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X-ray Irradiation-Induced Abnormal Development and DNA Damage in *Phthorimaea operculella* (Lepidoptera: Gelechiidae)

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Abstract: The potato tuber moth, *Phthorimaea operculella* (Zeller), is a destructive pest of Solanaceous crops. This study investigated the effects of X-ray irradiation on development, DNA damage and recovery in *P. operculella*. Eggs, larvae (*3rd and 5th), pupae, and adults were irradiated with various doses of X-ray irradiation. Egg hatching was inhibited at 70 Gy, and the pupation and adult emergence of 3rd-instar larvae were inhibited at 150 Gy and 70 Gy, respectively. Some 5th-instar larvae pupated at 150 Gy but failed to emerge as adults at 150 Gy. The adult emergence of pupae that spawned at 150 Gy, but egg hatching of F_1 generation was completely inhibited. In addition, the adult emergence of irradiated-pupae was completely inhibited at 200 Gy. Adults spawned at 150 Gy, but the hatching of the F_1 generation was completely suppressed. The levels of DNA damage and repair in *P. operculella* adults were investigated using the alkaline comet assay. The results indicated that X-ray irradiation increased DNA damage in a dose-dependent manner and showed that DNA damage was repaired in a time-dependent manner. However, damage from a high radiation doses was not completely repaired. This result suggests that at least 150 Gy radiation should be used for the control *P. operculella*.

Keywords: *Phthorimaea operculella*; X-ray; abnormal development; DNA damage

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1. Introduction

The potato tuber moth, *Phthorimaea operculella* (Zeller), is a major pest of Solanaceous crops, including potato, tomato, and eggplant [1–3]. *P. operculella* larvae are commonly known as 'potato tuber worms', and they inhabit plant growth sites and are found in tissues such as leaves, stems, and fruits [4,5]. *P. operculella* larvae cause problems mostly during the storage and distribution of agricultural commodities because they can reduce quantities and lower quality [6–8]. Secondary damage occurs in crops with wounds created by the larvae because fungi and bacteria grow in the wounds [9]. In addition, increased number of *P. operculella* are expected to occur in some regions of China and India due to climate change, so there is a need for a method to prevent massive damage caused by this pest during potato cultivation and storage [10].

P. operculella is regulated as a quarantine pest by the European and Mediterranean Plant Protection Organization (EPPO) and in Taiwan [11]. To control this insect pest, fumigants such as methyl bromide (MB), phosphine (PH_3), and ethanedinitrile (EDN) are used. However, MB was designated as an ozone layer-depleting substance in the Montreal Protocol, and its use has been banned worldwide. In addition to chemical methods, physical methods such as the application of extreme temperature, controlled atmospheric conditions, and irradiation have been employed as alternative methods [12,13].

Ionizing energy such as X-rays is being applied to quarantine pests overseas [14]. Whereas fumigation treatment requires a long treatment time and leaves pesticide residues behind, ionizing energy does not present these problems [15]. In addition, ionizing energy,

including X-rays, cannot immediately kill insect pests but is instead aimed at preventing their reproduction by inducing abnormal development and sterility [16–25]. When an insect pest is irradiated with ionizing energy, the DNA is damaged, but the damaged DNA stops the cell cycle, and recovery is attempted [26]. If the degree of damage is low, recovery to a normal level will occur, but if the degree of damage is high, normal conditions cannot be restored [18,22,23].

In this study, the effects of X-rays on the development and reproduction of *P. operculella* were investigated in each developmental stage. In addition, DNA damage and recovery were studied in *P. operculella* following the application of X-rays. Based on this approach, we aimed to provide basic data on the results of X-ray-based pest control techniques in agricultural products.

