Research Article

Received: 22 June 2024 Revised: 2 July 2025 Published online in Wiley Online Library: 6 August 2025

(wileyonlinelibrary.com) DOI 10.1002/ps.70068

Influence of overflooding ratios on fruit damage and population growth of *Thaumatotibia leucotreta* (Meyrick): implications for the sterile insect technique program

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Abstract

BACKGROUND: *Thaumatotibia leucotreta* (Meyrick) (Lepidoptera: Tortricidae) is a significant pest of citrus in South Africa. A key management strategy to control this pest is the sterile insect technique, which relies on releasing high numbers of sterile *T. leucotreta* in citrus orchards. The study investigated different release ratios of newly emerged sterile to fertile *T. leucotreta* adults (0:1, 10:1, 20:1, 40:1, 60:1), which were placed in insect-rearing cages and allowed to mate. After 4 weeks, the number of damaged fruit and larval entries per fruit were recorded. Infested fruits were incubated until all emerging F1 progeny were collected.

RESULTS: The cages with sterile *T. leucotreta* had significantly fewer infested fruits, larval entries, and F1 adults compared to the control. There was a negative correlation between the number of infested fruits, larval entries, and F1 adults with increasing ratios of sterile *T. leucotreta*. Control cages exhibited higher fecundity and fertility compared to treatment cages. The 40:1 and 60:1 treatment ratios showed the lowest per generation rate of increase (<1× from the parental to the F1 generation).

CONCLUSION: The study demonstrated that the 40:1 and 60:1 ratios were particularly effective, indicating that maintaining this ratio could significantly reduce the growth of the *T. leucotreta* fertile population, relative to lower ratios, albeit still effective.

Keywords: false codling moth; F1 progeny; fertility; fruit infestations; male competitiveness; sterile to fertile ratios

1 INTRODUCTION

The false codling moth (FCM), *Thaumatotibia leucotreta* (Meyrick) (Lepidoptera: Tortricidae), is an endemic pest to sub-Saharan Africa.[1] It is a polyphagous pest that infests a wide array of cultivated and wild fruits and nuts.[1] Amongst the cultivated fruit, citrus is a preferred host, particularly Navel oranges.[1–6] *Thaumatotibia leucotreta* infestation leads to premature fruit drop before harvest, and severe infestations can result in crop losses and potential rejections at packing houses.[1,7] However, advancements in field control measures over the past two decades have reduced the occurrence of severe infestations.[8–10]

One of the *T. leucotreta* management options is the use of the sterile insect technique (SIT). Globally, applied against a range of different pests, this technique has resulted in the production of higher-quality agricultural products, increased crop yields, created job opportunities, and expanded trade routes.[11,12] SIT is an autocidal pest control strategy that involves mass-rearing, sterilization, and release of sterile insect pests to mate with wild fertile insects resulting in pest suppression, eradication, or containment.[13,14] This technique is regarded as environmentally benign, because of its autocidal mode of action, eliminating the need for pesticides, and has led to its widespread adoption in pest control efforts worldwide.[11,13] In South Africa, SIT is currently being practiced in the Western Cape, Eastern Cape, and Northern Cape

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Provinces, to control *T. leucotreta*, thereby suppressing its population.[15,16]

The primary goal of SIT is to induce sterility in wild fertile populations as a way of controlling pests.[17–19] However, the effectiveness of SIT is dependent on various factors, including the quality of irradiated males, mating competitiveness and the overflooding ratio (OFR). Overflooding ratio involves the ratio of sterile insects released to the wild, fertile insect population in a target area, such as the orchards.[7] Ensuring that the ideal sterile-to-wild ratio is maintained is crucial for enhancing the effectiveness of most SIT programs. Therefore, considering the findings from the literature,[7,20] a study was conducted to determine the appropriate release ratio for *T. leucotreta* using walk-in field cage experiments. Newly emerged adult *T. leucotreta*, subjected to either 150 or 200 Gy gamma radiation, were released into the cages at ratios of five sterile to one fertile individual or 10:1 for a duration of 4 weeks. In control cages, only fertile moths were released. Specifically, the treatment with 150 Gy and a ratio of 10:1 had the lowest average number of fertile F1 adult females and males. Likewise, this treatment also exhibited the lowest rate of increase per generation (<1 from the P1 to F1), suggesting that maintaining *T. leucotreta* releases at this dosage and ratio in the field would suppress the growth of the fertile population. Consequently, an OFR of at least 10 sterile males to one wild male (10:1) was established as the benchmark ratio for effective *T. leucotreta* management.[7]

However, it is crucial to maintain the fitness of the released insects to enhance their mating competitiveness. Mating competitiveness pertains to the ability of released sterile males to successfully compete with wild males in order to mate with wild females, resulting in the production of non-viable eggs.[21–23] This is an important aspect to consider, as achieving high numbers of low-quality sterile insects may affect the effectiveness of the technique. The quality and capacity of mass-produced and sterilized males to mate with wild females play a crucial role in determining the success of SIT.[24,25] In various lepidopteran and dipteran species, improvements in the quality of sterile insects have been achieved by reducing the dose of ionizing gamma radiation. This has been recorded in the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae),[26] the fall armyworm, *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae),[27,28] the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae)[29–32] 32 and the spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae).[18,19]

