Eradication of the Australian Painted Apple Moth *Teia anartoides* in New Zealand: Trapping, Inherited Sterility, and Male Competitiveness

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ABSTRACT The incursion of the native Australian painted apple moth *Teia anartoides* Walker into Glendene, West Auckland in May 1999, prompted an area-wide eradication programme by the New Zealand Ministry of Agriculture and Forestry Biosecurity Authority. The Australian painted apple moth is a polyphagous pest of horticulture and plantation forestry and threatened New Zealand's native vegetation. The economic and ecological impact of the moth's incursion was estimated at NZD 50-350 million (approximately USD 30.5-212.9 million) over 20 years if no action was taken to eradicate the insect. The eradication programme (1999-2006) used a combination of tactics, including the first use of the sterile insect technique (SIT) in New Zealand. The SIT component was added to the eradication programme in 2002 but releases started in 2003 as an end game tactic once the pest population was brought down to ca 1% of the population level in 2001-2002, as indicated by trap catches. The aerial spray programme using *Bacillus thuringiensis* (Berliner), subsp. *kurstaki* (*Btk*) accompanied by release of sterile males drove the wild population to extinction, with overflooding ratios up to 100:1 based on trapping data. Sterility was assessed from the egg hatch of the F_1-F_3 generations and competitiveness examined using emergence rates and wind tunnel flight performance. When males exposed to 100 or 160 Gy mated with non-irradiated females, there was no significant effect on female egg production, but a lower egg hatch was observed for both doses. When F_1 and F_2 offspring were outcrossed to fertile moths, 100 Gy irradiation gave relatively similar inherited sterility levels to 160 Gy, with full mortality achieved at the F_3 generation. The lowest effective dose of radiation needed to induce inherited sterility is likely to offer the best competitiveness and mating success of the released males, representing a potential trade-off between sterility and competitiveness. Subsequently, the induced dominant lethal mutations carried by the released males (when mated to wild females), will be inherited through the surviving F_1 proportion of the progeny. Moth emergence rate was not affected at 100 Gy, but the response to seek and mate with wild calling females in the wind tunnel was reduced by 33%. The use of wind tunnel for quality assurance in integrated pest management programmes is discussed.

KEY WORDS Australian painted apple moth, *Teia anartoides*, eradication, aerial spray, trapping, *Btk*, sterile insect technique, fitness, wind tunnel

1. Introduction

The Australian painted apple moth *Teia anartoides* Walker has been the target of a large-scale (NZD 90 million equivalent to USD 54.7 million) eradication programme in Auckland, New Zealand since 1999 (Suckling et al. 2002, 2005). Female painted apple moths are flightless, and ballooning larvae are the main means of dispersal in this species. It

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has reached its widest host range in Auckland (Stephens et al. 2007). The insect was considered to have potential for significant economic and ecological damage in New Zealand because its host range includes plants of importance to horticulture and forestry, as well as to natural ecosystems. Estimates of NZD 50-350 million (approximately USD 30.5-212.9 million) of costs over 20 years were developed (Self 2003), and a response was mounted in mitigation.

1. 1. Operational Aspects of the Eradication Programme

The eradication programme operated by the Ministry of Agriculture and Forestry Biosecurity Authority ("Biosecurity New Zealand"), has included a pheromone trapping programme based on caged female moths, in order to map the distribution of the pest, from June 2001 onwards. The use of geographic information systems (GIS) proved invaluable for tracking the population spatially (ground finds and trap catches), as well as for managing the response (aerial spray flight lines and releases of sterile insects). Although the pheromone has been identified (El-Sayed et al. 2005), it is highly unstable and virgin females have been used to bait traps throughout this programme. The female moths were mass-reared for this purpose, and trap arrays of up to 2000 geo-referenced traps were serviced weekly (Suckling et al. 2005). There was concern at one point about bioterrorism through deliberate spread of the organism, and a solution was demonstrated which involved sterilizing females by irradiation, since this had no effect on male catch (Suckling et al. 2006).

The geographic area of the infestation was relatively small, ca 12 000 hectares (Fig. 1). Trap spacing varied from 1500 metres around the periphery, to 500 and 250 metres spacing in the central zone. By 2002, a male catch in a trap was followed immediately by the deployment of a higher density network of traps in order to locate the breeding population.

