Effects of Age and Length of Exposure on the Reproduction of Adult Codling Moth (Lepidoptera: Tortricidae) Exposed to Surfaces Treated with Ecdysone Agonists[1]

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Abstract The effects of age and length of exposure on the fecundity and fertility of codling moth, *Cydia pomonella* (L.), exposed as adults to surfaces treated with the ecdysone agonists tebufenozide and methoxyfenozide were examined. In addition, the development and reproduction of offspring (F_1 generation) whose parents were exposed to the ecdysone agonists were investigated. The length of exposure, but not moth age, significantly affected mean moth fecundity and fertility. A 6 h exposure period to treated surfaces did not negatively affect mean fecundity and fertility. However, exposure periods of 18 h and 30 h significantly reduced mean fecundity and fertility. Despite the significant negative impacts on the reproduction of the adults (parent generation) exposed to the treated surfaces, the mean development time and fecundity of the adult offspring (F_1 generation) were not affected; however, the mean fertility of the adult offspring in the methoxyfenozide treatment was significantly reduced.

Key Words Codling moth, *Cydia pomonella,* tebufenozide, methoxyfenozide, fecundity, fertility

Tebufenozide and methoxyfenozide belong to a novel class of insect growth regulators, bisacylhydrazine ecdysteroid agonists, discovered by the Rohm and Haas Co. (Spring House, PA), that mimic natural ecdysone (20-hydroxyecdysone) and induce a premature, lethal molt (Dhadialla et al. 1998, Carlson et al. 2001). These ecdysone agonists are highly specific to lepidopterous larvae, and their effectiveness (both in laboratory and field tests) against many such economically important horticultural, agronomic and forest pests have been reported (Chandler et al. 1992, Charmillot et al. 1994, Retnakaran et al. 1997, Trisyono and Chippendale 1997, 1998). In contrast, tebufenozide is reported to be safe to several species of beneficial arthropods (Brown 1994, Biddinger and Hull 1995, Dhadialla et al. 1998, Gurr et al. 1999, Medina et al. 2003), suggesting that ecdysone agonists could play a vital role in IPM programs.

Previous studies have shown that constant adult moth exposure to surfaces treated with tebufenozide and methoxyfenozide will significantly reduce the mean fecundity and fertility in the codling moth, *Cydia pomonella* (L.), redbanded leafroller, *Argyrotaenia velutinana* (Walker), and obliquebanded leafroller, *Choristoneura rosaceana* (Harris) (Sun and Barrett 1999, Sun et al. 2000). In addition, a sublethal exposure to methoxyfenozide-treated surfaces also have been reported to negatively

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impact the ability of a male moth to respond to a calling female (Hoelscher and Barrett 2003a,b).

There is little published information about how these reported negative sublethal effects are affected by moth age and length of exposure, and to what extent these ecdysone agonist compounds would affect the offspring of treated parents. Such information is critical before these sublethal effects can be fully understood and exploited in pest management programs utilizing ecdysone agonists. Consequently, the objectives of this study were to examine (1) the effects of moth age and length of exposure on mean fecundity and fertility of adult *C. pomonella* exposed to ecdysone agonist-treated surfaces; and (2) what similar effects, if any, would be exhibited in the subsequent (F_1) generation.

Materials and Methods

Insects. Adult *C. pomonella* used in this study were obtained as pupae from a colony at the Yakima Agricultural Research Laboratory, USDA-ARS, Wapato, WA. The pupae were separated by sex and placed individually into 18 × 50 mm clear glass, shell vials that were capped with a perforated plastic lid. The vials were housed in an environmental chamber set at 24°C with a photoperiod of 16L:8D.

