

Effects of Pyriproxyfen on Three Species of *Encarsia* (Hymenoptera: Aphelinidae), Endoparasitoids of *Bemisia argentifolii* (Homoptera: Aleyrodidae)

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ABSTRACT Effects of the phenoxy juvenile hormone analog pyriproxyfen were evaluated in the laboratory on larvae, pupae, and adults of the endoparasitoids *Encarsia pergandiella* Howard, *E. transvena* (Timberlake), and *E. formosa* Gahan, as well as on their host, *Bemisia argentifolii* Bellows & Perring. Although *B. argentifolii* nymphs reared on sweet potato leaves and treated as 1st, 2nd, or 3rd instars with pyriproxyfen developed to the pupal stage, <5% adult emergence was observed. However, when treated in the 4th instar, adult emergence was $\geq 70\%$, and when treated as pupae, $\geq 97\%$. Of the 3 parasitoids tested, pyriproxyfen was least harmful to *E. pergandiella* and most deleterious to *E. formosa*. Concentrations of 1.00, 0.05, and 0.01 mg (AI)/liter applied to whitefly nymphs 6.5 d after parasitization caused significant reduction in subsequent adult emergence of *E. formosa* at the greatest rate, but not of *E. pergandiella*. Effects of treatment of whitefly nymphs containing *E. formosa* pupae (11.4 d after parasitization) were even more striking—73.5 and 44.6% reduction in emergence at the 2 highest rates, with wing deformations observed in a large proportion of emerging adults. Development time of all 3 *Encarsia* species was increased significantly by exposure to pyriproxyfen shortly after oviposition, and parasitization of *B. argentifolii* by *E. formosa* adults treated as larvae was reduced 21.4–56.8% compared with untreated parasitoids. However, residues of 2 higher rates reduced the progeny by 30.7–42.3% and rate of emergence by 11.2–27.6% with *E. formosa*, and to a lesser extent the progeny by 21.7–29.3% and adult emergence by 3.2–11.0% of *E. transvena*. Thus, pyriproxyfen proved to be effective against *B. argentifolii*, safe to *E. pergandiella*, and relatively safe to *E. transvena*, but relatively toxic to *E. formosa*, especially pupae.

KEY WORDS *Encarsia* spp., *Bemisia argentifolii*, *Bemisia tabaci*, insect growth regulator, biological control

Bemisia argentifolii Bellows & Perring, formerly known as sweetpotato whitefly, *B. tabaci* (Gennadius) strain 'B', continues to be one of the most important insect pests of vegetable crops and cotton in the southern United States and many other countries. Economic loss in the United States was estimated to be >\$500 million in 1992, and >\$142 million in Florida (Perring et al. 1993). Although insecticides are used widely to control *B. argentifolii*, the potential of biological control to reduce whitefly populations through colonization from surrounding habitat (Stanly et al. 1994) or inundative release (Parrella et al. 1992) has been demonstrated. This potential might be integrated into conventionally managed systems by substituting broad-spectrum insecticides with selective materials that interfere only minimally with the activities of the most effective natural enemies.

Insect growth regulators (IGRs) have been used extensively in management of *Bemisia* on cotton in Israel (Ishaaya and Horowitz 1992, Horowitz and Ishaaya 1994). One of these, buprofezin with chitin

synthesis inhibitory activity, has been shown to be relatively innocuous to *Eretmocerus* sp. and *Encarsia luteola* Howard, endoparasitoids of *B. tabaci* (Gerling and Sinai 1994). Pyriproxyfen is a juvenile hormone analog with relatively low mammalian toxicity (Yokoyama and Miller 1991) that was first registered in Japan in 1991 for controlling public health pests (Miyamoto et al. 1993). The utility of pyriproxyfen in whitefly management was demonstrated based on suppression of embryogenesis and adult formation in *B. tabaci* (Ishaaya and Horowitz 1992) and *Trialeurodes vaporariorum* (Westwood) (Ishaaya et al. 1994). McMullen (1990) found that pyriproxyfen was safe to predators of pear psylla, *Cacopsylla pyricola* Foerster, such as *Anthocoris antevoles* White, *A. nemoralis* (F.), *Deraeocoris verbasci* Uhler, *Campylomma verbasci* (Meyer-Dür), and *Chrysopa* spp. However, pyriproxyfen at 12.5 mg (AI)/liter inhibited growth and development of *Cryptochaetum iceryae* Williston, a parasitoid fly of cottony cushion scale, *Icerya purchasi* Maskell, and caused total suppression of egg hatch

