Effect of X-ray irradiation on development, flight, and reproduction of *Spodoptera litura*

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*Spodoptera litura* is an omnivorous pest that has spread globally. Because irradiation sterilization technology has a great potential for control of *S. litura*, the effect of 25–150 Gy doses of X-rays on pupal survival, flight and reproductive variables of adult moths were analyzed in this research. The X-ray irradiation with the dose of 25–150 Gy significantly affected the reproductive ability of females. Irradiating male pupae with 25–150 Gy doses of X-rays had no effect on mating, life span, or flight ability of adult moths, but significantly reduced survival and fecundity of their offspring, and the sterility rate of the F₁ generation was 52.65%–99.9%. The results of logistic curve fitting showed that the sterility impact was 84% at the most appropriate irradiation dose (71.26 Gy). The sterility control was 91% in an indoor mating competition experiment when the release ratio of irradiated males (75 Gy) to nonirradiated males reached 12.6:1. The effects of X-ray irradiation doses on biological variables of *S. litura* and the most effective release ratio determined here provide a theoretical foundation for using radiation sterilization technology to control *S. litura*.

**KEYWORDS**

*Spodoptera litura*, sterile insect technology, X-ray, radiation biology, release ratios

**1 Introduction**

*Spodoptera litura* (Fabricius) (Noctuidae; Lepidoptera) is a worldwide pest (Bishara, 1934; Aitkenhead et al., 1974; Tojo et al., 2013) that can feed on 389 plant species from 109 families (Qin et al., 2006), it is also widely dispersed in China, where it breeds all year in Yunnan and other tropical areas of China (Wu et al., 2016). Chemical pesticides are the most common way to control *S. litura*, but resistance to a range of chemical insecticides (Srivastava and Joshi, 1965; Zhou and Huang, 2002; Ahmad et al., 2008), particularly carbamates and pyrethroids, has been reported since 1965 (Zhou and Huang, 2002; Ahmad et al., 2007a; Ahmad et al., 2007b). As a result, strategies for integrated pest
management (IPM) of S. litura have been widely accepted by all stakeholders (Rao et al., 1993; Klassen, 2005; Ehler, 2006).

One measure for IPM is sterilizing insect pests by irradiation with X-rays, electron beams, or γ-rays, then releasing a large number of sterile insects into the field (Knipling, 1955; LaChance et al., 1975). Since the 1950s, this eco-friendly technology has been used in wide range of IPM applications to control pests (Hendrichs et al., 2002) such as the dipterans Cochliomyia hominivorax (Coquerel) (Knipling, 1960; Wyss, 2006), Ceratitis capitata (Wiedemann) (De Longo et al., 2000; Hendrichs et al., 1983), Bactrocera cucurbitae (Coquillett) (Yosiaki et al., 2003; Koyama et al., 2004).

The use of radiation sterilization has lagged for lepidopterans, however, because of their high resistance to radiation (LaChance, 1967). As a result, a method to generate inherited sterility (IS) was developed for lepidopteran insects (Proverbs and Newton, 1962; North, 1975) and has been used to control a group of lepidopteran insects such as Cydia pomonella (Bloom et al., 2007), Teia anartoides (Walker) (Suckling et al., 2007), Pectinophora gossypella (Saunders) (Bloom et al., 2005; Tabashnik et al., 2021). However, because radioisotopes cannot be guaranteed to be safe, their usage is becoming increasingly limited. Many SIT programs, which rely on ionizing radiation from radioisotopes for insect sterilization, are severely hampered. As a result, finding a replacement for radioisotopes radiation source is critical. Because of its higher safety, lack of radioactive residue, and ease of portability, X-rays are commonly used in the past (Bakri et al., 2005; Yamada et al., 2014; Light et al., 2015).

The method of employing X-rays to irradiate insects has gradually gained traction in recent years, and considerable research has been reported. Cagnotti et al. (2012) used X-rays to sterilize Tuta absoluta pupae and found that 200 Gy was the best dose for sterility. Urquidi et al. (2015) used different wavelengths of X-rays to irradiate mosquitoes, finding that long wavelengths were more effective at mosquito sterilization. Adult orangeworm moths were irradiated with X-rays by Light et al. (2015), the research showed that 125 Gy could cause sterility in both parents and F1 generations. Aedes albopictus irradiated with X-ray at a dose of 40 Gy by Du et al. (2019) also had a high sterility effect. Haff et al. (2020) discovered that X-rays and γ-rays were biologically equivalent after irradiating Amyelois transitella larvae with X-rays. With 200 Gy X-ray treatment, Ephestia elutella can be sterilized, and a 15:1 ratio of irradiated male insects to normal male insects can prevent 71.91% of the wild population from reproducing (Zhao et al., 2022). In 1974, scientists discovered that 40 Gy of 60Co radiation had a significant impact on the offspring development of male S. litura (Mochida and Miyahara, 1974). In 1993, Seth and Sehgal explored the influence of radiation on the longevity of male S. litura and its F1 generation larvae, proving that IS may be used to manage S. litura (Seth and Sehgal, 1993). However, no any study on the optimal irradiation dose of X-rays to control S.litura was reported until now. In this study, we determined the effects of X-ray irradiation doses on critical biological variables and the best release ratio of irradiated to nonirradiated males to provide a theoretical basis for the development of S. litura green control technology.

2 Materials and methods

2.1 Experimental insect

Adults of S. litura were obtained from the Langfang Experimental Station, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, where field populations were collected on a regular basis for rejuvenation. After eclosion, adults were placed in a 450 ml disposable plastic bottle with a cotton ball dipped in 5% v/v honey water, and then the bottle was sealed with gauze. Daily, any eggs in the bottle were removed and placed in a self-sealed bag to await hatching, and the cotton ball was replaced with a fresh one. After eggs hatched, each larva was placed in a separate transparent plastic box (diameter: 50 mm; height: 40 mm) and an artificial feed made of soybean powder and wheat germ powder (Greene et al., 1976). On the fifth day after pupation, males and females were identified as described by Zhao et al. (2011). All insect stages were grown in an MGC intelligent program artificial climate box (MGC-450HP, Shanghai Yiheng Scientific Instrument Co., Ltd.) at 25°C ± 1°C, 70% ± 5% RH, and photoperiod of L: D = 16:8 h.

