Variation in Susceptibility of *Diadegma insulare* (Hymenoptera: Ichneumonidae) to Permethrin

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ABSTRACT Six field populations of the parasitoid *Diadegma insulare* (Cresson) were collected from Mexico and the United States and tested for their susceptibility to permethrin by using a glass-vial residue bioassay. Significant differences existed in susceptibility, with one population significantly more susceptible than the other five. Susceptibility of *D. insulare* increased when they were reared for several generations in the greenhouse in the absence of selection. *D. insulare* was less susceptible to permethrin than the adult stage of its host, *Plutella xylostella* (L.), from a laboratory colony, but more susceptible than those hosts collected from a commercial field. Our data suggest that a field population of *D. insulare* appeared to increase its tolerance to permethrin much more slowly than *P. xylostella*.

KEY WORDS *Diadegma insulare*, permethrin, *Plutella xylostella*

NATURAL CONTROL AGENTS are important components of integrated pest management systems. However, insecticides, especially broad-spectrum insecticides, frequently disrupt the balance between a host and its natural enemies because the natural enemies are often more susceptible than the pest species (Croft and Brown 1975, Croft 1990). Compared with resistance in pests, insecticide resistance in beneficial arthropods is rare and less well documented (Georghiou 1986, Tabashnik and Johnson 1995). However, natural enemies do not lack mechanisms required for detoxifying insecticides (Brattsten and Metcalf 1970). Decreased susceptibility of natural enemies to pesticides has been achieved through selection in the laboratory (Croft 1982, 1990; Hoy 1985, 1990; Havron et al. 1991) and the field (Spollen and Hoy 1992, Baker and Arbogast 1995, Rathman et al. 1995).

The diamondback moth, *Plutella xylostella* (L.), is the most destructive insect of cruciferous plants throughout the world and many populations have developed resistance to most classes of insecticides used against them (Talekar and Shelton 1993). The nearly sole reliance on insecticides has also led to severe disruption of its natural enemy complex. Natural control agents, especially parasitoids, can play an important role in *P. xylostella* management and efforts are underway in several countries to integrate biological and chemical control of *P. xylostella* (Talekar and Shelton 1993). In Europe, it has been reported that parasitoids alone may keep *P. xylostella* populations under control (Mustata 1992).

Diadegma insulare (Cresson) (Hymenoptera: Ichneumonidae) is one of the most important parasitoids of *P. xylostella* in North America (Harcourt 1986, Lasota and Kok 1986, Hu et al. 1998). In fields, parasitism of *P. xylostella* by *D. insulare* may reach 80% (Idris and Grafius 1993b). However, because of its high susceptibility to many insecticides (including fenvalerate, permethrin, cypermethrin, azinphosmethyl and methomyl), *D. insulare* could be severely reduced in crucifer fields that are sprayed frequently (Idris and Grafius 1993a, 1993b). It is likely that insecticides will remain a major tool for managing *P. xylostella* and other crucifer pests in the near future, so assessing the variation in susceptibility of *D. insulare* populations may provide insight into the potential for integrating insecticides and *D. insulare.*

For parasitoids, the development of resistance to insecticides largely depends on the resistance of their host insects (Tabashnik and Croft 1985, Tabashnik 1986). *Plutella xylostella* has developed high levels of resistance to many insecticides and, in a survey evaluating >40 populations of *P. xylostella* collected from throughout North America for their susceptibilities to commonly used insecticides, Shelton et al. (1993) found large differences based on collection location. Based on results of the *P. xylostella* study and the hypothesis that host and parasitoid susceptibility are related, we investigated whether there is variation in susceptibility to permethrin among six *D. insulare* populations collected from different areas within the United States and Mexico. Permethrin was chosen because it has been one of the most widely used insecticides for control of crucifer pests in both countries over the last decade.

