Radiation biology of *Eldana saccharina* (Lepidoptera: Pyralidae)

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Abstract

Laboratory-reared male and female *Eldana saccharina* Walker (Lepidoptera: Pyralidae: Gallerinae)—a major pest of sugarcane (*Saccharum* spp.; Poales: Poaceae) in South Africa—were exposed to increasing doses of γ-radiation to assess this species' suitability for the sterile insect technique as part of an area-wide integrated pest management (AW-IPM) program. Irradiated male and female moths were crossed with non-irradiated counterparts and irradiated counterparts at the same radiation dose. Male and female moths were treated with radiation doses of 150, 200, 250, 300 and 350 Gy, and the following crosses were made: irradiated males (T♂) mated with untreated females (U♀) and irradiated females (T♀) mated with untreated males (U♂). Males and females of the T♀ × T♂ cross were exposed to the same radiation doses except in the 350 Gy treatment. Fertility (egg hatch) declined significantly with increasing doses of radiation in all crosses. Female progeny from the T♀ × U♂ and T♀ × T♂ crosses were more sensitive to irradiation than female progeny from the U♀ × U♂ and U♀ × T♂ crosses and were completely sterile when treated with either 200 Gy or 150 Gy. Treated males mated with untreated females still had a residual fertility of 0.19% when exposed to 350 Gy of radiation. The fertility of *E. saccharina* is therefore sensitive to increasing doses of ionizing radiation and this species is a suitable candidate for further development of the SIT as a component of an AW-IPM program. The fecundity of untreated *E. saccharina* females mated with irradiated males was not affected by radiation. The availability of a great number of infertile eggs can be regarded as a benefit in a program where natural enemies are combined with the SIT because non-fertile eggs can provide additional hosts for egg parasitoids and be a food source for predators.

Key Words: fertility; fecundity; sugarcane borers; gamma rays; dose response; sterile insect technique

Resumen

Machos y hembras de *Eldana saccharina* Walker (Lepidoptera: Pyralidae: Gallerinae) criados en el laboratorio—una de las principales plagas de la caña de azúcar (*Saccharum* spp.; Poales: Poaceae) en Sudáfrica—fueron expuestos a dosis crecientes de γ-radiación para evaluar si esta especie es adecuada para la técnica de los insectos estériles como parte de un programa de manejo de integrado de plagas en todo el área (MIP-TA). Polillas machos y hembras fueron irradiados y luego cruzados con sus contrapartes no irradiados y contrapartes irradiados en la misma dosis de radiación. Las polillas machos y hembras fueron tratados con dosis de radiación de 150, 200, 250, 300 y 350 Gy, y se hicieron los siguientes cruces: machos irradiados (T♂) aparearon con hembras no tratadas (U♀) y hembras irradiadas (T♀) apareadas con machos no tratados (U♂). Los machos y las hembras del cruce T♀ × T♂ fueron expuestos a las mismas dosis de radiación, excepto en el tratamiento de 350 Gy. La fertilidad (eclosión de los huevos) se redujo significativamente al aumentar la dosis de radiación en todos los cruces. La progenie de las hembras de los cruces de T♀ × U♂ y de T♀ × T♂ fueron más sensibles a la irradiación de la progenie hembra de los cruces U♀ × U♂ y de U♀ × T♂ y estaban completamente estéril cuando se tratan con ya sea 200 Gy o 150 Gy. Los machos tratados se aparearon con hembras no tratadas todavía tenían una fertilidad residual de 0.19% cuando fueron expuestos a 350 Gy de radiación. Entonces, la fertilidad de *Eldana saccharina* es sensible a dosis crecientes de radiación ionizante y es un candidato adecuado para un mayor desarrollo del componente de la TIE en un programa MIP-TA. La fecundidad de las hembras de *E. saccharina* no tratadas apareadas con machos irradiados no fue afectada por la radiación. La disponibilidad de un gran número de huevos infértiles puede ser considerado como un beneficio en un programa donde los enemigos naturales se combinan con la TIE porque los huevos no fértiles pueden proveer hospderos adicionales para los parasitoides de huevos y ser una fuente de alimento para los depredadores.