A targeted programme of ground searches was also used to define the area occupied by the pest, and host removal was used where possible. Insecticides applied from the ground to host trees (e.g. *Acacia mearnsii*) included chlorpyrifos, deltamethrin and the insecticidal pathogen *Bacillus thuringiensis* (Berliner), subsp. *kurstaki* (*Btk*), which was also aerially applied on a regular basis from January 2003 onwards (Charles et al. 2005, Richardson et al. 2005). The sterile insect technique (SIT) was proposed as part of an end game strategy, once densities had been lowered with other tactics (Suckling 2003).

In New Zealand, the SIT has the advantage of meeting the stringent requirements of the Hazardous Substances and New Organisms Act (1996), which seriously limits the application of many technologies with potential value for eradication (Suckling 2003), such as exotic organisms (e.g. insect pathogens), or unregistered pesticides. The SIT had the advantage that the mass-rearing was already underway to provide female moths for the surveillance trapping programme.

Male moth trap catches well outside the known area of breeding populations raised questions about moth dispersal, since it was possible that the infested area was much wider than had been thought. A dispersal study was therefore undertaken, using marked irradiated males, after it was shown that the progeny of males irradiated at 160 Gy were essentially sterile by the F_2 generation (Suckling et al. 2002, Wee et al. 2005). Released moths dispersed up to five kilometres, and 17% of irradiated males released were recaptured (Suckling et al. 2005). This indicated that irradiated insects were sufficiently fit for field recapture, and therefore a full programme of sterile insect release was proposed. Subsequently, releases of a total of around 350 000 male moths irradiated as pupae at 100 Gy were made from January 2003 until April 2004 (Suckling et al. 2005). The lower dose was chosen in an attempt to increase the field competitiveness, while work was being done to quantify the difference in competitiveness from the two doses.