2.2 Irradiation equipment

An X-ray irradiator (JYK-001 type), newly developed by Hebi Jiaduoke Industry and Trade Co., Ltd., Hebi, China, was used. The dose of X-ray was selected as 1.790 mGy/s (180 kV/10 mA) in this study. The samples were placed on an irradiation table (210 mm × 210 mm) at a distance of 400 mm from the X-ray source to receive X-rays. The temperature in the irradiation chamber was 25°C ± 1°C, and the irradiation gradient was 0 Gy (unirradiated), 25 Gy (13,416 s), 50 Gy (26,831 s), 75 Gy (40,247 s), 100 Gy (53,662 s), 125 Gy (67,078 s), and 150 Gy (80,494 s). When the cumulative dose was attained, the irradiation was halted and the sample was taken out. During irradiation, the dosage rate was monitored in real-time and ranged from 1.731 to 1.864 mGy/s.

2.3 Experimental methods

2.3.1 Effects of irradiation on S. litura pupa

Healthy male and female pupae with a pupal mass >300 mg near eclosion (8 days old) (Bushland and Hopkins, 1951; Ouye et al., 1964) were placed in different transparent boxes (length: 100 mm; width: 100 mm; height: 10 mm) according to the irradiation dose with wet gauze to maintain humidity.
30 female and 30 male pupae were irradiated for each of the five doses (25 Gy, 50 Gy, 75 Gy, 100 Gy, 150 Gy), using unirradiated insects cultured in the lab at the same time as the control. The experiment was repeated six times. Each pupa was then placed in a 450 ml bottle to wait for eclosion after being irradiated. Dead and deformed pupae were used to calculate mortality and deformity rates; pupae were considered deformed if moths could not expand their wings after eclosion.

2.3.2 Effects of X-ray irradiation on mating and reproduction of the parent moths of S. litura

Pupa were irradiated as described in Section 2.3.1. After the adult emerged, they were paired with unirradiated females; the pair was placed in a 450 ml plastic bottle, eggs collected and food replaced as described in Section 2.1. The pairing methods of moths are as follows: N0 × N0 (control), N0 × T5, and T5 × N0 (N, nonirradiated, T, irradiation treatment); 15 pairs were treated per dose, and the experiment was done 4 times. The spermatophores within the spermathecae were counted and the mating history of the dead female moths was determined using a stereoscope with 1× objective (TS-63X, Shanghai Shangguang New Optical Technology Co., Ltd., Shanghai, China). When spermatophore was found to exist in the female moth’s spermatheca, the moth mating was identified successfully. Pre-oviposition, oviposition, and post-oviposition periods (the time between the last egg laying and the female’s death), the number of eggs deposited, eggs hatched, male adult lifespan, and mating time for each group were all recorded. Finally, the infertility rate was calculated (the probability that the eggs laid by female moth did not hatch was referred as the infertility rate).

2.3.3 Effects of different X-ray irradiation doses on flight ability of S. litura adults

Flying ability was assessed using the FXMD-24-USB insect flight information system (Henan Hebi Jiaduoke Industry and Trade Co., Ltd.) and the hoisting test based on the method of Ge et al. (2019). Male pupae were irradiated as described in Section 2.3.1. After emergence of the adults, 3-day-old adults that developed from the irradiated pupae and had intact wings were loaded into the finger tube and numbered. Twenty to thirty adults were selected from each treatment dose. The moths were removed carefully from the tubes, the wings of the moth were stretched out, the scales on the abdomen and thorax were brushed away, and the thorax was attached to the flight mill with a small droplet of cyanoacrylate glue (Deli Group Co., Ltd., Zhejiang, China). The test insect was inserted vertically at 90 degrees onto the crane arm of the flight mill and allowed to fly continuously for 24 h in the dark at 25°C ± 1°C and 70% ± 5% RH.

2.3.4 Effects of different X-ray irradiation on F1 generations of S. litura

F1 generation larvae (the male parent was irradiated [see Section 2.3.1], the female parent was not) were provided artificial feed (see Section 2.1 for insect rearing methods), their development was observed every day, and the duration of each stage was recorded. Also, the 3-days-old pupae were weighed. Once the F1 adults had emerged, they were paired with nonirradiated heterosexual adults that emerged on the same day as F1 adults, and reproductive variables (such as the periods of pre-oviposition, oviposition, and post-oviposition; the number of eggs deposited, eggs hatched, adult lifespan, and mating rate) were recorded. Growth of at least 200 eggs and 80 first-instar larvae were observed for each treatment, and the experiment was repeated three times. Mating rate and sterility rate were calculated for the F1 generation. Finally, the life table parameters for the F1 population were calculated. The net reproductive rate ($R_0$), generation time ($T$), intrinsic rate of increase ($r$), and finite rate of increase ($\lambda$) of the S.litura F1 populations were estimated using the formulas below (Chi and Liu, 1985; Chi 1988; Asiimwe et al., 2007):

$$
\lambda = e^r
$$

$$
R_0 = \sum_{x=0}^{\infty} l_x m_x
$$

$$
T = \frac{\ln R_0}{r}
$$

$$
l_x = \sum_{j=1}^{m} S_{xj}
$$

$$
m_x = \frac{\sum_{j=1}^{m} S_{xj} f_{xj}}{\sum_{j=1}^{m} S_{xj}}
$$

$$
\sum_{x=0}^{\infty} l_x m_x e^{-r(x+1)} = 1
$$

The $x$ is the number of days, $l_x$ is the S. litura survival probability from egg to $x$ days old $f_x$ is the age-specific fecundity at age $x$, $m_x$ is the average population fecundity from egg to $x$ days old, and $l_x m_x$ is the population age-specific maternity, and $e$ is the Euler number.

