

Effect of Irradiation on Mexican Leafroller (Lepidoptera: Tortricidae) Development and Reproduction

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ABSTRACT The effects of irradiation on egg, larval, and pupal development, and adult reproduction in Mexican leafroller, *Amorbia emigratella* Busck (Lepidoptera: Tortricidae), were examined. Eggs, neonates, early instars, late instars, early pupae, and late pupae were irradiated at target doses of 60, 90, 120, or 150 Gy, or they were left untreated as controls in replicated factorial experiments. Survival to the adult stage was recorded. Tolerance to radiation increased with increasing age and developmental stage. A radiation dose of 90 Gy applied to neonates and early instars prevented adult emergence. A dose of 150 Gy was not sufficient to prevent adult emergence in late instars or pupae. The effect of irradiation on sterility was examined in late pupae and adult moths. For progeny produced by insects treated as late pupae, a total of three out of 3,130 eggs hatched at 90 Gy, 0 out of 2,900 eggs hatched at 120 Gy, and 0 out of 1,700 eggs hatched at 150 Gy. From regression analysis, the dose predicted to prevent egg hatch from the progeny of irradiated late pupae was 120 Gy, with a 95% confidence interval of 101-149 Gy. The late pupa is the most radiotolerant stage likely to occur with exported commodities; therefore, a minimum absorbed radiation dose of 149 Gy (nominally 150 Gy) has potential as a quarantine treatment. Reciprocal crosses between irradiated and unirradiated moths demonstrated that males were more radiotolerant than females. Irradiation of female moths at a target dose of 90 Gy before pairing and mating with irradiated or unirradiated males resulted in no viable eggs, whereas irradiated males paired with unirradiated females produced viable eggs at 90 and 150 Gy.

KEY WORDS *Amorbia emigratella*, quarantine pest, phytosanitary treatment, postharvest

Mexican leafroller, *Amorbia emigratella* Busck (Lepidoptera: Tortricidae), was first described from Hawaii, but it is thought to be native to Mexico and Central America (Fullaway and Krauss 1945). Mexican leafroller has a wide host range, including many ornamental plants and tropical fruit such as avocado, guava, macadamia, papaya, pineapple, and rambutan (Pena et al. 2002, McQuate et al. 2000). Damage is typically to the foliage as larvae roll the leaves and feed on leaf edges, but it may extend to the fruit surface if leaves contact the fruit or when two fruit are close together (Wysocki et al. 2002). Mexican leafroller will occasionally travel with imported commodities (e.g., papayas, cut flowers, foliage), and in some countries, it is an actionable quarantine pest. For example, Mexican leafroller is a prohibited pest on any commodity exported from the United States to Korea, and on papayas and cut foliage exported from the United States to New Zealand (J. Clapp, personal communication). Irradiation is a postharvest treatment option for exported commodities to prevent movement of viable Mexican leafrollers.

In 2006, the USDA-APHIS published a landmark rule providing generic irradiation quarantine treat-

ments for insect pests infesting fresh fruit and vegetable and other horticultural commodities (USDA-APHIS 2006, Follett and Neven 2006). The rule approved radiation doses of 150 Gy for any tephritid fruit fly and 400 Gy for all other insects except the pupa and adult stages of Lepidoptera. Generic irradiation treatments are under consideration at the International Plant Protection Convention. Exported commodities may carry the egg, larva, and pupal stages of Mexican leafroller. Before irradiation can be used as a quarantine treatment for a commodity that may carry lepidopteran pupae, specific information establishing an effective dose is needed (Hollingsworth and Follett 2007).

The objective of the study with Mexican leafroller reported here was to examine the effects of irradiation on egg, larval, and pupal development, and adult reproduction, and thereby to identify a potential quarantine treatment dose.

Materials and Methods

Insect Rearing. A laboratory colony of *A. emigratella* was started using larvae (≈ 120) collected from blueberry (*Vaccinium corymbosum* \times *V. darrowii* hybrid complex) leaves from Waimea, HI. Larvae were re-

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moved from rolled leaves and placed directly on a generic lepidopteran diet in 350-ml plastic tubs (Rubbermaid, Wooster, OH) with lids (Follett and Lower 2000). *A. emigratella* typically pupates in the diet. Emerging adults were cooled and transferred to new 350-ml plastic tubs with ventilated lids for mating. Approximately 20 adult moths (50:50 sex ratio) were transferred to each tub without diet and provided with water through a wick; also, two 28-ml plastic cups turned upside down were placed in the tubs as an oviposition substrate. Female moths began laying eggs within 24 h and completed laying eggs within 3 d. Eggs were laid on the sides of the tub or on the cups. Emerging neonates were transferred individually to 28-ml plastic cups with laboratory diet for testing or were transferred in groups of 50–100 into new 350-ml tubs for colony rearing. Rearing conditions were $25 \pm 2^\circ\text{C}$ and a photoperiod of 12:12 (L:D) h for the duration of the experiments.