Importantly, the information on recaptures

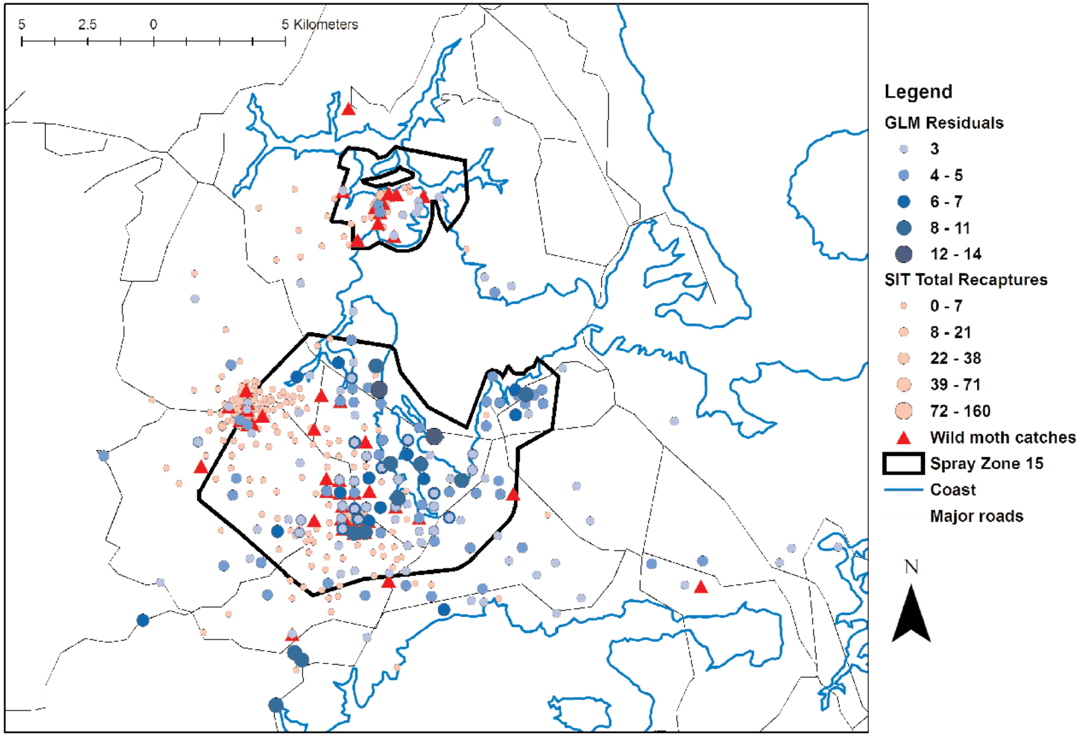

Figure 1. *Distribution of Australian painted apple moth trap catches, in relation to the spray zone at the 15th aerial application of* Btk *in west Auckland New Zealand (solid black lines). Wild moth catches (light to dark blue circles) expressed as general linear model residuals scaled to the observed catch rate corrected for trap location, distance from larval finds, and time of catch over the 2001-2002 period (courtesy D. Baird, AgResearch) with the locations of the final 19 catches of male painted apple moth in 2003 (red circles). SIT recaptures (pink circles) tended to cluster within one kilometre at the three release sites shown.*

was used to assist with the development and use of a decision-support tool for managers of the eradication programme, to estimate changing confidence levels in the success of the eradication programme over time (Kean and Suckling 2005). This model relies on sterile moth recaptures for the best quality estimate of trap efficiency, and takes into account weather, the relative competitiveness of irradiated insects, insect development rate, spatial deployment of trapping effort, duration of trapping effort in the absence of any recent wild catches and other factors. Further work has examined the cost effectiveness of release strategies (Wee et al. 2006) and ways of improving sterile insect quality (Stephens et al. 2006).

The work reported here outlines the trapping programme used for catching both wild and released males since 2001, and looks at the occurrence of catches over time and space, as part of the operational programme from 2001. The releases were continued until May 2004, they were terminated, fifteen months after the last catch. Subsequent trap catches are still under forensic biosecurity examinations of various kinds.

1.2. Competitiveness

Competitiveness of the irradiated insects is a key requirement for the success of the SIT (Lance and McInnes 2005, Itô and Yamamura 2005). The application of irradiation should not diminish the longevity or significantly impair the ability of treated insects to fly, mate and transfer sperm. The lowest effective irradiation dose to achieve sterility is more likely to optimize the mating competitiveness of the released insects (i.e. maximizing mating with the target population), representing a potential trade-off between sterility and competitiveness. With the codling moth *Cydia pomonella* (L.), as with Lepidoptera in general, a high radiation dose resulted in complete sterility but considerably reduced competitiveness, but the application of a lower dose yielded partially sterile insects of superior competitiveness, which were more effective in population suppression in the F_1 generation (Bloem et al. 2001).

A range of radiation doses produced different levels of inherited sterility in *T. anartoides* (Suckling et al. 2002). A 100 Gy treatment was projected to give 80% sterility of the F_1 generation and more than 99.5% sterility in the F_2 generation. The few viable individuals from the F_1 or F_2 generation would carry the inherited sterility into the population which, when crossed with wild-type insects, would later lead to eradication of the target population. Suckling et al. (2004a) showed that exposure of 6-day old pupae to 100 Gy did not increase wing deformities (which at even a low level would correlate with an effect on the flying ability of adult males).

The work reported here was instigated to determine the impact of irradiation on male competitiveness; female fecundity and fertility were assessed as well as the inherited genetic damage, expressed as mortality in the F_1 and F_2 generations (inherited sterility).

2. Materials and Methods

2.1. Trapping

Pheromone traps were deployed at 500 metres spacing, baited with virgin females (Suckling et al. 2005), and operated weekly from 2001 until 2006, although only the period immediately before the *Btk* spraying operations and then the SIT component is presented here. The phenology of *T. anartoides* was determined from a subsample of 102 traps in 2001/02, but in the 2002/03 year all traps were included due to the scarcity of wild moths, after densities fell dramatically. A generalized linear model with Poisson errors was fitted to the weekly counts of moths caught in the traps (D. Baird, personal communication). The components to the model were a smoothing spline on the distance from the trap to the closest larval find, which modelled the dispersion of the male moths, a factor for the week of the catch, allowing for a changing population of male moths. The fitted values from this model were subtracted from the observed catches to give a residual. This was fitted with Genstat® ver-