Materials and Methods

Collection and Rearing of *D. insulare*. Six colonies were used in the experiments (Table 1). *Diadegma*

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Table 1. *D. insulare* colonies used in the experiments

Colony	Collection site	Collection date	No. collected	Source of *D. insulare*
Texas	Weslaco, TX	3 May 1999	164	*P. xylostella* larvae and *D. insulare* pupae collected from a commercial cabbage field
SC	Charleston, SC	12 May 1999	160	Pupae collected from a commercial collard field
Celaya 1	Celaya, Mexico	20 May 1999	45	Pupae collected from large outdoor rearing cage, in which insects from nearby commercial fields were introduced every 3–6 months
Celaya 2	Celaya, Mexico	29 Nov. 1999	229	Pupae collected from a commercial broccoli field
S.L.P.	San Luis Potosi, Mexico	29 Nov. 1999	85	Pupae collected from a commercial cabbage field
Geneva	Geneva, NY	26 July 1999	100	Pupae and *P. xylostella* larvae were collected from an unsprayed cabbage field on a research farm

insulare pupae were collected in 1999 by cooperators and taken to Cornell University's New York State Agricultural Experiment Station in Geneva, NY, where they were placed in a growth chamber for emergence at $27 \pm 1°C$, $35 \pm 2\%$ RH, and a photoperiod of 16:8 (L:D) h. After emergence, 8–12 pairs of male and female parasitoids were transferred into a clear plastic cylinder cage (12 cm diameter by 15 cm tall) and allowed to mate. A colony of *P. xylostella* (Geneva 88) (Shelton et al. 1991) was used as a host for maintaining the *D. insulare* colonies. A tray (24 by 34 by 6 cm) of 5- to 6-wk-old oilseed rape (*Brassica napus* L. ssp. *oleifera*) seedlings was infested with ≈300 *P. xylostella* eggs and placed into a wooden rearing cage (45 by 50 by 76 cm, with a glass top and screen-covered openings on three sides) in a greenhouse at $27 \pm 5°C$ and a photoperiod of 14:10 (L:D) h. When the *P. xylostella* had reached the second to third instar, and after the *D. insulare* had been allowed to mate in the cylinder cages for 1 d, six to eight pairs of male and female parasitoids were transferred from the cylinder cages into the wooden cage with the *P. xylostella* larvae. A 10% sugar solution was provided as food for the wasps while they parasitized the host larvae. With these rearing conditions, the next generation of wasps emerged in 15–20 d.

Bioassays. For each *D. insulare* population, the susceptibility of adults to permethrin (Ambush 2E, Zeneca Ag Products, Wilmington, DE) was assessed using a direct contact residual method with glass vials (2.5 cm diameter by 9.5 cm long). Preliminary bioassays with the insecticide were conducted so that an appropriate range of concentrations (10–90% mortality range) could be selected for a full-scale test. For each formal test, six to seven concentrations of the insecticide were prepared in distilled water, including a control, and five to six vials were treated with each concentration. A volume of 5 ml was poured into each vial and the vial was swirled for 10–20 s. The excess solution was poured off and the residue was air-dried inside a hood for 4–5 h. Distilled water was used as a control. After they were anesthetized with CO_2 for ≈3 s, six randomly selected 1- to 2-d-old adults of both sexes were placed into each of the treated vials. Each vial was capped with nylon gauze and a cotton wick, soaked with 10% sugar solution, was pinned to the gauze on the inside of the vial to provide food for the wasps. The test vials were placed in a growth chamber at $27 \pm 1°C$, $35 \pm 2\%$ RH, and a photoperiod of 16:8

(L:D) h. Mortality was recorded after 24 h. Individuals were considered dead if they were unable to maintain a normal posture or walk normally, covering at least 1 mm/s.

To compare the susceptibility of *D. insulare* to that of its host, *P. xylostella* adults were tested using the same method. Adults, 1–2 d old, of two *P. xylostella* colonies were used in the bioassay: Geneva 88 and Celaya F_0. The Geneva 88 colony was started from individuals collected from untreated fields in 1988 at Geneva, NY. This colony has been used as a susceptible reference population in several studies of insecticide resistance in *P. xylostella* (e.g., Shelton et al. 1993). It was the same colony as we used for rearing the *D. insulare* cultures. The Celaya F_0 population was collected from a commercial broccoli field in Celaya, Mexico. To compare the susceptibility of these two populations, we used a resistance ratio, calculated by dividing the LC_{50} of the Celaya F_0 population by the LC_{50} of the Geneva 88 population.