2.3.5 Mating competition test between irradiated and nonirradiated males of S. litura

We set up a total of 13 groups with differing numbers of irradiated males (75 Gy X-rays in the pupal stage) to nonirradiated males to nonirradiated normal females: 0:1:1 (control), 1:1:1, 2:1:1, 3:1:1, 4:1:1, 5:1:1, 6:1:1, 7:1:1, 8:1:1, 9:1:1, 10:1:1, 11:1:1, and 12:1:1 in feeding buckets (diameter: 25 cm; height: 30 cm) with cotton balls dipped in 5% v/v honey water. The pail was sealed with gauze, eggs were collected and counted and fresh food supplied daily. The number of eggs which hatched larva was also recorded for calculating the infertility rate.

2.4 Data analyses

A two-way analysis of variance was used to examine the deformity rate and adjusted mortality of irradiated pupae, and the reproductive parameters of parental adult moths, with different radiation doses and sex as factors. If the difference was significant, Tukey’s HSD multiple comparison test was
performed. The one-way ANOVA was used to analyze the effects of different irradiation doses on mean adult flight ability, and F1 insect development of *S. litura* in software SPSS (version 26.0; IBM, Armonk, NY, United States). Percentage data were arcsine square-root transformed before the analysis of variance. If the difference among doses was significant for a variable, multiple Tukey’s HSD comparisons were carried out, and the Log-rank test was used to analyze the survival of the F1 generation of *S. litura* with different dose treatments in GraphPad (version 8.0; GraphPad Software Inc., San Diego, CA, United States).

Logistic regression was used to fit the sterility rate of *S. litura* at different doses of X-rays, and the sterility rate of *S. litura* with different release ratios was fitted by logistic in Origin software (version 2019; Origin Lab Corporation, Northampton, MA, United States). The model equation was \( y = \frac{1}{1 + e^{\beta_0 + \beta_1 x}} \), where \( y \) is the sterility rate, \( k \) is the theoretical highest percentage, \( x \) is irradiation dose or irradiation insect release ratio, \( r \) is the growth rate coefficient, \( a \) is a shape parameter. All the figures were drawn using Graphpad 8.0. The experimental population’s life table parameters were calculated using the software TWOSEX-MSChart (Chi, 2009; Chi et al., 2020). Life table parameters were analyzed for significant differences among different treatments using a paired bootstrap test (\( n = 100,000 \)) (Akca et al., 2015; Wei et al., 2020).

### 3 Results

#### 3.1 Effect of irradiation on pupae

The deformity rate of *S. litura* pupae did not differ significantly by irradiation doses and irradiation dose \( \times \) sex (irradiation doses: \( F_{6, 42} = 0.539, p = 0.777 \); irradiation dose \( \times \) sex: \( F_{6, 84} = 0.790, p = 0.581 \)), but did significantly by sex (\( F_{1, 84} = 7.424, p = 0.008 \)), according to two-way ANOVA (Table 1). The adjusted mortality rate of *S. litura* pupae did not differ significantly by irradiation doses, sex, and irradiation dose \( \times \) sex (irradiation doses: \( F_{6, 72} = 0.361, p = 0.900 \); sex: \( F_{1, 72} = 0.181, p = 0.672 \); irradiation dose \( \times \) sex: \( F_{6, 72} = 0.168, p = 0.984 \)).

#### 3.2 *S. litura* reproductive parameters and adult longevity after various X-ray doses

The mating rate of *S. litura* parents was not affected by irradiation doses and irradiation dose \( \times \) sex interaction, but it did significantly by sex (irradiation doses: \( F_{6, 42} = 0.241, p = 0.9602 \); sex: \( F_{1, 42} = 7.574, p = 0.009 \); irradiation dose \( \times \) sex: \( F_{6, 42} = 0.459, p = 0.834 \); Figure 1A). The oviposition of *S. litura* parents was affected by irradiation dose and sex, but not by irradiation dose \( \times \) sex interaction (irradiation doses: \( F_{6, 42} = 5.469, p = 0.0003 \); sex: \( F_{1, 42} = 10.460, p = 0.002 \); irradiation dose \( \times \) sex: \( F_{6, 42} = 1.180, p = 0.064 \); Figure 1B). The irradiation dose \( \times \) sex interaction had a significant influence on the pre-oviposition duration, while the irradiation dose had no effect (irradiation doses: \( F_{6, 42} = 1.292, p = 0.282 \); sex: \( F_{1, 42} = 45.30, p < 0.0001 \); irradiation dose \( \times \) sex: \( F_{6, 42} = 3.106, p = 0.013 \); Figure 1C). The sex had a significant effect on the post-oviposition duration, while the irradiation dose and irradiation dose \( \times \) sex interaction had no effect (irradiation doses: \( F_{6, 42} = 1.525, p = 0.194 \); sex: \( F_{1, 42} = 7.796, p = 0.008 \); irradiation dose \( \times \) sex: \( F_{6, 42} = 0.909, p = 0.498 \); Figure 1D). The eggs deposited per female was affected significantly by irradiation dose and sex, but not by the interaction of irradiation dose and sex (irradiation doses: \( F_{6, 42} = 7.519, p < 0.0001 \); sex: \( F_{1, 42} = 23.250, p < 0.0001 \); irradiation dose \( \times \) sex: \( F_{6, 42} = 2.113, p = 0.0718 \); Figure 1E).

The longevity of *S. litura* adults was affected significantly by sex, but not by irradiation dose and irradiation dose \( \times \) sex interaction (irradiation doses: \( F_{6, 42} = 0.2928, p = 0.9370 \); sex: \( F_{1, 42} = 8.746, p = 0.0051 \); irradiation dose \( \times \) sex: \( F_{6, 42} = 0.2499, p = 0.9566 \); Figure 1F).