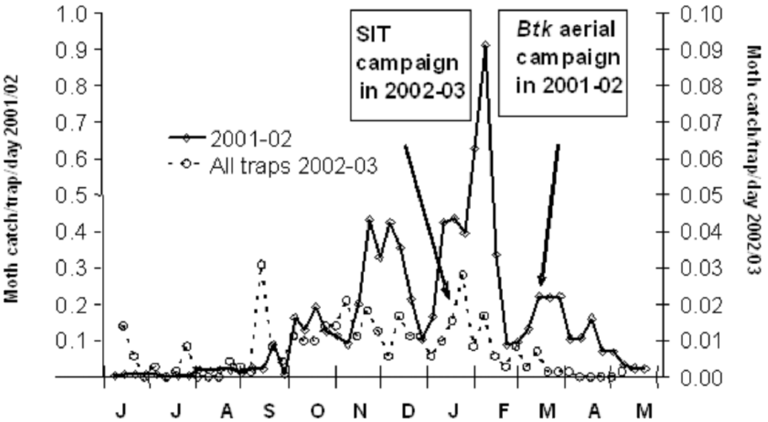

*Figure 2. Pheromone trap catch of the Australian painted apple moth from June to May in 2001/02 (*Btk *aerial campaign commenced in January 2002) and 2002/03 (SIT commenced 17 January 2003). There was a minimum of 100 traps for each data point.*

sion 8 (Payne 2005). High residual values from the model indicated spatial and temporal hot spots of trap catch.

2.2. Release Programme

Male moths were irradiated as pupae (below), dyed with fluorescent powder, emerged and released weekly from paper bags from 17 January 2003 until April 2004 (Suckling et al. 2005). Males were released at four main locations in Auckland, using a single release point but after 2005 multiple release points were used a few hundred metres apart from single nearby trap catches.

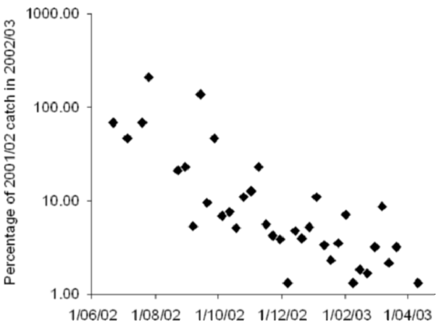

Figure 3. Log-linear change of Australian painted apple moth trap catches over time as a function of the previous year (2002/03 compared to 2001/02) due to the aerial Btk *spraying programme, prior to the commencement of the releases of sterile moths in Auckland, New Zealand.*

2.3. Irradiation of Insects

Male and female Australian painted apple moth pupae were obtained from the quarantine facility in Mount Albert Research Centre, HortResearch, Auckland. The colony was established from field-collected insects, and reared on an artificial diet (Charles et al. 2006). Six-day old male pupae were irradiated using 1.25 MeV gamma rays from a ^{60}Co source. Larvae were separated by sex during rearing. The pupae were irradiated for 5015 seconds, giving a dose of 100 Gy, or 8024 seconds, resulting in 160 Gy (Wee et al. 2005).

2.4. Female Fecundity and Fertility

Newly emerged males were mated singly with untreated females for each treatment dose. Total eggs laid (fecundity) and hatch rate (fertility) per female per treatment were assessed

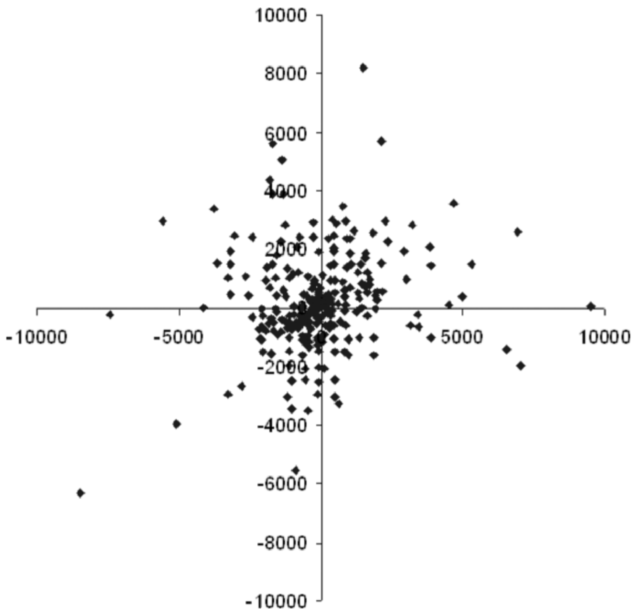

Figure 4. *Dispersal distances (metres) and directions of sterile male Australian painted apple moth, released and recaptured (n = 2145) in Auckland from 17 January to 9 May 2003.*

with 12 to 54 replicates for each cross, depending on survival rates. Egg counts were transformed using log10(n+1), and the proportion of eggs that hatched was angular-transformed (Anscombe 1948) and analysed using one-way ANOVA, with mean comparisons using Tukey's test ($P < 0.05$).