of *Elatophilus hebraicus* Pericart, a predator of *Matsucoccus josephi* Bodenheimer & Harpaz (Mendel et al. 1994). Some economically important coccinellid biological control agents have also been found to be highly sensitive to pyriproxyfen (Hattingh and Tate 1995). Pyriproxyfen was considered "very harmful" to pupae, and "slightly harmful" to adults of *E. formosa* in the Koppert Side Effect List (Anonymous 1995).

Our objectives were to evaluate insecticidal activity of pyriproxyfen on *B. argentifolii*, and compatibility of this insect growth regulator with some principal parasitoids of the whitefly in the genus *Encarsia*.

Materials and Methods

***Bemisia argentifolii* Culture.** *B. argentifolii* was obtained originally from D. J. Schuster (University of Florida, Bradenton) in 1990, and was identified as *B. tabaci* biotype 'B' in 1992 and as *B. argentifolii* in 1994. The colony has been maintained since then in a greenhouse culture on various potted host plants including the following: collard, *Brassica oleracea* L. variety *acephala*, 'Georgia LS'; hibiscus, *Hibiscus rosa-sinensis* L., 'Brilliant Red'; salvia, *Salvia splendens* L.; and sweet potato, *Ipomoea batata* (L.) Lam., 'Carolina Bunch'. Plants were grown singly in 15-cm pots in Metro-Mix 300 growing medium (Grace-Sierra, Horticultural Products, Milpitas, CA) and watered weekly with 0.1% (wt:vol) of Stern's Miracle-Gro (N:P:K, 15:30:15) (Stern's Miracle-Gro Products, Port Washington, NY).

***Encarsia* spp. Culture.** *Encarsia pergandiella* Howard (identified by G. A. Evans, University of Florida, Gainesville) was initially obtained from the whitefly colony that had been parasitized from natural sources in 1993, and later maintained in 60-cm³ wood frame cages enclosed with 52-mesh Lumite polyethylene screen (Chicopee, Gainesville, GA). *Encarsia transvena* (Timberlake) from the surrounding environment displaced *E. pergandiella* in the greenhouse colony in 1995 and was subsequently maintained in the same type of wooden cages. *Encarsia formosa* Gahan was provided by J. Nelson (University of California, Davis) from a greenhouse colony of *B. argentifolii* on poinsettia (*Euphorbia pulcherrima* Wild.), and also was maintained on *B. argentifolii* in wood frame cages. Voucher specimens of parasitoids and whiteflies were deposited in the insect collection at Southwest Florida Research and Education Center, University of Florida at Immokalee.

Individual sweet potato leaf cuttings were used as hosts for *B. argentifolii* in all experiments. Leaves were cut from the vine and the petiole inserted into root cubes (3.75 cm³, OASIS Growing Medium, Smithers-Oasis, Kent, OH), then placed in plastic trays (T. O. Plastics, Minneapolis, MN; 52 by 26 by 6 cm) into which water and fertilizer (0.1% Miracle-Gro) were added once a week. Ex-

periments were conducted in an air-conditioned insectary at 26.7 ± 2°C, 55 ± 5% RH, and a photoperiod of 14:10 (L:D) h. Light intensity was measured as photosynthetically active radiation at 39–44 μmol m⁻² s⁻¹ inside cages (Steady State Porometer, Model LI-1600, LI-COR, Lincoln, NE).

Whitefly Cohorts. Sweet potato leaves were placed in 0.9-liter clear plastic cups, each with an opening (9 cm diameter) opening on top screened with nylon organdy and a corked access hole (1.2 cm diameter) on the side. Whitefly adults aspirated from the greenhouse colony were introduced for oviposition periods of 24 h (whitefly experiments) or 12 h (parasitoid experiments). Cohorts were inspected daily until desired stages had been obtained—6 d for 1st instar, 9 d for 2nd instar, 11 d for early 3rd instar (appropriate for parasitization), 15 d for 4th instar, and 18 d for pupae (red-eyed nymphs).