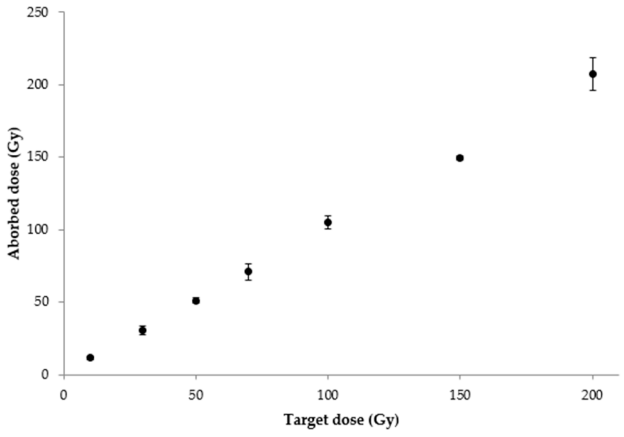
2. Materials and Methods

2.1. Test Insects

A susceptible strain of *P. operculella* was obtained from the National Institute of Highland Agriculture (Pyeongchang, Korea) in July 2011. *P. operculella* was reared on potato tubers (*Solanum tuberosum*) without exposure to any known pesticides in the laboratory. *P. operculella* were successively reared in a breeding cage (30 by 30 by 30 cm), for more than 9 years and were provided with potato tubers as food under the following conditions: 25 ± 2 °C, 55 ± 5%, and a 16 L:8 D photoperiod cycle.

2.2. X-ray Irradiation

X-ray irradiation in air was conducted at EB-Tech Co., Ltd. (Daejeon, Republic of Korea) using a high-energy linear accelerator (UEL V10S, 7.5 MeV, 1 mA, 10 Kw). Target doses were monitored by dosimetry with an alanine pellet dosimeter (ES 200-2106, Bruker Biospin Co., Billerica, MA, USA). The target doses were set at 10, 30, 50, 70, 100, 150, and 200 Gy and were measured using a radiochromic film dosimeter (GEXGAF3002DS, USA) [ISO/ASTM512752004(E)]. The range of absorbed irradiation doses is shown in Figure 1.



Dese (Gy)	10	30	50	70	100	150	200
Dose rate (Gy/sec)	34.7	104.2	173.8	260	403.3	559.2	806.6

Figure 1. X-ray dosimetry.

Thirty female and thirty male *P. operculella* adults were placed in a breeding cage (30 × 30 × 60 cm) containing cotton soaked in a sugar solution (5%) with coarse filter paper attached to the ceiling. They were permitted to lay eggs for 12 h. The filter paper with attached eggs (0–12 h old) was then exposed to X-ray irradiation. Ten *P. operculella* larvae (3rd and 5th instars) were placed in a plastic Petri dish (∅ 9 × 4 cm) with a potato tuber (5 × 1 cm) and exposed to X-ray irradiation. Ten *P. operculella* pupae (less than 1 day

after pupation) were placed in a plastic Petri dish (∅ 9 × 4 cm) and exposed to X-ray irradiation. Ten *P. operculella* adults (5 females and 5 males, 0–24 h after emergence) were separately placed in circular plastic cages (∅ 9 × 8 cm) and exposed to X-ray irradiation. To investigate the lethal effects on various developmental stages, we studied the rates of egg hatching and emergence suppression. The rate of egg hatching was recorded in X-ray-irradiated eggs. In X-ray-irradiated 3rd-instar larvae, the pupation rate, adult emergence rate, larval period, and larval mortality were recorded. In X-ray-irradiated 5th-instar larvae, the pupation rate, adult emergence rate, larval period, larval mortality, and newly emerged adult longevity were recorded. In X-ray-irradiated pupae, the rate of new adult emergence and the longevity of newly emerged adults were recorded. Furthermore, the fecundity and F_1 egg hatchability were recorded that adults emerged and copulated successfully from the irradiated pupae. In X-ray-irradiated adults (female and males), the longevity of irradiated adults, and the fecundity and F_1 egg hatchability were recorded. Trials on the different stages of *P. operculella* were performed with three replicates.

