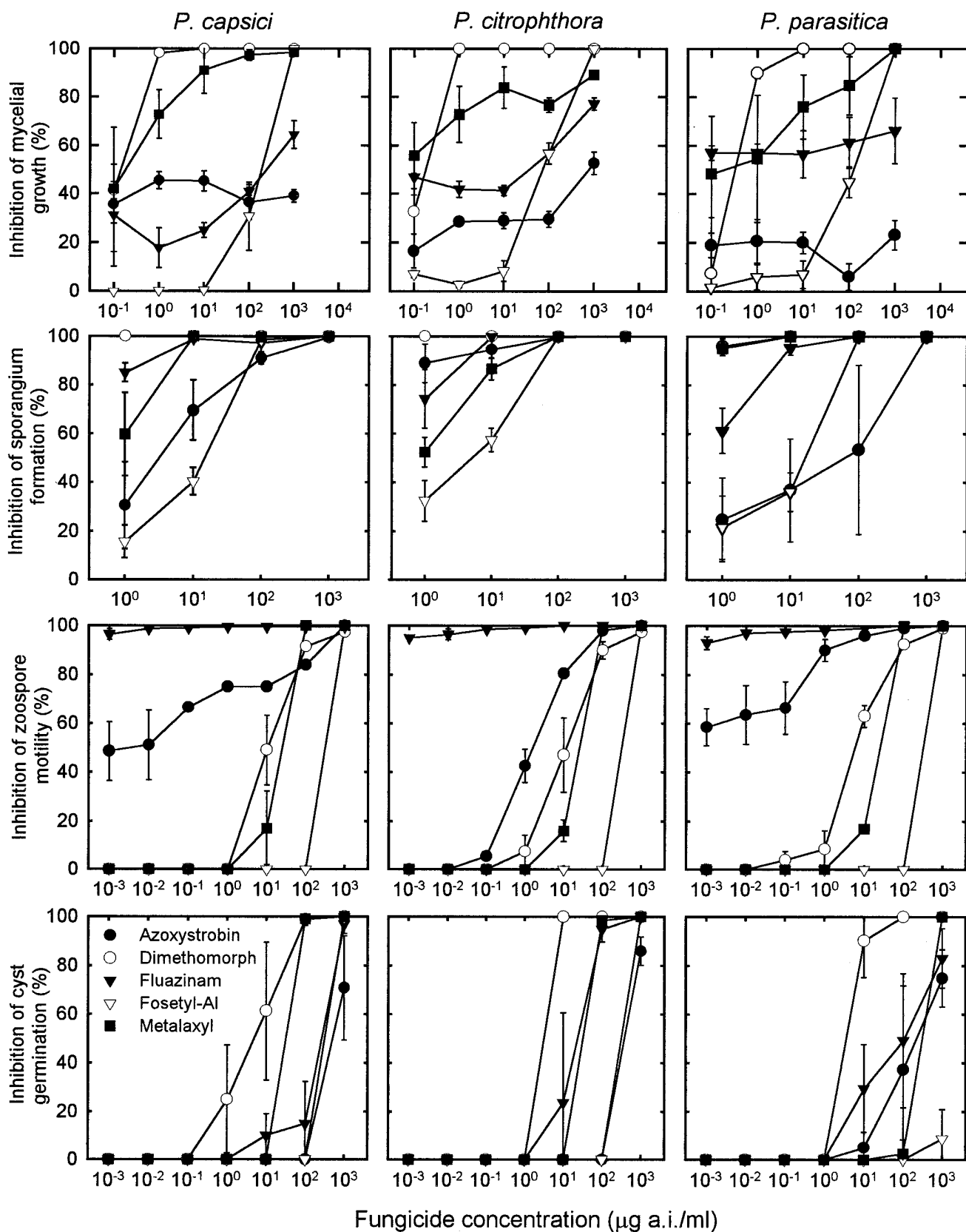


Fig. 1. Influence of dose of azoxystrobin, dimethomorph, fluazinam, fosetyl-Al, and metalaxyl on inhibition of mycelial growth, sporangium formation, zoospore motility, and germination of encysted zoospores of *Phytophthora capsici*, *P. citrophthora*, and *P. parasitica*.

cause disease. At appropriate concentrations, azoxystrobin, dimethomorph, fluazinam, fosetyl-Al, and metalaxyl completely prevented sporangium formation and normally reduced the duration of zoospore motility and germination of encysted zoospores significantly compared to non-treated controls, thus severely restricting the potential of *P. capsici*, *P. citrophthora*, and *P. parasitica* to infect plant tissue and cause disease. Among the components of the life cycle of the *Phytophthora* spp. tested, all five fungicides had the greatest impact on inhibition of sporangium formation.