2.5. Post-Embryonic Mortality

All possible crosses of emerging F_1 adults were made according to the number of surviving insects in each line, and were conducted as described above (between nine and 33 emerged F_1 adults of each gender from each treatment were outcrossed to wild-type). The total number of eggs oviposited per female (fecundity) and the number of eggs that hatched (fertility) were counted for each treatment.

All larvae that hatched for each female from each cross were counted to obtain fertility data. Neonates from each P and F_1 cross were reared at 25 ± 2°C, a photoperiod of 16:8 (L:D), and 60% relative humidity. Daily observations were made to ascertain insect development and mortality. The total number of larvae that pupated and the number of pupae that successfully emerged as adults were recorded daily. Data from each developmental stage (egg-larval-pupal mortality for F_1 to F_2, and egg mortality at F_3 generations) were corrected using Abbott's formula to account for control mortality (Abbott 1925). Subsequently, the cumulative mortality at different life stages was calculated as the product of the proportional survivorship of each stage. Results were pooled for reciprocal crosses with no significant difference.

2.6. Male Flight Ability

A perspex flight tunnel (50 x 50 x 50 centimetres) operating at a wind speed of 25-30 cm/sec under fluorescent light was used to determine the flight ability of male moths (Suckling et al. 2004a). Comparisons of treated and untreated males were done weekly as

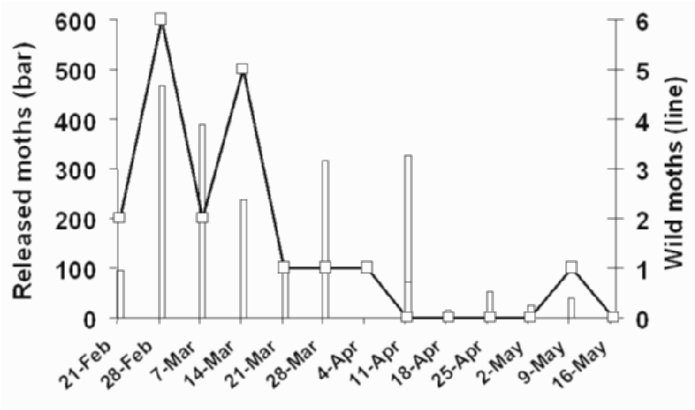

Figure 5. *Comparison of the last catches of wild and dyed released male Australian painted apple moth in Auckland from 17 January to 16 May 2003.*

part of the quality assurance programme. A single calling female (1-2-day old) was placed in a small wire-mesh cage (4 centimetres diameter x 5 centimetres height) with a sticky lid, which was then placed on a sticky base (18 x 19 centimetres) in the upwind area. At a distance of 130 centimetres from the upwind source, ten newly emerged (1-2-day old) irradiated males were released from a plastic tube placed at the downwind area, and their responses to the calling female were observed for six minutes. Similar procedures were repeated for control males, with 128 replicates of groups of males for each treatment. Flight ability expressed as arrival success was defined as when a male moth responded to the female pheromone plume by flying in "zig-zag" anemotaxis and successfully landed on

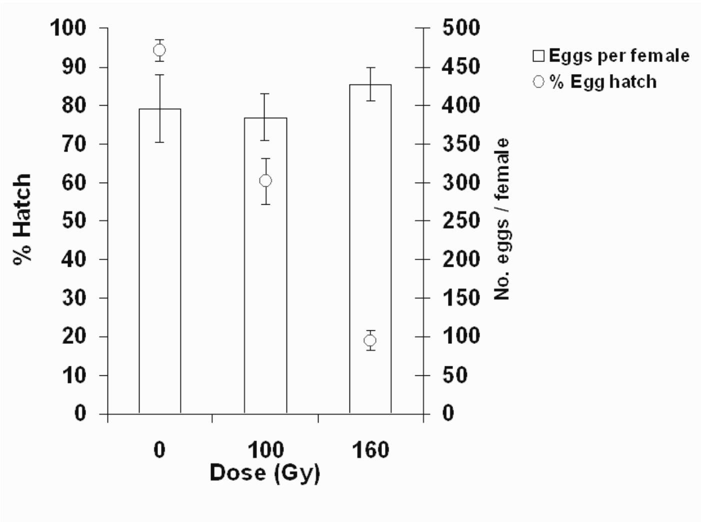

Figure 6. *Effect of 100 and 160 Gy gamma radiation of male pupae on female egg production and F_1 egg hatch of the Australian painted apple moth* Teia anartoides. *Bars show SE.*