Effect of Sex on Mortality of *D. insulare* Adults Caused by Permethrin. To evaluate the possible effect of sex on susceptibility of wasps in the bioassay, 1- to 2-d-old male and female parasitoids were tested concurrently but in different vials. Parasitoid adults of Geneva F_5 and Celaya 2 F_1 were used in these tests. Three concentrations, which had killed 20–30, 50–60, and 70–90% adults of both sexes in previous tests, were used, and distilled water was used as control. For each permethrin concentration we used three replications, with each replication having five vials and six adults in each vial.

Statistical Analysis. Concentration-mortality regressions were estimated by probit analysis using POLO (LeOra Software 1997). Differences in susceptibility were considered significant when 95% fiducial limits did not overlap. Analysis of variance (ANOVA) was used to test differences in the mortalities between male and female *D. insulare* (PROC ANOVA, SAS Institute 1985). Mortality data were transformed (arcsine square root) before the ANOVA.

Results

Variation in Susceptibility of *D. insulare* to Permethrin Between Locations. Adult *D. insulare* from the different geographic populations exhibited variation in their susceptibility to permethrin (Table 2). To eliminate the effect of generation removed from the

Table 2. Susceptibility of *D. insulare* adults from different locations to permethrin residues

Colony	Generation	n	LC_{50} (ppm [AI])	95% FL	Slope $\pm$ SE	χ^2
Celaya 2	F_0	168	22.28	19.76–25.41	4.29 $\pm$ 0.74	0.97
	F_2	168	11.81	10.37–13.33	4.27 $\pm$ 0.74	1.26
Celaya 1	F_3	164	10.34	7.95–13.76	2.17 $\pm$ 0.54	1.50
	F_5	154	6.81	5.63–7.91	3.30 $\pm$ 0.60	1.91
	F_7	168	5.02	4.53–5.54	5.46 $\pm$ 0.82	2.48
	F_9	198	4.93	4.43–5.52	4.48 $\pm$ 0.61	0.75
	F_{11}	168	5.10	4.45–5.78	4.10 $\pm$ 0.74	0.46
SC	F_3	212	7.20	6.22–8.52	3.10 $\pm$ 0.54	2.26
Texas	F_3	209	10.28	7.33–12.47	3.59 $\pm$ 0.83	2.48
Geneva	F_1	129	7.46	5.91–9.67	2.38 $\pm$ 0.37	2.63
	F_3	215	3.95	3.19–4.91	2.91 $\pm$ 0.53	1.80
	F_5	204	4.86	4.36–5.42	4.63 $\pm$ 0.61	2.87
	F_7	174	4.55	4.03–5.03	5.27 $\pm$ 0.83	0.77

field, we compared the LC_{50} of the same generation. In F_3 adults we found that LC_{50}s for Celaya 1, SC, and Texas colonies were significantly higher than that of the Geneva colony. We did not have enough adults from the S.L.P colony to do a complete dose–response bioassay, but the mortality of F_0 was 40.0% at 16 ppm and 70.0% at 27 ppm, which was similar to Celaya 2 F_0, indicating that the S.L.P. colony probably did not differ from Celaya 2 in susceptibility to permethrin.

Variation in Susceptibility of *D. insulare* Over Generations. Bioassay results indicated that susceptibility of *D. insulare* to permethrin increased when the wasps were reared without chemical selection (Table 2). For the Celaya 2 colony, the LC_{50} value decreased approximately twofold from F_0 to F_2, a significant difference based on the nonoverlap of the 95% fiducial limits. A similar and significant twofold decrease also occurred in Celaya 1 from F_3 to F_7. The data from the Celaya 1 colony and the Geneva colony indicate that the LC_{50} for *D. insulare* may have stabilized at about 4–6 ppm after five generations.