2.3. DNA Comet Assays

DNA damage in *P. operculella* female adults was determined under alkaline conditions using the Comet Assay Kit from Trevigen (Gaithersburg, MD, USA) according to Yun et al. [19]. After X-ray irradiation, females of *P. operculella* adults were homogenized. The images were analyzed using CASP software (Comet Assay Software Project 1.2.2). At least 100 comets were analyzed from each sample. All experiments were performed three times.

2.4. Recovery of Damaged DNA

After X-ray irradiation, female *P. operculella* adults were sampled at 5, 24, 72, 144, and 212 h, and the differences in DNA damage and DNA repair were investigated using the comet assay. The comet assay was performed in the same way as the DNA damage assay; 100 cells from each sample were randomly selected for observation, and the tail moment was measured using CASP software. Tail length/(tail length + head length) ratios were compared, and the degrees of DNA damage and recovery compared to untreated DNA were evaluated. All experiments were performed three times.

2.5. Statistical Analysis

Data were recorded and transformed to arcsine square-root values for the analysis of variance (ANOVA). Treatment means were compared and separated by Tukey's studentized range test at $P = 0.05$. Effective dose (ED) values for inhibition in different developmental stages were considered to be significantly different from one another when the 95% confidence limits failed to overlap. All statistical analyses were conducted using SAS ver. 9.4 [27].

3. Results

3.1. Effect of X-ray Irradiation on Each Developmental Stages of P. operculella

The effects of X-ray irradiation on the eggs are shown in Table 1. Hatchability decreased as the irradiation dose increased, and hatching was completely suppressed above 70 Gy. The median ED (ED_{50}) value for the X-ray irradiation of eggs was 6.6.

The effects of X-ray irradiation on the 3rd- and 5th-instar larvae are shown in Tables 2 and 3, respectively. When 3rd-instar larvae were irradiated at 150 Gy, pupation was completely suppressed. At doses of 70 Gy and above, no adult emergence was observed. The ED_{50} values for the pupation, emergence, and mortality of the 3rd-instar *P. operculella* were 30.3 Gy, 38.8 Gy, and 74.7 Gy, respectively. When 5th-instar larvae were irradiated at 150 Gy, although some larvae pupated, they did not emerge to adults. The adult longevity of *P. operculella* when irradiated at 100 Gy was significantly different than that of the untreated control moths. Additionally, the ED_{50} values for the pupation,

emergence, and mortality of 5th-instar *P. operculella* larvae were 189.6 Gy, 46.8 Gy, and 194.7 Gy, respectively.

Table 1. Effect of X-ray irradiation on hatchability in *P. operculella* eggs.

Dose (Gy)	n	Hatchability (%) (Mean ± SD)
100	800	- [1]
70	827	0.0 ± 0.0 c [2]
50	667	0.3 ± 0.3 c
30	832	2.3 ± 1.1 c
10	797	28.5 ± 1.8 b
0	686	98.0 ± 1.3 a
ED_{50} (Gy)	-	6.6 (4.5–8.3)
ED_{99} (Gy)	-	37.0 (27.7–62.6)

[1] Not determined [2] Different letter indicate statistically significant differences among doses.

Table 2. Effect of X-ray irradiation on pupation, emergence, larval period, and mortality in *P. operculella* 3rd instar larvae.