Effects on *B. argentifolii*. Pyriproxyfen (S-56716, 0.83 EC; Sumitomo, Osaka, Japan) was used in all experiments at 3 concentrations of 1.00, 0.05, and 0.01 mg (AI)/liter with water (reversed osmosis, 7 ppm solid) as control. The 2 lower concentrations were chosen on either side of the 0.04-mg (AI)/liter rate reported by Ishaaya and Horowitz (1992) to cause 91% suppression of adult development when applied to 2nd and 3rd instars of *B. tabaci*. An additional rate of 1.00 mg (AI)/liter was included to test for possible effects of high concentrations on parasitoids.

Leaves containing appropriate whitefly cohorts were dipped in the 3 pyriproxyfen dilutions or water control for 5 s and allowed to air dry for 1 h. Leaves were reconfined in the cup cages for incubation in the insectary and evaluated for adult emergence after all live whiteflies had emerged. Each treatment for each stage had 10 single-leaf replicates.

Parasitoid Cohorts. Sweet potato leaves infested with 3rd instar whitefly (11 d old) cohorts were placed into cup cages. Ten parasitoid females (plus 2–3 males in the case of *E. pergandiella* and *E. transvena*), collected with an aspirator from greenhouse and insectary colonies, were placed into each cup cage for a 24-h oviposition period. Adult wasps were removed, and parasitoid cohorts were allowed to develop into appropriate stages for treatments.

Treatment of Parasitoid Larvae. Parasitoid cohorts were incubated for 6 d after removal of adult wasps and examined under a stereoscopic microscope to identify 20 parasitized whitefly nymphs containing 2nd- or 3rd-instar parasitoid larvae that were circled with an india ink pen on each of 8 leaves per treatment per parasitoid species. Leaves were dipped for 5 s in dilutions of 1.00, 0.05, and 0.01 mg (AI)/liter pyriproxyfen or a water control, air dried for 2 h, and individually confined in cup cages. Newly emerged parasitoids were removed to prevent possible mortality of remaining pupae through host feeding

Table 1. Percentage (mean \pm SE) emergence of *B. argentifolii* on sweetpotato leaves following treatment by dipping different stages in various pyriproxyfen concentrations

Rate, mg (AI)/ liter	1st instars		2nd instars		3rd instars		4th instars		Pupae	
	n	Emergence	n	Emergence	n	Emergence	n	Emergence	n	Emergence
1.00	1,249	0.0 \pm 0.0Bc	1,054	0.0 \pm 0.0Bc	1,179	1.2 \pm 0.8Cc	1,503	70.0 \pm 2.5Cb	1,456	98.0 \pm 0.6Aa
0.05	887	0.0 \pm 0.0Bc	1,021	0.0 \pm 0.0Bc	1,176	1.7 \pm 0.5BCc	1,534	69.1 \pm 3.5Cb	1,476	98.7 \pm 0.4Aa
0.01	1,098	0.0 \pm 0.0Bd	622	0.0 \pm 0.0Bd	1,106	3.1 \pm 2.6Bc	1,204	79.5 \pm 1.4Bb	1,439	98.4 \pm 0.3Aa
Water	1,793	93.1 \pm 1.2Ab	773	95.1 \pm 1.2Aab	1,505	98.4 \pm 0.5Aa	1,270	96.4 \pm 1.2Aab	1,499	97.7 \pm 0.5Aab

Values in the same column with the same uppercase letters, and in the same row with the same lowercase letters, do not differ significantly ($P > 0.05$, LSD [SAS Institute 1988]).

and oviposition. Parasitoid emergence was evaluated 2 wk after parasitization, and emerged adults were examined for physical abnormalities with the stereoscopic microscope.

Treatment of Parasitoid Pupae. Sweetpotato leaves containing cohorts of parasitized whiteflies were monitored daily until parasitoids had pupated (11 d after removal of wasps). The leaf surface in proximity to each parasitized pupa was marked with india ink for identification, and leaves were dipped in pyriproxyfen, dried, and incubated as above. Emergence and mortality of the marked parasitoid pupae were evaluated 1 wk later by microscopic examination, and adults were examined for physical abnormalities. Each rate of pyriproxyfen was applied to 8 leaves (replicates) for each parasitoid species with 29.8 ± 2.5 (mean \pm SE; range, 17–42) pupae on each leaf.

