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Sensitivity of *Meloidogyne incognita* and *Rotylenchulus reniformis* to Fluopyram

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Abstract: Fluopyram is a succinate dehydrogenase inhibitor (SDHI) fungicide that is being evaluated as a seed treatment and in-furrow spray at planting on row crops for management of fungal diseases and its effect on plant-parasitic nematodes. Currently, there are no data on nematode toxicity, nematode recovery, or effects on nematode infection for *Meloidogyne incognita* or *Rotylenchulus reniformis* after exposure to low concentrations of fluopyram. Nematode toxicity and recovery experiments were conducted in aqueous solutions of fluopyram, while root infection assays were conducted on tomato. Nematode paralysis was observed after 2 hr of exposure at 1.0 μg/ml fluopyram for both nematode species. Using an assay of nematode motility, 2-hr EC_{50} values of 5.18 and 12.99 μg/ml fluopyram were calculated for *M. incognita* and *R. reniformis*, respectively. Nematode recovery in motility was greater than 50% for *M. incognita* and *R. reniformis* 24 hr after nematodes were rinsed and removed from a 1-hr treatment of 5.18 and 12.99 μg/ml fluopyram, respectively. Nematode infection of tomato roots was reduced and inversely proportional to 1-hr treatments with water solutions of fluopyram at low concentrations, which ranged from 1.3 to 5.2 μg/ml for *M. incognita* and 3.3 to 13.0 μg/ml for *R. reniformis*. Though fluopyram is nematistatic, low concentrations of the fungicide were effective at reducing the ability of both nematode species to infect tomato roots.

Key words: behavior, EC_{50}, fluopyram, fungicide, *Meloidogyne incognita*, nematistatic, nematicides, recovery, reniform nematode, *Rotylenchulus reniformis*, SDHI fungicides, sensitivity, southern root-knot nematode, toxicity.

The southern root-knot nematode, *Meloidogyne incognita*, and reniform nematode, *Rotylenchulus reniformis*, are two of the most important plant-parasitic nematodes that affect agricultural crop production in the United States (Nickle, 1991; Luc et al., 2005). Yield losses by these two nematode species can be substantial and often occur as a result of direct feeding on roots or indirectly through an interaction with soilborne fungal pathogens (Sasser, 1979; Luc et al., 2005).

Management strategies for these nematodes continue to rely on nematicides whether used as part of an integrated management program or as a solo control agent. Fumigant nematicides are highly effective, but often require specialized application equipment and have higher production costs than nonfumigant nematicides. Nonfumigant nematicides are the most common nematicides used in agricultural production and the most effective nonfumigants like aldicarb and oxamyl are highly toxic. The use of highly toxic nematicides has been criticized by the public due to potential risk to human health and environmental concerns. Thus, a pesticide with a lower risk to human health and environmental impact is desirable. Currently, one such pesticide being evaluated for its effect on plant-parasitic nematodes is fluopyram.

Fluopyram is an SDHI fungicide that is being evaluated for management of soilborne fungi and plant-parasitic nematodes in agronomic crops. However, it was not the first fungicide investigated for its effect on plant-parasitic nematodes. Benomyl and thiabendazole were reported to have no effect on the motility of *Heterodera tabacum* or *M. graminicola* (Miller, 1969; Krishna-Prasad and Rao, 1980). Thiophanate-methyl was shown to suppress *H. glycines* on soybean (*Glycine max*), but had no significant effect on nematode densities in field trials (Faghihi et al., 2007). Pentachloronitrobenzene (PCNB) and tetrachloronitrobenzene (TCNB) were reported to suppress root galling by *M. incognita* on cotton (*Gossypium hirsutum*) (Rodriguez-Kabana et al., 1977; Adams et al., 1979). Iprodione, a dicarboximide fungicide, was somewhat effective at reducing early season galling by *M. incognita* on tomato (*Solanum lycopersicum*) (Moore and Lawrence, 2010; Becker and Ploeg, 2012, 2013), but had no significant effect on nematode densities in turf (Dernoeden et al., 1990). Recently, a formulation that consists of fluopyram + imidacloprid (Velum Total®, Bayer CropScience, Research Triangle Park, NC) has been evaluated as an in-furrow spray for suppression of *M. incognita* and *R. reniformis* in cotton (Lawrence et al., 2014, 2015). In these field trials, fluopyram was reported to suppress nematode densities at levels that were numerically more effective than those achieved by thiodicarb applied as a seed treatment. This formulation was registered in 2015 for use against nematodes and insects in cotton and peanut. In addition, fluopyram-treated seed (ILeVO®, Bayer CropScience) was registered in 2014 for use against sudden death syndrome, which is caused by the fungal pathogen *Fusarium virguliforme* and nematodes in soybean. Though a few studies have evaluated the effect of fluopyram on the suppression of plant-parasitic nematodes in the field, currently there are no data on the sensitivity or behavior of *M. incognita* or *R. reniformis* to fluopyram. Given the recent registration of fluopyram for nematicide use, additional data on the sensitivity of target species are needed.