### Table 1 Mean (±SE) deformity rates and adjusted mortality of pupae of *Spodoptera litura* after irradiation with different doses of X-rays.

| Irradiation dose (Gy) | Male |   | Female |   |
|----------------------|------|---|--------|---|
|                      | Deformity rate (%) | Adjusted mortality (%) | Deformity rate (%) | Adjusted mortality (%) |
| 0 (control)          | 11.65 ± 2.02a       | —                        | 16.82 ± 3.39a       | —                        |
| 25                   | 13.81 ± 4.22a       | 0.02 ± 0.06a             | 25.40 ± 4.22a       | —0.05 ± 0.03a            |
| 50                   | 19.21 ± 2.73a       | 0.07 ± 0.05a             | 16.73 ± 1.83a       | 0.10 ± 0.06a             |
| 75                   | 14.06 ± 3.01a       | 0.08 ± 0.10a             | 20.23 ± 3.88a       | 0.09 ± 0.08a             |
| 100                  | 13.46 ± 2.51a       | 0.18 ± 0.10a             | 21.07 ± 2.53a       | 0.00 ± 0.05a             |
| 125                  | 13.91 ± 4.22a       | 0.12 ± 0.11a             | 18.8 ± 5.67a        | 0.14 ± 0.08a             |
| 150                  | 13.82 ± 3.62a       | 0.09 ± 0.10a             | 16.25 ± 2.59a       | 0.01 ± 0.03a             |

Note: Among different irradiation doses, significant differences in pupal deformity and adjusted mortality of *S. litura* (two-way ANOVA, Tukey’s HSD; \( p < 0.05 \)) are shown by different lowercase letters.
3.3 Effects of different doses on sterility of S. litura

According to a one-way ANOVA, the sterility rate for irradiated moths that mated with nonirradiated heterosexual moths increased significantly at higher irradiation doses (T × N: F6, 21 = 5.514, p = 0.001; N × T: F6, 21 = 13.611, p < 0.001) (N = nonirradiated, T = irradiation treatment), and both the growth dynamics fit the logistic curve (T × N: R² = 0.879, p < 0.001; N × T: R² = 0.981, p < 0.001, Figure 2). The equation that fits the mating sterility rate of irradiated male moths and nonirradiated female moths was
3.4 Effects of X-ray irradiation on the flight ability of *S. litura*

In the one-way analysis of variance, none of the flight variables differed significantly among the irradiation doses (flight mass loss: $F_{6, 125} = 0.241, p = 0.962$; flight speed: $F_{6, 125} = 1.147, p = 0.339$; flight time: $F_{6, 125} = 0.963, p = 0.453$; flight distance: $F_{6, 125} = 0.992, p = 0.434$) (Table 2).

3.5 Development of *S. litura* F$_1$ generations after males were irradiated with different doses of X-rays

After males that were irradiated at doses from 25 to 150 Gy at the pupal stage mated with nonirradiated females, the developmental duration of the F$_1$ generation insects was significantly affected. As shown in the ANOVA, different doses of irradiation had significant effects on the duration of egg stage ($F_{6, 2658} = 87.842, p < 0.001$), 1st instar larva ($F_{6, 2653} = 94.382, p < 0.001$), 2nd instar larva ($F_{6, 2653} = 29.079, p < 0.001$), 3rd instar larva ($F_{6, 2792} = 18.472, p < 0.001$), 4th instar larva ($F_{6, 2792} = 18.472, p < 0.001$), 5th instar larva ($F_{6, 2653} = 9.166, p < 0.001$), 6th instar larva ($F_{6, 2650} = 5.362, p < 0.001$), adult duration ($F_{6, 125} = 3.283, p = 0.003$), and generation period ($F_{6, 2658} = 14.016, p < 0.001$), the duration of pre-oviposition stage of females ($F_{6, 125} = 3.921, p = 0.001$), number of eggs deposited per female ($F_{6, 265} = 4.522, p < 0.001$) of insects, but had no significant effect on the duration of post-oviposition stage ($F_{6, 265} = 1.304, p = 0.255$) (Table 3). Compared with the control, the pupal mass of the F$_1$ generation in the 25–150 Gy irradiation treatments group was significantly reduced (386.45–421.76 mg), and the sex ratio was significantly inclined to males (male: female = 1.04–2); the oviposition period (4–4.68 days) for the 50 Gy, 75 Gy, and 125 Gy treatment groups was significantly lower compared with the control (6.7 days); and the 100 Gy and 150 Gy treatment groups had significantly lower pre-oviposition (1.5–1.76 days) than the control group (3.32). Significantly fewer eggs were deposited per female (99.5–316.78) compared with the control (1028.3) when the irradiation dose was >125 Gy, and at 150 Gy, the insect generation duration (26.19 days) was significantly lower than that of the nonirradiated insects (35.01 days) (Table 3). The mating rate for the 25–150 Gy dose groups was not significantly different from that of the nonirradiated insects by different mating types ($N_4 \times T_{6C}: F_{6, 14} = 0.166, p = 0.982; T_{6C} \times N_4: F_{6, 14} = 0.479, p = 0.813; T_{6C} \times T_{6C}: F_{6, 14} = 1.311, p = 0.315$) ($N$ = normal individual whose parents were both unirradiated; $T = F_1$ individual whose male parent was irradiated with 250 Gy dose of X-ray); however,
TABLE 2 Means (±SE) for flight performance variables of Spodoptera litura adults exposed to different doses of X-ray during pupal stage.

| Irradiation dose (Gy) | Mass loss (mg)       | Velocity (km/h) | Duration (h) | Distance (km) |
|-----------------------|----------------------|-----------------|--------------|---------------|
| 0 (control)           | 56.87 ± 5.44a        | 2.05 ± 0.25a    | 8.56 ± 1.62a | 19.51 ± 4.41a |
| 25                    | 51.33 ± 1.92a        | 1.56 ± 0.15a    | 6.15 ± 1.57a | 10.40 ± 2.85a |
| 50                    | 51.48 ± 4.00a        | 1.90 ± 0.26a    | 10.25 ± 1.99a| 21.98 ± 5.64a |
| 75                    | 52.62 ± 4.29a        | 1.73 ± 0.20a    | 7.45 ± 1.95a | 14.84 ± 6.28a |
| 100                   | 47.36 ± 4.89a        | 1.31 ± 0.20a    | 3.09 ± 0.81a | 3.90 ± 0.86a  |
| 125                   | 54.58 ± 3.48a        | 1.96 ± 0.26a    | 4.56 ± 1.94a | 8.99 ± 3.80a  |
| 150                   | 58.70 ± 2.20a        | 2.19 ± 0.46a    | 7.60 ± 1.29a | 18.32 ± 5.32a |

Note: Among different irradiation doses, significant differences in flight performance of S. litura (one-way ANOVA, Tukey’s HSD, p < 0.05) are shown by different lowercase letters.