Chemicals and treatments. Formulated tebufenozide (RH-5992 2F), methoxyfenozide (RH-2485 80WP), and Latron B-1956® (a resin-based nonionic surfactant) were obtained from the Rohm and Haas Co. (Spring House, PA). Small volume quantities (250 ml) of 360 ppm tebufenozide and 180 ppm methoxyfenozide were prepared in water and corresponded to recommended field rates. Because field applications of tebufenozide and methoxyfenozide are recommended to include Latron B-1956 (Rohm and Haas Co., Philadelphia, PA) (or a similar spreader-sticker), a proportionate field rate of Latron B-1956 (0.125% v/v) was added to both the tebufenozide and methoxyfenozide treatment solutions. However, no Latron B-1956 was added to the water-control solution because a previous study indicated that it did not affect adult *C. pomonella* fecundity, fertility and longevity (Sun 1998).

Exposure cages. Each bioassay cage used to expose moths to treated surfaces consisted of a 10 cm long section of polyvinyl chloride (PVC) pipe, 9 cm wide, and two end lids. Each cage was lined with removable plastic-mesh screening (2 × 2 mm). The end lids consisted of thin PVC rings covered with the same plastic-mesh screening. The mesh cage liners and end lids were immersed in a treatment solution for 30 s and allowed to air-dry.

Moth age and length of exposure effects on reproduction. The experimental design consisted of three main factors and three levels within each factor: chemical treatment (tebufenozide, methoxyfenozide and water control), moth age (0 to 6 h, 18 to 24 h and 30 to 42 h), and length of exposure (6 h, 18 h and 30 h). Due to limited environmental chamber space, exposure cages and pupae, an incomplete block design was established that resulted in 36 blocks with seven (of the 27) treatments being examined in each block, each treatment being replicated nine times (Cochran and Cox 1957).

Emerged moths of the three age groups were placed by sex into the treatment exposure cages. In addition to the treated mesh liners, each cage contained 2 or 3 red delicious apple leaves that had also been dipped in the treatment solution for 30 s and allowed to air dry. After the appropriate exposure period, a female was paired with two males of the same treatment regime and placed inside a nontreated cage lined with

clear plastic transparency film that served as an oviposition surface. These cages were housed in an environmental chamber maintained at 24°C on a photoperiod of 16L:8D.

The transparency film liners were replaced every 24 h until female death. The eggs oviposited on the plastic cage liners were counted and considered as a measure of fecundity. Liners with eggs were trimmed and stored in sealed Petri dishes (90 × 20 mm) and stored in an environmental chamber maintained at 24°C on a photoperiod of 16L:8D. Fertility was determined by enumerating egg hatch. After initial eclosion the eggs in the Petri dishes were examined daily and any neonates were removed. This procedure was followed for at least 10 days after first eggs hatched.

Parental exposure effects on F_1 development and reproduction. Eggs from adult moths that had been exposed continuously to treated surfaces were obtained in the following manner. Newly-emerged virgin male and female moths (less than 48 h old) were placed randomly in treated exposure cages. Each exposure cage received 2 or 3 females and at least the same number of males. At least 10 cages were used for each treatment. The cages were placed in an environmental chamber maintained at 24°C on a photoperiod of 16L:8D.

After the adults had been exposed to the treated surfaces for at least 48 h, narrow strips of nontreated wax paper were placed in each cage to serve as oviposition sites. To measure development of the F_1 generation from egg to adult, the wax paper strips were removed every 24 h and placed in sealable plastic containers maintained in an environmental chamber (24°C, 16L:8D). The eggs were checked daily for eclosion. Within 24 h of hatching, larvae were collected and placed individually into 30-ml plastic cups containing commercial *C. pomonella* diet (Southland Products, Incorp, Lake Village, AR). Each treatment replicate consisted of at least 30 larvae monitored for development (three replicates per treatment). The cups were examined daily for larval and pupal survival and adult emergence.

To measure adult F_1 reproduction, newly-emerged moths (≤24 h old) were collected from the 30-ml cups and placed inside a cage (10 × 9 cm) lined with a clear, plastic transparency film that served as an oviposition site. Each cage (replicate) contained one female and two males that were developed from eggs oviposited by parents exposed to the same treatment surface. Each treatment had at least 10 replicates. The clear plastic liner in each cage was replaced daily, and portions of it with eggs attached were placed within sealable plastic containers kept in an environmental chamber (24°C, 16L:8D). The total number of eggs oviposited and the number of eclosed larvae for each cage replicate were recorded.