Dose (Gy)	n	Pupation (%)(Mean ± SD)	Emergence (%)(Mean ± SD)	Larval Period (day) (Mean ± SD)	Mortality (%)(Mean ± SD)
150	30	0.0 ± 0.0 d [1]	0.0 ± 0.0 c	- [2]	100.0 ± 0.0 d
100	30	6.7 ± 5.8 d	0.0 ± 0.0 c	17.7 ± 0.6 b	93.3 ± 5.8 d
70	30	13.3 ± 5.8 d	0.0 ± 0.0 c	16.6 ± 1.5 b	86.7 ± 5.8 d
50	30	30.0 ± 0.0 c	33.3 ± 33.3 bc	10.9 ± 0.3 a	70.0 ± 0.0 c
30	30	46.7 ± 11.5 b	66.7 ± 28.9 ab	9.8 ± 0.2 a	53.3 ± 11.5 b
0	30	100.0 ± 0.0 a	86.7 ± 15.3 a	9.4 ± 0.2 a	0.0 ± 0.0 a
ED_{50} (Gy)		30.3 (24.9–34.8)	38.8 (33.3–42.7)	-	74.7 (71.6–78.0)
ED_{99} ($Gy_{)}$		174.6 (137.3–252.0)	88.7 (75.8–118.1)	-	130.4 (119.1–147.4)

[1] Different letter indicate statistically significant differences among doses [2] Not determined.

Table 3. Effect of X-ray irradiation on pupation, emergence, larval period, mortality, and adult longevity in *P. operculella* 5th instar larvae.

Dose (Gy)	n	Pupation (%)(Mean ± SD)	Emergence (%)(Mean ± SD)	Larval Period (day)(Mean ± SD)	Mortality (%)(Mean ± SD)	Adult Longevity (day)(Mean ± SD)
150	30	66.7 ± 5.8bc [1]	0.0 ± 0.0d	4.2 ± 0.2b	33.3 ± 5.8c	- [2]
100	30	80.0 ± 10.0b	22.2 ± 17.9c	3.4 ± 0.1a	16.7 ± 5.8b	3.8 ± 1.3b
70	30	86.7 ± 5.8ab	38.9 ± 14.7bc	3.2 ± 0.1a	13.3 ± 5.8b	8.4 ± 0.8a
50	30	100.0 ± 0.0a	60.0 ± 17.3ab	3.2 ± 0.1a	0.0 ± 0.0a	9.0 ± 0.8a
30	30	100.0 ± 0.0a	83.3 ± 11.5a	3.1 ± 0.1a	0.0 ± 0.0a	9.8 ± 0.5a
0	30	100.0 ± 0.0a	93.3 ± 5.8a	3.3 ± 0.1a	0.0 ± 0.0a	9.9 ± 0.5a
ED_{50} (Gy)		189.6 (160.0–249.1)	46.8 (43.0–50.4)	-	194.7 (163.3–259.4)	-
ED_{99} (Gy)		467.7 (331.0–847.6)	162.4 (145.6–185.6)	-	480.4 (336.8–891.2)	-

[1] Different letter indicate statistically significant differences among doses.[2] Not determined.

The effects of X-ray irradiation on the pupae are shown in Table 4. At 200 Gy, no adult emergence was observed. The adult longevity of females and males and the fecundity of females decreased with increasing X-ray doses. At 150 Gy, F_1 eggs did not hatch. Additionally, the ED_{50} values for the emergence and F_1 egg hatchability of the *P. operculella* pupae were 73.1 Gy and 41.0 Gy, respectively.

Table 4. Effect of X-ray irradiation on emergence, adult longevity, fecundity, and hatchability in *P. operculella* pupae.

Dose (Gy)	n	Emergence (%)(Mean ± SD)	Adult Longevity (♀, day) (Mean ± SD)	Adult Longevity (♂, day) (Mean ± SD)	No. Eggs (♀/total) (Mean ± SD)	Hatchability (%) (F_1) (Mean ± SD)
200	30	0.0 ± 0.0c [1]	- [2]	-	-	-
150	30	15.6 ± 12.6c	2.5 ± 0.2c	2.4 ± 0.5c	5.2 ± 1.0b	0.0 ± 0.0c
100	30	42.2 ± 16.8b	6.5 ± 0.3b	7.1 ± 0.1b	9.2 ± 1.3b	4.5 ± 3.8c
50	30	67.8 ± 5.1b	7.7 ± 0.5b	9.1 ± 0.6a	19.2 ± 1.5b	35.5 ± 4.8b
0	30	98.9 ± 1.9a	9.9 ± 0.3a	9.4 ± 0.3a	62.3 ± 4.6a	99.3 ± 0.5a
ED_{50} (Gy)		73.1 (62.6–82.3)	-	-	-	41.0 (32.8–44.5)
ED_{99} (Gy)		200.2 (179.1–231.4)	-	-	-	145.0 (129.0–167.6)

[1] Different letters indicate statistically significant differences among doses [2] Not determined.