The objectives of this study were to (i) characterize the toxicity of fluopyram to *M. incognita* and *R. reniformis*, (ii) evaluate the toxicity of other SDHI fungicides to *M. incognita* and *R. reniformis*, (iii) determine if the effects of fluopyram on each nematode species are

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reversible, and (iv) determine the effect of low concentrations of fluopyram on the infectivity of each nematode species.

Materials and Methods

Nematode inoculum: Meloidogyne incognita and *R. reniformis* were originally isolated from cotton and maintained on tomato (*S. lycopersicum* 'Rutgers') and cotton (*G. hirsutum* 'DP 0912 B2RF'), respectively. Eggs of *M. incognita* were collected from tomato roots with 0.5% NaOCl (Hussey and Barker, 1973) and J2 were collected in a hatching chamber (Vrain, 1977). Only 24-hr-old J2 were used as inoculum. Inoculum of *R. reniformis* was collected from infested soil using a Baermann tray system. Mixed life stages were collected with a 25-μm-pore sieve after 48 hr and used immediately.

Effects of fluopyram on nematode motility: Meloidogyne incognita and *R. reniformis* were treated for 2 and 24 hr with water solutions of 10.0, 1.0, 0.1, and 0.0 μg/ml of fluopyram. An agricultural grade fluopyram (Bayer CropScience) was used in this experiment. These experiments were performed in 24-well Falcon tissue culture plates (Corning Life Science, Tewksbury, MA); each well received 500 μl of a 2× concentration of the test solution, which contained 30 to 40 nematodes in 500 μl of distilled water. The experimental design was a completely randomized design (CRD), each treatment was replicated four times and the experiment was conducted three times per nematode species. Incubation temperatures of 28°C for *M. incognita* and 30°C for *R. reniformis* were maintained throughout these experiments. Motile and immotile nematodes were determined visually at each sample time with an inverted compound microscope (Axio Vert.A1, Carl Zeiss Microscopy, Thornwood, NY). Nematodes were considered immotile if they did not respond to being touched by a small probe and the percentage of immotile nematodes was calculated for each species.

Effects of several fungicides on nematode motility: To determine the sensitivity of *M. incognita* and *R. reniformis* to a few selected fungicides, a motility assay similar to that described above was conducted. Fungicides were selected because they were in the same fungicide class as fluopyram (SDHI) or marketed for use as a nematicide (i.e., iprodione). The six fungicides included boscalid (BASF Ag Products, Research Triangle Park, NC), flutolanil (Nichino America, Inc., Wilmington, DE), penthiopyrad (DuPont Crop Protection, Wilmington, DE), solatenol (Syngenta Crop Protection, Greensboro, NC), fluxapyroxad (BASF Ag Products), and iprodione (Bayer CropScience). An agricultural grade of each fungicide was used in this experiment. Nematode inoculum for each species was treated for 24 hr with water solutions of 1.0 μg a.i./ml for each fungicide. Fungicides were divided into three groups that consisted of two randomly selected fungicides and fluopyram as a control treatment per experiment. The experimental design was a CRD, each treatment was replicated four times and the experiment was conducted once per nematode species. Motile and immotile nematodes were determined visually with an inverted compound microscope. Nematodes were considered immotile if they did not respond to being touched by a small probe and the percentage of immotile nematodes was calculated for each species.

