Carbamate and Pyrethroid Resistance in the Leafminer Parasitoid *Diglyphus begini* (Hymenoptera: Eulophidae)

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J. Econ. Entomol. 83(6): 2153–2158 (1990)

ABSTRACT Populations of *Diglyphus begini* (Ashmead), a parasitoid of *Liriomyza* spp. leafminers, showed resistance to oxamyl, methomyl, fenvalerate, and permethrin in laboratory bioassays. Relative to a susceptible strain from California, maximum resistance ratios for these pesticides were 20, 21, 17, and 13, respectively. Three populations that had been treated frequently with insecticides were significantly more resistant to all four insecticides compared with an untreated Hawaii population and a California population with an unknown spray history. 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. Populations resistant to oxamyl and methomyl had LC_{50}'s two- and sixfold below the field rate, respectively. *D. begini* is one of the few parasitoids resistant to pyrethroids, with LC_{50}'s exceeding field application rates. Resistant *D. begini* may be useful for controlling leafminers in management programs that integrate biological and chemical controls.

KEY WORDS Insecta, IPM, pesticide resistance, *Liriomyza* spp.

INSECTICIDE RESISTANCE in beneficial arthropods is rare compared with resistance in pests (Croft & Strickler 1983, Georghiou 1986, Croft 1990, Hoy in press, Tabashnik & Johnson in press). Based on survey results, Georghiou (1986) concluded that natural enemies accounted for <3% of the 447 species of insects and mites known to be resistant to one or more pesticides. Few hymenopterous parasitoids are resistant to insecticides (Croft 1990, Tabashnik & Johnson in press).

During the past several years, studies of insecticide resistance in leafminers in the genus *Liriomyza* (Diptera: Agromyzidae) (Mason et al. 1987, 1989) and their hymenopterous parasitoids (Mason & Johnson 1988) have been conducted in Hawaii. The leafminers *Liriomyza sativae* Blanchard and *L. trifolii* (Burgess) are major pests of tomatoes, cucurbits, legumes, and ornamentals in Hawaii (Mothershead 1978, Hara 1986, Johnson 1987) and throughout the world (Parrella 1987). Insecticides commonly used in vegetable and ornamental production in Hawaii and the continental United States include carbamates (methomyl and oxamyl) and pyrethroids (fenvalerate and permethrin). Use of these pesticides has led to control problems with *L. sativae* and *L. trifolii* resulting from the development of resistance (Parrella et al. 1984, Keil et al. 1985) and decimation of effective natural enemies (Oatman 1959; Johnson et al. 1980a,b; Mason et al. 1987).

In a previous study, five species of parasitic Hymenoptera associated with *L. sativae* and *L. trifolii* in Hawaii were tested to determine their tolerances to permethrin and fenvalerate (Mason & Johnson 1988). The eulophid *Diglyphus begini* (Ashmead), which was accidently introduced into Hawaii in the early 1900s (Timberlake 1923), and reintroduced from Mexico in 1976 (Funasaki et al. 1988), had higher LC_{50}'s to both pyrethroids than those reported earlier for *L. trifolii* and *L. sativae* (Mason et al. 1987). These results were consistent with a study that showed *D. begini* survived spray treatments with permethrin in California (Allen & Charlton 1981). In Florida, a related species, *Diglyphus intermedius* (Girsault) (Eulophidae), was highly tolerant to fenvalerate in laboratory bioassays of contact toxicity (Waddill 1978). In these studies, intraspecific comparisons between parasitoid populations were not made. Therefore, it could not be determined if pyrethroid resistance in *Diglyphus* spp. was an innate characteristic (i.e., natural tolerance) or if resistance resulted from selection with pesticides.

The objectives of our study were to examine variation in susceptibility to methomyl, oxamyl, permethrin, and fenvalerate in the leafminer parasitoid *D. begini*. LC_{50}'s were compared among five *D. begini* populations to examine whether resis-

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tance was a function of the history of insecticide treatment for each population.

