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Interactions Among the Aphid *Diuraphis noxia*, the Entomopathogenic Fungus *Paecilomyces fumosoroseus* and the Coccinellid *Hippodamia convergens*

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Paecilomyces fumosoroseus *(Wize) Brown & Smith is under development as a mycoinsecticide for control of the Russian wheat aphid,* Diuraphis noxia *Kurdjumov. Interactions with other natural enemies within the agro-ecosystem, such as the coccinellid* Hippodamia convergens *Guerin, require evaluation before its potential can be realized. In laboratory bioassays* H. convergens *adults were sprayed with suspensions of* P. fumosoroseus *conidia at different concentrations (including potential field rates) and mortality assessed. Although a proportion of coccinellids succumbed to infection (the greatest proportion was 22% when the ladybirds had suffered stress) it is unlikely that they would be at risk from infection as a direct result of a spray application unless there were prolonged periods of high humidity or the coccinellids were stressed. When provided with uninfected or* P. fumosoroseus*-infected* D. noxia *cadavers as prey, coccinellids consumed more uninfected aphids. The predators never consumed aphid cadavers from which the fungus was erupting or sporulating.* Hippodamia convergens *is, therefore, unlikely to be a significant intraguild predator of* P. fumosoroseus*. Predators contaminated with conidia of* P. fumosoroseus *using different methods (sprayed coccinellids, coccinellids foraging on sprayed aphids, and those foraging in the presence of sporulating* D. noxia *cadavers) were able to transfer conidia to healthy* D. noxia *populations and initiate infection in a proportion of those aphids. The proportion of aphids becoming infected was greatest when the coccinellids became contaminated when foraging amongst sporulating cadavers. Some coccinellids also succumbed to infection under these conditions.*

Keywords: Paecilomyces fumosoroseus, Hippodamia convergens, Diuraphis noxia, *coccinellid, Russian wheat aphid, susceptibility, feeding behaviour, epizootiology, vector*

INTRODUCTION

Entomopathogenic hyphomycete fungi have great potential as biological control agents of insects (mycoinsecticides) and as one component within integrated pest management systems.

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As such, their efficacy against a range of aphid species, particularly in cereals, has been evaluated (Feng & Johnson, 1990; Feng *et al*., 1990; Vandenberg, 1996; Vandenberg *et al*., 2001). *Paecilomyces fumosoroseus* (Wize) Brown & Smith is registered in the USA and Europe for use against glasshouse pests and has been tested in the field for control of the Russian wheat aphid, *Diuraphis noxia* Kurdjumov (Vandenberg *et al*., 2001). If the potential of this pathogen is to be realized its effect on non-target and beneficial organisms requires evaluation. Most of the literature on non-target effects have related to direct susceptibility tests (Cook *et al*., 1996). In this study interactions among *D. noxia*, *P. fumosoroseus* and the coccinellid, *Hippodamia convergens* Guerin are described, which determine the relative susceptibility of the predator to the fungus and other potential interactions between these two natural enemies in the presence of *D. noxia*.

MATERIALS AND METHODS

Fungus and Insect Cultures

Paecilomyces fumosoroseus (Strain 612) was obtained as a technical-grade spore powder from Mycotech Inc. (Butte, MT, USA) and isolated and maintained on Sabouraud dextrose agar supplemented with 2% yeast extract (SDAY) at 24ºC and 15L:9D. Conidia were used to infect *D. noxia*, reisolated, and subcultured no more than four times prior to use in the experiments described here. Suspensions were prepared by scraping conidia from the surface of plates and vortexing in 0.01% Tween 80 for 1 min. Concentrations were estimated using a Reichert haemocytometer and appropriate dilutions made.

Diuraphis noxia colonies were maintained on barley, and 0- to 2-day old adult apterae produced for experiments, using established methods (Vandenberg, 1996). Adult *H. convergens* were purchased from IPM Laboratories, Inc. (Locke, NY, USA) and were maintained at 10ºC and 15L:9D for up to 7 days or until required for experimentation. Prior to experimentation coccinellids were provided with water on damp cotton wool and the pea aphid, *Acyrthosiphon pisum* Harris, as prey.