Reversible effect of fluopyram: A large population (i.e., 2,000 individuals) of *M. incognita* or *R. reniformis* was treated for 1 hr with a water solution respective to their 2-hr EC_{50} value of fluopyram, poured over a 25-μm pore sieve, and rinsed twice with distilled water. Rinsed nematodes were transferred to a 24-well tissue culture plate containing distilled water. Nematodes treated with distilled water served as the negative control and nematodes treated for 2 hr to their respective 2-hr EC_{50} value of fluopyram served as the positive control. The experimental design was a CRD, each treatment was replicated four times and the experiment was conducted twice per nematode species. Motile and immotile nematodes were determined visually at 1 and 24 hr after rinse with an inverted compound microscope. Nematodes were considered immotile if they did not respond to being touched by a small probe and the percentage of immotile nematodes was calculated for each species.

Effect of low concentrations of fluopyram on nematode infectivity: The impact of fluopyram on the infectivity of *M. incognita* and *R. reniformis* on tomato roots was evaluated in a greenhouse experiment. A large population (i.e., 4,000 individuals) of each nematode species was treated for 1 hr with water solutions of fluopyram at concentrations at or below their respective 2-hr EC_{50}. Fluopyram concentrations of 5.2, 3.9, 2.6, and 1.3 μg/ml were used for *M. incognita* and 13.0, 9.8, 6.5, and 3.3 μg/ml were used for *R. reniformis*. Nematodes were inoculated onto 2-wk-old tomato seedlings growing in sand:peat (12:1 v/v) soil mix in seedling tray with 84 cm^3 cells. Each seedling received 2 ml of the fluopyram solution containing 500 nematodes. Inoculum was distributed among three holes created by pushing a 1-ml pipette tip 3 cm into the root zone around the seedlings. Nematodes treated with distilled water served as the positive control. The experimental design was a randomized complete block design, each treatment was replicated six times and the experiment conducted twice per nematode species. Tomato plants were incubated at 28°C to 30°C on a greenhouse bench and sampled 3 wk after inoculation to determine infectivity. A root gall rating was used to determine infectivity by *M. incognita* using a 6-point scale where 0 = no galls, 1 = trace infection with a few small galls, 2 = <25% roots galled, 3 = 25% to 50%, 4 = 51% to 75%, and 5 = >75% of roots galled (Hussey and Janssen, 2002). Females of

R. reniformis were stained with acid fuchsin (Byrd et al., 1983) to aid in counting the total females per root system.

Statistical analysis: Data from the repeated experiments were similar ($P \geq 0.20$) and combined for final analysis. For these preliminary analyses, experiment repetitions were modeled as a random variable. Data from the nematode motility experiments were subjected to probit analysis, while data from nematode infectivity experiments were subjected to chi-square analysis, specifically Kruskal–Wallis and Mann–Whitney *U*-test and Pearson's correlation coefficient test. Data from the effect of several fungicides on nematode motility and reversible effects of fluopyram experiments were ln $(x + 1)$ transformed to normalize for statistical analysis and nontransformed data are reported. These data were subjected to general linear model analysis of variance and mean differences ($P = 0.05$) are reported according to Tukey's honestly significant difference (HSD) test using SPSS 19.0 (SPSS Inc., Chicago, IL).

Results

Meloidogyne incognita was more sensitive to fluopyram than *R. reniformis*. Based on the nematode motility assays, 78% of *M. incognita* were immotile after 2 hr of continuous exposure at 10.0 µg/ml fluopyram, while 48% of *R. reniformis* were immotile. Nematode paralysis increased for both species after 24 hr of continuous exposure at 10.0 µg/ml fluopyram to 91% for *M. incognita* and 87% for *R. reniformis*. The 2-hr EC_{50} values for fluopyram were 5.18 and 12.99 µg/ml for *M. incognita* and *R. reniformis*, respectively (Fig. 1). As expected, the increased duration of exposure required less fluopyram to achieve an EC_{50}. The 24-hr EC_{50} values were 1.18 µg/ml for *M. incognita* and 1.97 µg/ml for *R. reniformis*. The EC_{90} values at 24-hr exposure for *M. incognita* and *R. reniformis* were 5.31 and 9.68 µg/ml, respectively (Fig. 1).

Meloidogyne incognita and *R. reniformis* were more sensitive ($P = 0.05$) to fluopyram than any of the other SDHI fungicides (boscalid, flutolanil, penthiopyrad, fluxapyroxad, and solatenol) or the dicarboximide fungicide iprodione tested in this experiment (Fig. 2). Of these other fungicides tested, fluxapyroxad had the highest numeric percentage of immotility at 9% for *M. incognita*, while boscalid had the highest numeric percentage of immotility at 25% for *R. reniformis*. The response by each nematode species to fluopyram was similar in the three fungicide groups where it was tested and averaged 78% and 52% immotility for *M. incognita* and *R. reniformis*, respectively (Fig. 2).