The OFR needs to be maintained over time to ensure the success of the SIT programs. Therefore, to maintain this ratio in orchards, the numbers of *T. leucotreta* released may need to be adjusted, depending on wild population density, by either increasing the frequency of releases per week or expanding the width of release zones.[33] In the *T. leucotreta* SIT program, a total of 2000 sterile moths are released per week per hectare, but this can be adjusted depending on the season, environmental conditions, and wild population levels.[16] However, achieving this in a typical field setting might pose challenges that are not encountered in a controlled field cage design. Moreover, certain field trials involving *T. leucotreta* SIT have suggested that employing higher ratios could yield better results.[34–36] While it is true that ratios higher than 10:1 are typically maintained in field applications,[37] it would be prudent to further investigate the effectiveness of these higher ratios. Therefore, this study aimed to investigate whether higher than 10:1 *T. leucotreta* ratios (sterile: fertile) would improve the effectiveness of the technique and reduce the rate of pest population growth, through laboratory cage experiments. The results obtained are discussed in the context of improving the *T. leucotreta* SIT program to aid in suppressing the pest in South Africa and anywhere else where it may occur.

2 MATERIALS AND METHODS

2.1 Test insects

Adult sterile and fertile *T. leucotreta* were sourced from X Sterile Insect Technique (XSIT) (Pty) Ltd., Citrusdal, South Africa. To render them sterile, the moths were placed into cardboard boxes (140 mm × 140 mm × 50 mm) and were exposed to a dose of 180 Gy of gamma radiation in a 20 kCi[38] Co source panoramic irradiator.[16] This dosage is used in the mass-rearing facility to sterilize moths for large-scale releases across South African citrus growing regions. Thereafter, the moths were transported to Rhodes University, Makhanda, South Africa (~840 km, 13–14 h) in a polystyrene cooler box with dry ice bricks, maintaining a temperature of 4–6 °C. This controlled temperature was crucial in minimizing the moths' activity and preventing mating while in transit.[39]

The moths were approximately 48 h old upon arrival and were immediately sorted by sex using a dissection microscope (Zeiss Microscopy, South Africa), at a magnification of 40× to prevent any unintended mating. Distinguishing characteristics included the presence of black tufts on the hind tibiae in males, which are absent in females.[40]

2.2 Release of sterile *T. Leucotreta* into the laboratory cages

The laboratory cage studies were conducted following the methodology outlined by Hofmeyr *et al.*[7] in a controlled environment (CE) room at approximately 26 ± 1 °C, 70 ± 5% relative humidity (RH) and photoperiod of 16:8 (L:D) h. A total of 15 foldable insect-rearing cages (40 cm × 40 cm × 60 cm) were used. The moths were released into the cages, which contained 35 ripe Washington Navel oranges each. Before release into the cages, the adult sterile and fertile *T. leucotreta* were sorted into different ratios (Table 1). This grouping was done 1 day prior to the actual release, with male and female *T. leucotreta* being released on opposite sides of the cage. The selection of treatments within the cages was randomized, with each treatment being replicated three times, and the experiment repeated three times. Petri dishes (90 mm × 15 mm) with wet cotton wool were placed in each cage, to provide water for the moths. Throughout the experiment period, the insects were allowed to mate and lay eggs without any disturbance. The experiment was conducted for approximately 4 weeks. Thereafter, the fruits were thoroughly examined for any *T. leucotreta* infestation (brown larval penetration holes/spots with frass). Any fruits showing *T. leucotreta* infestation were identified and removed. The total number of infested fruits per cage and the number of larval entries per fruit were recorded for each treatment.

2.3 Determination of F1 sterility

The infested fruit was placed in individual 500-mL round plastic containers (10 cm × 8 cm) with mesh lids and incubated. To provide the larvae with suitable cocooning sites, wads of cotton wool were placed inside each container. Rapidly decaying fruits were cut open, and any larvae found were carefully transferred into diet jars (13 cm × 7 cm) (one diet jar per infested fruit), to enable the larvae to complete their development under optimum

Table 1. Randomly assigned treatments to 15 insect-rearing cages to examine the effect of release ratios of sterile (S) to fertile (F) *T. leucotreta* on the incidence of fruit damage and the sterile male's competitiveness

		Number of sterile *T. leucotreta*		Number of fertile *T. leucotreta*		
Treatment	Release ratio S: F	S male	S female	F male	F female	Total moths
A	0:1 (Control)	0	0	10	10	20
B	10:1	100	100	10	10	220
C	20:1	200	200	10	10	420
D	40:1	400	400	10	10	820
E	60:1	600	600	10	10	1220

conditions.[41] Pupae collected from cotton wool and diet jars were transferred to individual 90-ml clear plastic containers (5 cm × 5 cm) and allowed to eclose.

After sexing, all the emerged adults (F1 generation) were coupled with fertile *T. leucotreta* adult counterparts of the opposite sex from XSIT. The pairs were placed in 90-mL clear plastic containers with snap-on lids, perforated to hold a moistened cotton dental wick and placed in the CE room for them to copulate. Copulation between the pairs was allowed to occur, followed by egg-laying on the smooth inner sides of the containers until the death of the females (~8–10 days). Afterwards, the containers were opened, and the total number of eggs laid (fecundity) was counted and recorded. After 5 days, the number of neonates that hatched (fertility) was counted and recorded from each container.