Developmental Rate of Parasitoid Immatures. Treatments were applied 24 h after the end of the 24-h parasitization period when parasitoid eggs were 1–2 d old. Leaves bearing parasitized whitefly nymphs were immersed in the 3 pyriproxyfen dilutions or water control for 5 s, air dried, and incubated as above. When the parasitoid larvae became visible through the whitefly cuticle (usually 7 d after parasitization), 20 parasitized nymphs were identified on each leaf with india ink dots on the nearby leaf surface. Parasitized nymphs were examined daily with the stereoscopic microscope until all parasitoids either died or emerged. There were 4 replicates (leaves), or a total of 80 parasitized nymphs for each treatment \times parasitoid combination.

Treatment of Parasitoid Adults. Sufficient *E. pergandiella* were not available, so only *E. formosa* and *E. transvena* were used for this experiment. Parasitoid adults were confined to the abaxial leaf surface in clip cages made from a 12-ml polystyrene medicine cup on which the bottom (2.5 cm diameter) had been replaced with a 60-mesh plastic screen. A metal hair clip was glued to the cup and held the mouth (4.0 cm diameter) in contact with the leaf surface. A cohort of whitefly eggs was established by introducing 60 whitefly adults (sex undetermined) from the greenhouse culture into each clip cage for a 24-h oviposition period. Whitefly adults were removed, and ≈ 150 nymphs were allowed to develop within each clip cage for 11 d (early 3rd instar). Leaves were dipped in 1 of 3 concentrations of pyriproxyfen for 5 s, and air dried for 4 h. Female parasitoids (15–18) (plus 2–3 males of *E. transvena*) were introduced into each clip-on cage, and mortality was evaluated 24 h later. Whitefly nymphs were recaged, and parasitization and emergence of parasitoid adults were recorded after 2 wk under a stereoscopic microscope. Each treatment \times parasitoid combination had 8 replicates (leaves).

Second-Generation Effects. Based on results from the experiments described above, *E. formosa* was selected as the most susceptible of the 3 spe-

Table 2. Percentage (mean \pm SE) emergence of adult *Encarsia* spp. from *B. argentifolii* treated with pyriproxyfen 6.5 d after parasitization

Rate, mg (AI)/ liter	<i>E. pergandiella</i>		<i>E. transvena</i>		<i>E. formosa</i>	
	n	Emergence	n	Emergence	n	Emergence
1.00	170	95.3 \pm 1.8a	349	89.9 \pm 5.0a	154	86.5 \pm 3.6b
0.05	167	96.4 \pm 1.4a	313	98.8 \pm 0.6a	164	94.4 \pm 1.8a
0.01	248	98.4 \pm 0.8a	212	97.4 \pm 1.3a	143	97.9 \pm 1.1a
Water	213	97.2 \pm 1.1a	248	98.0 \pm 1.1a	164	99.3 \pm 0.7a

Values in the same column with the same letter do not differ significantly ($P > 0.05$ [SAS Institute 1988]).

cies tested. A 6-d-old cohort of *E. formosa* was treated with 3 dilutions of pyriproxyfen or the water control (8 single-leaf replications each) as described above. Development was monitored daily, and 10–11 newly emerged adult females (<48 h old) were aspirated from each treatment into cup cages containing sweet potato leaves infested with ≈ 200 third-instar *B. argentifolii* each for a 24-h oviposition period. This test had 4 replications. Parasitoid emergence from the succeeding generation was recorded 3 wk later.

Data Analysis. Numbers of parasitized, unparasitized-live, and unparasitized-dead whitefly nymphs expressed as percentages in all experiments were analyzed using the general linear model (PROC GLM), and means were separated using the Fisher protected least significant difference test (LSD) (SAS Institute 1988). Percentage emergence fell between 0 and 30% in the experiment on parasitoid pupae; therefore, corresponding proportions were transformed to their arcsine $\sqrt{}$ before analysis (Gomez and Gomez 1984).