Recovery in nematode motility was observed for *M. incognita* and *R. reniformis* when removed from fluopyram after a 1-hr treatment with their respective 2-hr EC_{50} concentration (Fig. 3). This was a significant ($P = 0.05$) effect as 58% of *M. incognita* and 54% of *R. reniformis* recovered in motility 24 hr after being rinsed and removed from the fluopyram. Nematode posture for immotile nematodes exposed to fluopyram was rigid and straight for *M. incognita* and rigid and slightly curved for *R. reniformis*, but nematodes regained their undulated and relaxed posture when removed from the fluopyram. All life stages of *R. reniformis* responded similarly to the onset and development of paralysis and subsequent recovery. Furthermore, paralysis and recovery were casually observed for free-living nematodes collected from cultures of *R. reniformis*.

Fluopyram was effective at reducing *M. incognita* and *R. reniformis* infection on tomato roots. All fluopyram rates of 1.3 to 5.3 µg/ml reduced ($P = 0.05$) and were negatively correlated ($r = -0.62$, $P = 0.001$) to root galling by *M. incognita*. Moreover, root galling was reduced by 31% to 84% at concentrations of 1.3 to 5.3 µg/ml fluopyram, respectively (Fig. 4). Similarly, concentrations of 3.3 to 13.0 µg/ml fluopyram reduced ($P = 0.05$) and were negatively correlated ($r = -0.42$, $P = 0.001$) to the number of *R. reniformis* females observed per root system. A reduction in root infection by

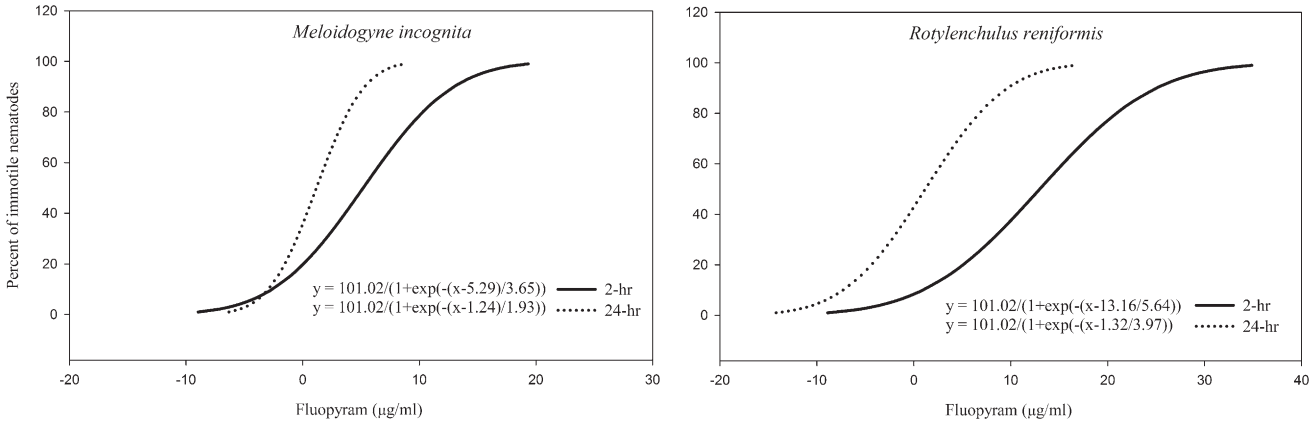

Fig. 1. Relationship between paralysis of *Meloidogyne incognita* and *Rotylenchulus reniformis* treated for 2 and 24 hr with water solutions of fluopyram. Equations were derived by nonlinear regression of probit analysis. For each equation the R^2 value was 0.99 ($P = 0.0001$).