In the release ratio trials, the percentage egg hatch was used to categorize the parentage of the F1 male, or female reared from the infested fruit. If the percentage egg hatch was <5%, the F1 adult was designated as the progeny of a sterile male (SM) and fertile female (FF), and if the egg hatch was >5%, the F1 was designated as the progeny of a fertile male (FM) and an FF.[20] In these trials, it was assumed that sterile females (SF) were completely sterile, and as such, produced no F1 progeny.[20] The per generation rate of increase occurring from the P1 to the F1 generation in each cage was calculated by dividing the number of F1 male and female progeny produced by a fertile (FM × FF) mating by the number of P1 FM (10) and FF (10) released into each cage.

2.4 Statistical analysis

Data collected from the experiment were checked for homogeneity of variance (F test, Levene's test) and the residual deviations for non-normality were determined using the Shapiro–Wilk test, revealing that the data were not normally distributed.[42] The data were analyzed using a negative binomial generalized linear model analysis as an extension of the Poisson distribution to allow for count data with a significant proportion of zero values, with different ratios as the sources of variation, as recommended by O'Hara and Kotze.[43] Analysis of deviance (log-likelihood ratio statistic) was used to assess the goodness of fit of the Poisson regression model, which has a distribution similar to that of chi-squared (χ^2). The dependent variables used in the statistical model included the number of larval entries, the number of damaged fruit and the number of F1 *T. leucotreta* adults emerging from the infested fruit from the different treatments. The data were also sorted by release ratios, where Spearman's rank correlation analysis was used to examine the relationship between the number of sterile *T. leucotreta* released into each cage and the number of larval entries, the number of damaged fruit, and the number of F1 adult *T. leucotreta* emerging from each treatment.

The model was used to analyze data from the number and percentage of hatched eggs laid by the F1 moths (that emerged from infested fruit and were crossed with fertile adults of the opposite sex), where the F1 adult sex and cage treatment were the sources of variation. Similarly, the model was also used to analyze the percentage of F1 males and females that were fathered by a fertile male, where the cage treatment was the source of variation. Differences among treatment means were separated using the Tukey–Kramer statistic ($P \leq 0.05$) for multiple comparisons when the statistical model indicated significant treatment effects. All analyses were performed in R. 4.2.2.[44]

3 RESULTS

3.1 Fruit damage, larval entries, and F1 progeny

The ratio of sterile to fertile *T. leucotreta* assigned to the laboratory cages had a significant effect on the mean number of damaged fruit ($\chi^2 = 198.06$; df = 4; $P < 0.05$) (Fig. 1), the mean number of larval entries ($\chi^2 = 111.29$; df = 4; $P < 0.05$) (Fig. 2(A)), and the mean number of emerged F1 *T. leucotreta* adults ($\chi^2 = 41.43$; df = 4; $P < 0.05$) (Fig. 2(B)). There was a significant decrease in the number of infested fruit and larval entries between control and all treatments ($P < 0.05$) (Fig. 1; 2A). In addition, significantly lower mean number of infested fruit and larval entries were recorded in 40:1 compared to 20:1. The highest percentage of infested (damaged) fruit (98.40 ± 4.20%) and the mean number of larval entries (397.70 ± 64.80 in 35 fruit per treatment replicate)

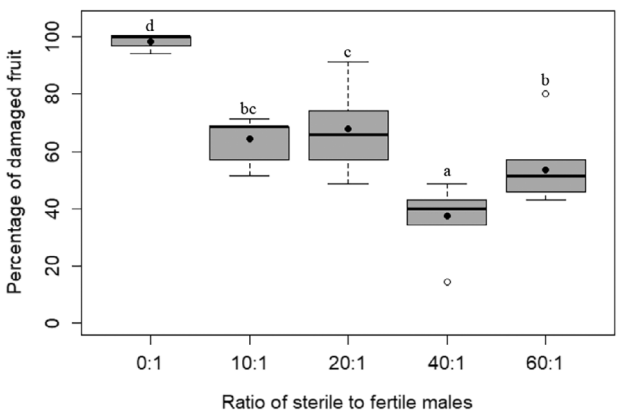

Figure 1. The percentage of damaged fruit from different ratios of sterile to fertile males. Boxplots show median values (solid lines), and whiskers show the range of the data. The black dots indicate the mean percentage of damaged fruit per treatment, while the white dots represent the outliers. Different letters across the treatments indicate a statistically significant difference ($P < 0.05$).