TABLE 3 Mean duration (±SE) for developmental stages of F1 generation of Spodoptera litura after male parent was irradiated with different X-ray doses during pupal stage.

| Developmental stage | 0 Gy (control) | 25 Gy | 50 Gy | 75 Gy | 100 Gy | 125 Gy | 150 Gy |
|---------------------|---------------|-------|-------|-------|--------|--------|--------|
| Egg                 | 3.60 ± 0.02a  | 3.33 ± 0.03c | 3.49 ± 0.03b | 3.44 ± 0.02b | 3.00 ± 0.00e | 3.40 ± 0.03bc | 3.06 ± 0.02d |
| 1st instar larva    | 3.02 ± 0.02c  | 3.33 ± 0.04b | 3.09 ± 0.03c | 2.87 ± 0.03d | 4.10 ± 0.06a | 3.38 ± 0.05b | 3.35 ± 0.06b |
| 2nd instar larva    | 2.36 ± 0.03c  | 2.62 ± 0.04b | 2.34 ± 0.04cd | 2.21 ± 0.03e | 2.65 ± 0.07b | 2.93 ± 0.06a | 2.67 ± 0.06b |
| 3rd instar larva    | 2.49 ± 0.04b  | 2.70 ± 0.05a | 2.86 ± 0.07a | 2.26 ± 0.03c | 2.83 ± 0.06a | 2.23 ± 0.06c | 2.92 ± 0.09a |
| 4th instar larva    | 2.20 ± 0.03bc | 2.06 ± 0.05c | 2.26 ± 0.07bc | 2.12 ± 0.03c | 2.28 ± 0.07bc | 2.79 ± 0.07a | 2.42 ± 0.09b |
| 5th instar larva    | 2.15 ± 0.03b  | 2.17 ± 0.06ab | 2.09 ± 0.06b | 2.31 ± 0.03a | 1.83 ± 0.05c | 2.06 ± 0.08bc | 2.10 ± 0.08bc |
| 6th instar larva    | 5.17 ± 0.04a  | 4.93 ± 0.07abc | 5.06 ± 0.07ab | 5.05 ± 0.04ab | 4.89 ± 0.06bc | 4.76 ± 0.07c | 5.03 ± 0.09ab |
| Larval stage        | 19.90 ± 0.14ab | 20.44 ± 0.17a | 20.03 ± 0.20ab | 19.51 ± 0.11b | 19.92 ± 0.23ab | 20.08 ± 0.24ab | 19.21 ± 0.28b |
| Pupa                | 10.22 ± 0.09b  | 10.22 ± 0.08b | 10.35 ± 0.10b | 10.16 ± 0.07b | 10.35 ± 0.09b | 10.35 ± 0.16b | 11.17 ± 0.16a |
| Egg-pupa            | 24.06 ± 0.26bc | 27.38 ± 0.37 a | 25.21 ± 0.38b | 23.79 ± 0.23c | 24.64 ± 0.42bc | 24.43 ± 0.44bc | 22.75 ± 0.48c |
| Pupa mass (mg)      | 440.38 ± 3.74a | 397.77 ± 3.89c | 394.12 ± 5.16c | 421.76 ± 3.72b | 402.54 ± 5.10bc | 386.45 ± 5.12c | 394.97 ± 6.26c |
| Adult               | 13.15 ± 0.38a  | 11.68 ± 0.51ab | 11.51 ± 0.68ab | 10.88 ± 0.38ab | 10.98 ± 0.58b | 12.55 ± 0.81b | 10.82 ± 0.95b |
| Total generation    | 29.42 ± 0.51b  | 35.33 ± 0.75a | 30.97 ± 0.76b | 28.37 ± 0.44bc | 29.66 ± 0.76b | 29.7 ± 0.87b | 26.19 ± 0.84c |
| Sex ratio (♂:♀)     | 0.97 ± 0.12b   | 1.04 ± 0.15a   | 1.24 ± 0.21a  | 1.48 ± 0.17a  | 1.74 ± 0.32a | 1.16 ± 0.33a | 0.96 ± 0.57a |
| Pre-oviposition      | 6.70 ± 0.36a   | 5.69 ± 0.45ab  | 5.40 ± 0.69b  | 4.68 ± 0.38b  | 5.38 ± 0.49ab | 4.00 ± 0.88b | 6.13 ± 0.64ab |
| Post-oviposition     | 3.32 ± 0.27a   | 1.88 ± 0.47ab  | 1.57 ± 0.77ab | 8.88 ± 0.49b  | 5.91 ± 0.32b | 3.02 ± 0.27b |
| Eggs deposited per female | 1.028 ± 0.30 | 80.79a | 838.43 ± 116.74ab | 511.94 ± 157.27ab | 647.02 ± 103.67ab | 529.33 ± 132.20b | 316.78 ± 130.39b | 99.5 ± 40.76b |

Note: Values in the same row followed by different lowercase letters indicate a significant difference among doses (one-way ANOVA, Tukey’s HSD, p < 0.05).

when the irradiation dose ≥50 Gy, the sterility rate of the F1 generation with two mating types was significantly higher than that of the control (N5 × T2: F5,159 = 8.973, p < 0.001; T5 × T2: F5,159 = 10.238, p < 0.001). The sterility rate of the 100 Gy, 125 Gy, and 150 Gy treatment groups was significantly higher than that of the control group when the mating mode was T2 × N5 (F5,159 = 5.654, p < 0.001) (Table 4).