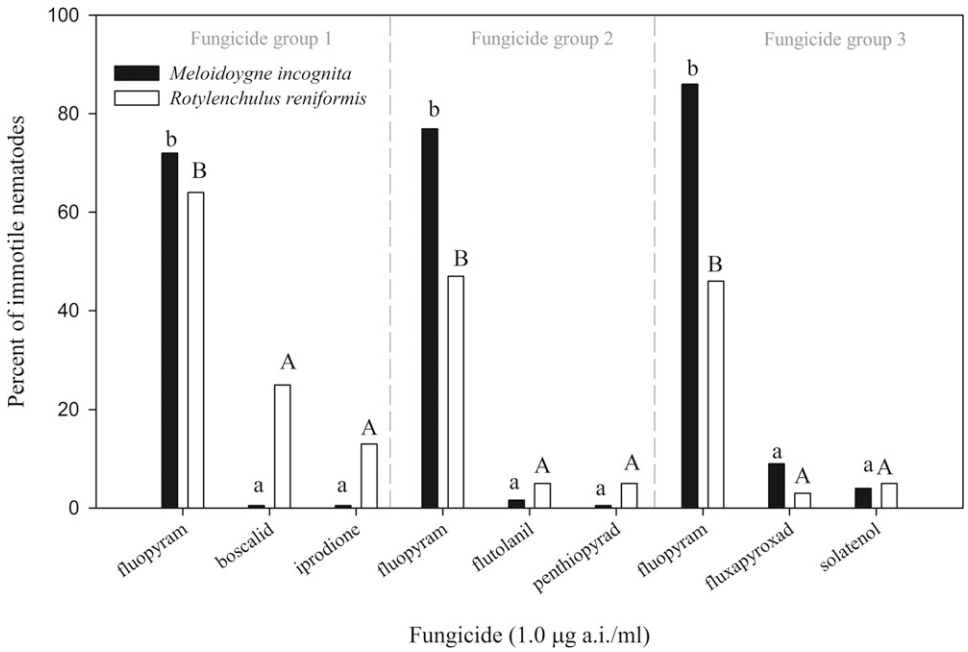

FIG. 2. Effect of seven fungicides on paralysis of *Meloidogyne incognita* and *Rotylenchulus reniformis* treated for 24 h with water solutions of 1.0 µg a.i./ml for each fungicide. Within each fungicide group and nematode species, different letters over bars indicate significant differences at $\alpha = 0.05$ according to Tukey's HSD test.

R. reniformis ranged from 38% to 96% at 3.3 to 13.0 µg/ml fluopyram, respectively (Fig. 4). Over the range of fluopyram concentrations tested, average reductions in infection by 60% and 77% were observed for *M. incognita* and *R. reniformis*, respectively.

DISCUSSION

Fluopyram had a negative effect on the motility of *M. incognita* and *R. reniformis*, which was affected by the concentration and duration of exposure to the fungicide. Sixty percent of *M. incognita* were immotile after a 24 hr of exposure to 2.0 µg/ml fluopyram, which is similar to that reported for aldicarb at 5.0 µg/ml and abamectin at 0.5 µg/ml for *M. javanica and M. incognita*, respectively (Nordmeyer and Dickson, 1989; Faske and Starr, 2006). These findings indicate the toxicity of fluopyram to some species of *Meloidogyne* is similar to that of aldicarb and abamectin.

The motility of free-living nematodes was affected by fluopyram as paralyzed free-living nematodes were observed in the nematode motility assays. The sensitivity of free-living nematodes has been reported for other nonfumigant nematicides and fungicides with anthelmintic properties (Adams et al., 1979; Simpkin and Coles, 1981). Thus, fluopyram is a nonselective