Palabras Clave: fertilidad; fecundidad; barrenadores de caña de azúcar; rayos gamma; respuesta a la dosis, técnica del insecto estéril

Informed decisions need to be made on the correct ionizing radiation dose to induce sterility in the wild population for an effective sterile insect technique (SIT) program to be implemented against a target insect pest (Bakri et al. 2005). Dose responses are species-specific and therefore need to be tested on each species considered a target before a program that contains a SIT component can be implemented against a pest insect (Robinson 2005). Dose response curves for sterility by exposure to different doses of radiation are measured using fecundity (number of eggs oviposited) and fertility (egg hatch) as parameters, from pairs of adults mated in the following combinations, 1) irradiated females with non-irradiated males and 2) non-irradiated females with irradiated males. The shape of a dose-response curve, which is calculated by measuring fertility of insects exposed to increasing doses of radiation, is characteristic of the types of initial chromosomal lesion that occurs (Klassen 2005). There is a linear relationship between the dose response and the induction of dominant lethal effects. At higher doses,

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the curve reaches 100% sterility asymptotically, due the induction of multiple lethal events in the same cell. The shape of the curve also assists in selecting a dose for release of sterile insects (Robinson 2005).

In an area-wide integrated pest management (AW-IPM) program with a SIT component (Klassen 2005; Vreysen et al. 2007) it is important that the released females have no residual fertility, as this may increase the wild population. Residual fertility in males is less important as this will only reduce the rate at which the population is suppressed. Male and female insects often respond differently to radiation because sperm are haploid post-meiotic cells and eggs are pre-meiotic (Robinson 2005). In the female, mature eggs are more resistant to radiation as compared with oocytes. Consequently, a radiation dose that induces full sterility in mature eggs can lead to cessation of oogenesis and an increase in the lifespan of the female. This is generally not a problem, unless the female stage is a pest such as the tsetse fly (*Glossina* spp. Wiedemann (Diptera: Glossinidae)) (Robinson 2005). Generally female insects are more sensitive to radiation than males, and it should therefore be possible to select a radiation dose that ensures that all released females are fully sterile. In order to maximize genetic damage to mature germ cells and minimize somatic damage, insects should be irradiated as late as possible in the development pathway, ideally as fully differentiated adults, where insects are most resistant to somatic damage. Certain somatic cells, especially in the gut, continue to divide and this can compromise their competitiveness (Robinson 2005).

The proportion of females in a wild population that is rendered sterile by a given number of sterile males released depends on both the released male's residual fertility and their success in competing with wild males to mate with wild females. Therefore, to optimize the balance between competitiveness and genetic sterility, it may be advisable to select a radiation dose that maximizes the successful mating of released sterilized males with wild females. Of course, the released irradiated males must have a level of sterility sufficient to cause a downward trend in the wild population at over-flooding ratios that are practical. The selected optimal radiation dose might therefore be one that does not give 100% sterility (Robinson 2005).

Because Lepidoptera are very radiation resistant (Carpenter et al. 2005), higher doses of radiation may result in less competitive individuals and can induce unfavorable physiological and behavioral changes. These include failure of irradiated males to disperse widely enough, to seek out appropriate niches, to compete with wild males for mates, to respond to calling mates and to mate, to form a spermatophore and to transfer sufficient sterile sperm to the female (North 1975; Omar & Mansour 1993; Carpenter et al. 2005).

This study aimed to determine the effect of increasing doses of radiation on the fertility and fecundity of *Eldana saccharina* Walker (Lepidoptera: Pyralidae: Gallerinae)—a major pest of sugarcane (*Saccharum* spp.; Poales: Poaceae) in South Africa—in order to assess whether this pest is a suitable candidate for the SIT in an AW-IPM program in the South African sugar industry. This study also aimed to determine at which radiation dose *E. saccharina* females are sterile, so that irradiated females that are released into sugarcane do not oviposit fertile eggs.

Materials and Methods

COLONY REARING CONDITIONS

Eldana saccharina was routinely reared at the South African Sugar Cane Research Institute (SASRI) using the methods described by Graham & Conlong (1988). The modified *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) diet described by Graham & Conlong (1988) was further modified by Gillespie (1993), and ferric citrate and formaldehyde were

removed (Walton & Conlong 2016). Plastic multicell trays (32 cavities) containing 8 mL of artificial diet in each cell and developing *E. saccharina* larvae were routinely maintained in rearing rooms held at 28 ± 2 °C, 75 ± 5% RH and 0:24 h L:D photoperiod for approximately 619 degree days (DD), which is the time for peak pupal production (Way 1995).