Susceptibility of *H. convergens* to *P. fumosoroseus*

Two bioassays were done using a modification of the method described by Vandenberg (1996). The conidia were applied in an atomized spray using a spray tower (Burgerjon, 1956) calibrated to deposit approximately 100 conidia mm^{-2} using 5 mL of a suspension containing 8×10^6 conidia mL^{-1} (Vandenberg, 1996). Petri dishes containing coccinellids were covered with nylon netting to prevent escape; preliminary experiments demonstrated that this did not significantly reduce conidial deposition. Coccinellids were sprayed in groups of 10 and there were four replicate groups per treatment. *Diuraphis noxia* aphids in groups of 15 on excised barley leaves set in water agar, were sprayed at the same time as the coccinellids were treated, at all dosages, as a positive control. Dosages applied were control (0.01% aqueous Tween 80), and 1.6, 12.5, 100 and 200 conidia mm^{-2}. The lowest two dosages approximated an LC_{50} and LC_{95} for *D. noxia* in the laboratory (Vandenberg, 1996) while higher dosages approximated possible field application rates. Coccinellids were maintained at 25ºC, 15L:9D and 100% relative humidity (RH) for 72 h following inoculation and then at ambient RH (40-60%) for the remaining 5 days of the assay. They were provided with water on damp cotton wool but no prey during the experiment. Aphids were maintained on barley leaves set in water agar at 24ºC, 15L:9D, 100% RH for the first 24 h after inoculation and at ambient RH (40-60%) for the remainder of the assay (Vandenberg, 1996). Mortality of aphids and coccinellids was assessed daily for 8 days. The second assay included an additional, higher dosage of 1000 conidia mm^{-2}. For the second assay, six replicates of 10 coccinellids each were included per dosage and aphids were sprayed only for the control and lowest two dosages (four replicates of 15 aphids each for each dosage). Half the coccinellids (three replicates) in each treatment were held at 100% RH for 72 h (as in the first assay) and the other half held at 100% RH only for the first 24 h post-inoculation

but otherwise monitored as previously described. On both occasions germination tests on plates of SDAY confirmed viability of conidia (> 90% germination).

Foraging Behaviour of *H. convergens* on *P. fumosoroseus*-infected Aphids

In the 5 days prior to this experiment, half of the coccinellids were starved by supplying them with water on damp cotton wool but no prey; the other half (non-starved) were supplied with water in the same way and fed twice with excess aphid prey (*A. pisum*). For the experiment, coccinellids were placed individually in 60 mm Petri dish arenas with 10 items of one of four prey types: (1) uninfected *D. noxia* cadavers (killed by freezing); (2) infected *D. noxia* cadavers that had only recently died but remained green in colour; (3) infected *D. noxia* cadavers with the fungus emerging; or (4) *D. noxia* cadavers on which the fungus was sporulating profusely. The experiment was done twice; in each, five starved and five non-starved coccinellids were tested with each prey type. The number of prey items either entirely or partially consumed after 90 min and 24 h was recorded. The experiments were done under ambient conditions (≈25ºC and 40-60% RH and fluorescent lighting). The number of aphids consumed at the two observation times was analysed by repeated measures analysis of variance.

Capability of *H. convergens* as Vectors of *P. fumosoroseus* After Foraging on *D. noxia* Sprayed With Conidia

Seven starved coccinellids were allowed to forage for 4 h in individual 60 mm Petri dishes containing a piece of barley leaf bearing 10 adult *D. noxia* aphids that had been sprayed at a dosage of 1000 conidia mm^{-2}. The coccinellids were then transferred into individual Petri dishes containing ten pieces of barley on damp filter paper bearing 30 unsprayed *D. noxia* aphids. Three starved coccinellids foraged on Tween 80-sprayed *D. noxia* aphids and served as controls. After 18 h aphids and coccinellids were separated; beetles were maintained individually with water but without prey under conditions described for the susceptibility bioassay and monitored daily. Surviving aphids were maintained in groups on barley leaves as described for the susceptibility bioassay. Mortality was assessed daily for 7 days. A further 20 (approximately) untreated *D. noxia* aphids were then placed for 24 h on five of the original ten leaf pieces on which contaminated beetles and aphids had been maintained together. After this time, this second group of aphids was transferred to fresh leaves and maintained and assessed as described above.

Capability of *H. convergens* as Vectors of *P. fumosoroseus* After Being Sprayed With Conidia

Five starved coccinellids were sprayed at a dosage of 1000 conidia mm^{-2}. They were then transferred individually into 60 mm Petri dishes containing ten pieces of barley on damp filter paper bearing 20 unsprayed *D. noxia* aphids. Five starved coccinellids were sprayed with Tween 80 and allowed to forage on *D. noxia* aphids; these served as controls. After 18 h coccinellids were removed. Surviving aphids were transferred to fresh leaves and maintained and monitored as described above. A further 20 (approximately) untreated *D. noxia* aphids were then placed for 24 h onto five of the original ten leaf pieces on which contaminated beetles and aphids had been maintained together. After this time, this second group of aphids was transferred to fresh leaves and maintained and assessed as described above.