Materials and Methods

Sources of Parasitoids. Leaves containing mixed populations of *Liriomyza sativae* and *L. trifolii* larvae were collected from three locations (PO, HO, and MO) on the island of Oahu, Hawaii, from February to July 1989. Two of these sites, PO and HO, had previously received weekly pesticide applications. PO was at the University of Hawaii Experiment Station farm at Poamoho, Oahu. The HO site was a private commercial farm in Hawaii Kai, Oahu. MO, the third collection site on Oahu, was an isolated organic garden containing tomatoes and beans in the Manoa Valley near the University of Hawaii. The owner of this property reported that no chemicals had been applied for the past 20 yr. Leaves infested with *Liriomyza* spp were also collected from a heavily sprayed commercial greenhouse (GH) north of Hilo on the island of Hawaii during August to October 1989. The GH greenhouse had received 34 pesticide treatments between December 1988 and May 1989, including 16 applications of fenvalerate (Asana XL 0.66 emulsifiable concentrate [EC]; E. I. du Pont de Nemours & Company, Wilmington, Del.), 11 applications of methomyl (Lannate 1.8 EC; Du Pont), and 7 applications of oxamyl (Vydate 2.0 EC; Du Pont). Application rates were 5.0–10.0 ml/liter for Vydate and Lannate and 320–640 µl/liter for Asana.

Long bean (HO and PO) or tomato leaves (PO, GH) were sampled, brought into the laboratory, dried at 24°C for 2–3 d, and placed in emergence cages. Adult parasitoids were aspirated daily from the cages into glass vials and held at 24°C with honey for 1–4 d before the bioassays were done. Because the MO site was a private backyard garden, plant material infested with *Liriomyza* was difficult to collect. Therefore, a different technique was used to obtain parasitoids for the bioassays. Bean plants (12 d old) ('Henderson Bush,' Burpee Seed, Warminster, Pa.) grown in a greenhouse in vermiculite and infested with second- and third-instar *L. trifolii* were placed at the MO site for 24–48 h. After removal from the field, plants were kept in a holding cage in the laboratory for 7–10 d. Leaves were removed from the plants, dried, and placed in emergence cartons. Adult parasitoids were aspirated and handled in the same manner as parasitoids from the HO, PO, and GH sites.

The California *D. begini* colony was established in April 1989 at the Department of Entomology, University of California, Davis, from 569 males and 362 females collected from weeds surrounding a greenhouse in Salinas, Calif. These greenhouses were bordered by artichokes and other vegetable crops. *D. begini* were reared at Davis on chrysanthemum for several generations before overnight shipment to Hawaii in June and July 1989. This colony's pesticide exposure history was not known. Parasitoids used in the bioassays were 2–4 d old (CA) and 1–4 d old (PO, HO, MO, and GH).

Insecticides. Four formulated insecticides were used: methomyl (Lannate 1.8 EC, Du Pont), oxamyl (Vydate 2.0 EC, Du Pont), permethrin (Ambush 2.0 water soluble liquid [L]; ICI Americas, Inc., Wilmington, Del.), and fenvalerate (Pydrin 2.4 L; Shell, Houston, Tex.).

Field rates for methomyl and oxamyl were calculated as 1,080 and 1,200 mg (AI) per liter, respectively, based upon recommended label rates of 216 (methomyl) and 240 (oxamyl) g (AI)/liter or 1.0 and 1.1 kg formulated material/ha, respectively. Field rates for permethrin and fenvalerate were calculated as 240 mg (AI) per liter, based upon recommended label rates of 240 (permethrin) and 288 (fenvalerate) g (AI)/liter or 0.24 kg formulated material/ha.

Bioassays. The bioassay procedure was similar to that described by Rosenheim & Hoy (1986). Adult parasitoids anesthetized with CO_2 for 30 s were sorted by sex 24 h before they were exposed to pesticide residue. *D. begini* females were placed in 36-ml clear plastic cups (Anchor Hocking, Minneapolis, Minn.) with a fine camel's-hair brush. The cups were covered with an organdy square and capped with a plastic lid, the center portion removed. All insects were kept in an environmental chamber at 24°C at a photoperiod of 16:8 (L:D) and were provided with honey before testing.