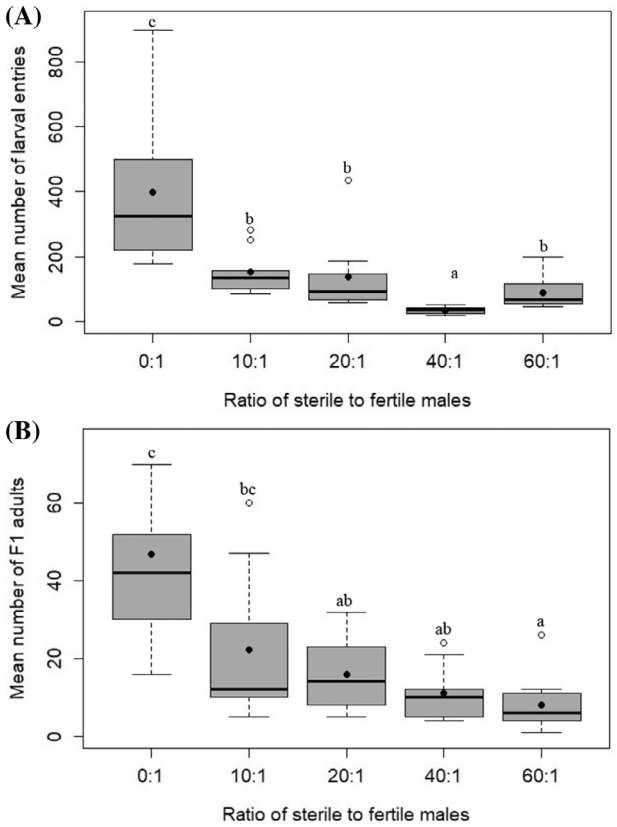

Figure 2. The effects of different treatment ratios of sterile and fertile *T. leucotreta* males on (A) the mean number of larval entries and (B) the mean number of F1 *T. leucotreta* adults. Boxplots show median values (solid lines), and whiskers show the range of the data. The black dots indicate the mean number of larval entries and F1 *T. leucotreta* adults per treatment, while the white dots represent the outliers. Different letters across the treatments indicate a statistically significant difference ($P < 0.05$).

were recorded from the control, while the lowest (37.50 ± 2.26% of fruit infested; 33.10 ± 5.70 larval entries in 35 fruit per the treatment replicate) were recorded in 40:1 cages (Fig. 1; 2A). However, no significant differences in infested fruit and larval entries were recorded between 10:1 and 20:1 as well as 10:1 and 60:1 (Fig. 1; 2A). The number of F1 progeny decreased with an increase in ratios (Fig. 2(B)). The highest mean number of F1 progeny was recorded in control (46.89 ± 9.76) while the lowest number was recorded in 60:1 (8.10 ± 1.90) (Fig. 2(B)). There was a significantly lower mean number of F1 progeny between control and 20:1, 40:1 and 60:1. Similarly, there was a significantly lower mean number of F1 progeny between release ratio 60:1 and 10:1. However, there was no significant difference in the F1 progeny between control and 10:1 (Fig. 2(B)).

The Spearman's rank correlation revealed a significant linear relationship between the number of sterile *T. leucotreta* adults released into each cage and the number of larval entries, the number of damaged fruit, as well as the number of F1 adults emerging from infested fruit. There was a negative correlation between the number of damaged fruit and the number of sterile to fertile *T. leucotreta* in the cages ($P < 0.05$) (Fig. 3(A)). Likewise, the number of larval entries per treatment decreased as the number of sterile to fertile *T. leucotreta* in the cages increased ($P < 0.05$) (Fig. 3(B)). Moreover, as the number of sterile to fertile