For the assessment of parental fertility, pupae were harvested from artificial diet after approximately 619 DD of development, and placed singly into individual empty cells of the multicell trays. The trays were wrapped with cling wrap (Handywrap®, Chipkins Catering Supplies, P.O. Box 12767, Jacobs, 4026, KZN, South Africa) and the wrap was aerated with a pin-prick above each cell. This ensured that virgin adults were available to be paired, as each sex emerged singly in the separate cells. The packed *E. saccharina* pupae were transported by air and road to the Deciduous Fruit Producer's Trust (DFPT) mass-rearing facility, Stellenbosch, Western Cape, South Africa (S 33° 55' 26", E 18° 52' 25") where the irradiator was located on the Agricultural Research Council (ARC) Infruitec premises. Emerged adults of the same sex and < 24 h old were each placed into a single cell of a multicell tray and exposed to increasing doses of γ-radiation delivered at a rate of 3.7536 Gy/min from a ⁶⁰Co source. The multicell tray was wrapped with cling wrap and aerated with a pin-prick above each cell. Ten males and 10 females were exposed to γ-radiation doses of 100, 150, 200, 250, 300 and 350 Gy. Five males from each irradiated group and 5 females from each irradiated group (labeled "T" for "Treated by irradiation") were mated with adults of the opposite sex that did not receive any radiation (labeled "U" for "Untreated"). The remaining 5 males from each irradiated group were mated with the remaining 5 females that were irradiated at the same radiation dose. Crosses were therefore made as follows at each radiation dose, U♀ × T♂; T♀ × U♂ and T♀ × T♂. This resulted in 5 replicates for each cross at each radiation dose. There was one exception, i.e., at 350 Gy, the T♀ × T♂ cross was not made, based on unpublished data acquired the previous year that no progeny emerged from this cross. Five pairs of untreated adults were crossed as a control, U♀ × U♂.

Pairs were placed individually into a 500 mL paper cup for mating, with a pleated cardboard oviposition substrate (50 × 10 mm when pleated 5 times), secured with a paperclip to maintain the pleats, and a 10 mm cotton dental wick soaked with water for the adults. Plastic lids were then placed on the paper cups. Moths were held at the DFPT laboratories (26 ± 2 °C; 65 ± 5% RH; 16:8 h L:D photoperiod) for mating and oviposition. Oviposition substrates were changed daily until the female died or until the pair was 5 days old (as by then the majority of eggs had been oviposited) (Dick 1945; Betbeder-Matibet 1981; Sampson & Kumar 1985; Walton & Conlong 2016). The removed oviposition substrates were placed into re-sealable transparent plastic bags and labelled with the date, sex irradiated (either male or female) and radiation dose received. After oviposition was complete, females were killed by freezing and dissected for spermatophore presence in the bursa copulatrix to assess mating status. The eggs oviposited on the substrates were counted to measure fecundity and the substrates were placed back into their corresponding plastic bag for neonate emergence. The eggs were packaged in their labelled plastic bags and put into a cardboard box and transported back to SASRI at Mount Edgecombe, KwaZulu-Natal (S 29° 42' 24", E 31° 02' 45") by air and road. Eggs were placed into an incubator at SASRI (26 ± 2 °C; 60 ± 5% RH; 0:24 h L:D photoperiod) for hatching. The neonate larvae hatching from the eggs were counted to measure fertility. For the measurement of development time, survival and sex ratio, hatched neonate larvae were inoculated onto the same artificial diet described above, dispensed in 25 mL plastic vials with aerated screw-cap lids, to prevent larvae of the various treatments from escaping. Due to space constraints and to avoid mixing the experimental larvae with the routine colony at SASRI, the plastic vials containing the neonate larvae were placed in a separate temperature controlled rearing room (26 ± 2

°C; 70 ± 5% RH; 8:16 h L:D photoperiod). Developing larvae were checked daily for pupation and adult emergence.

STATISTICAL ANALYSES

Genstat 12.1© (2009) was used for REML (Residual Maximum Likelihood) variance component analysis. The statistic is reported with a χ^2 value. Sigmaplot 9.0© (2004) was used for regression analysis and calculation of mean development time, percent survival and sex ratio.