Results

Effects on *B. argentifolii*. Affected whitefly nymphs appeared to develop normally, but died in the pupal stage, turning dark and wet. Response to pyriproxyfen decreased with whitefly age at treatment—no emergence if treated as 1st and 2nd instars, $<4\%$ emergence if treated as 3rd instars, $>69\%$ emergence if treated as 4th instars, and $>98\%$ emergence if treated as pupae—which was not significantly different from the water control (Table 1). Third- and 4th-instar *B. argentifolii* exhibited significantly increased response to greater concentrations of pyriproxyfen.

Effects on Parasitoid Larvae. Emergence of *E. pergandiella* was unaffected by application of pyriproxyfen to nymphs parasitized with 6.5-d-old larvae at the tested rates, whereas emergence of *E. formosa* was reduced by the greatest (1.00 mg [AI]/liter) concentration applied (Table 2). The response of *E. transvena* appeared to be intermediate but was not significantly different from the water-treated control. Affected *E. formosa* failed to emerge, although those that did emerge appeared normal. Abortive pupae appeared normal at first but later desiccated and shrank.

Effects on Parasitoid Pupae. Pyriproxyfen produced no noticeable response in *E. pergandiella* and *E. transvena* when applied to whitefly nymphs containing pupae of these species, and parasitoids emerged normally (Table 3). In contrast, pyriproxyfen applied to the pupal stage at rates of 0.05 and 1.00 mg (AI)/liter reduced emergence of *E. formosa* by 44.6% and 73.5%, respectively, although response to 0.01 mg (AI)/liter was not significantly different from the water control. Deformed wings, particularly front wings, were observed on $\approx 40\%$ of *E. formosa* adults emerging from pupae treated with 1.00 mg (AI)/liter pyriproxyfen (Fig. 1). Aside from their inability to fly, deformed wasps behaved normally in regard to grooming, searching, probing, host-feeding, and oviposition.

Developmental Rate of Parasitoid Immatures. Significant increases in developmental period from oviposition to emergence were observed in all 3 parasitoid species tested in response to applications of pyriproxyfen made to whitefly nymphs 1 d after parasitization (Table 4). Developmental time was lengthened in response to the greatest rate by 10.2% for *E. pergandiella* and 20.7% for *E. transvena*. Increases

Table 3. Percentage (mean \pm SE) emergence of adult *Encarsia* spp. from *B. argentifolii* treated with pyriproxyfen 11.5 d after parasitization (parasitoids in pupal stage)

Rate mg (AI)/ liter	<i>E. pergandiella</i>		<i>E. transvena</i>		<i>E. formosa</i>	
	n	Emergence	n	Emergence	n	Emergence
1.00	275	97.6 \pm 1.2a	277	99.4 \pm 0.6a	327	26.5 \pm 15.4c
0.05	176	100.0 \pm 0.0a	202	100.0 \pm 0.0a	287	55.4 \pm 10.8b
0.01	239	99.7 \pm 0.2a	253	100.0 \pm 0.0a	247	94.8 \pm 1.8a
Water	143	98.6 \pm 0.8a	277	100.0 \pm 0.0a	160	100.0 \pm 0.0a

Values in the same column with the same letters do not differ significantly ($P > 0.05$, LSD [SAS Institute 1988]).