Serial dilutions of formulated insecticide were prepared in 50 ml of distilled water plus 1 ml of 0.2% Triton Ag-98 (Rohm & Haas Company, Newark, N.J.), a wetting agent. Control treatments contained distilled water plus 0.2% Triton Ag-98. Dilutions were poured into 36-ml clear plastic cups and poured back into the original beaker after 10 s. The cups had an inner surface area of 50 cm^2. Treated cups were inverted on a wire rack inside a ventilated hood for 2 h to dry. We estimated that 95 ± 4.0 mg of solution (n = 10) was deposited on the inner surface of each cup by weighing the cups before and immediately after treatment with a 0.2% solution of Triton Ag-98.

Unanesthetized insects set up in untreated cups 24 h earlier were gently introduced into the treated cups. These cups were then covered with an untreated square of organdy and capped with plastic snap-top lid, the center portion removed. A single drop of honey was placed in the center of the organdy, and the cup was inverted on a wire screen.

All tests were conducted in an environmental chamber at 24°C under constant light. Mortality was recorded at 24 and 48 h. Parasitoids not moving legs and antennae were scored as dead. On a given date, a series of five or six concentrations plus an untreated control were tested; each concentration was replicated four times, with five individuals per replicate. Experiments were done with ≈120 females per test date. Tests were repeated on at least two different dates (except HO tested with per-

Table 1. Toxicity of oxamyl and methomyl to *D. begini* females

Population[a]	n	Slope ± SE	LC_{50} (95% CL)[b]	Resistance ratios[c]
		Oxamyl		
PO	210	2.3 ± 0.3	280 (210–400)c	10
HO	240	2.0 ± 0.3	570 (430–830)d	20
GH	229	2.6 ± 0.3	420 (350–510)cd	15
MO	214	1.8 ± 0.3	68 (46–96)b	2.4
CA	332	3.1 ± 0.4	28 (22–34)a	1.0
		Methomyl		
PO	259	2.6 ± 0.4	130 (110–170)b	16
HO	239	3.2 ± 0.4	120 (95–150)b	15
GH	240	3.0 ± 0.4	180 (130–260)b	21
MO	217	2.8 ± 0.4	15 (11–20)a	1.9
CA	246	2.3 ± 0.3	8.4 (6.0–12)a	1.0

[a] PO, Poamoho, Oahu; HO, Hawaii Kai, Oahu; GH, Glenwood, Hawaii; MO, Manoa, Oahu; CA, California.
[b] Mg (AI) per liter. LC_{50}'s followed by the same letter are not significantly different based on overlap of 95% CL.
[c] LC_{50} of a population divided by LC_{50} of most susceptible population (CA).

Table 2. Toxicity of fenvalerate and permethrin to *D. begini* females

Population[a]	n	Slope ± SE	LC_{50} (95% FL)[b]	Resistance ratios[c]
		Fenvalerate		
PO	193	1.9 ± 0.5	5,700 (4,000–16,000)d	14
HO	340	2.9 ± 0.4	3,100 (2,700–3,700)c	7.8
GH	240	1.8 ± 0.3	6,900 (5,000–11,000)d	17
MO	298	1.7 ± 0.2	1,400 (1,000–1,900)b	3.5
CA	227	2.7 ± 0.5	400 (240–580)a	1.0
		Permethrin		
PO	239	2.9 ± 0.4	1,100 (850–1,300)b	5.8
HO	120	2.5 ± 0.4	620 (200–2,300)abc	3.3
GH	240	3.2 ± 0.4	2,400 (2,000–2,900)c	13
CA	290	1.6 ± 0.2	190 (130–310)a	1.0

[a] PO, Poamoho, Oahu; HO, Hawaii Kai, Oahu; GH, Glenwood, Hawaii; MO, Manoa, Oahu; CA, California.
[b] Mg (AI) per liter. LC_{50}'s followed by the same letter are not significantly different based on overlap of 95% CL.
[c] LC_{50} of a population divided by LC_{50} of most susceptible population (CA).

methrin), with data pooled across dates for the analysis. The MO population was not tested with permethrin because of the limited number of parasitoids.