Survival analysis showed that the age-specific survival rate curves (l) of the population under different irradiation doses had highly significant differences (χ² = 904.655, df = 6, p < 0.0001), and there was a significant linear trend (χ² = 697.500, df = 1, p < 0.0001) (Figure 3). The m curve and the ln_m curve showed that the peak reproductive age of insects in the treatment group and nonirradiated insects was similar, the maximum age-specific fecundity (m) for the 0–150 Gy treatment group was, respectively, on the 35th, 34th, 33rd, 35th, 33rd, 33rd day, and the age-specific pregnancy rate (l_m) maximum was, respectively, on 32nd, 32nd, 33rd, 32nd, 33rd, 33rd, 33rd day. For the 25–150 Gy doses, the age-specific pregnancy rate of female adults (l_m) decreased as the dose increased (highest
TABLE 4  Mean (±SE) mating rate and sterility rate for F1 offspring adults of Spodoptera litura by different mating types: \( T \times N \), \( T \times T \), and \( N \times N \) (N = normal individual whose parents were both unirradiated; T = F1 individual whose male parent was irradiated with 250 Gy dose of X-ray).

| Irradiation dose (Gy) | \( N \times T \) | \( T \times N \) | \( T \times T \) |
|----------------------|----------------|----------------|----------------|
|                      | Mating rate (%) | Sterility rate (%) | Mating rate (%) | Sterility rate (%) | Mating rate (%) | Sterility rate (%) |
| 0 (control)          | 55.59 ± 3a      | 34.46 ± 6.44c    | 55.59 ± 3a      | 34.46 ± 6.44c    | 55.59 ± 3a      | 34.46 ± 6.44c    |
| 25 Gy                | 64.44 ± 16.02a  | 57.65 ± 7.28bc   | 73.33 ± 10.18a  | 52.65 ± 6.11bc   | 72.22 ± 4.01a   | 60.61 ± 7.95bc   |
| 50 Gy                | 53.82 ± 11.78a  | 72.3 ± 7.34ab    | 55.56 ± 19.44a  | 65.36 ± 7.56abc  | 66.67 ± 13.33a  | 89.19 ± 5.47ab   |
| 75 Gy                | 63.19 ± 3.03a   | 79.49 ± 5.48ab   | 68.89 ± 12.37a  | 65.69 ± 7.52abc  | 51.52 ± 3.03a   | 79.77 ± 7.16ab   |
| 100 Gy               | 53.33 ± 21.43a  | 79.8 ± 5.8ab     | 72.02 ± 14.59a  | 83.74 ± 5.85ab   | 77.38 ± 4.29a   | 81.21 ± 5.57ab   |
| 125 Gy               | 50.43 ± 17.09a  | 87.68 ± 5.53a    | 54.76 ± 2.38a   | 83.71 ± 7.03ab   | 46.67 ± 13.33a  | 99.9 ± 0.06a     |
| 150 Gy               | 54.17 ± 4.17a   | 92.09 ± 5.53a    | 55 ± 16.07a     | 94.46 ± 2.22a    | 53.33 ± 17.64a  | 98.02 ± 1.21a    |

Note: Values in the same column followed by different lowercase letters indicate a significantly difference among doses (one-way ANOVA, Tukey’s HSD, \( p < 0.05 \)).

3.6 Competitive release ratio between irradiated males and nonirradiated males

There were significant differences in the number of eggs laid by females after different release ratios of irradiated males (75 Gy) and nonirradiated males (\( F_{12,82} = 2.515, p = 0.007, \) Figure 4A). The sterility rate increased significantly with an increase in proportion of irradiated males (\( F_{12,82} = 11.914, p < 0.001; \) Figure 4B). When the irradiation release ratio (\( T/N: N\times T \)) was 5:1 to 12:1, the sterility rate (59.85%–88.44%) was significantly higher than that in the control group (24.55%) (\( N = \) nonirradiated, \( T = \) irradiation treatment). The growth dynamics in relation to the sterility rate conformed to the logistic curve as follows (Figure 4C).

\[
y = \frac{100}{1+e^{-k(x-x_0)}}
\]

where \( y \) is the sterility rate, \( x \) is the release ratio, and \( k \) is a growth rate constant. Thus, the turning point of the graph occurs when the radiation insect to normal insect ratio reaches 12.61. The ideal release ratio should be greater than or equal to 12.6:1:1.

4 Discussion

After \( S. \) litura pupae (8 day old) were irradiated with 25–150 Gy X-rays, our analyses of pupal survival, reproductive variables of adults, adult life span, flight ability, and offspring developmental durations showed that none of the doses altered the emergence, reproductive ability, adult life span, or flight ability of male \( S. \) litura. However, survival rate and fecundity of its offspring were reduced compared with nonirradiated controls, and the sex ratio of the F1 generation tended toward males. The X-ray of 25–150 Gy dose had no effect on the emergence rate of female pupae, but significantly affected their reproduction. However, a dose of 150 Gy still did not reach the point of female sterilization. According to the logistic curve fit, the appropriate sterilizing effect would be achieved with 71.26 Gy in theory, and the best control effect could be achieved with a release ratio of 12.6:1:1 irradiated (75 Gy) males to nonirradiated males.