Capability of *H. convergens* as Vectors of *P. fumosoroseus* After Foraging on *D. noxia* Among Aphid Cadavers Sporulating With *P. fumosoroseus*

Seven starved coccinellids were allowed to forage for 4 h in a 60 mm Petri dish containing a barley leaf bearing ten healthy, unsprayed *D. noxia* aphids and five sporulating *P. fumosoroseus*-infected *D. noxia* cadavers. Coccinellids were then transferred individually into Petri dishes containing 10 pieces of barley on damp filter paper bearing 30 *D. noxia* aphids. Three starved coccinellids were treated similarly, but foraged in the presence of no

sporulating aphid cadavers, and served as controls. After 18 h aphids and coccinellids were separated; coccinellids were maintained and monitored individually as described above. The surviving aphids were transferred to fresh leaves and monitored as described above. A further 20 (approximately) untreated *D. noxia* aphids were then placed for 24 h onto five of the original 10 leaf pieces on which contaminated beetles and aphids had been maintained together. After this time, this second group of aphids was transferred to fresh leaves and maintained and assessed as described above.

RESULTS AND DISCUSSION

Susceptibility of *H. convergens* to *P. fumosoroseus*

In the first bioassay, *P. fumosoroseus*-induced mortality of coccinellids averaged 5, 22 and 10% (SD = 6, 19 and 1%, respectively) at dosages of 12.5, 100 and 200 conidia mm^{-2}, respectively. In the second bioassay, no beetle mortality occurred at dosages less than 1000 conidia mm^{-2}; 6.7% mortality (2 of 30 coccinellids; SD = 11.5%) occurred at this dosage only after initial incubation for 72 h at 100% RH. No mortality occurred among the 28 coccinellids inoculated at this dosage and incubated at 100% RH for only 24 h. At dosages above 12.5 conidia mm^{-2}, 69-97% of aphids succumbed to infection confirming the efficacy of the treatment. Coccinellids used for the first assay had been delayed in transit and may have suffered temperature and desiccation stresses prior to assay, which could account for the higher infection rates observed in this assay. Other studies have shown changes in susceptibility of insects to fungal pathogens as a result of stressful conditions such as starvation and changes in temperature (Donegan & Lighthart, 1989). At the high dosages of conidia (similar to field rates) of *P. fumosoroseus*, *H. convergens* adults are unlikely to be at risk from infection as a direct result of a spray application unless there are prolonged periods of high humidity or the insects are stressed. This is supported by studies examining the pathogenicity of *Beauveria bassiana* (Balsamo) Vuillemin isolates against *H. convergens* in the laboratory and field (James & Lighthart, 1994). *Beauveria bassiana* was pathogenic to *H. convergens* in the laboratory, but pathogenicity in the field varied with weather conditions: early in the season the incidence of the predator was reduced by 75-93% even at low concentrations of the fungus, but was not affected later in the season (James *et al*., 1995). A low level of mortality due to *B. bassiana* infection was observed in coccinellids, but not aphids, in both assays. These infections probably originated from *B. bassiana* infection of the original field-collected beetles. Overwintering coccinellid populations are commonly attacked by *B. bassiana* (Hodek, 1973; Mills, 1981) and laboratory bioassays against coccinellids have demonstrated their susceptibility to isolates of *B. bassiana* (Magalhaes *et al*., 1988; Poprawski *et al*., 1998; Yeo, 2000). Increased use of mycoinsecticides, such as *B. bassiana*, may increase the level of overwintering mortality in many hibernating non-target insects (Flexner *et al*., 1986).