Host Plant Effects. To determine if host plants influenced insecticide susceptibility, *D. begini* were reared for one generation in the laboratory on chrysanthemum and bean before conducting the bioassays. Bean leaves from PO infested with *Liriomyza* were collected and dried as described previously. Parasitoids emerging from these leaves were released into a Plexiglas-topped wooden cage (122 cm long, 61 cm wide, and 43 cm high) containing 12-d-old beans ('Henderson Bush') grown in vermiculite or 25–30 cm tall chrysanthemums ('Florida Marble' and 'Iceberg') grown in a 50:50 mixture of potting soil and vermiculite. These plants, infested with late second- or early third-instar *L. trifolii*, were exposed to *D. begini* for 24 h. The plants were then removed and kept in holding cages for 7 d to allow the parasitoids to develop. The mined leaves were then pinched and placed in drying boxes (≈17 by 16 by 8 cm) on wire racks for 3–4 d before they were transferred to emergence cartons. Parasitoids 1–4 d old were used in the bioassays. Individuals were exposed to fenvalerate using methods identical to those described for field-collected *D. begini*. Because of an extreme male-biased sex ratio, only male *D. begini* were available for use in the tests for host plant effects.

Analysis. Concentration–mortality data were analyzed with the probit option of POLO-PC (LeOra Software 1987). Control mortality was always <3%. LC_{50}'s were compared among populations to determine intraspecific variability. Differences were considered significant if 95% CL for the LC_{50}'s did not overlap. Resistance ratios were calculated for each insecticide by dividing the LC_{50} of each field population by the LC_{50} of the most susceptible population. LC_{50} and resistance ratio data were rounded to two significant digits.

Results

Susceptibility Differences Between Populations. The CA and MO populations had significantly lower LC_{50}'s than the three sprayed populations (PO, HO, and GH) for methomyl, oxamyl, and fenvalerate. The CA population was the most susceptible to all four insecticides (Tables 1 and 2).

The maximum LC_{50} for oxamyl (HO, 570 mg [AI] per liter) was 20 times higher than the LC_{50} for CA and 8 times higher than the LC_{50} for MO. The maximum LC_{50} for methomyl (GH, 180 mg [AI] per liter) was 21 times higher than the LC_{50} for the CA strain and 12 times higher than the LC_{50} for MO. The maximum LC_{50} for fenvalerate (GH, 6,900 mg [AI] per liter) was 17 times greater than the LC_{50} for the CA strain and five times higher than the LC_{50} for MO. The second highest LC_{50} for fenvalerate (PO, 5,700 mg [AI] per liter) was 14 times greater than the LC_{50} for the CA strain. The maximum LC_{50} for permethrin (GH, 2,400 mg [AI] per liter) was 13 times higher than the CA strain.

Comparisons with Field Rates. All five populations of *D. begini* had LC_{50}'s below the field rates for both oxamyl (1,200 mg [AI] per liter) and methomyl (1,080 mg [AI] per liter). For fenvalerate, all five populations had LC_{50}'s above the field rate of 240 mg (AI) per liter. For permethrin, only one population (CA) had an LC_{50} below the field rate (240 mg [AI] per liter). LC_{50}'s for GH were 29 times higher than the field rate for fenvalerate and 10 times higher than the field rate for permethrin. For the MO and CA populations, LC_{50}'s for fenvalerate were 5.7 and 1.7 times higher than the field rate, respectively.

Comparisons Among Insecticides. The trend in toxicity among insecticides was methomyl > oxamyl > permethrin > fenvalerate (Tables 1 and 2). All populations tested had lower LC_{50}'s for methomyl than oxamyl and lower LC_{50}'s for permethrin and fenvalerate. For the susceptible CA population, the relative toxicities at LC_{50} were 1:2:14:50 for fenvalerate, permethrin, oxamyl, and methomyl, respectively; methomyl had 50 times greater toxicity than fenvalerate. For the resistant GH population, the relative toxicities at LC_{50} were 1:3:16:39 for fenvalerate, permethrin, oxamyl, and methomyl, respectively.

Host Plant Effects. No significant differences in LC_{50}'s for fenvalerate were found between field *D. begini* from bean at PO and *D. begini* from bean at PO reared for one generation in the laboratory on *L. trifolii* on chrysanthemum or 'Henderson Bush' bean before testing (Table 3).