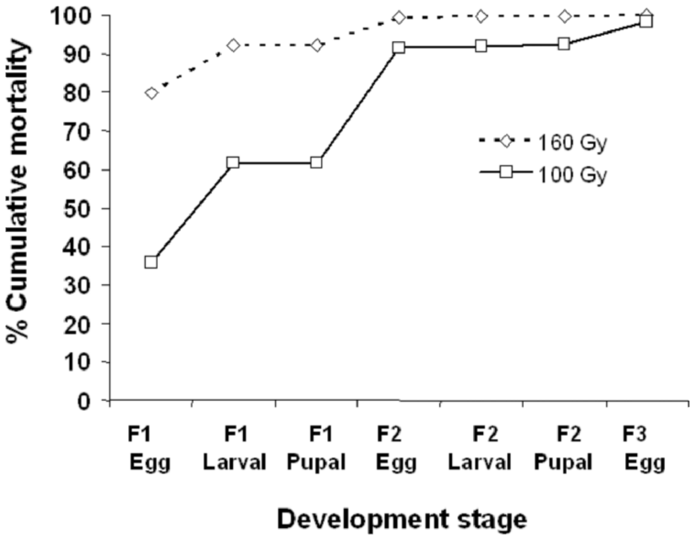

Figure 7. *Cumulative Abbott's corrected mortality at different life stages of Australian painted apple moth* Teia anartoides*, irradiated as male pupae at 100 and 160 Gy.*

the sticky base (female source) within the stipulated time. Numbers of successful male arrivals were noted for each replicate. A simple flight ability ratio was derived by dividing the mean arrival success of irradiated males by that of untreated males.

3. Results

3.1. Population Assessment from Trap Catches

The map (Fig. 1) shows a solid core where there was a breeding population that generated moth catches, followed by circles indicating significance of the catch outwards indicated as residuals from the generalized linear model. The area within the aerial spray zone (the solid black line, approximately 12 000 hectares) can be compared with the spatial distribution of the final 19 catches of male moths (red circles), that occurred between 17 January 2003 and 9 May 2003, and also the recaptures of sterile males.

The population in 2002/03 was much lower, and showed a 100-fold decline in catch to ca 1% of that in the previous year, over several months (301 days) that led up to the releases of irradiated moths in January 2003 (Fig. 3). This was likely to be predominantly due to the applications of *Btk* (Charles et al. 2005, Richardson et al. 2005), although some areas such as Waikumete Cemetery had heavy vegetation cover with less efficacy, evident as the region with the last catches of wild males (Fig. 1). The relative catch compared to the same week in the previous year shows how quickly the population dropped (Fig. 2).

3.2. Phenology

The phenology of painted apple moth was assessed in a geo-referenced grid of 102 traps from June 2001 to May 2002 and assessed from all traps in the second year (Fig. 2). In the first year of trapping, the population showed evidence of several apparently doubling generations of increase, before the

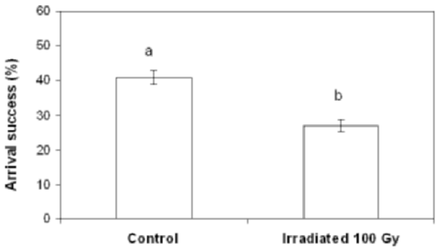

Figure 8. *Arrival success of control and irradiated (100 Gy) males, flown separately to a calling virgin female in a flight tunnel. Bars (SE) topped with different letters were significantly different at* P *= 0.01, Student's* t*-test (128 replicates of each treatment; each replicate consisted of 10 males).*

effect of the regular aerial *Btk* spray programme, started in January 2002, began to measurably reduce the moth population after one generation by May 2002 (Fig. 2). A total of more than 9300 male moths were caught in the first 35 weeks of trapping from June 2001 onwards (Suckling et al. 2005).