The mortality of male and female parasitoid adults treated with permethrin did not differ significantly (Table 3), both in Geneva F_5 ($F = 0.17$; df = 1, 12; $P = 0.913$) and in the relatively tolerant colony, Celaya 2 F_1 ($F = 0.07$; df = 1, 12; $P = 0.977$).

Comparison of Susceptibility of *D. insulare* with Its Host-*P. xylostella*. The LC_{50} of Geneva 88 *P. xylostella* adults to permethrin was 0.59 ppm, which was seven times lower than that of the Geneva F_7 *D. insulare* (Tables 1 and 4). Our data indicate that, compared with *P. xylostella* adults of the Geneva 88 colony, *D. insulare* adults were less susceptible to permethrin. For *P. xylostella* adults, the LC_{50} of the Celaya field

population (F_0) for permethrin was 132 times higher than that of the Geneva 88 colony, whereas for *D. insulare* adults, the LC_{50} of Celaya 2 F_0 for permethrin was only four times higher than that of the Celaya 1 F_{11}.

Discussion

Pesticide-resistant beneficial insects may be an important component of pest management programs (Metcalf and Luckmann 1982), but previous investigations of the evolution of resistance to insecticides among field populations of parasitoids have yielded mixed results (Krukierek et al. 1975, Schoonees and Giliomee 1982, Rosenheim and Hoy 1986). Some parasitoid populations have developed high levels of resistance to insecticides, with LC_{50}s exceeding field application rates. For example, populations of *Diglyphus begini* (Ashmead), a parasitoid of *Liriomyza* spp. leafminers, showed resistance to oxamyl, methomyl, fenvalerate, and permethrin, and parasitoids from a heavily sprayed tomato greenhouse on the island of Hawaii had LC_{50}s for permethrin and fenvalerate that were 10 and 29 times higher than the field rate, respectively (Rathman et al. 1990). A field population of *Anisopteromalus calandrae* (Howard) was shown to be 2,800-fold more resistant to malathion, compared with a susceptible laboratory strain (Baker and Weaver 1993, Baker 1995). For *D. insulare*, our investigation documented variability in susceptibility to permethrin among different field populations. Once parasitoids were removed from the field and reared without insecticide selection in the greenhouse, however, the susceptibility to permethrin increased. In contrast,

Table 3. Mortality of *D. insulare* adults by sex in glass vials treated with permethrin

	Geneva F_5			Celaya 2 F_1	
Concn (ppm [AI])	Mortality (%) Mean $\pm$ SE		Concn (ppm [AI])	Mortality (%) Mean $\pm$ SE	
	Female	Male		Female	Male
3.0	18.34 $\pm$ 1.67a	18.89 $\pm$ 1.57a	8.0	11.11 $\pm$ 3.14a	11.11 $\pm$ 1.57a
5.0	45.55 $\pm$ 5.66b	47.78 $\pm$ 6.85b	12.0	44.44 $\pm$ 4.16b	45.56 $\pm$ 4.16b
8.0	82.22 $\pm$ 3.14c	83.33 $\pm$ 5.44c	20.0	73.33 $\pm$ 7.20c	70.00 $\pm$ 8.16c

Means by sex or by concentration in rows and columns of each colony followed by the same letter are not significantly different ($P > 0.05$).

Table 4.   Susceptibility of *P. xylostella* adults to permethrin

Colony	n	LC$_{50}$ (ppm [AI]) (95% FL)	Slope $\pm$ SE	χ^2	RR
Geneva 88	170	0.59 (0.48–0.72)	2.19 $\pm$ 0.39	0.82	
Celaya	175	77.95 (65.92–93.17)	3.14 $\pm$ 0.50	0.80	132.1

RR = LC$_{50}$ of Celaya colony / LC$_{50}$ of Geneva 88 colony.

populations of several other parasitoid species have been shown to have stable resistance to insecticide in the absence of selection in laboratory (Hoy et al.1991, Spollen and Hoy 1992). Spollen et al. (1995) reported that resistance of a laboratory-selected strain of *Aphytis melinus* Debach was relatively stable in the absence of selection after 10 mo ($\approx$15 generations). Obviously, tolerance in the field population of *D. insulare* used in our bioassays was not fixed, and the relatively small number of individuals used to initiate our colonies may have contributed to the rapid increase in susceptibility.