The effects of X-ray irradiation on the adults are shown in Table 5. The adult longevity of *P. operculella* irradiated at any dose was not significantly different from that of the untreated control moths. However, fecundity and F_1 egg hatchability decreased with increasing X-ray doses. At 150 Gy, no eggs hatched. The ED_{50} value for the F_1 egg hatchability of *P. operculella* adults was 32.9 Gy.

Table 5. Effect of X-ray irradiation on adult longevity, fecundity, and hatchability in *P. operculella* adults.

Dose (Gy)	n	Adult Longevity (♀, day) (Mean±SD)	Adult Longevity (♂, day) (Mean±SD)	No. Eggs (♀/total) (Mean±SD)	Hatchability (%)(Mean±SD)
200	30	9.9 ± 0.4a [1]	9.8 ± 0.2a	5.3 ± 0.5d	0.0 ± 0.0c
150	30	10.0 ± 0.5a	9.8 ± 0.4a	9.4 ± 5.0d	0.0 ± 0.0c
100	30	9.9 ± 0.4a	9.5 ± 0.2a	21.0 ± 2.3c	16.9 ± 7.4b
50	30	10.3 ± 0.1a	10.2 ± 0.4a	34.7 ± 2.4b	20.5 ± 1.6b
0	30	10.0 ± 0.1a	9.6 ± 0.2a	57.5 ± 6.3a	98.8 ± 1.1a
ED_{50} (Gy)		- [2]	-	-	32.9 (26.0–39.5)
ED_{99} (Gy)		-	-	-	177.7 (139.8–247.8)

[1] Different letters indicate statistically significant differences among doses [2] Not determined.

3.2. Effects of X-ray Irradiation on DNA Damage and Repair

DNA damage was evaluated in *P. operculella* adults after 5 h of X-ray irradiation using a DNA comet assay. Comet images for cells obtained from *P. operculella* adults are presented in Figure 2. Untreated cells showed a round shape with a very small tail in comet images, indicating little or no DNA damage; on the other hand, the comet tail lengths of X-ray-irradiated cells increased a dose-dependent manner. At doses of 100 Gy and above, most of the comet tails were long, but comets without a long tail were also frequently observed (Figure 2A). The results of calculations based on the observations are portrayed in graphs (Figure 2B). The increase in the tail moment observed in the comet assay indicated that DNA damage increased as the X-ray dose increased.

Thereafter, to conduct a time-series analysis of the repair of DNA damage induced by X-ray irradiation, a comet assay was carried out using *P. operculella* adults. Cells from *P. operculella* adults were sampled 5, 24, 72, 144, and 212 h after X-ray irradiation (0, 50, 100, and 150 Gy) and analyzed under alkaline conditions using the Comet Assay Kit. Frequency histograms of the ratios of individual cells are shown in Figure 3. The increase in the frequency of ratios close to one associated with an increasing radiation dose after 5 h of X-ray irradiation indicated increased DNA damage. At 212 h after X-ray irradiation, the frequency of the ratios observed under a 50 Gy irradiation dose did not indicate a level of repair, similar to that in the control.