Recaptures have been reported elsewhere in detail (Suckling et al. 2005), and this information has been used in a model of trap efficiency and therefore the success of the eradication effort (Kean and Suckling 2005). There was no overwhelming evidence of a directional component to overall released male dispersal (Fig. 4), although individual release points could expect some effect of topographic features, and local wind conditions would likely play a large part in a given catch. Geographic bias is obvious as apparently reduced catches in the south-eastern quadrant which includes the harbour at Hobsonville, so cannot be compared with catch in traps present at other quadrants. This leaves room for further analysis at greater resolution.

The estimated ratio of substerile to wild males caught varied with weekly catch (Fig. 5), but was frequently over 100:1, as can be seen by comparison of the axes. The temperature flight threshold of 17ºC (Suckling et al. 2005) was not met later in the season.

3.3. Effect of Gamma Radiation on Fecundity and Fertility

There was no significant difference between the fecundity of females mated with males from the two radiation treatments or the controls (F = 0.650, d.f. = 2, 88, $P > 0.05$) (Fig. 6). However, the percentage of F_1 egg hatch (fertility) decreased significantly with increasing radiation dose (F = 44.06, d.f. = 2, 88, $P < 0.001$) (Fig.6).

3.4. Post-Embryonic Mortality

The cumulative mortality for the post-embryonic development stages from the F_1 to the F_3 generations was calculated for the partially sterile P males (irradiated as pupae at 100 and 160 Gy) and their progeny (Fig. 7). For 160 Gy, the cumulative F_1 egg mortality was twice that calculated for insects treated at 100 Gy. By the end of the F_1 pupal stage, more than 90% cumulative mortality was recorded at 160 Gy (Fig. 7). Beginning from the egg stage of the F_2 generation, the cumulative percentage mortality for both male and female lines reached 99% (Abbott's corrected). These results were used to choose 100 Gy for the operational programme.

3.5. Male Flight Ability

Both irradiated and control males exhibited similar behavioural responses to the calling females. Responding males initiated wing activation, followed by take-off and flying upwind via zig-zag anemotaxis towards the females. At the up-wind end, upon arriving at the females, males would be stuck on either the sticky base or the sticky lid of the cage. The irradiated males showed 27.0 ± 1.8% arrival success (334 out of 1236 males tested) compared to 40.9 ± 1.9% in the untreated controls (504 out of 1233 males tested) ($t = 5.34$, $P < 0.001$) (Fig. 8). In terms of irradiated/non-irradiated male competitiveness, the simple competitiveness ratio showed that irradiated males were approximately 66% as successful as the untreated males. These values were tied to the fixed duration of the bioassay, but would be expected to remain constant over time.

4. Discussion

The population of the Australian painted apple moth was dramatically reduced by various measures, including delimitation using virgin female-baited traps, ground searches, habitat removal, and aerial application of *Btk*. The population reduction was an essential precursor to the SIT component of the programme, and it is clear that the combination of these measures was effective in reducing the wild moth population as shown by trap catches in the treated areas, although in some areas heavy vegetation cover affected deposition and impeded the spray programme (Richardson et al. 2005). Sterile releases began with declining catches of wild moths, and only very few were subsequently caught, enabling overflooding ratios in excess of 100:1 to be achieved. Whether the contribution of the releases to eradication was significant compared to the Allee effect acting at such a low insect density (Allee 1938) is unclear, although overflooding was readily achieved at an insect density numbering less than six catches in 12 months to May 2006. As an ongoing case study in mid 2006, it faces operational and scientific challenges similar to other programmes.

Mortality from irradiation treatment of male pupae accumulated across several life stages up to the F_3 generation, but the biggest effect was on eggs at the F_1 and F_2 generations. The level of inherited sterility at the dose chosen for the field programme (100 Gy) was capable of providing nearly complete cumulative sterility of all progeny by the F_3 generation.

In general, sterilizing doses do not alter the lifespan of adult moths (Snow et al. 1972, Lu et al. 2002), and a related study on the Australian painted apple moth showed no effect on the longevity of irradiated males or their progeny under laboratory conditions (Wee et al. 2005), suggesting that this parameter was not a useful measure of competitiveness. Flight and mating competitiveness were therefore used in routine quality assurance (Stephens et al. 2006).

