

Developing a Sterile Insect Release Program for *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae): Effective Overflooding Ratios and Release-Recapture Field Studies

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ABSTRACT In an effort to continue the development of a sterile insect release program against the invasive cactus moth, *Cactoblastis cactorum* (Berg), we released partially sterile males alone or in combination with fully sterile females at a 5:1 or 10:1 (treated:fertile) overflooding ratio inside large field cages containing *Opuntia stricta* Haworth (Haworth) host plants. Insects were allowed to mate and lay eggs, and all eggsticks were collected daily. Percent egg hatch and reduction in F₁ fertile larvae were used to ascertain the effectiveness of each release combination. In addition, limited field release-recapture experiments were conducted to examine the dispersal ability of untreated and treated cactus moth males. Results suggest that an overflooding ratio as low as 5:1 can effectively suppress *C. cactorum* in field cages and that releasing both genders together is more effective than releasing males only. In open field releases, the dispersal ability of *C. cactorum* was not significantly affected by treating the adults with gamma radiation.

KEY WORDS cactus moth, inherited sterility, sterile insect technique, control, invasive species

THE UNINTENTIONAL ARRIVAL OF the South American cactus moth, *Cactoblastis cactorum* (Berg), into Florida from the Caribbean was first detected in 1989. Immediate concerns were raised about the westward dispersal of *C. cactorum* and the threat to native *Opuntia* in the southern United States and Mexico (Habeck and Bennett 1990, Dickel 1991, Pemberton 1995, Johnson and Stiling 1998, Zimmermann et al. 2001). Until its appearance in the United States as an invasive insect, *C. cactorum* was considered the undisputed poster child for biological control of weeds because of its role in the annihilation of invasive *Opuntia* in Australia in the 1930s. Only a few years after its release in Australia, millions of hectares of cactus-infested lands were returned to agriculture and cattle farming (Dodd 1940). As such, concerns for the safety and survival of the many species of native *Opuntia* in southern North America has heightened considerably as *C. cactorum* continues its geographical expansion along the United

States coastline (Hight et al. 2002, 2003; Zimmermann et al. 2004).

No satisfactory method of control is presently available for *C. cactorum* (Stiling 2002). The current infestation is affecting native cacti distributed throughout large expanses of natural lands as well as ornamental cactus plants in urban settings (Hight et al. 2002). Hand removal of infested cladodes and eggsticks and application of insecticides against hatching neonates has been used in *Opuntia* plantations for control of *C. cactorum* in South Africa (Zimmermann et al. 2004). However, Leibe and Osborne (2001) concluded that the biology of *C. cactorum* and its occurrence in natural settings precluded the use of insecticides in the management of populations over vast areas of the United States. Pemberton and Cordo (2001a, b) reviewed the available literature on natural enemies and concluded that, although biological control could reduce the abundance of *C. cactorum*, it was unlikely to help in preventing its spread.

The use of the sterile insect technique (SIT) and, in particular, the variation of the SIT known as inherited or F₁ sterility, offers great potential for managing the spread of *C. cactorum* in North America (Carpenter et al. 2001a,b). Inherited sterility takes advantage of two unique genetic phenomena in Lepidoptera (Lachance 1985, Bloem and Bloem 2000). First, females are more sensitive to radiation than are males of the same species. This differential sensitivity allows for treatment with a particular dose of radiation to result in females that are completely sterile and males that

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Table 1. Treatments used to examine the effect of different overflooding ratios and release options on the suppression of populations of *C. cactorum* inside field cages

Treatment	Treatment designation	No. U♀	No. U♂	No. T♀	No. T♂	Total no. adults
Control (N)	N	10	10	0	0	20
5:1 ratio males	N + 5:1 T♂	10	10	0	50	70
5:1 ratio males and females	N + 5:1 T♂♀	10	10	50	50	120
10:1 ratio males	N + 10:1 T♂	10	10	0	100	120
10:1 ratio males and females	N + 10:1 T♂♀	10	10	100	100	220

N, untreated "population" of 10 males and 10 females; U♀, untreated female; U♂, untreated male; T♀, female treated with 200 Gy gamma radiation; T♂, male treated with 200 Gy gamma radiation.

are only partially sterile. A benefit of using lower doses of radiation (i.e., doses lower than would be necessary to fully sterilize males) is that the quality and competitiveness of the irradiated insects is improved (North 1975). Second, when partially sterile males mate with wild fertile females in the field, the radiation-induced deleterious effects in the male are inherited by his offspring (F_1 generation). The resulting field-produced fully sterile F_1 progeny resulting from these matings combined with regular releases of partially sterile males (and fully sterile females) offer greater suppressive potential than the release of fully sterile insects by themselves (LaChance 1985).