Foraging Behaviour of *H. convergens* on *P. fumosoroseus*-infected Aphids

Prey type and coccinellid starvation status interacted significantly in determining the number of aphid prey consumed using a repeated measures analysis of variance ($F = 11.4$; df = 1,36; $P < 0.02$ within coccinellids at a single observation time; $F = 39.2$; df = 1,36; $P < 0.04$ among coccinellids across observation times). There were several types of interactions. Starved coccinellids fed on uninfected aphids immediately but consumed only a few more prey after 90 min (Table 1). Non-starved beetles ate few uninfected prey in the first 90 min, but ate significantly more over the remainder of the 24 h. The freeze-killed aphids probably began to decay during the 24 h of the test, but they still remained acceptable to coccinellids. Starved cocinellids consumed almost as many newly-dead fungus-infected cadavers as they did uninfected freeze-killed aphids in the first 90 min, but they consumed no additional infected aphids for the rest of the experiment. This may be due to the continuing growth of the fungus during the 24-h test, making the cadavers less appealing to coccinellids. Non-

TABLE 1. Number of adult *Diuraphis noxia* consumed by individual adult *Hippodamia convergens* foraging in Petri dish arenas

	Mean Number (SEM) of Prey Consumed by *H. convergens*[a] coccinellids			
	within 90 min when:		within 24 h by:	
Prey Type Offered	Starved[b]	Non-starved	Starved	Non-starved
Uninfected, freeze-killed *D. noxia*	8.0 (0.9)	2.8 (1.0)	9.4 (0.5)	7.4 (0.7)
Infected *D. noxia*:[c]				
Newly-dead	6.5 (0.9)	0.1 (0.1)	6.8 (0.8)	0.4 (0.2)
Fungus erupted	0	0	0	0
Fungus sporulated	0	0	0	0

[a]10 aphids offered per coccinellid. Significant interaction of prey type and starvation status; see text for statistics.

[b]'Starved' coccinellids deprived of food and 'non-starved' coccinellids fed twice to satiation in the 5 days prior to the experiment. There were 5 coccinellids tested per treatment combination and the experiment was done twice.

[c]'Newly dead' aphids remained green in colour but contained fungus mycelium. 'Fungus erupted' cadavers had fungal hyphae beginning to emerge through the host cuticle. 'Fungus sporulated' cadavers were covered with conidia and hyphae.

starved beetles consumed very few infected aphids. No coccinellids consumed cadavers from which the fungus was emerging or sporulating.

Roy *et al*. (1998) tested the foraging choices of larvae of *Coccinella septempunctata* L. presented with *A. pisum* as prey. The suitability of living and dead, uninfected and *Erynia neoaphidis*-infected aphids as prey were compared. Both infected and uninfected aphids were consumed although infected aphids were less palatable. Hungry beetle larvae did attempt to feed on sporulating *E. neoaphidis*-infected cadavers but never entirely consumed them. Similar results were observed for adult *C. septempunctata* (Pell *et al*., 1997). Although partially-consumed infected aphids did not produce as many *E. neoaphidis* conidia, the rate of secondary transmission in aphid populations was unaffected compared to undamaged cadavers, and in fact the presence of the beetle actually encouraged secondary transmission (Roy *et al*., 1998). Similar results were obtained with the interactions studied here; aphid cadavers infected and killed by *P. fumosoroseus* were not consumed once the fungus had erupted through the cuticle and those aphids that had been recently killed by the fungus were less palatable than recently killed uninfected aphids. Similarly, a proportion of aphids were only partially consumed (10 of 72) although sporulation was not quantified. *Hippodamia convergens* is therefore unlikely to be a significant intraguild predator of *P. fumosoroseus*. The presence of foraging *H. convergens* may encourage transmission of *P. fumosoroseus*, particularly if beetle foraging disturbs aphids sufficiently to cause them to move out from cryptic feeding sites in the unfolded leaves of cereals (Burd & Burton, 1992) and into greater contact with fungal inoculum.

Capability of *H. convergens* as Vectors of *P. fumosoroseus*

The seven coccinellids allowed to forage on aphids sprayed with *P. fumosoroseus* conidia transferred the fungus and caused infection in a total of 3 of 148 aphids in their new arenas (average of 0.4 aphids per arena; Table 2). An additional 4 of 141 aphids (average of 0.6 aphids per arena; Table 2) became infected after being transferred into these foraging arenas after coccinellid removal. Three out of the seven coccinellids contaminated in this way became infected with *P. fumosoroseus*. Coccinellids sprayed with *P. fumosoroseus* conidia transferred conidia to healthy aphids initiating infection in a total of 9 out of 60 aphids (average of 1.8 aphids per arena; Table 2). An additional 6 of 50 aphids (average of 1.2 aphids per arena; Table 2) became infected after being transferred into the foraging arenas after coccinellid removal. None of the coccinellids sprayed with *P. fumosoroseus* succumbed

TABLE 2. Mean number (SEM) of adult *Diuraphis noxia* infected by *Paecilomyces fumosoroseus* vectored by individual adult *Hippodamia convergens* foraging in Petri dish arenas