Table 3. Toxicity of fenvalerate to *D. begini* males from Poamoho, Oahu (PO) reared from *Liriomyza* spp. on different host plants

Host	*n*	Slope ± SE	LC_{50} (95% CL)
Chrysanthemum (F_1)[a,b]	120	1.2 ± 0.3	480 (260–1,000)a
Henderson bush bean (F_1)[a,b]	120	1.8 ± 0.4	350 (180–530)a
Long bean (field)[c]	598	1.1 ± 0.1	440 (310–640)a

LC_{50}'s followed by the same letter are not significantly different based on overlap of 95% CL.
[a] Original field collection from long bean.
[b] *Liriomyza trifolii.*
[c] *Liriomyza* spp.

Discussion

Susceptibility Differences Between Populations. Three heavily treated populations of *D. begini* (PO, HO, and GH) were more resistant than one untreated population (MO) and one population with an unknown spray history (CA). The Hawaii data support the hypothesis that variation in treatment history caused differences in susceptibility. Large differences occurred between populations on Oahu separated by <50 km (distance from MO to PO) and by <16 km (distance from MO to HO), which suggests that local variation in selection was an important parameter. Similar effects of treatment history on geographical patterns of resistance have also been reported for *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae), a parasitoid of citrus scale (Rosenheim & Hoy 1986) and several pests (e.g., Tabashnik et al. 1987, 1990).

Exposure of *D. begini* to methomyl and oxamyl has been considerable in Hawaii. Methomyl, a broad-spectrum insecticide, is one of the principal materials used to control lepidopterous pests such as the tomato fruitworm, *Helicoverpa zea* (Boddie) and the tomato pinworm, *Keiferia lycopersicella* (Walsingham). Oxamyl, also a broad spectrum insecticide, has been used for aphid, whitefly, and leafminer control on vegetables in Hawaii for about 10 yr (Mau 1983; M.W.J., unpublished data).

Fenvalerate and permethrin have been used extensively on the United States mainland, but their use on vegetables in Hawaii was limited until 1984 (Mason et al. 1987). Thus, direct selection of *D. begini* by pyrethroids in Hawaii has probably occurred during the past 5 yr. Cross-resistance may have developed from prior use of chlorinated hydrocarbon insecticides such as DDT (Farnham & Sawicki 1976, Vijverberg et al. 1982).

The maximum resistance ratios for *D. begini* (20 for oxamyl, 21 for methomyl, 17 for fenvalerate, and 13 for permethrin) are among the highest recorded for any parasitoid species. Maximum insecticide resistance ratios for seven Hymenoptera parasitoids reviewed by Tabashnik & Johnson (in press) were <8 in 12 of 13 cases (median, 3.1; 2–12 populations tested per pesticide–species combination). An exceptional case was 66-fold resistance to methidathion in a field population of *Comperiella bifasciata* Howard (Hymenoptera: Encyrtidae) relative to a laboratory strain of the same species (Schoonees & Giliomee 1982). However, LC_{50}'s for two populations of this resistant parasitoid were 12 and 18 times below the recommended field rate. In contrast, LC_{50}'s for resistant *D. begini* were 29- and 10-fold higher than the field application rates for fenvalerate and permethrin, respectively. These data provide one of the few examples of a hymenopterous parasitoid surviving field rates of an insecticide in a laboratory bioassay.

Relative Insecticide Toxicity. Our laboratory bioassays indicated that methomyl was highly toxic to *D. begini* compared with oxamyl, permethrin, and fenvalerate. These data are consistent with results from previous field studies (Oatman & Kennedy 1976; Johnson et al. 1980a,b). Oatman & Kennedy (1976) reported that methomyl induced leafminer outbreaks because of adverse effects on *D. begini* and ineffectiveness against *Liriomyza sativae.* Johnson et al. (1980a,b) found that all rates of methomyl applied to tomatoes resulted in an increase in leafminer densities and reduced populations of *D. begini.* High tolerance of *D. begini* to fenvalerate and permethrin is consistent with tolerance to pyrethroids in other hymenopterous parasitoids (Plapp & Vinson 1977, Waddill 1978, Mason & Johnson 1988).

Host Plant Effect. The results suggest that differences in susceptibility among populations were probably caused by variation in insecticide treatment history and were not related to host plant (Table 3).