Irradiation Treatment. Irradiation treatment was conducted at a nearby commercial x-ray facility (CW Hawaii Pride LLC, Keaau, HI) using an electron linear accelerator (5 MeV, model TB-5/15, L-3 Communications Titan Corp., San Diego, CA) at ambient temperature. Dosimeters (Opti-chromic detectors, FWT-70–83M, Far West Technology, Goleta, CA) were placed in between diet cups containing leafrollers at each dose in each replicate. The dosimeters were read with a FWT-200 reader (Far West Technology) at 600-nm absorbance to verify the minimum absorbed dose and dose variation in each replicate. To minimize the dose uniformity ratio (the ratio of the maximum/minimum dose), plastic cups with leafrollers were placed in a double row perpendicular to the x-ray beam. Dose mapping demonstrated that doses were sometimes lower near the sides and floor of the metal carrier, so the cups with leafrollers on diet were elevated by placement on a cardboard box and positioned in the center of the carrier. Each carrier passed in front of the beam in a forward then reverse orientation. The dose uniformity ratio during the Mexican leafroller research was generally <1.2 . After irradiation treatment, Mexican leafrollers in diet cups were returned to the laboratory and held under standard rearing conditions.

Experimental Design. All irradiation tests used F_{3-4} generation laboratory-reared Mexican leafrollers. For stage-specific tests, larvae were placed into categories based on size and known developmental rates (unpublished data). Eggs (6 d old [normally eggs hatch after 9 d]) and larvae (neonates, second/third instars, and fourth/fifth instars) were irradiated at target doses of 60, 90, 120, and 150 Gy in replicated factorial experiments. These are the stages that usually occur with exported commodities. Although the pupal stage of Mexican leafroller is not typically found on fruits, we tested the effects of irradiation against this stage in the event a mature larva pupated within a box of fruit before receiving irradiation treatment. Pupal development to the adult stage is 11 d under our rearing conditions ($25 \pm 2^\circ\text{C}$). Early (1–3 d old) and late (8–10 d old) stage pupae were tested at the same

Table 1. Mexican leafroller egg eclosion after irradiation at various doses

Target dose (Gy)	No. eggs treated ^a	No. hatching	Mean % hatch \pm SE
0	515	332	64.5 \pm 7.2
60	465	13	1.9 \pm 1.9
90	675	0	0.0
120	665	0	0.0
150	1105	0	0.0

^a Total number of eggs irradiated in four replicates.

series of doses. For each larval or pupal age/stage, three replicates were irradiated on different dates, and in each replicate a control group of 25–50 insects was not irradiated and held under the same conditions.

Larvae and pupae were tested in 28-ml plastic cups with diet, whereas eggs were tested in diet cups without diet. After treatment, development of eggs was followed until hatch or until they became discolored, indicating nonviability. Larvae were followed until pupation and adult emergence. Early pupae were followed until adult emergence. Late pupae were scored for adult emergence, and individuals that developed to the adult stage were mated inter se, and the number of eggs laid (fecundity) and egg hatch (fertility) was recorded.

Adult sterility tests were conducted using a reciprocal crosses design. Individuals were isolated in individual 56 ml plastic cups as pupae, and after emergence, unmated moths (≤ 2 -d-old) were irradiated with a target dose of 90 or 150 Gy or left untreated. Irradiated and unirradiated males and females in all combinations were then mated as pairs in individual cups for 24 h. The number of eggs laid and the number of eggs hatched were recorded two weeks after all moths had died. This test was replicated three times.