The type of irradiation source and the age of insects can affect the sterilization dose of insects, according to the studies on the irradiation sterility of a range of species (IDIDAS Database: https://nucleus.iaea.org/sites/naipc/ididas/Pages/Browse-IDIDAS.aspx). With a similar research on \( S. \) litura also presented this point. In 1974, researchers discovered that exposing 3–5-day-old male pupae of \( S. \) litura to an 80 Gy dose of \( \gamma \)-rays sterilized all pupae (Mochida and Miyahara, 1974). When 3-day-old \( S. \) litura pupae were irradiated with a 150 Gy electron beam, the hatching rate of the eggs produced by their offspring was 0% (Yun et al., 2014). Evaluating the radiation biological characteristics of insects while using different radiation sources than in prior studies is critical. In addition, when young pupae were used, the impact of insect sterility could be achieved at a lower dose, but pupae mortality was considerable. As a result, using older pupae for irradiation would be a more cost-effective way to increase insect pupae survival after irradiation (Bushland and Hopkins, 1951; Ouye et al., 1964; Ducoff and Bosma, 1966). Among the numerous studies on irradiation-induced sterility in \( S. \) litura, few have focused on the effect of X-rays. We therefore focused here on X-ray irradiation of 8-day-old male pupae of \( S. \) litura and determined that the appropriate sub-sterilizing dose is around 75 Gy. The sub-irradiation dose for males was usually equal to the sterilization dose for females of this species, because fertile radiation females were thought to cause unpredictably significant population increase in the wild (Bloem et al., 1999). In our study, we discovered that even at the dose of 150 Gy employed in the experiment, the female could not be sterilized. Seth and Sehgal (1993) found that 100 Gy and 130 Gy...
FIGURE 3
Age-specific survival rate ($l_x$), age-specific fecundity of female adult ($f_x$), age-specific fecundity ($m_x$), and age-specific maternity ($l_xm_x$) of $F_1$ generation of *Spodoptera litura* after male parent was irradiated with different doses of X-rays. (A) Survival rate of $F_1$ generation of nonirradiated parents ($N \times N$). (B–G) $F_1$ generation after mating with nonirradiated females and males irradiated with 25 Gy, 50 Gy, 75 Gy, 100 Gy, 125 Gy, or 150 Gy doses of X-rays during pupal stage ($N \times T$) (N, nonirradiated; T, irradiation treatment).
doses of γ-ray irradiation were good sub-sterilisation doses of S. litura, but that the γ-ray of 130 Gy did not reach the sterilization dose of females, which is similar to our findings. That was because studies have showed that after 130 Gy of γ-ray irradiation, the male sperm competitiveness of S. litura decreased (Seth et al., 2002). Similar effects have been observed in other Lepidoptera insects. In Spodoptera frugiperda, males exposed to 100 Gy γ-ray dos exhibit better sperm competitiveness than males exposed to 150 Gy dose (Carpenter and Gross, 1993). As a result, if the female sterilization dose is used as the male sub-sterility dose, the competitive ability of S. litura may be seriously impacted. As a result, populations for genetic sex separation (GSS) from released insects should be developed before SIT technology can be used on a large scale, such as C. capitata, Bombyx mori, P. gossypiella (Peloquin et al., 2000; Tamura et al., 2000; Sahara et al., 2003; Augustinos et al., 2017). Furthermore, flying ability is an essential factor to be concerned in the SIT program (Seth et al., 2016b). According to Stephens et al. (2006), the flight ability of sterile painted apple moths was not significantly affected after being irradiated with γ-rays at 100 Gy. The flight capacity of Teia anortoides was unaffected by γ-ray radiation of 160 Gy (Suckling et al., 2002). The flying ability of S. frugiperda was not affected when the dose of X-ray was lower than 300 Gy (jiang et al., 2022). Their findings are nearly identical to ours. Lepidopteran insects are more resistant to radiation than insects in other orders (LaChance et al., 1975) because, after irradiation, the shattered chromosomal fragments attach to the centromere and are passed to the next generation through germ cells (Proverbs and Newton, 1962; Marec and Traut, 1993). As a result, using substerile doses to irradiate insects can not only inhibit the development of parental populations but also reduce the number of their offspring (Seth et al., 1997; 2016a). This inherited sterility has provided remarkable advancement in the control of lepidopteran pests, such as Trichoplusia ni and Helicoverpa zea (North and Holt, 1969; Carpenter and Gross, 1993). The reproductive peak of F1 females was similar to that of normal insects, and there was no significant variation in the development duration of F1 generations in different stages by irradiation with the dose range of 25 Gy–75 Gy in this study. This

### TABLE 5 Means (±SE) for life table parameters of Spodoptera litura F1 generation after male parent was irradiated with different X-ray doses during pupal stage.

| Irradiation dose (Gy) | Net reproductive rate R₀ | Intrinsic rate of increase r | Mean generation time T | Finite rate of increase λ |
|-----------------------|--------------------------|-----------------------------|------------------------|--------------------------|
| 0 (control)           | 163.032 ± 19.141a        | 0.144 ± 0.004a              | 35.258 ± 0.244a        | 1.155 ± 0.004a           |
| 25 Gy                 | 108.943 ± 21.640a        | 0.140 ± 0.007a              | 33.304 ± 0.438c        | 1.150 ± 0.008a           |
| 50 Gy                 | 22.327 ± 8.409bc         | 0.089 ± 0.013b              | 33.905 ± 0.603bc       | 1.093 ± 0.014bc          |
| 75 Gy                 | 38.022 ± 7.690b          | 0.103 ± 0.006b              | 35.139 ± 0.404ab       | 1.108 ± 0.007b           |
| 100 Gy                | 13.806 ± 4.531c          | 0.074 ± 0.010c              | 34.484 ± 0.458abc      | 1.077 ± 0.011cd          |
| 125 Gy                | 4.944 ± 2.501cd          | 0.046 ± 0.021cd             | 35.431 ± 1.488abc      | 1.042 ± 0.021de          |
| 150 Gy                | 0.792 ± 0.410cd          | 0.006 ± 0.019d              | 35.272 ± 1.076a        | 0.989 ± 0.019e           |

Note: Values in the same row followed by different letters differed significantly (paired bootstrap test, p < 0.05).