Assessment of Parental Fecundity and Fertility

Because not all *E. saccharina* pairs were mated (Table 1), the data were unbalanced and an ANOVA test could not be used. A REML variance component analysis was performed on the fecundity and fertility data from these pairs with dose and type of cross as variables. The fecundity data were normal, while the fertility data were square root transformed to attain normality. For fertility, where a dose by type of cross interaction was found to be significant, data from each type of cross were subjected to a polynomial regression.

Development Time of F_1 Neonates to Adulthood

Individual F_1 development time from each parental cross pair was not followed to adult emergence; instead the data were pooled at each radiation dose for each type of parental cross. The average development time at each dose for each type of cross was not normal and could not be transformed to attain normality for the purposes of a regression analysis. Because of this, data were not statistically analysed.

Survival of F_1 Neonates to Adulthood

As for development time individual repetitions were not followed through for this assessment. Total survival to adulthood was calculated from neonates placed onto artificial diet for each radiation dose.

Sex Ratio of F_1 Adults

As for survival of F_1 neonates, total % males in the surviving offspring was calculated collectively for each radiation dose from the total adults that emerged from the neonates placed onto artificial diet for each radiation dose.

Results

PARENTAL FECUNDITY

There was a significant interaction between the dose and type of cross on mean fecundity per female with increasing radiation dose (χ^2 = 18.66; df = 9; P = 0.05) (Fig. 1). Females were more sensitive to radiation as compared with males, as treated females mated with untreated males oviposited fewer eggs with increasing radiation dose as compared

Table 1. Percentage of successfully mated *Eldana saccharina* pairs (5 crosses) with one of either sex irradiated with increasing doses of gamma radiation (T = Treated by irradiation; U = Untreated).

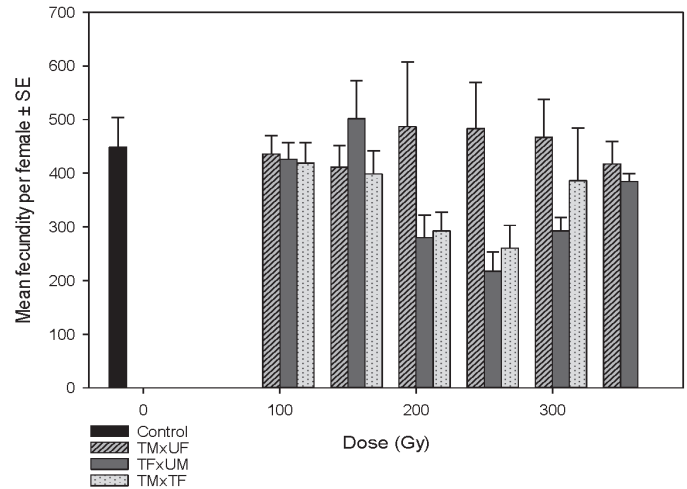| Dose	U♀ × U♂	U♀ × T♂	T♀ × U♂	T♀ × T♂
0	100			
100		100	80	100
150		100	100	100
200		100	80	100
250		100	80	80
300		100	100	60
350		100	100	

Fig. 1. Mean fecundity per *Eldana saccharina* female from 3 parental crosses treated with increasing radiation doses (T = Treated by irradiation; U = Untreated; M = Male; F = Female).

with untreated females that had mated with treated males at the same dose. Females treated with 200 Gy and mated with either untreated or treated males had a mean fecundity (± SE) of 280 ± 121.0 and 292 ± 34.7 eggs, respectively. The number of eggs oviposited was therefore reduced by half compared with the untreated control (448 ± 55.4 eggs), and treated males crossed with untreated females (486 ± 41.8 eggs).

Treating males and females with 250 Gy resulted in similar fecundity as with the 200 Gy treatment. Surprisingly, females treated with 350 Gy and crossed with treated males and females treated with 300 Gy and crossed with untreated and treated males (both crosses) showed a fecundity that was similar to that of the control (Fig. 1).