Statistical Analysis. To make comparisons of radiotolerance between life stages, dose–response data on percentage of survival to pupa and adult for each replicate were arcsine transformed and subjected to linear regression and analysis of covariance (ANCOVA) by using the standard least squares model (SAS Institute 2002). Data used in the regression model included any radiation dose causing mortality between 0 and 100%, and the lowest dose causing 100% mortality. For each replicate, mortality values $<100\%$ were adjusted for control mortality using Abbott's formula (Abbott 1925). Residual plots were evaluated to ensure regression model assumptions were met for each treatment combination. Covariance analysis requires the slopes of the regression lines fitted to each group to be parallel, so the assumption of parallelism (nonsignificant life stage \times dose interaction effect) was tested before evaluating intercepts (life stage effects) (Sokal and Rohlf 1981). For irradiated late pupae, data on adult emergence, eggs per female, and percentage of egg eclosion were subjected to analysis of variance (ANOVA), and mean separation tests were done using a Tukey's test at the 0.05% level of probability. For the reciprocal matings study, log-transformed data on eggs per female and arcsine-transformed data on percent-

Table 2. Maturation of Mexican leafroller larvae and early pupae after irradiation

Stage ^a	Target dose (Gy) ^b	No. treated ^c	Pupae recovered		Adults recovered	
			No.	% ± SE	No.	% ± SE
L1	0	154	108	69.0 ± 6.0	83	53.4 ± 6.4
	60	168	46	27.4 ± 6.6	11	6.5 ± 6.4
	90	168	16	9.5 ± 2.6	0	0.0
	120	168	0	0.0	0	0.0
	150	168	0	0.0	0	0.0
L2/3	0	168	105	62.5 ± 9.3	94	56.0 ± 11.4
	60	168	61	36.3 ± 5.7	25	14.9 ± 4.9
	90	168	52	31.0 ± 6.3	9	5.4 ± 0.0
	120	168	20	11.9 ± 1.6	0	0.0
	150	168	10	6.0 ± 0.6	0	0.0
L4/5	0	162	124	76.5 ± 5.8	113	69.5 ± 9.1
	60	162	103	64.0 ± 6.8	63	38.8 ± 2.1
	90	162	91	56.1 ± 7.3	39	23.9 ± 2.0
	120	162	86	53.5 ± 5.7	25	15.3 ± 1.7
	150	162	93	57.5 ± 2.9	5	3.2 ± 1.7
Pupae (early)	0	95			68	72.3 ± 9.6
	60	90			69	76.6 ± 5.1
	90	90			72	80.0 ± 8.8
	120	146			69	48.1 ± 16.4
	150	148			59	41.0 ± 18.7

^a L1, neonates; L2/3, second and third instars; L4/5, fourth and fifth instars; pupae (early), 1–2-d-old pupae.

^b Measured doses for the 60-, 90-, 120-, and 150-Gy treatments had extremes of 59–74, 81–92, 112–126, and 138–157 Gy, respectively.

^c Total number of individuals irradiated in three replicates.

age of egg eclosion were subjected to ANOVA, and means separations were done using Tukey's test at the 0.05% level of probability.

Results

In general, the pattern of tolerance to irradiation in Mexican leafroller was eggs < neonates < second and third (early) instars < fourth and fifth (late) instars < pupae. A radiation dose of 90 Gy prevented eggs from hatching (Table 1). No neonates developed to the adult stage after radiation treatment at doses ≥90 Gy, and no early instars developed to the adult stage at doses ≥120 Gy (Table 2). For late instars, survival to the adult stage decreased with increasing dose, but it was not prevented in any of the irradiation treatments tested. Adult emergence also was not prevented in any of the irradiation treatments for early pupae (Table 2). Late pupae irradiated at even the highest dose (150 Gy) readily completed development and emerged as adults, mated, and laid eggs (Table 3). There were no significant differences among treatments in the number of adults emerging or the number of eggs laid per

female ($P < 0.05$; Tukey's test). In late pupae, egg hatch was significantly reduced in the 60- and 90-Gy treatments compared with untreated controls, and no eggs hatched in the 120- or 150-Gy treatments (Table 3); a total of three out of 3,130 eggs hatched at 90 Gy, 0 out of 2,900 eggs hatched at 120 Gy, and 0 out of 1,700 eggs hatched at 150 Gy. The mean numbers of male and female adults emerging from treated late pupae were not significant at any dose level ($P < 0.05$; t -tests).

Linear regression on the data shown in Tables 2–4 was used to test whether slopes were significantly different from 0 (significant effect of radiation dose), and to predict a radiation dose needed to prevent adult emergence in Mexican leafroller. Slopes were positive and significant for neonates, early instars and late instars ($P < 0.05$), indicating that success in developing to the adult stage decreased with increasing dose (Table 4). Slope was not significant for early pupae ($P = 0.18$) or late pupae ($P = 0.07$), indicating that irradiation at the dose levels used in these tests did not strongly affect pupal development to adult. The late pupa was predicted to require the highest radiation

Table 3. Maturation and reproduction of Mexican leafroller late-stage pupae^a after irradiation

Target dose (Gy)	No. pupae treated ^b	No. adults			No. eggs ^c	No. eggs/female ± SE	No. eggs hatched ^b
		Male	Female	Total			
0	128	53	56	109a	3,100	52.3 ± 17.2a	1,875a
60	128	54	47	101a	4,210	88.2 ± 5.8a	130b
90	128	44	44	88a	3,130	71.2 ± 17.9a	3c
120	128	43	39	82a	2,900	73.3 ± 15.2a	0c
150	130	45	39	84a	1,700	44.0 ± 2.1a	0c

^a Late stage pupae were 8–10 d old, and some members of the cohort were beginning to emerge as adults. Means followed by a different letter were significantly different by a Tukey's test at $P < 0.05$.