Once infection has occurred, suppression of mycelial growth within host tissue becomes an important disease management consideration. Among the tested chemicals, mycelial growth of the three tested *Phytophthora* spp. was most sensitive to dimethomorph at 1 µg/ml. At higher concentrations, fosetyl-Al and metalaxyl effectively suppressed mycelial growth as well, whereas azoxystrobin and fluazinam were significantly less effective.

The effect of fosetyl-Al and metalaxyl on growth and sporulation of *Phytophthora* spp. has been studied extensively (11). For inhibition of mycelial growth of *P. capsici* by fosetyl-Al, Fenn and Coffey (14) found EC₅₀ and EC₉₀ values of 50 and 196 µg/ml, respectively. For the same compound, Farih and Menge (12) calculated EC₅₀ values of 56 and 285 µg/ml for inhibition of mycelial growth of *P. citrophthora* and 929 and 1,146 µg/ml for *P. parasitica*, where the smaller value for each pathogen was determined after a 3-day period of

growth on V-8 juice agar containing the fungicide and the larger value was ascertained after 7 days. Sporangium formation by *P. citrophthora* and *P. parasitica* was prevented by fosetyl-Al at 5 and 10 µg/ml, respectively, whereas germination of zoospores of these two pathogens was reduced 53 and 99%, respectively, by 1,000 µg/ml of the compound (12). In another published report (6), fosetyl-Al at a concentration of 2.9 µg/ml resulted in 56 and 75% inhibition of sporangium formation by *P. cinnamomi* and *P. citricola*, respectively. Our findings on the relative sensitivity of mycelial growth, sporangium formation, and zoospore cyst germination to fosetyl-Al generally agree with these other published data.

Previously determined EC₅₀ values for inhibition of mycelial growth of *P. cinnamomi*, *P. citrophthora*, and *P. parasitica* by metalaxyl ranged from 0.04 to 0.56 µg/ml (2,13). Furthermore, Fariah et al. (13) reported that sporangium formation by *P. citrophthora* and *P. parasitica* was reduced 67 and 85%, respectively, in the presence of metalaxyl at 0.1 µg/ml, whereas zoospore germination was reduced 52 and 7%, respectively, in the presence of metalaxyl at 100 µg/ml. These concentrations of metalaxyl are in the same order of magnitude as our determinations of EC₅₀ for mycelial growth as well as inhibition of sporangium formation and zoospore germination for *P. citrophthora* and *P. parasitica*.

Published accounts on the impact of azoxystrobin, dimethomorph, and fluazinam on growth and sporulation of *Phy-*

tophthora spp. are less numerous than those concerning fosetyl-Al and metalaxyl. Godwin et al. (17) reported that azoxystrobin affects *Phytophthora* spp. primarily by inhibiting germination of sporangia and zoospores. In contrast, our data suggest that azoxystrobin is more active in suppression of sporangium formation (mean EC₉₀ value of 29.2 µg/ml) and zoospore motility (mean EC₉₀ value of 14.5 µg/ml) than inhibition of zoospore cyst germination (EC₉₀ value >1,000 µg/ml). For dimethomorph, Chabane et al (5) calculated an EC₅₀ of 0.7 µg/ml for inhibition of mycelial growth of *P. parasitica*. Schwinn and Staub (27) report that dimethomorph is more inhibitory to mycelial growth and sporulation than to spore germination *in vitro*. Our results for *P. capsici*, *P. citrophthora*, and *P. parasitica* are similar, with mycelial growth (EC₉₀ <1.0 µg/ml) and sporulation (EC₉₀ ranging from 0.32 to 1.6 µg/ml) appearing to be more sensitive to dimethomorph than germination of zoospore cysts (EC₉₀ ranging from 5.6 to 21 µg/ml). On the other hand, Cohen et al. (7) found that, for *P. infestans*, dimethomorph was more inhibitory to zoospore cyst germination (97% reduction at a concentration of 0.015 µg/ml) than to mycelial growth (90% reduction at 0.3 µg/ml) and sporulation (52% reduction at 500 µg/ml). Fluazinam has been reported to strongly inhibit germination of zoospores of *P. infestans* (1). Our data suggest that zoospore motility and sporangium formation by *P. capsici*, *P. citrophthora*, and *P. parasitica* are more sensitive than zoospore cyst germination to this compound.