Conclusions. Our data strongly suggest that *D. begini* in the field has developed resistance to at least two pyrethroids and significant resistance to two oxime carbamates in Hawaii in response to selection with insecticides. It has been hypothesized that parasitoids are slow to evolve resistance because they starve or emigrate because of lack of hosts following insecticide treatments (Huffaker 1971, Georghiou 1972). In contrast, *Liriomyza* spp.

in Hawaii have developed resistance (Mason et al. 1987) and persist at high densities following treatments. Furthermore, *Liriomyza* spp. are indirect pests, and high densities are acceptable to most growers. Several other factors that may promote resistance in *D. begini* in Hawaii include the isolation of the Hawaiian islands, isolation of farms within the Hawaiian archipelago, and year-round insecticide spraying. Because of their exceptional ability to survive field rates of permethrin and fenvalerate and lower rates of oxamyl and methomyl, resistant strains of *D. begini* may be useful for controlling *Liriomyza* spp. leafminers in management programs that integrate biological and chemical techniques.

Acknowledgment

We thank M. P. Parrella and K. M. Heinz (University of California, Davis) for providing *Diglyphus begini* from their California culture. We are grateful to J. F. Brunner (Washington State University) and T. F. Watson (University of Arizona) for earlier reviews of this paper. Special thanks go to L. Oride and L. Caprio for technical assistance. Yoder Brothers of Barberton, Ohio, supplied the chrysanthemum plants. This work was supported by the USDA under CSRS Special Grant 88-34135-3600 managed by the Pacific Basin Advisory Group. This is Journal Series 3428 of the Hawaii Institute of Tropical Agriculture and Human Resources Journal Series.

References Cited

Allen, W. W. & C. A. Charlton. 1981. The biology of *Diglyphus begini* and its performance in caged releases on chrysanthemums, pp. 75–81. *In* D. J. Shuster [ed.], Proceedings Institute of Food and Agricultural Sciences-Industry conference on biological control of *Liriomyza* leafminers. Lake Buena Vista, Fla.

Croft, B. A. 1990. Pesticide resistance documentation, pp. 357–381. *In* B. A. Croft [ed.], Arthropod biological control agents and pesticides. Wiley-Interscience, New York.

Croft, B. A. & K. Strickler. 1983. Natural enemy resistance to pesticides; documentation, characterization, theory and application, pp. 669–702. *In* G. P. Georghiou & T. Saito [eds.], Pest resistance to pesticides. Plenum, New York.

Farnham, A. M. & R. M. Sawicki. 1976. Development of resistance to pyrethroids in insects resistant to other insecticides. Pestic. Sci. 7: 278–282.

Funasaki, G. Y., P. Y. Lai, L. M. Nakahara, J. W. Beardsley & A. K. Ota. 1988. A review of biological control introductions in Hawaii: 1890 to 1985. Proc. Hawaii. Entomol. Soc. 18: 105–160.

Georghiou, G. P. 1972. The evolution of resistance to pesticides. Annu. Rev. Ecol. Syst. 3: 133–168.

1986. The magnitude of the resistance problem, pp. 14–43. *In* National Research Council, Pesticide resistance: strategies and tactics for management. National Academy of Sciences, Washington, D.C.

Hara, A. H. 1986. Effects of certain insecticides on *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae) and its parasitoids on chrysanthemums in Hawaii. Proc. Hawaii. Entomol. Soc. 26: 65–70.

Hoy, M. A. In press. Pesticide resistance in arthropod natural enemies: variability and selection. *In* R. T. Roush & B. E. Tabashnik [eds.], Pesticide resistance in arthropods. Chapman & Hall, London.

Huffaker, C. B. 1971. The ecology of pesticide interference with insect populations, pp. 92–107. *In* J. E. Swift [ed.], Agricultural chemicals—harmony or discord for food people environment. University of California Division of Agricultural Sciences Publications, Berkeley.

Johnson, M. W. 1987. Parasitization of *Liriomyza* spp. infesting commercial watermelon planting in Hawaii. J. Econ. Entomol. 80: 56–61.

Johnson, M. W., E. R. Oatman & J. R. Wyman. 1980a. Natural control of *Liriomyza sativae* in pole tomatoes in southern California. J. Econ. Entomol. 73: 193–198.

1980b. Effects of insecticides on populations of the vegetable leafminer and associated parasites on summer pole tomatoes. J. Econ. Entomol. 73: 61–66.