PARENTAL FERTILITY

There was a significant interaction of radiation dose and type of cross on fertility (χ^2 = 25.92; df = 9; P = 0.006). In the U♀ × T♂ cross, fertility declined significantly (y = 7.41 - 0.019x; F = 60.97; df = 34; P < 0.001; R^2 = 0.65) with increasing radiation dose, i.e., from 31.3% to 3.1% for males treated with 100 and 350 Gy, respectively as compared with the untreated control group (65.4%) (Fig. 2). In the T♀ × U♂ cross,
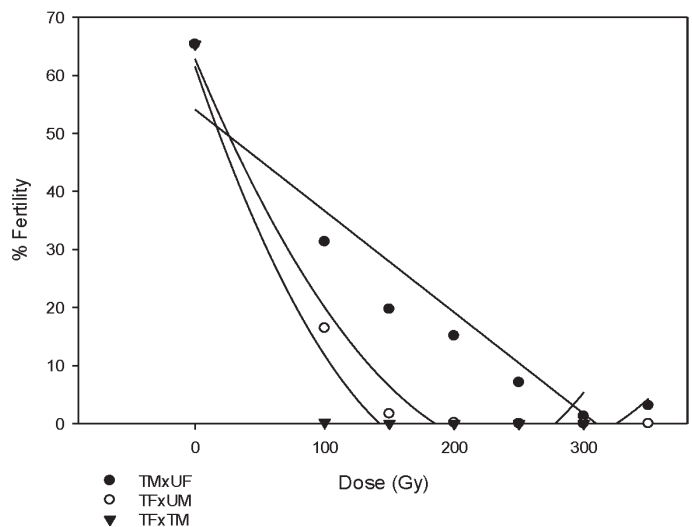

Fig. 2. Mean percent fertility of *Eldana saccharina* females from 3 parental crosses treated with increasing radiation doses (T = Treated by irradiation; U = Untreated; M = Male; F = Female).

fertility declined significantly with increasing radiation dose, as treated females oviposited even fewer fertile eggs than untreated females mated with treated males (i.e., 16.4%, 0.2% and 0.04% for females treated with 100, 200 and 300 Gy, respectively, as compared with the untreated control (65.4%)) (Fig. 2) ($y = 8.055 - 0.0611x + 0.00112x^2$; $F = 195.27$; df = 31; $P < 0.001$; $R^2 = 0.93$).

In the T♀ × T♂ cross, fertility was significantly reduced with increasing radiation dose and was for the same dose lower than the T♀ × U♂ cross, i.e., fertility was 0.23% and 0% for females treated with 100 and 200 Gy, respectively, as compared with the untreated control (65.4%) (Fig. 2) ($y = 7.698 - 0.0826x + 0.000202x^2$; $F = 192.34$; df = 26; $P < 0.001$; $R^2 = 0.94$). It is clear from these results that percentage fertility in all crosses declined significantly with increasing radiation dose and that females were more sensitive to radiation than males.

DEVELOPMENT TIME OF F$_1$ NEONATES TO ADULTHOOD

In the U♀ × T♂ cross, the resulting F$_1$ neonates showed an increased mean development time when parental males were treated with 250 and 300 Gy, i.e., 69.2 and 68.5 days, respectively as compared with 59.3 days for the untreated control (Fig. 3). However when males were treated with 350 Gy, mean development time was 60.5 days which was similar to the untreated control (Fig. 3). The development time, in days, of F$_1$ neonates from the T♀ × U♂ cross also increased at the higher radiation doses reaching a mean of 65.5 and 68.0 days for the 150 and 200 Gy treatments, respectively as compared with the untreated control group (Fig. 4). There was just one F$_1$ neonate that completed development from the T♀ × T♂ cross where a dose rate of 100 Gy was administered. Development time for this individual was 63 days compared with 59.3 days for the untreated control. Data for this T♀ × T♂ cross is thus not presented in Fig. 3 as there was only one data point.

SURVIVAL OF F$_1$ NEONATES TO ADULTHOOD

The total percentage survival of F$_1$ neonates, i.e., those reaching adulthood in the U♀ × T♂ cross declined significantly with increasing radiation dose, i.e., from 31.1% in the untreated control to 11.8% for those where the male parents had been treated with 350 Gy (Fig. 5) ($y = 29.445 - 0.579x$; $F = 14.64$; df = 1; $P = 0.012$; $R^2 = 0.70$). In the T♀ × U♂ cross, where the parental females had been treated with 200 Gy, survival of F$_1$ neonates increased to 66.6%,

Fig. 4. Mean development time to adulthood of *Eldana saccharina* F$_1$ neonates descendants from females treated with increasing radiation doses and mated with untreated males. (0 Gy, *n* = 450; 100 Gy, *n* = 61; 150 Gy, *n* = 13 and 200 Gy, *n* = 2).

but then declined to 0% when the dose was increased to 250 Gy. However, only 3 neonates hatched from eggs oviposited by females irradiated with 200 Gy and mated with untreated males. Of these 3 neonate larvae that hatched, 2 adults emerged. In the T♀ × T♂ cross survival of the F$_1$ neonates when the parents were treated with 100 Gy remained similar to that of the untreated control, i.e., 31.1% and 33.0% respectively, but when the dose was increased to 150 Gy, survival decreased to 0% (Fig. 5). Three F$_1$ larvae, descendants of parents treated with 100 Gy, were inoculated on the artificial diet, and of those, 1 individual emerged which indicated a survival of 33%, which was similar to the control (31.1%).