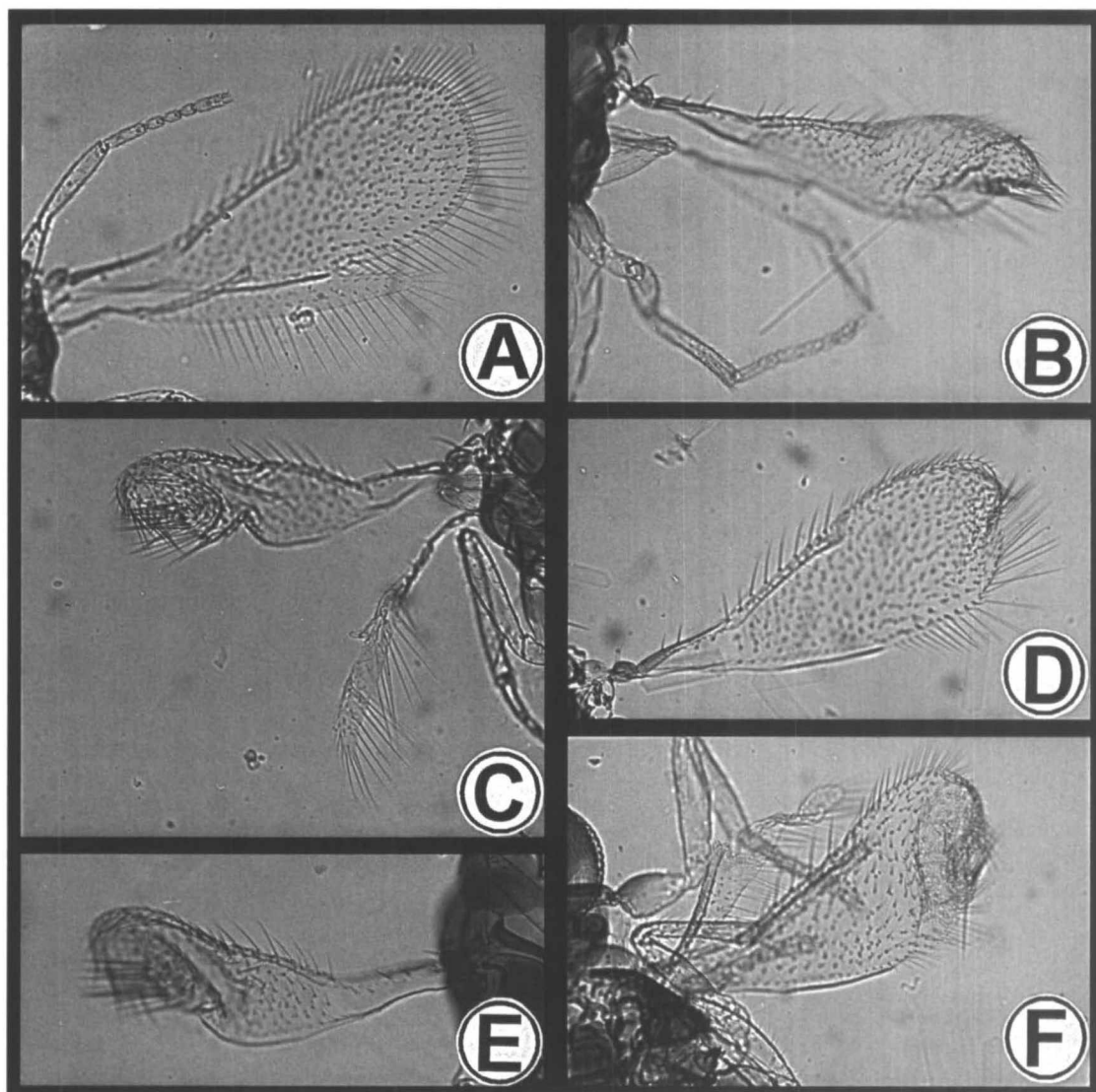


Fig. 1. Wings of female *E. formosa*. (A) Normal front wing and hind wing. (B–C) Abnormal front wing and hind wing (D–F) Abnormal front wing.

in development time of *E. pergandiella* occurred in the pupal stage, whereas pupal stage, egg, and larval stages of *E. transvena* and *E. formosa* were lengthened. Mortality was low for all treatments, ranging from 0 to 2 individuals within each species \times treatment group, with no obvious trends among species or treatments.

Effects on Parasitoid Adults. No statistically significant mortality of adult *E. transvena* and *E. formosa* was observed in response to contact with residues of pyriproxyfen. However, these data suggested a low-level response, especially by *E. formosa* (Table 5).

Unexposed wasps successfully parasitized more whitefly nymphs than exposed wasps, significantly so in the case of *E. formosa* ($F = 3.36$; $df = 3, 28$; $P = 0.0326$), which were more susceptible to

pyriproxyfen than *E. transvena* ($F = 3.48$; $df = 3, 28$; $P = 0.029$). Reduction of progeny per female was significantly reduced by 30.7 and 42.3% with *E. formosa* and by 21.7–29.3% for *E. transvena* in the 2 greater rates. Emergence of subsequent progeny was significantly reduced for both species—27.6% reduction for *E. formosa* at the greatest rate, and 11.0% for *E. transvena* at the same rate.