Keil, C. B., M. P. Parrella & J. G. Morse. 1985. A method for establishing base-line insecticide resistance data for *Liriomyza trifolii* and other Agromyzidae. J. Econ. Entomol. 78: 419–422.

LeOra Software. 1987. POLO-PC. A user's guide to Probit Or LOgit analysis. Berkeley, Calif.

Mason, G. A. & M. W. Johnson. 1988. Tolerance to permethrin and fenvalerate in hymenopterous parasitoids associated with *Liriomyza* spp. (Diptera: Agromyzidae). J. Econ. Entomol. 81: 123–126.

Mason, G. A., M. W. Johnson & B. E. Tabashnik. 1987. Susceptibility of *Liriomyza sativae* and *L. trifolii* (Diptera: Agromyzidae) to permethrin and fenvalerate. J. Econ. Entomol. 80: 1262–1266.

Mason, G. A., B. E. Tabashnik & M. W. Johnson. 1989. Effects of biological and operational factors on evolution of insecticide resistance in *Liriomyza* (Diptera: Agromyzidae). J. Econ. Entomol. 82: 368–373.

Mau, R. F. 1983. Tomato insecticide guide for commercial producers. Hawaii Institute of Tropical Agriculture and Human Resources Brief 042.

Mothershead, P. D. 1978. An evaluation of the effectiveness of established and recently introduced parasites on *Liriomyza* on Oahu, Honolulu. M.S. thesis, University of Hawaii, Honolulu.

Oatman, E. R. 1959. Natural control studies of the melon leafminer, *Liriomyza pictella* (Thompson). J. Econ. Entomol. 52: 895–898.

Oatman, E. R. & G. G. Kennedy. 1976. Methomyl induced outbreaks of *Liriomyza sativae* on tomato. J. Econ. Entomol. 69: 667–668.

Parrella, M. P. 1987. Biology of *Liriomyza*. Annu. Rev. Entomol. 32: 201–224.

Parrella, M. P., C. B. Keil & J. G. Morse. 1984. Insecticide resistance in *Liriomyza trifolii*. Calif. Agric. 38(1 & 2): 22–23.

Plapp, F. W., Jr., & S. B. Vinson. 1977. Comparative toxicities of some insecticides to the tobacco budworm and its ichneumonid parasitoid, *Campoletis sonorensis*. Environ. Entomol. 6: 381–384.

Rosenheim, J. A. & M. A. Hoy. 1986. Intraspecific variation in levels of pesticide resistance in field populations of a parasitoid, *Aphytis melinus* (Hymenoptera: Aphelinidae): the role of past selection pressures. J. Econ. Entomol. 79: 1161–1173.

Schoonees, J. & J. H. Giliomee. 1982. The toxicity of methidathion to parasitoids of red scale, *Aonidiella aurantii* (Hemiptera: Diaspididae). J. Entomol. Soc. S. Afr. 45: 261–273.

Tabashnik, B. E. & M. W. Johnson. In press. Evolution of pesticide resistance in natural enemies. *In* T. Fisher [ed.], Principles and application of biological control. Univ. Calif. Press, Berkeley.

Tabashnik, B. E., N. L. Cushing & M. W. Johnson. 1987. Diamondback moth (Lepidoptera: Plutellidae) resistance to insecticides in Hawaii: intra-island variation and cross-resistance. J. Econ. Entomol. 80: 1091–1099.

Tabashnik, B. E., B. A. Croft & J. A. Rosenheim. 1990. Spatial scale of fenvalerate resistance in pear psylla (Homoptera: Psyllidae) and its relationship to treatment history. J. Econ. Entomol. 83: 1177–1183.

Timberlake, P. H. 1923. Records of the introduced and imigrant chalcid flies of the Hawaiian islands (Hymenoptera). Proc. Hawaii. Entomol. Soc. 5: 418–449.

Vijverberg, H. P. M., J. M. van der Zalm & J. van den Berken. 1982. Similar mode of action of pyrethroids and DDT on sodium channel gating in mylinated nerves. Nature 295: 601–603.

Waddill, V. H. 1978. Contact toxicity of four synthetic pyrethroids and methomyl to some adult insect parasitoids. Fla. Entomol. 61: 27–30.

Received for publication 29 November 1989; accepted 11 May 1990.