^b Total number of pupae irradiated in three replicates.

^c Egg hatch data were log + 1 transformed before analysis.

Table 4. Linear regressions on prevention of development to adult when various life stages of Mexican leafroller were irradiated at 60, 90, 120, and 150 Gy

Target dose (Gy)	Obs.	y-intercept \pm SE	Slope \pm SE	R^2	Predicted dose for 100% mortality (Gy)
L1	6	63.7 \pm 6.0	0.40 \pm 0.07	0.87	90
L2/3	9	49.7 \pm 8.3	0.43 \pm 0.09	0.77	118
L4/5	12	10.9 \pm 5.8	0.56 \pm 0.05	0.92	158
Pupae (early)	12	-31.5 \pm 19.2	0.54 \pm 0.17	0.48	246
Pupae (late)	12	-0.11 \pm 10.7	0.17 \pm 0.10	0.24	581

Regression analysis used data from Tables 2 and 3 corrected for control mortality using Abbott's formula. Extrapolated values for 100% mortality are used for comparing stage-specific tolerance to irradiation, not to suggest a treatment dose to prevent adult emergence.

dose to prevent adult emergence (estimated 581 Gy), whereas the egg stage was predicted to require the lowest dose to prevent adult emergence (90 Gy) (Table 4). These extrapolated values are presented to illustrate relative differences in stage-specific response and tolerance to irradiation, not to suggest a treatment dose to prevent adult emergence.

Covariance analysis confirmed that tolerance increased with increasing age and developmental stage. The species by dose–interaction effects were not significant (at $P < 0.05$) for any of the life stage comparisons; therefore, the interaction term was dropped from the model in each case and life stage effects were compared. For development to the pupal stage, neonates were less radiotolerant than early instars ($F = 30.1$; $df = 1, 3$; $P = 0.0002$) and late instars ($F = 23.1$; $df = 1, 3$; $P = 0.0003$); and early instars were less tolerant than late instars ($F = 17.9$; $df = 1, 3$; $P = 0.0006$). For development to the adult stage, neonates were less radiotolerant than early instars ($F = 29.6$; $df = 1, 3$; $P = 0.0002$), late instars ($F = 120.0$; $df = 1, 3$; $P = 0.0001$), and early pupae ($F = 80.9$; $df = 1, 3$; $P = 0.0001$); early instars were less tolerant than late instars ($F = 65.1$; $df = 1, 3$; $P = 0.0001$) and early pupae ($F = 92.3$; $df = 1, 3$; $P = 0.0001$); and late instars were less tolerant than early pupae ($F = 49.7$; $df = 1, 3$; $P = 0.0001$). Late pupae were not significantly different from early pupae in terms of development to the adult stage ($F = 2.1$; $df = 1, 4$; $P = 0.17$).

Because the late pupa is the most radiotolerant stage (Table 4), linear regression on the percentage of eggs hatched (from Table 3) can be used to estimate a dose sufficient to provide quarantine security for Mexican leafroller. The equation describing the arcsine-transformed data were y (egg hatch) = $0.795 - 0.00661$

(dose) ($R^2 = 0.76$). The desired response for late pupae is sterility. The predicted dose to prevent egg hatch was 120 Gy, with a 95% confidence interval of 101–149 Gy. Therefore, a minimum absorbed radiation dose of 149 Gy (nominally 150 Gy) is predicted to be sufficient as a quarantine treatment.

In the reciprocal adult crosses experiment, radiation treatment at 90 and 150 Gy had no significant effect on the mean number of eggs laid (fecundity) per female ($F = 1.5$; $df = 6, 14$; $P = 0.24$) in any of the crosses compared with the untreated control (Table 5). However, the mean percentage of eggs hatching (fertility) was significantly reduced in all irradiation treatments ($F = 33.1$; $df = 6, 14$; $P < 0.0001$) compared with the controls; egg hatch was reduced by 60 and 54% in the 90- and 150-Gy treatments, respectively, for matings between unirradiated females and irradiated males, and no viable eggs were produced in matings between irradiated females and either irradiated or unirradiated males (Table 5).