Second-Generation Effects. Parasitization of whitefly nymphs by *E. formosa* wasps treated as larvae with 1 mg (AI)/liter pyriproxyfen was significantly reduced by 58.6%, and a reduction of 48.2% was evident with the 0.05 mg (AI)/liter rate (Table 6). A 21.4% reduction at the 0.01 mg (AI)/liter rate showed the same trend although the difference was not significant. Emergence of sub-

Table 4. Effect of pyriproxyfen treatment on 3rd-instar *B. argentifolii* 1.5 d after parasitization on developmental time (d) for egg-larval and pupal stages of *Encarsia* spp.

Rate, mg (A1)/ liter	<i>E. pergandiella</i>				<i>E. transvena</i>				<i>E. fornosa</i>			
	n	Egg + larval	Pupal	Total	n	Egg + larval	Pupal	Total	n	Egg + larval	Pupal	Total
1.00	21	10.5 ± 1.3a	5.6 ± 1.2a	16.2 ± 0.2a	30	11.1 ± 0.2a	5.3 ± 0.2a	16.3 ± 0.3a	25	11.3 ± 0.1a	7.3 ± 0.2a	18.6 ± 0.3a
0.05	18	9.9 ± 0.6a	5.4 ± 0.8ab	15.3 ± 0.2b	36	10.9 ± 0.2a	4.9 ± 0.3a	15.7 ± 0.3a	41	10.3 ± 0.1b	6.7 ± 0.1b	17.1 ± 0.2b
0.01	26	10.5 ± 1.3a	5.0 ± 0.7b	15.4 ± 0.2b	27	10.8 ± 0.3a	4.8 ± 0.2a	15.6 ± 0.3a	48	9.9 ± 0.1b	6.7 ± 0.1b	16.5 ± 0.1bc
Water	15	10.7 ± 0.5a	4.0 ± 0.8c	14.7 ± 0.3c	39	9.6 ± 0.2b	3.8 ± 0.2b	13.5 ± 0.3b	48	9.8 ± 0.1b	6.4 ± 0.1b	16.3 ± 0.1c

Values in the same column followed by the same letters do not differ significantly ($P > 0.05$, LSD [SAS Institute 1988]).

Table 5. Contact toxicity of pyriproxyfen to adult females of *E. transvena* and *E. formosa* in terms of direct mortality, and subsequent parasitization and emergence rates

Rate, mg (AI)/ liter	<i>E. transvena</i>						<i>E. formosa</i>					
	% ♀ mortality			Progeny/♀			% ♀ mortality			Progeny/♀		
	n	%	% reduction	n	%	% emergence	n	%	% reduction	n	%	% emergence
1.00	112	1.8 ± 1.7a	29.3	65 ± 0.7a	80.2 ± 3.5b	11.0	106	4.1 ± 2.6a	42.3	9.4 ± 1.1b	66.7 ± 3.1c	27.6
0.05	112	0.0 ± 0.0a	21.7	7.2 ± 1.4a	88.3 ± 2.0b	3.2	106	4.0 ± 2.3a	30.7	11.3 ± 1.9b	83.7 ± 4.8b	11.2
0.01	112	0.0 ± 0.0a	16.3	7.7 ± 1.0a	88.9 ± 1.9b	2.5	110	3.8 ± 2.3a	22.1	12.7 ± 1.5ab	90.0 ± 2.6ab	4.6
Water	112	0.0 ± 0.0a	0.0	9.2 ± 0.7a	91.2 ± 2.7a	0.0	112	0.0 ± 0.0a	0.0	16.3 ± 1.7a	94.3 ± 1.3a	0.0

Values \pm SE in the same column followed by the same letters do not differ significantly ($P > 0.05$, LSD [SAS Institute 1988]).