### FIGURE 4

Effects of different release ratios of substerilized males (irradiated with 75 Gy dose of X-rays) and nonirradiated males on fecundity (A), sterility rate (B) and logistic curve of sterility rate of Spodoptera litura (C). Data are means ± SE, significant differences (one-way ANOVA, Tukey’s HSD; p < 0.05) among doses for a variable are shown by different lowercase letters.

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shows that irradiated insects’ reproduction behavior can be synchronized with that of normal insects in the wild after being released in the field. The same effects were observed in research of Helicoverpa Armigera and A. transfretella F1 generation developmental stages (Kim et al., 2015; Light et al., 2015). The F1 generation of irradiated insects in this study still showed high sterility (>60%) and the mating rate was unaffected, confirming that 75 Gy was a suitable dose of sterility. Similar results were reported when S. litura was irradiated with gamma rays, the substerilizing irradiation 0–24 h old male adults of S. litura with 100 Gy and 130 Gy of γ-ray used by Seth achieved a higher sterility rate for the F1 generation than for the parents, and 130 Gy also affected larval and gonadal development of the F1 generation (Seth et al., 2000; Seth and Sharma, 2001).

The goal of SIT is to inhibit wild populations from expanding by providing large populations of irradiated individuals to mate with wild populations. As a result, determining the appropriate release ratio of irradiated males to nonirradiated wild males so that a substantial number of irradiated males compete with the wild population to suppress the pest population is essential for the highest efficiency (Bloem and Carpenter, 2001; Bloem et al., 2005). The release ratio is considered as part of the SIT program. Anopheles arabiensis exhibits better mating competitiveness when three times more irradiated males were exposed to 70 Gy doses of γ-rays than normal males, according to Helinski and Knols (2009). The hatching rate of A. albopictus females was less than 20% when the ratio of irradiated males (irradiated by γ-rays of 35 Gy dose) to normal males was 10:1. In this study, the release rate of male insects was also investigated. When the irradiated male moths (exposed to a 75 Gy X-ray during the pupal stage) to normal male release ratios were 10:1, 11:1, and 12:1, the sterility rate was greater than 85%, this is comparable to the effectiveness of pesticides such as profenofos and imidacloprid in controlling S. litura (Abbas et al., 2012; Abbas et al., 2014). In order to achieve a better control effect, we used logistic fitting to confirm that the rapid increase in sterility rate ended at a release ratio of 12.6:1, and that induced sterility rate might theoretically reach 91%. S. litura population growth will be severely hampered by this release ratio. An increase in the release rate is required to limit population expansion in many sterile insect release studies. After irradiating Anastrepha fraterculus with a 40 Gy X-ray dose, the ideal release ratio of irradiated male to normal male is 50:1 (Mastrangelo et al., 2018). The induced sterility rate can be increased to more than 70% by raising the release ratio of irradiated C. capitata male to normal male to 100:1 (Rendón et al., 2004). As mentioned earlier, with X-ray doses of 75 Gy, we theoretically determined the best release ratio to be 12.6:1 irradiated to nonirradiated males. However, because this ratio was determined in the laboratory, field testing is needed to determine the appropriate release ratio (Seth and Sehgal, 1993; Holmeyer et al., 2005).

Using SIT alone cannot adequately control insects that migrate long distances, but the release of substerilized pests is compatible with other pest control methods (Knipling, 1964), and can be part of synergistic management that includes, for example, the release of substerilized pest insects with natural enemies of the pests (Seth et al., 2009; Cagnotti et al., 2016). Area-wide integrated pest management (AW-IPM), in conjunction with SIT, has also provided remarkable control of lepidopteran pests, using Bacillus thuringiensis to control T. anartoides (Suckling et al., 2007) and using Bt cotton to eradicate P. gossypella (Saunders) in the continental United States and northern Mexico (Tabashnik et al., 2021). Such strategy also is good for the control of S. litura, which survives in winter season only in the tropical area of China (such as Hainan, Guangxi, Yunnan) (Fu et al., 2015; Bei et al., 2001). As a result, the activity range of S. litura is quite limited and isolated in the winter season, it should be a good option to manage the pest using the SIT strategy. The Bt corn planting is now legal in China (http://www.moa.gov.cn/ztzl/zyjqwgs/spzx/201912/t20191230_6334015.htm). By planting Bt corn in areas where S. litura overwinters and releasing sterile males in the winter in those areas, S. litura damage can be reduced there and nationwide as the moths migrate in the spring.

Although the radiation biology of S. litura was investigated in this study, there are still a number of issues to be resolved before the insect is released on a broad scale. Low-energy X-ray irradiators had a lower dose rate than γ-ray irradiators, and the relative efficiency of 30 kV–280 kV X-rays is about 8.9% lower than 60Co (Hjørringgaard, et al., 2020). This implies that X-rays might take a longer time to irradiate than 60Co. Current research indicated that the role of low-energy X-rays on insects was quite comparable to that of γ-rays, which could achieve high sterility (Tamada et al., 2014; Kumano et al., 2018). Recently, the X-ray irradiator had been upgraded, tweaked, and improved on a routine basis (Mastrangelo et al., 2010; Fan and Niemira, 2020). Furthermore, although there is a feasible feed for large-scale rearing of S. litura (Gupta et al., 2005), compared to easier rearing of dipteran insects, rearing S. litura on a large scale is expensive, so efficient, cheaper rearing methods need to be developed. Overall, X-ray irradiation technology to substerilize S. litura is safe and “green,” may play an important and special role compared to existing control methods to the pest. Therefore, there is a great necessity to take a field trial for establishing a mature method for deployment in a large-scale in southern China.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

KW and SJ designed the project. SJ and S-SJ did the indoor experiment, and H-YZ irradiated the experimental insects. SJ, X-WF, X-MY, and KW analyzed the data. SJ and KW wrote and edited the manuscript. All authors contributed to the article and approved the submitted version.
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Conflict of interest

The Author H-YZ was employed by the Hebi Jiadiou Industry and Trade Co., Ltd.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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