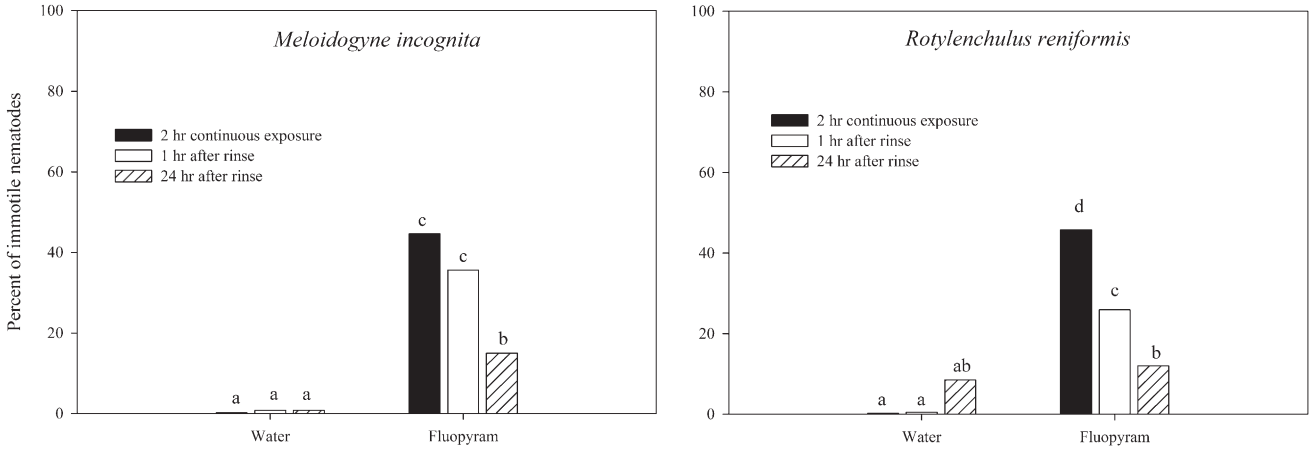

FIG. 3. Recovery of *Meloidogyne incognita* and *Rotylenchulus reniformis* at 2 and 24 hr after being treated with fluopyram. Each species was treated with a water solution of fluopyram respective to their 2-hr EC_{50} value of fluopyram (5.18 and 12.99 µg/ml for *M. incognita* and *R. reniformis*, respectively) for 1 hr, then rinsed and transferred to distilled water. Different letters over bars indicate significant differences at $\alpha = 0.05$ according to Tukey's HSD test.

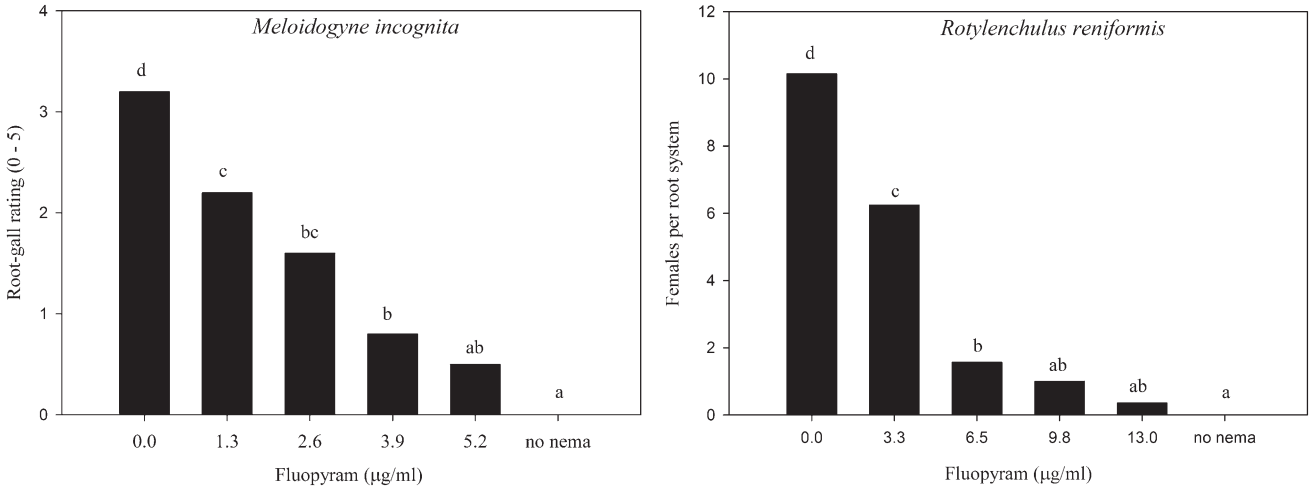

FIG. 4. Effect of low concentrations of fluopyram on infectivity of *Meloidogyne incognita* and *Rotylenchulus reniformis* on tomato roots. Root-gall ratings were based on a 6-point scale where 0 = no galling and 5 = >75% of roots galled. Different letters over bars indicate significant differences at $\alpha = 0.05$ based on chi-square analysis applied in pairs of treatments for root-gall ratings or females per root system.

nematicide affecting both plant-parasitic and free-living nematodes.

Based on the nematode motility assays, *M. incognita* was more sensitive to fluopyram than *R. reniformis*. The 24-hr EC_{90} value for *R. reniformis* (9.68 µg/ml) was 83% higher than that for *M. incognita* (5.31 µg/ml). It is not uncommon for species of nematodes to differ in sensitivity when challenged with a fungicide or insecticide with nematicidal activity. *Meloidogyne incognita* was reported to be more sensitive to PCNB and abamectin than *R. reniformis* (Adams et al., 1979; Faske and Starr, 2006). Similarly, *M. incognita* was shown to be more sensitive to TCNB compared to *Pratylenchulus brachyurus* (Rodriguez-Kabana et al., 1977). Though fluopyram will likely exhibit some toxicity to other species of plant-parasitic nematodes the concentration of fluopyram needed to initiate paralysis will likely vary among nematode genera. Thus, further studies are needed to determine the EC_{50} for other economically important genera.