Table 6. Parasitization of *B. argentifolii* by *E. formosa* wasps treated as larvae with pyriproxyfen

Rate, mg (AI)/liter	No. parasitoid ♀♀	No. whiteflies parasitized	Progeny per ♀	% reduction	% emergence
1.00	44	196	4.5 ± 12.1b	58.6	90.7
0.05	44	245	5.6 ± 14.9b	48.2	91.3
0.01	44	363	8.3 ± 6.8ab	21.4	93.1
Water	44	273	10.8 ± 24.9a	0.0	97.6

Progeny per ♀ (mean ± SE) followed by the same letters do not differ significantly ($P > 0.05$, LSD [SAS Institute 1988]).

sequent progeny was not significantly affected but also tended to decrease.

Discussion

There is much that we do not yet understand about the response of *Encarsia* species to pyriproxyfen. Why is uniparental *E. formosa* more sensitive to pyriproxyfen than biparental *E. pergandiella* and *E. transvena* in terms of adult development and embryogenesis? Why does toxicity increase with age of the *E. formosa* immatures at time of exposure, whereas the opposite is true of its whitefly host? The sensitivity of early instars of *Bemisia* to pyriproxyfen is shared by several species of scale insect, including California red scale, *Aonidiella aurantii* (Maskell); Florida wax scale, *Ceroplastes floridensis* Comstock; and cottony-cushion scale, *Icerya purchasi* Maskell (Peleg 1988, 1989), whereas other species, including mosquitos (Schaefer et al. 1988) and even the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Ishaaya et al. 1994), are more sensitive when treated as late instars.

In contrast to other parameters evaluated, the response to pyriproxyfen treatment 36 ± 12 h after oviposition was greatest for *E. transvena*, least for *E. pergandiella*, and intermediate for *E. formosa*. We anticipated a response for *E. pergandiella*, because females oviposit in 1st-instar *B. argentifolii* but egg eclosion or early larval development (or both) is delayed or arrested until the host reaches the 3rd instar (Liu and Stansly 1996). Could delayed development of *E. pergandiella* in 1st-instar nymphs be a response to high host titers of juvenile hormone? Perhaps *E. pergandiella* cannot make molting hormone and may depend instead on molting hormone from the host. If so, the effect might be mimicked by treatment with pyriproxyfen. However, we observed an increase development time of the egg and early larval stage in 1st-instar hosts, whereas only an increase in the pupal stage of *E. pergandiella* was observed in response to pyriproxyfen. However, both egg and larval stages of *E. transvena* and *E. formosa* were lengthened by treatment with pyriproxyfen. One factor obscuring the comparison is that treatment oc-

curred as much as 48 h after oviposition, so that many parasitoid eggs may have already matured past the point of sensitivity to pyriproxyfen at the time of application. Further research will be required to clarify the relationship between delayed development of parasitoids in young-instar hosts and in hosts treated with juvenile hormone analogue.

Despite mysteries surrounding mechanisms of pyriproxyfen selectivity, we now have better information to integrate the use of this material in conjunction with biological control of *B. argentifolii* by the 3 *Encarsia* species tested. No deleterious effects were noted on adult emergence to *E. pergandiella* or *E. transvena* at the rates applied to parasitized whitefly nymphs, although a modest lengthening of development time was observed. Also, contact toxicity to adult *E. transvena* was minimal, although some suppression of subsequent parasitization and adult emergence was noted. Therefore, pyriproxyfen could be applied with minimal deleterious effects when these 2 species are the principal natural enemies. This is a fortunate result, given that crops are currently colonized by these species from sources within the habitat. However, pyriproxyfen should not be applied when *E. formosa* is in its later stages of development. Because colonization by *E. formosa* is usually from commercial sources, parasitoid releases and pyriproxyfen applications could be coordinated to avoid deleterious effects to late-stage parasitoid immatures. However, a detrimental effect on the next generation could be expected.

Pyriproxyfen is known to be extremely persistent on citrus and highly detrimental to some coccinellid species and therefore disruptive to biological control of mealybugs and cottony cushion scale on citrus in South Africa, albeit at higher rates (30 mg [AI]/liter) than we used for whitefly control (Hattigh and Tate 1995). The *Encarsia* species we tested represent a single component of the natural enemy complex surrounding *B. argentifolii*. The net effect of foliar applications of pyriproxyfen on the entire complex must be evaluated before a general compatibility with biological control could be affirmed.

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