Table 1. Range of EC₅₀ and EC₉₀ values of five different fungicides for mycelial growth, sporangium formation, zoospore motility, and encysted zoospore germination of *Phytophthora capsici*, *P. citrophthora*, and *P. parasitica*^a

Fungicide	EC ₅₀ (µg/ml)			EC ₉₀ (µg/ml)		
	<i>P. capsici</i>	<i>P. citrophthora</i>	<i>P. parasitica</i>	<i>P. capsici</i>	<i>P. citrophthora</i>	<i>P. parasitica</i>
Mycelial growth						
Azoxystrobin	>3,000	138	>3,000	>3,000	>3,000	>3,000
Dimethomorph	<0.1	0.14	0.38	0.64	0.32	1.6
Fluazinam	80.5	2.9	<0.1	>3,000	>3,000	>3,000
Fosetyl-Al	103	23.6	30.8	402	404	381
Metalaxyl	0.16	<0.1	0.38	10.0	725	40.2
Sporangium formation						
Azoxystrobin	3.3	<1.0	5.0	57.8	1.9	27.8
Dimethomorph	<1.0	<1.0	<1.0	<1.0	<1.0	<1.0
Fluazinam	<1.0	<1.0	<1.0	<1.0	2.2	6.0
Fosetyl-Al	6.0	3.1	12.0	33.4	20.0	208
Metalaxyl	<1.0	1.1	<1.0	3.0	10.0	<1.0
Duration of zoospore motility						
Azoxystrobin	0.10	1.7	0.002	26.8	16.0	0.65
Dimethomorph	24.0	12.0	6.8	139	105	72
Fluazinam	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Fosetyl-Al	334	299	317	680	518	519
Metalaxyl	12.5	12.0	13.0	24.0	38.2	37.0
Zoospore cyst germination						
Azoxystrobin	700	530	256	>1,000	>1,000	>1,000
Dimethomorph	3.9	3.3	7.2	21.0	5.6	21.0
Fluazinam	108	18	100	820	67	>1,000
Fosetyl-Al	317	326	>1,000	510	545	>1,000
Metalaxyl	32	34	280	49	56	529

^a EC₅₀ and EC₉₀ values are the concentrations of each fungicide causing 50 and 90% reduction, respectively, in mycelial growth, sporangium formation, zoospore motility, and germination of encysted zoospores compared to the absence of a fungicide. These values were estimated from the fitted regression line of the logit-transformed percent inhibition plotted against the log-transformed fungicide concentration.

There is considerable diversity in the published data concerning the relative activity of each chemistry on mycelial growth, sporulation, and zoospore cyst germination. Possible reasons for these discrepancies could include variability due to the different *Phytophthora* spp. tested, variability among different isolates of the same species, and differences due to the techniques employed to assess fungicide activity.

Each of the chemistries tested in this study has a unique mode of action at the biochemical level. Strobilurin analogues, such as azoxystrobin, inhibit mitochondrial respiration by blocking electron transfer at the cytochrome bc₁ complex (3). Circumvention of this cytochrome bc₁ target site by induction of the alternative oxidase respiratory pathway has been proposed as the likely reason for low mycelial sensitivity to strobilurins displayed by several pathogens (26). This alternative oxidase respiratory pathway is utilized by fungi growing on agar, especially nutrient-rich agar, and could account for the low sensitivity to azoxystrobin that we observed for *P. capsici*, *P. citrophthora*, and *P. parasitica* grown on CMA containing this compound. Kune et al. (20) suggests that dimethomorph acts on the biochemical processes associated with cell wall biogenesis. Fluazinam has been shown to actively uncouple oxidative phosphorylation (19). The biochemical target area for fosetyl-Al is amino acid metabolism (27), whereas phenylamides, including metalaxyl, interfere with RNA synthesis of target fungi (8). Each compound has a different mode of action; therefore, these chemistries could be incorporated into a disease management program that could minimize the risk of development of resistance by *Phytophthora* spp. and, at the same time, maximize disease control.

In our investigations, the relationship between EC₅₀ and EC₉₀ values was highly dependent upon the chemical under evaluation as well as the species and biological function of *Phytophthora* that was being measured. These investigations revealed a difference between EC₅₀ and EC₉₀ values ranging from 0 to >1,000-fold. EC₅₀ values often are calculated in studies assessing the potential value of a molecule to control growth or sporulation of a pathogen. As a practical matter, reducing growth and especially sporulation or spore survival of *Phytophthora* spp. by 50% will not usually provide an acceptable level of disease control. For evaluation and comparison of molecules as potential chemical disease management tools, EC₉₀ rather than EC₅₀ values for growth and inoculum reduction would seem to be more beneficial.

The activity of azoxystrobin, dimethomorph, and fluazinam on one or more stages of the life cycle of *P. capsici*, *P. citrophthora*, and *P. parasitica* suggests that these compounds could provide *Phy-*

tophthora spp. disease control comparable to that of the established fungicides fosetyl-Al and metalaxyl. Evaluation of these compounds for control of some diseases caused by *P. capsici*, *P. citrophthora*, and *P. parasitica* are in progress.

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