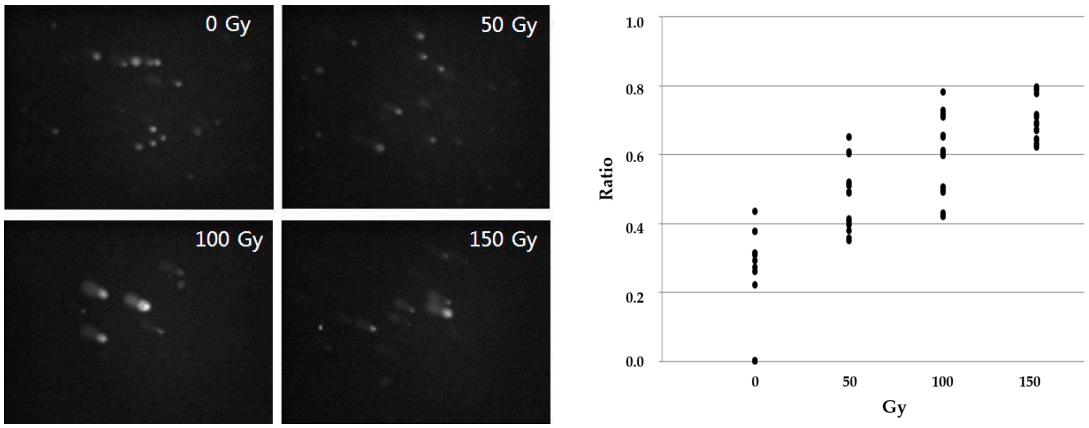


Figure 2. Comet assay of X-ray-induced DNA damage in *P. operculella* adults. The cells were harvested 5 h after *P. operculella* irradiation and analyzed under alkaline conditions using a Comet Assay Kit. (**A**) representative images of comets from *P. operculella* adults treated with X-ray irradiation at different doses. (**B**) graphic depiction of the calculated tail length from the analysis of alkaline comet assays. Data are shown for a representative experiment, in which at least 100 comets were quantified for each sample. Ratio, the percentage of fluorescence in the damaged area relative to overall luminance, including intact DNA (head) and the damaged area (tail) of a comet image. The X-axis represents the Gy, and the Y-axis represents the ratio.

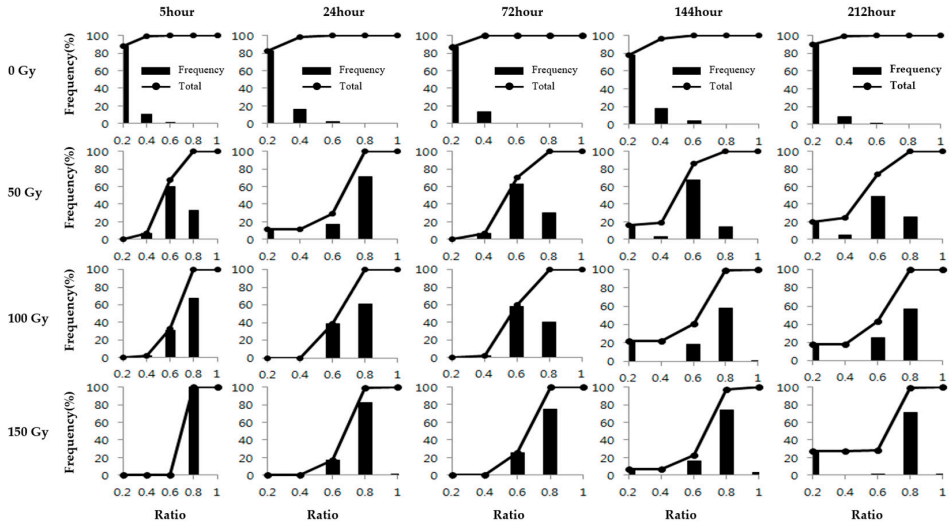


Figure 3. Frequency histogram of the parameter ratio at different time points before and after X-ray irradiation with various doses. The cells of *P. operculella* adults were harvested 5, 24, 72, 144, and 212 h after X-ray irradiation (0, 50, 100, and 150 Gy) and analyzed under alkaline conditions using a Comet Assay Kit. Ratio, the percentage of fluorescence in the damaged area relative to overall luminance, including intact DNA (head) and the damaged area (tail) of a comet image. The X-axis represents the ratio, and the Y-axis represents the frequency (%).