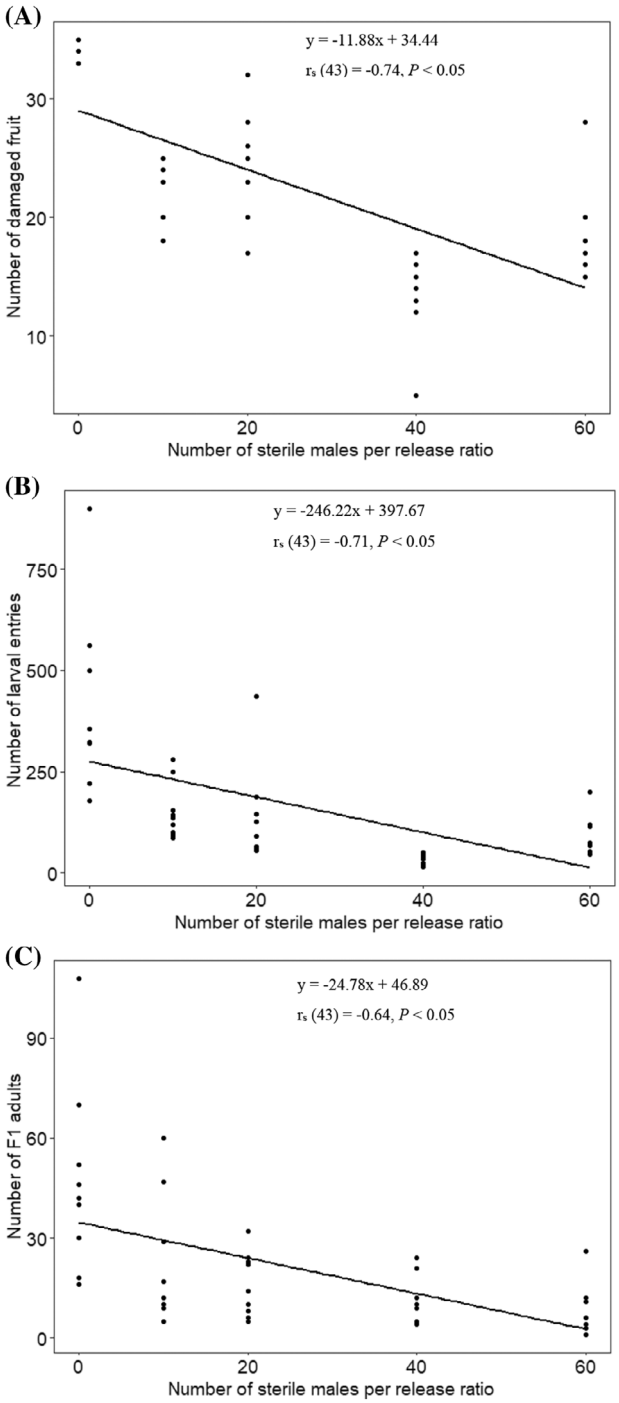

Figure 3. A negative correlation observed among (A) the number of damaged fruit, (B) the number of larval entries, and (C) the number of emerged F1 adults as the number of sterile to fertile *T. leucotreta* males increased per release ratio.

T. leucotreta in the cages increased, there was a decrease in the mean number of F1 *T. leucotreta* adults per treatment ($P < 0.05$) (Fig. 3(C)).

3.2 Fecundity and fertility

The mean number of eggs laid (fecundity) from F1 moths emerging from the infested fruit and paired with fertile *T. leucotreta* of the opposite sex was significantly influenced by the ratio of sterile

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Table 2. Effect of different ratios of sterile and fertile *T. leucotreta* released per cage, and the sex of F1 *T. leucotreta*, on the mean fecundity and fertility of F1 moths emerging from infested fruit paired with fertile *T. leucotreta* of the opposite sex

	Mean fecundity ± SE		Mean fertility ± SE (%)	
Cage treatment	F1 female	F1 male	F1 female	F1 male
0:1 (Control)	166.60 ± 1.02 g	128.00 ± 2.89 g	55.40 ± 0.59f	30.30 ± 0.43d
10:1	98.50 ± 1.73f	71.20 ± 1.06d	28.20 ± 0.94c	24.80 ± 0.63c
20:1	103.60 ± 1.55f	58.50 ± 1.37c	36.40 ± 0.92e	25.80 ± 0.91c
40:1	31.70 ± 1.26a	44.30 ± 1.20b	13.00 ± 0.81a	18.40 ± 0.77b
60:1	42.00 ± 2.16b	83.40 ± 2.44e	11.60 ± 1.34a	32.50 ± 1.52de

Means within each column followed by the same letter are not significantly different ($P \geq 0.05$).

to fertile males ($\chi^2 = 4233.2$; df = 4; $P < 0.05$), the sex of F1 adults ($\chi^2 = 4663.6$; df = 1; $P < 0.05$), and the interaction between the ratio of sterile to fertile males and the sex of F1 adults ($\chi^2 = 1278.6$; df = 4; $P < 0.05$) *T. leucotreta* (Table 2). There was a significant difference in fecundity resulting from F1 female and male crosses between the control and all the other treatments (Table 2). The highest fecundity from F1 female and male crosses was recorded for the control, while the lowest fecundity from both crosses was recorded for the 40:1. Significant higher fecundity of F1 female compared to F1 male crosses was observed in 10:1 and 20:1. However, 40:1 and 60:1 showed significant lower fecundity of F1 female compared to F1 male crosses (Table 2). No significant difference in fecundity was recorded between F1 female and F1 male crosses from the control. Similarly, the percentage fertility from F1 moths emerging from infested fruit and paired with fertile *T. leucotreta* of the opposite sex was significantly influenced by the ratio of sterile to fertile males ($\chi^2 = 1299.44$; df = 4; $P < 0.05$), the sex of F1 adults ($\chi^2 = 912.70$; df = 1; $P < 0.05$), and the interaction between the ratio of sterile to fertile males and the sex of F1 adults ($\chi^2 = 504.55$; df = 4; $P < 0.05$) (Table 2). The control had the highest mean percentage fertility from crosses involving F1 females than F1 males compared to other treatments. Similarly, the cages receiving different treatments of sterile to fertile ratios had significant differences in the percentage fertility involving crosses from F1 females and F1 males with fertile *T. leucotreta*, except treatment 10:1 (Table 2).

Table 3. Effect of different ratios of sterile and fertile *T. leucotreta* on the mean number of fertile F1 *T. leucotreta* adults emerging from fruit removed from the cages and the rate of increase for the P1-F1 generation

	Mean ± SE fertile moths (progeny of unsterile males)		P1-F1 reproductive rate of increase	
Cage treatment	F_1 male	F_1 female	Male	Female
0:1	23.22 ± 4.96c	23.67 ± 5.16c	2.32×	2.36×
10:1	13.89 ± 3.07b	8.22 ± 1.95b	1.38×	0.82×
20:1	9.44 ± 2.17b	6.56 ± 1.60b	0.94×	0.65×
40:1	7.11 ± 1.69a	4.00 ± 1.06a	0.71×	0.40×
60:1	5.67 ± 1.39a	2.44 ± 0.73a	0.56×	0.24×

Means within each column followed by the same letter are not significantly different ($P \geq 0.05$).