SEX RATIO OF F$_1$ ADULTS

The percentage of males emerging from F$_1$ neonate inoculations in the U♀ × T♂ cross increased from 52.8% in the untreated control to 60.7% for male parents irradiated with 150 Gy, but dropped to 35.7%, 50.0% and 50.0% when the dose was increased to 250, 300 and 350 Gy, respectively (Fig. 6). In the T♀ × U♂ cross, the percentage of surviving adult males declined to 0% with a treatment dose of 200 Gy. When males and females were treated with 100 Gy in the T♀ × T♂ cross, all offspring were male (Fig. 6).
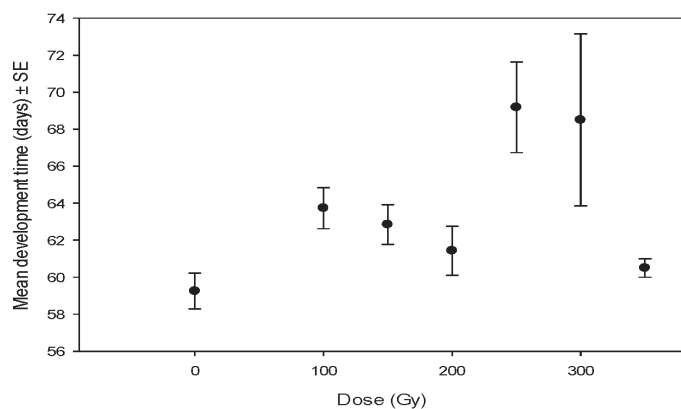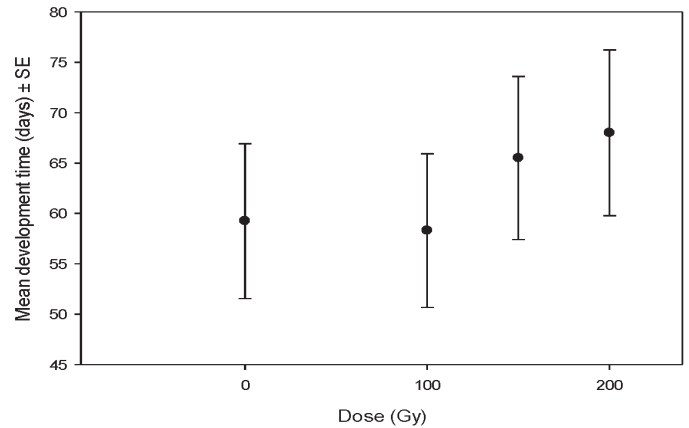

Fig. 3. Mean development time of *Eldana saccharina* F$_1$ neonates descendants from males treated with increasing radiation doses and mated with untreated females. (0 Gy, *n* = 450; 100 Gy, *n* = 182; 150 Gy, *n* = 112; 200 Gy, *n* = 47; 250 Gy, *n* = 14; 300 Gy, n = 4 and 350 Gy, *n* = 2).
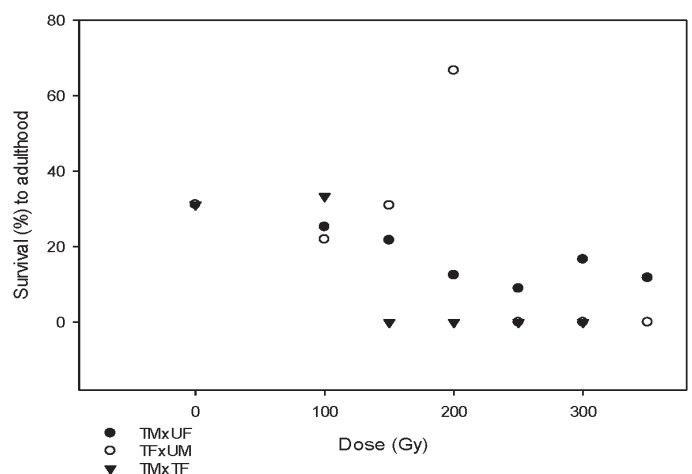