The field application of SIT/ F_1 sterility has been studied for many species of economically important Lepidoptera, including *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae) (North and Holt 1969), *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) (Carpenter et al. 1987, Carpenter and Gross 1993), *Lymantria dispar* L. (Lepidoptera: Lymantriidae) (Mastro 1993), and *Cydia pomonella* L. (Lepidoptera: Tortricidae) (Proverbs et al. 1978, Bloem et al. 1999a, b, 2001, 2004). Carpenter et al. (2001b) conducted radiation biology studies on *C. cactorum* and determined that a dose of 200 Gy results in completely sterile females and males that are 40–50% fertile. In this paper, we examined the effect of releasing different ratios of partially sterile *C. cactorum* males alone or in combination with releases of fully sterile females inside field cages containing potted host plants and a cohort of untreated *C. cactorum* males and females. In addition, we conducted field release-recapture tests using untreated and treated *C. cactorum* males to ascertain whether radiation is detrimental to dispersal. The results obtained are discussed in the context of launching an SIT/ F_1 sterility program to prevent the westward spread of *C. cactorum* into areas of the western United States and Mexico.

Materials and Methods

Test Insects. Cactus moths used in these studies came from a laboratory colony maintained at the USDA-ARS Crop Protection and Management Research Unit in Tifton, GA. Larvae were reared on cladodes of *Opuntia ficus-indica* L. Miller, inside rectangular plastic boxes as described by Carpenter et al. (2001b). As larvae matured, cocoons were collected every 2–3 d. For these experiments, pupae were extracted from the cocoons, sorted by gender, and

placed in separate screen cages (30.5 by 30.5 by 30.5 cm). Emerged, virgin adult males and females (<48 h old) were placed in individual 30-ml plastic cups and either left untreated (U) or treated (T) with 200 Gy of gamma radiation using a Cobalt⁶⁰ Gammacell 220 irradiator (J. L. Shepherd & Associates, San Fernando, CA; dose rate of ≈ 14.56 Gy/min). A dose of 200 Gy causes 100% sterility in adult females and ≈ 50 –60% sterility in adult males (Carpenter et al. 2001b).

Field Cage Experiments. Twenty large, high-density, polypropylene mesh field-cages (1.8 by 1.8 by 1.8 m; Synthetic Industries, Gainesville, GA) were erected in late September 2003 in a forest clearing at St. Marks National Wildlife Refuge (30°04' N, 84°10' W). The site was mowed before cage placement. Once erected, each cage was provisioned with a single unfested potted plant of *Opuntia stricta* (Haworth) Haworth (mean plant height 0.70 m). Four treatments and a control were randomly assigned to the field cages (Table 1). Treatments were based on (1) the overflooding ratio of treated to untreated moths (5:1 or 10:1) and (2) whether treated males only or treated males and females were released into cages containing an untreated population (see control = N in Table 1).

On the day of release, adults were counted and placed in cylindrical cardboard containers (0.5 liter) according to treatment requirements, transported to the field in a small cooler, and released in the cages during mid-afternoon (1500–1600 hours). Moths were gently tapped out onto the potted plants inside each cage. Each treatment was replicated four times, and replicates were initiated over four dates—02, 06, 08, and 10 October 2003. In all cases field cages were first checked 48 h after each release to allow for moth mating and oviposition. Thereafter, *O. stricta* plants and the surfaces of the cage screening were checked daily for eggsticks. Daily checks of each cage continued for 2 d after the last eggstick was found. Each eggstick was placed into an individual 30-ml plastic cup and taken back to the laboratory. Eggsticks were incubated at $30 \pm 1^\circ\text{C}$, a photoperiod of 14:10 (L:D), and 50% RH to allow for embryonic development and egg hatch.