Discussion

Unlike other disinfestation techniques, irradiation does not need to kill the pest immediately to provide quarantine security; therefore, live (but nonviable or sterile) insects may occur with the exported commodity. The objective of an irradiation quarantine treatment is to stop the insect's ability to reproduce and thereby prevent its introduction and establishment into new areas.

In general, tolerance to radiation in Mexican leafroller increased with increasing age and developmental stage. A radiation dose of 90 Gy applied to neonates and early instars prevented adult emergence. The late

Table 5. Reproductive performance of Mexican leafroller when irradiated and unirradiated adults are mated in reciprocal crosses

Dose (Gy)	Pairing ^a	No. pairs	No. females with eggs ^b	Total no. eggs	No. eggs/female (mean \pm SE)	Total no. eggs hatched	Mean \pm SE % eggs hatched
0	UF \times UM	42	22	1895	82.8 \pm 17.7a	1510	78.1 \pm 3.5a
90	IF \times IM	42	24	1095	44.5 \pm 2.1a	0	0.0c
	IF \times UM	42	23	1065	46.1 \pm 3.2a	0	0.0c
150	UF \times IM	45	17	770	44.8 \pm 1.4a	154	18.2 \pm 8.8b
	IF \times IM	42	16	820	52.0 \pm 6.9a	0	0.0c
	IF \times UM	42	20	880	39.5 \pm 10.1a	0	0.0c
	UF \times IM	45	18	780	43.3 \pm 13.8a	143	24.1 \pm 9.2b

Means \pm SE within a column followed by different letters are significantly different using a Tukey's test ($P < 0.05$).

^a I, irradiated; U, unirradiated; F, female; and M, male.

^b Some pairings resulted in no eggs.

(fifth) instar was the most tolerant larval stage, and the late pupa was the most tolerant of all the immature stages tested. A radiation dose of 120 Gy applied to late pupae prevented the production of viable eggs. Regression analysis of the data on egg hatch from irradiated late pupae suggested a dose ≥ 150 Gy would prevent egg hatch with 95% confidence. Reciprocal crosses between irradiated and unirradiated moths demonstrated that males were more radiotolerant than females. Irradiation of female moths at a target dose of 90 Gy before pairing and mating with irradiated or unirradiated males resulted in no viable eggs. Therefore, a minimum radiation dose of 150 Gy has potential as a treatment for control of Mexican leafroller infesting exported commodities. Large-scale validation tests at 150 Gy are needed before this dose can be recommended as a quarantine treatment (Follett and Neven 2006).

After fruit flies, tortricid moths are probably the most significant pests of economic and quarantine concern for fruit (Bloem et al. 1999, 2003). Several irradiation studies have been done on tortricid moths, suggesting control can be achieved at radiation doses between 120 and 200 Gy (IDIDAS 2007). A radiation dose of 200 Gy was shown to be sufficient to control codling moth, *Cydia pomonella* (L.) (Mansour 2003); *Ecdytoplopha aurantiana* (Lima) (Arthur 2004); oriental fruit moth, *Grapholita molesta* (Busck) (Hallman 2004); and light brown apple moth, *Epiphyas postvittana* (Walker) (Dentener et al. 1990). Recent research on light brown apple moth suggests that adult emergence is prevented when fifth instars are irradiated at 120–150 Gy (P.A.F. unpublished data). Irradiation tests with *Cryptophlebia illepidata* (Butler) indicated that 250 Gy prevented adult emergence from irradiated fourth and fifth instars, but 125 Gy was sufficient to cause sterility (Follett and Lower 2000). Information on several other tortricid species is available from studies to develop sterilizing doses for sterile insect release programs (e.g., Bloem et al. 1999, 2003, IDIDAS 2007, Suckling et al. 2007); these studies concur that radiation doses ≤ 200 Gy are sufficient to sterilize females.

Establishing a generic dose for tortricid moths below 400 Gy could reduce treatment time for certain commodities, thereby reducing costs and increasing capacity for irradiation facilities (Follett and Neven 2006). Also, lowering the required dose for commodities infested with tortricids would minimize any negative effects irradiation treatment may have on commodity quality (Follett and Griffin 2006). A radiation dose of 200 Gy would probably suffice as a generic dose for tortricids, but detailed studies including large-scale validation tests on several additional pest species in the family is desirable before making a recommendation.

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