Fig. 5. Percentage survival of *Eldana saccharina* F$_1$ larvae from neonate to adulthood from 3 parental crosses with increasing radiation doses (T = Treated by irradiation; U = Untreated; M = Male; F = Female).
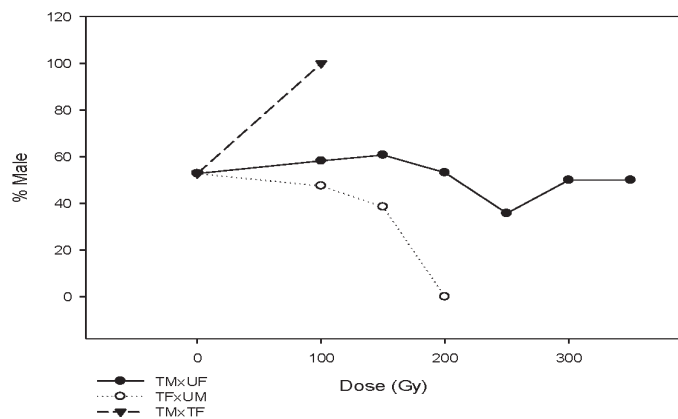
Fig. 6. Percentage males in the total *Eldana saccharina* F_1 larvae surviving to adulthood from 3 parental crosses with increasing radiation doses (T = Treated by irradiation; U = Untreated; M = Male; F = Female).

Discussion

Generally, irradiated *E. saccharina* females mated with untreated males oviposited fewer eggs than untreated females mated with treated males and the untreated control, when treated with radiation doses of 200 to 250 Gy. Thus, the fecundity of untreated *E. saccharina* females mated with irradiated males was not affected by radiation. This is consistent with the earlier published radiation biology studies on the codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae) (Bloem et al. 1999; Blomefield et al. 2010) and false codling moth (FCM) *Thaumatotibia leucotreta* Meyrick (Lepidoptera: Tortricidae) (Bloem et al. 2003), but not for the closely related sugarcane borer, *Diatraea saccharalis* F. (Lepidoptera: Crambidae), where untreated females mated with irradiated males produced significantly fewer eggs than the untreated control (Sanford 1976). However, in both tortricid species, treated female fecundity decreased almost linearly in response to increasing doses of radiation. In contrast, this type of cross in *E. saccharina*, especially with females treated with radiation doses of 300 and 350 Gy did not follow the trend reported for the tortricid species. In the cactus moth, *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae) the fecundity of irradiated females was not affected by increasing doses of radiation. This response was found for treated males and for treated females mated with their untreated counterparts respectively (Carpenter et al. 2001). A non-significant response of treated female fecundity of *E. saccharina* to increasing radiation dose indicates that there may be differences in fecundity response to radiation between insect families and this requires further investigation.

However, the result that the fecundity of *E. saccharina* does not decrease with increasing radiation dose is not detrimental to the implementation of a program that includes the release of sterile insects. The aim of the SIT is to induce sterility in the wild population, and therefore the number of eggs oviposited in the field is not important provided they do not hatch and cause damage to crops. However, the availability of a great number of infertile eggs can be regarded as a benefit in those programs where natural enemies are combined with the SIT as non-fertile eggs can provide additional hosts for egg parasitoids and be a food source for predators (Carpenter et al. 2005; Vreysen et al. 2006).

A linear decline in fertility with increasing radiation doses has been observed for males of the Indian meal moth, *Plodia interpunctella* Hübner (Lepidoptera: Pyralidae) (Ashcraft et al. 1972; Brower 1979), the pink bollworm, *Pectinophora gossypiella* Saunders (Lepidoptera: Gelechiidae) (LaChance et al. 1973; Henneberry & Clayton 1988), the sugarcane borer, *D. saccharalis* (Sanford 1976; 1977), the European corn

borer, *Ostrinia nubilalis* Hübner (Lepidoptera: Crambidae) (Nabors & Pless 1981), and the common cutworm, *Spodoptera litura* F. (Lepidoptera: Noctuidae) (Seth & Sharma 2001). These studies measured only fertility of untreated females mated with irradiated males and did not measure the impact of increasing radiation doses given to females on their fertility.