Data analysis. Mean differences in adult fecundity and fertility (both in the parent and F_1 generations), and the length of time from neonate to adult emergence were determined by an analysis of variance (ANOVA) (SAS Institute 1990). If the overall treatment F tests were significant, the treatment means were separated by the Fisher protected least significant difference (LSD) procedures (SAS Institute 1990). All data were transformed with appropriate procedures before being analyzed. Significant differences among treatments for mean percent F_1 adult eclosion were based a continuity adjusted chi-square test (SAS Institute 1990). Differences were considered statistically significant at the level of $P < 0.05$.

Results

Moth age effects on reproduction. There were no significant interactions between 'moth age' and 'treatment' regarding mean fecundity ($F = 0.98$; df = 4, 180; P

> 0.05) and fertility ($F = 0.42$; df = 4, 157; $P > 0.05$), indicating that the treatment effect on these mean reproductive parameters were not related to moth age. For the most part, there were no significant differences in mean fecundity and fertility within each treatment across the three age groups (Table 1). However, regarding differences within each age group across treatments, the ecdysone agonist treatment means were almost always significantly less than the control means, but usually not significantly different from each other (Table 1).

Exposure length effects on reproduction. There were significant interactions between 'length of exposure' and 'treatment' regarding mean fecundity ($F = 6.95$; df = 4, 180; $P = 0.0001$) and fertility ($F = 7.12$; df = 4, 157; $P = 0.0001$). This implies that the treatment effect on the mean reproductive parameters were affected by length of exposure of the moth to the chemicals. With the exception of the control, the mean fecundity and fertility levels of moths exposed to treated surfaces for 18 h and 30 h were generally significantly less than that for moths exposed for only 6 h (Table 2). In three of the four cases, the means from the 18-h exposure periods were not significantly different from the 30 h means. Regarding differences within each exposure period across treatments, there were no significant differences in mean fecundity and fertily among all treatments in the 6 h exposure period. However, during the 18-h and 30-h exposure periods, mean fecundity and fertility levels in the tebufenozide and methoxyfenozide treatments (while usually not significantly different from each other) were always significantly less than the control means (Table 2).

Parental exposure effects on F_1 development and reproduction. The mean percent of F_1 larvae (whose parents were exposed to treated surfaces for 48 h and

Table 1. Mean fecundity and percent fertility levels of adult *Cydia pomonella* exposed at different age groupings to surfaces treated with ecdysone agonists tebufenozide and methoxyfenozide

Treatment	Mean (±SE) fecundity* per moth age group**					
	n†	0-6 h	n†	18-24 h	n†	30-42 h
Control	27	101.1 ± 5.9 a	27	80.3 ± 7.3 ab	26	62.8 ± 6.8 bc
Tebufenozide	27	51.5 ± 10.3 cd	27	43.8 ± 6.6 de	27	37.8 ± 6.6 d
Methoxyfenozide	27	35.1 ± 9.3 de	27	32.3 ± 6.4 de	27	22.7 ± 6.1 e
	Mean (±SE) % fertility‡ per moth age group**					
	n§	0-6 h	n§	18-24 h	n§	30-42 h
Control	27	80.4 ± 2.4 a	26	73.6 ± 4.9 a	24	70.8 ± 4.3 ab
Tebufenozide	24	47.7 ± 7.5 c	25	60.0 ± 6.3 bc	25	59.0 ± 7.2 bc
Methoxyfenozide	19	40.0 ± 8.7 c	26	45.2 ± 7.9 c	23	39.6 ± 8.4 c

Means followed by the same letter within each column or treatment row (per reproductive parameter) are not significantly different (Fisher's protected LSD, $P < 0.05$).

* Mean number of eggs oviposited per female.