The flight ability of groups of sterile males treated at 100 Gy was only 66% of that of groups of untreated males (with over 1200 males tested per treatment). The estimate of the flight ability of irradiated males tested as a 1:1 pair with untreated males was even lower (32%), although the sample size was also lower (83 males per treatment) (Suckling et al. 2004b). Hence it is not clear whether the inferior performance of irradiated males in a competitive situation was really half of that of irradiated males alone, although reduced flight ability of irradiated males was statistically significant in both experiments. The more representative estimate of flight ability is likely to be from the larger sample size, given that simultaneous arrival of sterilized and wild males at a female would be rare. Some degree of reduced competitiveness of males is inevitable in return for the associated inherited sterility described above. However, it remains unclear whether the increased competitiveness associated with lower irradiation doses is "sufficient" as a trade-off to lower inherited sterility. Population suppression depends on both mating competitiveness (of treated and F_1 males), and the survival of potential non-sterile progeny. Modelling the impact of lower levels of inherited sterility may offer the best approach to optimizing this trade-off.

While the irradiated males showed a lower arrival success, presumably indicating a reduced ability to seek a female in the field, their ability to copulate was not affected (Sucking et al. 2004b). Generally, it is thought that total sperm transfer is positively correlated with copulation duration in insects. In the Mediterranean flour moth *Ephestia kuehniella* Zeller, total time *in copula* was dose (irradiation) and sperm volume-dependent (i.e. the higher the treatment dose and the lower the sperm number, the longer the total time *in* *copula*) (Koudelová and Cook 2001). Irradiated males tended to copulate for longer than did untreated controls in gamma irradiated cabbage looper *Trichoplusia ni* (Hübner) (Holt and North 1970).

This study used wind tunnel flight success as a surrogate for competitiveness estimates in the field. Irradiated males showed significantly reduced ability to arrive at calling females compared to untreated males. However, other experiments showed that upon arrival, they did not show a lower probability of mating compared to untreated males. This, together with the lack of other differences in mating behaviour, suggest that flight success may be an adequate surrogate for the probability of mating of irradiated males, and thereby introgression of inherited sterility into the population. It can therefore be concluded that wind tunnel assessment is a valuable tool for quality assurance, and can provide useful insights into the competitiveness of irradiated males in the implementation of the SIT.

The recapture rate from field releases of fluorescent dye-marked 100 Gy-treated males in a trapping grid was also used to assess the programme (Kean and Suckling 2005). Field recaptures of irradiated males indicated dispersal up to ten kilometres from the release point (Suckling et al. 2005), indicating a surprising level of flight capacity.

5. Conclusions

The eradication of Australian painted apple moths has been considered to be successful in West Auckland, with no breeding populations located since 2003, or males in this area trapped since January 2004. Formal eradication in this area was declared in 2006 (http://www.maf.govt.nz/mafnet/press/200306pam.htm). However, the simultaneous use of multiple eradication tactics prevents quantification of the contribution of the sterile releases. The more recent catches of several males (May, August, October, November and December 2005 and May 2006) in other parts of the city appears to be due to a separate incursion, although isotopic and mtDNA analysis is underway to determine point of origin of these catches (R. Frew, personal communication). This type of new forensic biosecurity tool appears to have potential and work is underway to extend the validation using another species of moth. Two mtDNA haplotypes have been identified (K. F. Armstrong, personal communication), but their frequency in Australia requires more work to assist interpretation. The response to the catches has been to recommence the releases of irradiated moths during 2005 and to increase trap density around each catch, but no other control tactics have been deployed.

The use of this approach against the Australian painted apple moth has highlighted the potential of the SIT in New Zealand to eradicate other exotic insect pests in the future. In addition, sterile recapture information can be used to assess the effectiveness of the surveillance grid (Kean and Suckling 2005). This programme has introduced the concept of "boutique" SIT, referring to a small-scale programme where only a few thousand sterile insects are released each week, targeted at the eradication of well delimited, small populations. There are considerable social advantages of the SIT over aerial spraying and other interventions in an urban setting, including the lack of inconvenience to the public (Dowell et al. 2000). Further work is underway on this and other areas of terrestrial plant biosecurity research in New Zealand under the heading "Better Border Biosecurity".

6. Acknowledgements

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