Where radiation effects have been assessed on both moth sexes, a linear decline in fertility with increasing radiation doses was shown for both irradiated males and irradiated females of the range caterpillar moth, *Hemileuca oliviae* Cockerell (Lepidoptera: Saturniidae) (Ward et al. 1986), *C. pomonella* (Bloem et al. 1999; Blomefield et al. 2010); *C. cactorum* (Carpenter et al. 2001); and *T. leucotreta* (Bloem et al. 2003). These studies showed that females were more sensitive than males to increasing doses of radiation. This is common in Lepidoptera, where fertility is a better indicator of radiation sensitivity than fecundity (North 1975; Carpenter et al. 2005). *Eldana saccharina* responded similarly, in that fertility was significantly reduced with increasing radiation dose in all parental crosses. Female *E. saccharina* were also much more sensitive to radiation than males, as fewer eggs oviposited by treated females hatched. The higher radiation sensitivity of *E. saccharina* females is an advantage for a potential SIT program over the above species in view of *E. saccharina*'s mating behaviour. In this species males release pheromones to attract females (Atkinson 1981), and released sterilised females will thus be able to respond to wild and sterile males. By them mating with wild males however, a certain percentage of the wild male population will be prevented from mating with wild females.

Other factors common to male Lepidoptera following radiation are extended F_1 development time, increased F_1 mortality during development and a sex ratio in favor of F_1 males (North 1975). These attributes have been reported for *D. saccharalis* (Sanford 1976, 1977), *P. gossypiella* (LaChance et al. 1973; Henneberry & Clayton 1988), *C. pomonella* (Bloem et al. 1999), and *T. leucotreta* (Bloem et al. 2003). The data on these parameters for *E. saccharina* were however quite variable because of the substantial reduction in parental fertility and poor survival of F_1 larvae with increasing radiation dose. Survival in the control group was also poor. This could have been due to handling stress at the time of inoculation. More data on development time, survival and sex ratio is therefore needed to test for statistical significance.

Some significant differences were found in *E. saccharina* F_1 survival as compared with other published literature. In the T♀ × U♂ cross, *E. saccharina* F_1 survival was 66.6% when parental females had been treated with 200 Gy (Fig. 5). North (1975) in contrast, reported that survival of lepidopteran F_1 progeny from irradiated parents was poor. However, data from the *E. saccharina* study was distorted because only 3 larvae hatched from this cross, 2 adults emerged and both were female.

Sex ratio of progeny of irradiated Lepidoptera males is generally male-biased (North 1975). In contrast, in the T♀ × U♂ cross, *E. saccharina* F_1 adult sex ratio remained relatively equal between males and females. Carpenter et al. (2001) similarly found that after radiation of *C. cactorum* parents, F_1 development time was not significantly affected and a shift in sex ratio towards males did not occur. In their study, they proposed that the decline in survival of the F_1 larval descendants from parents that had been treated with higher radiation doses affected their results. Similar results were obtained in this study with *E. saccharina,* as significantly fewer F_1 larvae survived to adulthood when male parents were treated with higher radiation doses, and so fewer replicates were completed. It is likely that in the field any larvae hatching from eggs oviposited by a female treated with a radiation dose of 200 Gy or higher would probably not survive due to predation (Leslie 1982) or other biotic and abiotic factors before completing development, because of their reduced fitness.

Conclusion

This study has shown that *E. saccharina* is sensitive to increasing doses of radiation, and that females are more sensitive to radiation than males. This is a particular advantage of this pyralid family, as *E. saccharina* males call the females. Wild females, thus being more competitive than released sterilized females, will be more likely to respond to laboratory reared, irradiated and released males in the field. This has been demonstrated in field cage studies, where it has also been shown that sterile males call earlier in the evening—and wild females respond to them—than wild males (Mudavanhu et al. 2016). The laboratory-reared irradiated females are significantly less fertile than males and almost completely sterile at 200 Gy, but are also available to mate with wild males in the release fields (which they may do as the wild females often have already responded to the calling sterile male), thereby potentially increasing the benefit of the sterile releases. *Eldana saccharina*, therefore, shows much promise as a potential candidate for being managed by programs that include a SIT component in the South African sugar industry.

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