** Moth age (in hours) after emergence.

† Number of cages (replicates) per treatment per age group.

‡ The number of eggs hatched divided by the number of eggs oviposited per cage, multiplied by 100.

§ Number of eggs (replicates) where eggs were laid per treatment per age group.

Table 2. Mean fecundity and percent fertility levels of adult *Cydia pomonella* exposed for different time periods (lengths) to surfaces treated with ecdysone agonists tebufenozide and methoxyfenozide

Treatment	n†	Mean (±SE) fecundity* per exposure period** 6 h	n†	18 h	n†	30 h
Control	26	80.3 ± 6.9 ab	27	91.3 ± 7.7 a	27	73.1 ± 7.0 ab
Tebufenozide	27	75.3 ± 8.4 ab	27	33.4 ± 7.3 c	27	24.5 ± 4.3 cd
Methoxyfenozide	27	66.5 ± 9.1 b	27	12.9 ± 2.9 cd	27	10.6 ± 1.8 d
		Mean (±SE) % fertility‡ per exposure period**				
	n§	6 h	n§	18 h	n§	30 h
Control	24	83.4 ± 1.9 a	27	66.7 ± 5.2 b	26	76.2 ± 3.1 ab
Tebufenozide	26	72.7 ± 5.2 ab	23	47.8 ± 7.7 c	25	45.3 ± 6.9 c
Methozyfenozide	27	73.5 ± 5.2 ab	18	39.9 ± 8.2 c	23	6.2 ± 3.9 d

Means followed by the same letter within each column or treatment row (per reproductive parameter) are not significantly different (Fisher's protected LSD, $P < 0.05$).

* Mean number of eggs oviposited per female.

** Length of moth exposure (in hours) to treated surfaces.

† Number of cages (replicates) per treatment per exposure period.

‡ The number of eggs hatched divided by the number of eggs oviposited per cage, multiplied by 100.

§ Number of eggs (replicates) where eggs were laid per treatment per exposure period.

the F_1 eggs being deposited on nontreated wax paper strips) that eventually developed into adults from the tebufenozide and methoxyfenozide treatments were 46.4% and 49.5%, respectively (Table 3). Neither of these values were significantly different from the control mean of 44.1% adult emergence. Similarly, there were no significant differences among the treatments in the mean number of days from F_1 eggs to adult emergence and in the mean fecundity of F_1 adults. For mean fertility levels of F_1 adults, no differences were found between the control and tebufenozide treatments. However, the mean fertility level in the methoxyfenozide treatment was significantly less than the other two treatments (Table 3).

Discussion

A previous study by Sun and Barrett (1999) revealed that continuous exposure to tebufenozide- or methoxyfenozide-treated surfaces significantly reduced the fecundity and fertility of *C. pomonella.* Similarly, the negative effects of ecdysone agonists on fecundity and/or fertility have been demonstrated in other species, either through topical application or ingestion of treated diet (Monthean and Potter 1992, Carpenter and Chandler 1994, Smagghe and Degheele 1994a,b, Biddinger and Hull 1999, Sun et al. 2000). Interestingly, Knight (2000) demonstrated that reductions in the reproduction of *C. pomonella* also can occur with exposure to tebufenozide-treated surfaces for as little as 1 h. Some suggest reductions in mean fecundity among female Lepidoptera are most likely caused by the ecdysone agonists having a

Table 3. Mean percent adult eclosion, days to adult eclosion, fecundity and fertility of F_1 generation *Cydia pomonella* whose parents were exposed to surfaces treated with the ecdysone agonists tebufenozide and methoxyfenozide for 48 h and who deposited the F_1 eggs on nontreated surfaces

Treatment	n*	Mean % adult eclosion**	n*	Mean days to adult eclosion from egg hatch (±SE)†	n‡	Mean fecundity (±SE)†	n§	Mean fertility (±SE)†
Control	120	44.1 a	53	38.6 ± 0.5 a	18	99.1 ± 10.1 a	17	85.5 ± 4.5 a
Tebufenozide	125	46.4 a	58	40.1 ± 0.6 a	14	97.0 ± 9.9 a	14	84.8 ± 2.5 a
Methoxyfenozide	117	49.5 a	58	40.1 ± 0.6 a	16	94.5 ± 11.0 a	15	70.4 ± 6.0 b

* Total number of F_1 neonates evaluated.