The ratio of sterile to fertile *T. leucotreta* per cage significantly influenced the mean number of fertile (= progeny of unsterile males) F1 male *T. leucotreta* ($\chi^2 = 25.68$; df = 4; $P < 0.05$) and F1 female *T. leucotreta* ($\chi^2 = 54.01$; df = 4; $P < 0.05$) emerging from the infested fruit (Table 3). The mean number of fertile F1 males and females decreased with an increase in ratio such that the control recorded the highest number while 60:1 recorded the lowest (Table 3). There were significant differences in the mean number of fertile F1 males and females between the control and all the other ratios. However, there were no significant differences in the mean number of fertile F1 males and females between ratios 10:1 and 20:1 as well as 40:1 and 60:1. A comparison of fertile F1 males and females showed no mean significant differences across all treatments (Table 3). Similarly, the P1-F1 reproductive rate of increase decreased with an increase in ratio (Table 3). The ratio of 60:1 had the lowest per generation rate of reproductive increase, while the control recorded the highest increase from P1 to F1 generation. The treatment, 60:1, resulted in a mean rate of increase <1 for both males (0.56×) and females (0.24×). From this, the mean per generation rate of reproductive increase for the fertile males and females was 0.4×, a value resulting in a slight decline from P1 to the F1 generation (Fig. 4).

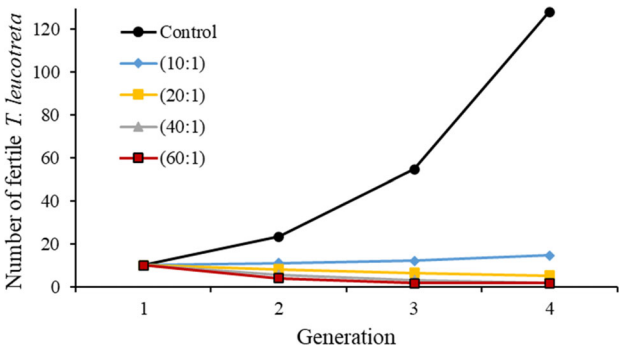

Figure 4. Comparison of the estimated increase in the number of fertile *T. leucotreta* in a control population and treatment populations subjected to releases of sterile *T. leucotreta*. The first generation in the control population started with 10 pairs of fertile (F) *T. leucotreta* males (0:1), with a reproductive rate of 2.34× per generation. The treatment population 60:1 (= with the lowest per generation rate of increase) started generation 1 with 10 pairs of fertile *T. leucotreta*, with a release of 600 pairs of sterile (S) *T. leucotreta* males at the onset of each of the three generations (60:1), which reduced the reproductive rate to 0.4× per generation.

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3.3 Discussion

An adequate OFR is one of the essential requirements for the successful implementation of an SIT program. For instance, Klassen[45] discussed the importance of 'substantial OFRs' while Lance and McInnis[46] emphasized the significance of 'a sufficiently high OFR (sterile: fertile insects)' for the success of SIT. Likewise, Steiner[47] demonstrated that pest eradication through SIT can be achieved only with a consistent overflooding of the native population. Despite this, there has been minimal effort to precisely connect OFR with the effectiveness of SIT. For example, Villaseñor *et al.*[48] indicated that an 80:1 ratio was the lowest OFR required for controlling *C. capitata* (Wiedemann) (Diptera: Tephritidae), while Steiner[47] suggested a 20:1 ratio as crucial for eradicating populations of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), *Zeugodacus cucurbitae* (Coquillett) (Diptera: Tephritidae), and *C. capitata*. Nevertheless, neither study offered substantial evidence on these proposed critical OFR values.

Conversely, there are mathematical models that have been created to explicitly determine the minimum OFR required to inhibit the reproduction of the target population. These models, first introduced by Knipling[21,49] essentially alter geometric population growth by incorporating factors such as the count of sterile and fertile males in the population (indicative of infertile matings) and a coefficient representing the competitive ability of sterile males, which adjusts their numerical prevalence.[50,51] Despite their accuracy, these models include variables like male and female population size and the population's inherent rate of growth, which are challenging to gauge in real-world settings. As a result, modelling strategies are not greatly employed in the establishment of specific OFR targets for field SIT programs targeting tephritid and tortricid pests.[51]