There was no significant difference in susceptibility of *D. insulare* to permethrin between male and female wasps. In other studies, sexual differences in susceptibility to pesticides have been noted in some parasitoids with male parasitoids being generally more susceptible to insecticides than females (Schoonees and Giliomee 1982, Scott and Rutz 1988, Rathman et al. 1992). The differences are thought to be related partly to differences in size and physiology between the sexes (Baker et al. 1995, Croft 1990). However, male parasitoids are not always more susceptible to insecticides than females (Spollen and Hoy 1992), and Baker et al. (1995) stated that such differences may be difficult to document with a typical dose–response assay. In another experiment, using a serial time-response bioassay with a single dose, which Baker et al. (1995) used, we still failed to find any significant sexual difference in susceptibility, although *D. insulare* males are usually smaller than the females (unpublished data).

Pyrethroids are considered highly toxic to many beneficial arthropods (Croft 1990). However, our results clearly demonstrate that *D. insulare* adults were less susceptible to permethrin than *P. xylostella* adults of the Geneva 88 colony, indicating that parasitoids do not always have higher susceptibilities to insecticides than host insects. This result is in line with at least one other report on *Liriomyza* spp. parasitoids (Mason and Johnson 1988). Although Geneva 88 is a laboratory-maintained strain, its susceptibility to permethrin is similar to some field populations of *P. xylostella* (Shelton et al. 1993, 2000). Using a similar method to ours, Idris and Grafius (1993a) reported that *D. insulare* was much more susceptible than *P. xylostella* to permethrin. The *P. xylostella* population used in their bioassay was collected from commercial cabbage fields in Monroe County, MI, during October 1989. One explanation for the difference between their result and ours with the Geneva 88 colony is that the *P. xylostella* used in their bioassay may have developed resistance to permethrin. As they mentioned, growers

in that area had reported control failures after applications of insecticides, including permethrin (Idris and Grafius 1993a). Our results indicated that although their susceptibility increased after seven generations the *D. insulare* colonies that we reared in the greenhouses were still more tolerant to permethrin than the Geneva 88 *P. xylostella* adults, suggesting that the higher tolerance to permethrin in *D. insulare*, compared with susceptible *P. xylostella*, may be an innate characteristic of the *D. insulare* species.

Although a field strain of *A. calandrae* was shown to be 200-fold more tolerant of malathion than the field strain of its insect-host (Baker 1995), this result may have been due to several unique characteristics of the interaction of the insecticides, host food and host insect within the stored grain ecosystem (Baker et al. 1995). Most field populations of parasitoids develop resistance slowly (if they develop resistance at all) and the level of resistance is usually low (Rosenheim and Hoy 1986). Our results demonstrate that, compared with *P. xylostella*, the increase in tolerance of *D. insulare* populations in fields may be much slower. For permethrin, the resistance ratio of *P. xylostella* adults collected from a crucifer field in Celaya, Mexico, was 132-fold. When the highest LC$_{50}$ we observed for any *D. insulare* population collected from fields (Celaya 2 F$_0$) was divided by the lowest LC$_{50}$ we obtained (Geneva F$_3$), the difference was only approximately fivefold. The lack of genetic flexibility among the ecologically specialized parasitoids and the relatively low activity of preadapting detoxifying enzyme systems may restrict the evolution of resistance (Georghiou 1972, Croft and Strickler 1983). Nevertheless, based on the differences in susceptibility of geographically separated populations of *D. insulare*, our results provide some indication of the possibility of developing field strains of *D. insulare* that are resistant to commonly used insecticides, although this may take an extended period. An insecticide tolerant strain of *D. insulare* may be valuable for integrating this parasitoid into a management system of the *P. xylostella*.

Acknowledgments

early draft of the manuscript. We greatly thank M. A. Schmaedick for his help and useful discussion during this research.

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