** Total number of F_1 neonates developed to adults divided by original number evaluated, multiplied by 100. Means within column followed by the same letter are not significantly different (Continuity Adjusted Chi-square Test, $P < 0.05$).

† Means within column followed by the same letter are not significantly different (Fisher's protected LSD, $P < 0.05$).

‡ Number of cages containing F_1 generation adults (1 female and 2 males)

§ Number of cages where F_2 eggs were laid.

chemosterilizing effect, i.e., the ecdysone agonists interfere with ovulation and oviposition, perhaps through a resorption of the ovarioles (Smagghe and Degheele 1994a), or that the compounds negatively impact the expression of the ecdysone receptor (EcR), ultraspiracle protein (USP) and other proteins in the reproductive tissues (Sun et al. 2003). The decline in fertility may be caused partially by the ovicidal effect of ecdysone agonists (Trisyono and Chippendale 1997, 1998, Pons et al. 1999) or by the failure of sperm transfer during copulation (Carpenter and Chandler 1994).

For the current study, the age of the moth (0 to 6, 18 to 24 or 30 to 42 h) within each treatment did not appear to affect the mean fecundity and fertility of *C. pomonella* adults exposed to tebufenozide and methoxyfenozide. Despite the decline in mean fecundity and fertility values as the moths aged, the differences were almost always not significant. In contrast, the between-treatment comparisons within each age group usually revealed significant differences. In most cases, the mean fecundity and fertility values in the tebufenzoide and methoxyfenozide treatments (while not significantly different from each other) were significantly less than the control. These data were somewhat different from our previous study that showed a continuous exposure to treated surfaces resulted in a mean reduction in reproduction in the methoxyfenozide treatment that was significantly less than the tebudenozide treatment (Sun and Barrett 1999).

In terms of the length of moth exposure within each treatment, the fecundity and fertility means found in the 6-h exposure period of both the tebufenozide and methoxyfenozide treatments were always significantly higher than the means from the 18-h and 30-h exposure periods. The differences between the 18-h and 30-h exposure periods within each treatment were usually not significant. Among the treatments within the 6-h exposure period, there were no significant differences in mean fecundity and fertility. This contradicts the results of Knight (2000) where he reported that only a 1 h exposure by *C. pomonella* adults to a tebufenozide-treated surface significantly reduced mean fecundity and fertility.

Adult individuals from the F_1 generation (resulting from eggs that were oviposited on nontreated surfaces by parent moths exposed to treated surfaces for 48 h) did not differ significantly among all treatments in terms of mean percent adult eclosion, days to adult eclosion, and fecundity. However, the mean fertility level of the F_1 adults in the methoxyfenzoide treatment was significantly less than that of the tebufenozide and control treatments. The physiological mechanism of how methoxyfenozide, a significantly more active compound than tebufenozide (Dhadiall et al. 1998), might reduce the mean fertility in the F_1 generation is unknown.

In summary, previous work done by the authors and others have reported a significant decline in the reproduction, and attractiveness and responsiveness, of some important tortricid fruit pests when as adults they are exposed to surfaces treated with the ecdysone agonists tebufenozide and/or methoxyfenozide. The current study has demonstrated that the resulting negative reproductive effects found within each treatment were more related to the length of time the moths were exposed to the ecdysone agonists than the age at which the moths were exposed to the treatments. Also, despite the significant negative impacts on the reproduction of the adults exposed to the ecdysone-treated surfaces, the mean development and fecundity of their adult offspring were not affected; however, the mean fertility of the adult offspring in the methoxyfenzoide treatment was significantly reduced.

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