Fluopyram had the greatest negative effect on the motility of *M. incognita* and *R. reniformis* than any of the other fungicides tested. Seventy-eight percent of *M. incognita* were immotile when treated for 24 hr at 1.0 µg/ml fluopyram compared to the average immotility of 3% for the five SDHI fungicides. Similarly, 52% of *R. reniformis* were immotile when exposed to fluopyram compared to an average of 9% for the five SDHI fungicides. These findings indicate fluopyram has a mode of action toward nematode motility that is unique among these SDHI fungicides. Iprodione caused 0.7% and 20% immotility for *M. incognita* and *R. reniformis*, respectively, which was significantly lower than that of fluopyram. Thus, fluopyram is more toxic to these nematode species than iprodione, another fungicide marketed for use as a nematicide.

Currently, there is no information on the effects of iprodione on the behavior of plant-parasitic nematodes. In field trials, iprodione was somewhat effective at suppressing galling by *M. incognita* on tomato (Moore and Lawrence, 2010; Becker and Ploeg, 2012, 2013). In this study, based on nematode motility, *R. reniformis* was more sensitive to iprodione than *M. incognita*. Thus, although iprodione does affect nematode motility, a higher rate may be needed to affect *M. incognita*. In addition, iprodione may act as a repellent to protect the developing root system from nematode infection, which was reported as the mode of action for benomyl (Miller, 1969). However, additional studies are needed to confirm the possible repellent effect of iprodione.

Nematode paralysis was reversible with over 54% recovery in motility within a 24-hr period after removal from the fluopyram solution for both *M. incognita* and *R. reniformis*. This reversible effect indicates fluopyram is nematistatic, which is similar to other nonfumigant nematicides (e.g. aldicarb). The reversible effects of aldicarb have been reported for *M. incognita* and *Heterodera rostochiensis* (Nelmes, 1970; Faske and Starr, 2006). Few fungicides with nematicidal activity have been evaluated for reversible effects, but benomyl and thiabendazole were reported to act as a repellent of *H. tabacum* rather than directly affecting nematode motility (Miller, 1969). Abamectin is one of the only nonfumigant nematicides that are truly nematicidal as its impact on nematode paralysis is irreversible (Faske and Starr, 2006).

Though fluopyram is nematistatic, low concentrations of fluopyram were effective at inhibiting infection of tomato roots by *M. incognita* and *R. reniformis*. These effects are similar to other nematistatic, nonfumigant nematicides, which suggest fluopyram may share a similar mode of action by disrupting the chemoreception and the ability of both nematode species to infect a host root system (Haydock et al., 2013). A low concentration of 1.0 µg/ml aldicarb inhibited infection by *M. javanica*

on tomato roots (Hough and Thomason, 1975). Similarly, a sublethal concentration of 0.4 and 8.2 μg/ml abamectin inhibited tomato root infection by *M. incognita* and *R. reniformis*, respectively (Faske and Starr, 2006). The concentration of fluopyram needed to cause paralysis and inhibit infection of *M. incognita* and *R. reniformis* on tomato was low and similar to that of aldicarb and abamectin.

The toxicity of fluopyram is similar to aldicarb and abamectin in vitro and like aldicarb its effects on *M. incognita* and *R. reniformis* are reversible. Fluopyram has limited xylem movement, which indicates direct contact will be important for nematode suppression rather than systemic nematicides like aldicarb, which are translocated to the roots to inhibit nematode infection or repel nematodes from the root. Currently, fluopyram is commercially available for use as an in-furrow spray in cotton and peanut, and as a seed treatment in soybean for suppression of plant-parasitic nematodes. Based on the labeled rates of these products, the concentration of fluopyram applied in-furrow or per seed would exceed the effective concentration to cause nematode paralysis for either nematode species. Though the concentration of fluopyram protecting the developing root system has yet to be quantified, even low concentrations of fluopyram can limit the ability of both nematode species to infect a host root.

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