In this study, we explored the impact of different ratios of sterile to fertile *T. leucotreta* adults on fruit damage and the sterile male competitiveness in the treatments. The findings revealed a consistent decrease in the mean number of damaged fruit, larval entries, and F1 *T. leucotreta* adults that were recorded across all treatments receiving sterile *T. leucotreta*, in contrast to the control cages. These results closely align with reports by Hofmeyr *et al.*,[7] suggesting that the sterile males released per cage demonstrated competitive ability, effectively inducing high levels of sterility in their fertile counterparts within the cages.[52] Therefore, this resulted in the reduction of fruit damage and ultimately, fewer F1 progeny, due to their reduced reproductive capacity, thereby potentially aiding in pest population suppression.[20] Our results support findings by Hofmeyr *et al.*[15] and Boersma,[16] indicating that the incidence of infested fruit and fruit drop per tree was notably lower in Navel orange orchards under SIT compared to non-SIT orchards in an SIT pilot project. Additionally, a study by Yazid *et al.*[53] corroborates our findings, demonstrating that higher densities of *C. capitata* resulted in lower fruit infestation compared to the control treatment. Likewise, Gard *et al.*[54] demonstrated that a 5:1 ratio of sterile to wild *D. suzukii* significantly reduced the number of infested strawberries compared to a 1:1 ratio. The infestation of wild cucurbit fruit on Kume-Zima Island by *Z. cucurbitae* significantly decreased following the release of sterile *Z. cucurbitae* at a release ratio of 50:1, ultimately resulting in the eradication of the flies on the island.[55] Similarly, in *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae), a 10:1 sterile: wild ratio resulted in a significantly lower number of flies trapped per day compared to the control, inducing about 80% sterility in *A. obliqua* cohorts,[56] indicating that an increase in the number of sterile insects can improve the effectiveness of SIT programs.

From our findings, the ratio of sterile to fertile *T. leucotreta* in the cage treatments led to a reduced number of F1 adults compared to the control. This suggests that the sterile *T. leucotreta* males released in the cages effectively outcompeted the fertile males for access to the fertile females. The findings corroborate with those of Hofmeyr *et al.*,[7] depicting that the mean number of fertile *T. leucotreta* males and females produced in the F1 generation was significantly lower in cages receiving sterile *T. leucotreta* as compared to control cages, resulting in a lower per generation rate of reproductive increase (from the P1 to the F1 generation) in these cages. Our findings are consistent with previous studies, such as those by Bloem *et al.*[31] on *C. pomonella* (L.) (Lepidoptera: Tortricidae), where a 10:1 sterile-to-wild ratio led to reduced fruit damage and lower F1 progeny production. Similarly, Hight *et al.*[57] observed a decline in wild *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) populations when sterile insects were released at ratios of between 10:1 and 20:1. Flores *et al.*[58] found that a 30:1 (sterile: wild) ratio in *Anastrepha ludens* (Loew) (Diptera: Tephritidae) induced 90% sterility in the wild population. Likewise, Shelley *et al.*[22] demonstrated that a 100:1 (sterile: wild) ratio in *C. capitata* achieved 79% sterility, whereas in *Z. cucurbitae*, a 50:1 (sterile: wild) ratio resulted in an egg sterility of about 80%. Additionally, Peng *et al.*[59] showed that a 3:1 (sterile: wild) ratio in *B. dorsalis* induced 66% egg sterility. These studies collectively depict that the population growth of these respective pests can be influenced by the release of sterile conspecifics, even when the release ratios used are relatively low. However, increasing the ratio of sterile to fertile males (OFR) will not necessarily yield desired outcomes if released males, irrespective of their abundance, fail to meet a certain minimum threshold of 'acceptable' courtship performance required by most or all wild females.[22,58] This is crucial because the irradiation dose used directly affects the mating competitiveness of the released males. Bloem *et al.*[20] demonstrated that *T. leucotreta* males exhibited a residual fertility rate of 5.2% when sterilized at 350 Gy, indicating their radioresistance, which in turn impacts their field fitness. However, the irradiation dose varies among species. For instance, Krüger *et al.*[18] and Costa *et al.*[60] showed that radiation doses of 200 and 60 Gy induced nearly 100% sterility in *D. suzukii* and *A. obliqua* (Schiner) (Diptera: Tephritidae) males, respectively. Furthermore, a significantly lower number of F1 adults emerged from the 60:1 ratio compared to the 10:1 ratio. This reduction could be attributed to the higher number of sterile *T. leucotreta* males in the 60:1 release ratio, which effectively outcompeted the fertile males, thereby inducing sterility.

In the study, a simulation was conducted to emulate the real-world scenario of an SIT program, wherein sterile *T. leucotreta* would be continuously released from the onset of a growing season when the population of fertile wild *T. leucotreta* would be at its lowest. The investigation compared the projected rate of reproductive increase in the number of fertile *T. leucotreta* within a 'control' population against the number of fertile (unsterile) *T. leucotreta* within a population subject to releases of sterile *T. leucotreta* treated with a radiation dosage of 180 Gy. Currently, the irradiation dose fluctuates between 150 and 200 Gy during winter and summer seasons to maintain the fitness of male sterile *T. leucotreta*, ensuring they remain competitive against their wild counterparts.[16,20] The moths used in this study were sterilized at a

radiation dose of 180 Gy, as used by the XSIT mass-rearing facility to sterilize moths for large-scale releases in citrus-growing regions in South Africa[16] This ensured that the females were completely sterile, while males were partially sterile.