4. Discussion

These results demonstrated that the suppression of the development and reproduction of *P. operculella* increased with increasing X-ray doses. The most radiotolerant stages were pupae and adults, and the most radiosensitive stage was eggs. Similar to our findings, Kim et al. [28] reported that all stages of *Helicoverpa armigera* and its reproduction were inhibited by X-ray irradiation. In the present study, the hatching rate of the F_1 generation was investigated for pupae and adults, which means that the pupae and adults are generally studied to be more radiotolerant than the eggs and larvae [17–19]. Moreover, the population of emerged adults from the irradiated eggs and larvae was smaller than the irradiated pupae and adults. In addition, the emerged adults (female and male) were difficult to successfully copulated that the mating timing of female and male are not right. So, the results were difficult to investigate until the next generation.

While the research on the effects of ionizing energy on *P. operculella* following X-ray irradiation is insufficient, many studies have been performed on gamma-rays [29–33]. Although gamma-irradiation was not performed in this study, Mahto et al. [33] reported that the gamma-irradiation of the eggs and larvae of *P. operculella* at 120 Gy inhibited adult emergence and that emerged adults were deformed following gamma-irradiation at 80 Gy. In addition, Rananavare et al. [29] reported that *P. operculella* male adults irradiated with gamma-rays at 500 Gy showed no difference in mating ability from normal adults. However, other authors reported that the mating ability and frequency of mating decreased under 25 Gy of gamma-irradiation, and at 45 Gy, the sterility of *P. operculella* male adults was 91% [31]. In addition, Haiba et al. [30,32] suggested that 150 Gy of gamma-irradiation should be applied to completely control *P. operculella.* When X-ray irradiation was applied to the pupae, the lifespan of newly emerged adults was shortened as the dose increased. This result was similar to the results of a study on gamma rays [33].

The comet assay is likely to be used in genotoxicology and biological monitoring studies to detect DNA damage under various pest control strategies [34]. In this study, X-ray irradiation was shown to induce DNA damage in *P. operculella* adults. The induction of DNA damage in insect pests irradiated with ionizing energy has also been observed in previous studies [17–20,23,35,36]. Yun et al. [19] reported that DNA damage in *Spodoptera litura* was not complete at electron beam irradiation doses of 100 Gy and above. However, the frequency of the ratios recorded at 30 and 50 Gy indicated repair to almost the same level observed in the control (0 Gy). In this study, DNA damage was not completely repaired 212 h after irradiation at a dose of 150 Gy or above. In addition, at doses of 50 and 100 Gy, irradiated adults were not repaired at 0 Gy. Yun et al. [19] confirmed that DNA damage caused by low-dose irradiation (30 and 50 Gy) was repaired by multiple DNA repair systems and did not affect the hatchability of the F_1 adults when irradiation was performed at low doses. In this study, the induction of DNA damage in *P. operculella* adults by X-ray irradiation was confirmed only in females. However, according to the results reported in female and male *H. armigera* adults exposed to gamma-irradiation, females showed higher radiotolerance than males, as males exhibited longer tail moments than females [20].

In addition, only the susceptibility of *P. operculella* to X-rays was evaluated, and it is still necessary to perform an empirical evaluation, as in previous studies [21,24,25,37,38]. At quarantine sites, empirical tests for radiotolerant stages should be carried out, excluding inspection for pupal and adult insects that can be seen with the naked eye [39]. Taken together, the results of this study suggest that radiation treatment with at least 150 Gy could be required to control *P. operculella*.

5. Conclusions

The results of this study suggest that radiation treatment with at least 150 Gy could be required to control *P. operculella*.

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