Method of *H. convergens* exposure to *P. fumosoroseus*	Aphids exposed to foraging coccinellids[a]			Aphids transferred into arenas after coccinellid foraging[a]		
	No. exposed	% infected	Range[b] %	No. exposed	% infected	Range[c] %
Coccinellids foraging on sprayed aphids	21.1 (3.3)	2 (2)	0 to 12	20.1 (0.6)	3 (2)	0 to 14
Coccinellids sprayed before foraging	12.0 (3.2)	15 (7)	5 to 38	10.0 (1.8)	12 (6)	0 to 38
Coccinellids foraging near cadavers	20.7 (2.6)	53 (18)	0 to 100	20.1 (0.5)	59 (14)	0 to 95

[a]No aphid infection occurred among controls.
[b]Infection rates in 5 or 7 arenas among aphids not consumed by the sole foraging coccinellid.
[c]Infection rates in 5 or 7 arenas among aphids placed in arenas after coccinellid removal.

to infection, confirming results of bioassays described previously. Coccinellids contaminated with *P. fumosoroseus* by foraging in the presence of sporulated aphid cadavers vectored conidia to healthy aphids initiating infection in a total of 77 out of 145 aphids (average of 11 aphids per arena; Table 2). An additional 83 of 141 aphids (an average of 11.9 per arena; Table 2) became infected after transfer into the arenas after beetle removal. Four out of the seven coccinellids contaminated in this way later became infected with *P. fumosoroseus*.

This study demonstrates that, as with similar studies on the ability of other coccinellid predators to act as vectors (Pell *et al*., 1997; Roy *et al*., 2001), adult *H. convergens* contaminated with conidia were able to transfer these conidia to healthy aphid populations and initiate infection in a proportion of the population. The proportion of aphids that became infected was particularly large when the coccinellid had become contaminated when foraging amongst sporulating cadavers. This may facilitate the spread of inoculum within and between fields and therefore improve the efficacy of an application. Moreover, predators acting as vectors may allow movement of fungal inoculum into cryptic aphid feeding sites. Unlike previous studies in which the fungus used (*E. neoaphidis*) did not infect the coccinellid, our studies did demonstrate infection by *P. fumosoroseus* of a proportion of beetles foraging in the presence of sprayed aphids or sporulating cadavers. These beetles may have become heavily contaminated by conidia that concentrated around their mouthparts during feeding. Here there are numerous intersegmental membranes making penetration of the fungus easier than elsewhere on the cuticle. Similar high levels of mortality in predators have been recorded in other systems when the predator fed on infected hosts (Kiselek, 1975; Poprawski *et al*., 1998). Conidia may also have germinated within the alimentary canal and penetrated the haemocoel to cause infection (Feng *et al*., 1994). Further studies are needed to determine the relative importance of coccinellids acting as vectors in relation to cocinellid infection in the field.

In summary, a number of potentially synergistic, antagonistic and additive interactions have been demonstrated among Russian wheat aphid, *P. fumosoroseus* and *H. convergens* in the laboratory. The coccinellid was not a significant intraguild predator of *P. fumosoroseus*; it never consumed overtly infected aphids and would therefore not remove inoculum from the environment thereby reducing secondary transmission. In addition, coccinellids contaminated with conidia were able to transfer these conidia to healthy aphid populations and initiate infection in a proportion of the population. However, in extended periods of high humidity and stress, coccinellids were susceptible to infection by *P. fumosoroseus* in laboratory assays. Even in these individuals mortality never exceeded 22% at dosages that killed almost all test aphids. Coccinellids foraging in close proximity to sporulating *P. fumosoroseus*-infected aphids, and therefore more likely to acquire large numbers of conidia around potentially vulnerable mouthparts, were most at risk from infection but also most likely to transfer infection to healthy aphid populations.

The safety of microbial control agents is directly linked to their physiological and ecological host range (Goettel, 1994); the physiological host range is defined under laboratory conditions, as we did here, but the ecological host range is the range of hosts that will actually be infected in the field (Hajek & Butler, 2000). This can be influenced by environment (e.g. James *et al*., 1995) but also the biology and ecology of the hosts (Roy & Pell, 2000). Predators serving as effective vectors of fungal inoculum might partially compensate for predator susceptibility to infection by the same fungi in terms of total mortality of the target pest. However, further studies under more realistic conditions are necessary to determine whether these laboratory studies are indicative of interactions that might be important in the field in the long term. They do suggest that direct susceptibility to infection is only one parameter that should be assessed when considering the safety of a microbial control agent.

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