In the control population, the first generation commenced with 10 pairs of fertile *T. leucotreta*, exhibiting an average reproductive increase rate of 2.34× per generation. Likewise, the treatment involving the sterile population started the first generation with 10 pairs of fertile (unsterile) *T. leucotreta* and received a release ratio of 600 pairs of sterile *T. leucotreta* irradiated with a dosage of 180 Gy at the onset of each of the three generations (equivalent to a ratio of 60: 1 for each generation) resulting in a reduced mean reproductive increase rate for both males and females of 0.4× per generation. According to the model, derived from data obtained from our laboratory cage trial, the population of fertile moths receiving treatment with sterile moths experienced a slight decline, whereas the number of fertile *T. leucotreta* in the control population increased by over 14%. Our findings align with those of Hofmeyr *et al.*,[7] demonstrating that treatment with a sufficient ratio of sterile to fertile *T. leucotreta* can significantly reduce the growth of a fertile population across several generations.

In summary, our findings confirm those of Hofmeyr *et al.*[7] who recommended a 10:1 ratio, which has been used commercially since 2007 in controlling *T. leucotreta* in citrus orchards.[37] However, our laboratory study demonstrated that ratios of 40:1 and 60:1 can significantly decrease the multiplication of the wild fertile population, relative to lower ratios, resulting in enhanced suppression of *T. leucotreta*.[38] Additionally, field trials conducted by Hofmeyr and Hofmeyr,[34] Hofmeyr and Hofmeyr,[35] and Moore,[36] reported dramatic reductions in fruit infestation with a 40:1 ratio under field conditions. Our study also showed that any release ratio can have a suppressant effect on *T. leucotreta*, as it provides an opportunity for fertile-sterile pairings, rather than fertile-fertile pairings. Notwithstanding this, the findings from our study suggest that a ratio higher than 10:1, particularly at 40:1 and 60:1, can further enhance the efficacy of SIT. The study showed that a release ratio of 40:1 or higher can provide enough sterile males to effectively outcompete wild males, thereby inducing sufficient sterility to suppress the pest population.

The findings of this study have important practical implications for the optimization of an SIT program against *T. leucotreta*. The release ratio of 40:1 has been reported in various field studies[34–36] 36 and therefore it may not have significant implications for production costs, provided that other control strategies against *T. leucotreta* are well implemented to reduce the wild population. In South Africa, *T. leucotreta* area-wide integrated pest management (AW-IPM) strategy uses a systems-based approach to achieve effective control. Preharvest measures are diverse and include the use of sex pheromone-based tools such as attract-and-kill, mating disruption, and SIT.[61] Therefore, combining high release ratios of sterile *T. leucotreta* with pheromone-based methods can enhance control efforts, especially given the presence of geographically separated populations of *T. leucotreta* across South Africa. Importantly, these populations still maintain consistent sexual communication, allowing sterile males to effectively compete for wild females in the release sites.[61,62] Moreover, combining high sterile release ratios with pheromone-based tools may produce a synergistic effect, as the sterile females produce pheromones attracting wild males for mating resulting in the production of non-viable eggs.[61,62]

As a result, these new proposed ratios can lower the wild population densities aiding in achieving the required sterile:wild release ratio in citrus orchards. Establishing an effective and economically viable release ratio ensures that SIT remains a sustainable pest management strategy. Moreover, the success of a *T. leucotreta* SIT program depends not only on the release ratio but also on the fitness of sterile males. Continuous quality control assessments should be conducted to confirm that sterile *T. leucotreta* released at a ratio of 40:1 and 60:1 remain competitive against wild males. Ensuring high mating competitiveness will maximize sterility induction and increase the long-term efficacy of the *T. leucotreta* SIT program. These findings can guide future SIT implementations in citrus orchards, supporting more targeted and cost-effective pest management strategies. This will ensure that the effectiveness of the *T. leucotreta* SIT program is achieved, suppressing *T. leucotreta* in citrus orchards. Nevertheless, additional research is necessary to thoroughly evaluate the effectiveness and feasibility of these findings under real-world field conditions. The findings of our study support the continued improvement of the efficacy and effectiveness of the SIT program as a control and management strategy for *T. leucotreta* in South Africa.

ACKNOWLEDGEMENTS

Primary funding for this work was provided by Citrus Research International. The South African Research Chairs Initiative, of the Department of Science and Innovation and the National Research Foundation of South Africa (Grant 84643) also provided further funding for the work. The assistance of XSIT (Pty) Ltd. and River Bioscience (Pty) Ltd. for supplying sterile and fertile *T. leucotreta*; Rhodes University for financial and technical support, are acknowledged. Any opinion, funding, conclusion, or recommendation expressed in this material is that of the authors, and the National Research Foundation does not accept any liability in this regard. The authors thank Deric Vershiyi Tanka and Dr Natanah Gusha for the technical assistance; Dr Lenin Chari for proofreading the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

AUTHOR CONTRIBUTIONS

Conceptualization: MMG, Methodology: MMG, Data curation: MMG, Investigation: MMG, Funding acquisition: SDM and MPH, Supervision: CAC, RM, SDM, and MPH, Formal analysis: MMG, Writing – original draft: MMG, Writing – editing: MMG, CAC, RM, SDM, and MPH, Validation: MMG, CAC, RM, SDM and MPH, Visualization: MMG, CAC, RM, SDM and MPH.

CONFLICTS OF INTEREST

The authors declare they do not have any conflicts of interest.

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Pest Management Science published by John Wiley & Sons Ltd on behalf of Society of Chemical Industry.