The following data were collected for each treatment: total number of eggsticks, mean number of eggsticks per female, mean number of eggs per eggstick, and number of eggs from each eggstick that hatched. The identity of the parental cross involved in producing all eggsticks collected from each treatment cage was determined according to a decision tree, where

U♀ or U♂ = untreated mother or father, respectively, and T♀ or T♂ = treated mother or father with 200 Gy of gamma radiation. The decision tree progressed as follows: if the percentage of eggs hatching from an eggstick was >49.9%, the parental cross was identified as U♀ × U♂; if the percentage of eggs hatching from an eggstick was >5% but ≤49.9%, the parental cross was identified as U♀ × T♂; if the percentage of eggs hatching from an eggstick was <5% but >70.0% of the unhatched eggs exhibited embryonic development, the parental cross was also identified as U♀ × T♂; if the percentage of eggs hatching from an eggstick was <5% but ≤70.0% of the unhatched eggs exhibited embryonic development, the parental cross was identified as either T♀ × T♂ or T♀ × U♂. The values in this decision tree were derived from the egg hatch found in the control cages ($N = 10 \text{ U♀} + 10 \text{ U♂}$), in cages receiving only T♂, and from egg hatch and developmental data reported by Carpenter et al. (2001b). Once the parental cross was identified for each eggstick, only the number of larvae emerging from eggsticks laid by U♀ × T♂ mating pairs (F_1 sterile larvae) and by U♀ × U♂ mating pairs (F_1 normal) were tabulated and used in the data analysis. The percentage of eggs that hatched and the number of F_1 larvae produced were used to assess the effectiveness of the different treatments. In cages receiving treated males (T♂) and treated females (T♀), the same data were used to assess the role of fully sterile females in population suppression.

Release-Recapture of Treated and Untreated Male Cactus Moths. Experiments were conducted during mid-October 2003 along the edge of a salt marsh estuary on the southern banks of the Brunswick River, Glynn County, GA. An area along the edge of the salt marsh estuary and the Jekyll Island causeway containing naturally occurring patches of *O. stricta* (between 0.5 and 1.5 m in height) was chosen for the study. Ten Pherocon 1-C wing traps were baited with one or two 48-h-old fertile *C. cactorum* females as described in Bloem et al. (2003). Each trap was mounted to a hollow metal stake placed within a cactus patch at a height of ≈0.75 m. All traps were separated from one another by at least 10 m. This area containing the 10 traps was designated as the "release site." In addition to the 10 traps at the release site, 3 similar traps were placed at distances of 1.4, 1.5, and 2.5 km from the release site along the easterly oriented Jekyll Island causeway. These distances were chosen because of the presence of host plants. *Opuntia stricta* were common but occurred in widely separated patches in this general area.

On the day of release, adult males were counted, placed in 475-ml plastic cups according to treatment requirements (U♂ = untreated male; T♂ = male treated with 200 Gy of gamma radiation), transported to the field in a small cooler, and released during mid-afternoon (1500–1600 hours). To distinguish between male treatment type and day of release, males from each release date and treatment were marked with a different color fluorescent powder (Day-Glo Color, Cleveland, OH). Five releases of equal num-

Table 2. Date and no. untreated (U♂) and treated (T♂) (at 200 Gy) adult male *C. cactorum* released in the release-recapture study conducted at Glynn County, GA, in 2003

Release no.	Date in 2003	No. U♂	No. T♂	Total ♂
1	17 October	180	180	360
2	20 October	120	120	240
3	23 October	106	106	212
4	27 October	127	127	254
5	31 October	78	78	156

bers of untreated (U♂) and treated (T♂) male cactus moths were made by hand along the salt marsh estuary by gently tapping out the insects from the plastic containers onto the estuary vegetation at a point between each trap at the release site. The minimum distance between the release points and a trap was 5 m. The date and number of released *C. cactorum* males is summarized in Table 2.

Virgin female-baited traps were first deployed on 17 October and serviced every 3 d until 6 November 2003. During each trap servicing, the number of *C. cactorum* males captured per trap was recorded, and the traps were rebaited with fresh virgin females. Sticky trap bottoms that captured at least one male moth were taken back to the laboratory where the color, and thus the treatment and release date of the captured males, was ascertained under UV light. Traps were serviced a total of six times, and the numbers of males recaptured per treatment per release were recorded. The length of time over which males from a particular treatment release were captured in traps was also noted and used as a further assessment of male moth competitiveness.

Statistical Analysis. Field-cage data were analyzed using analysis of variance (ANOVA) and regression analysis, with treatment and replication as sources of variation (PROC ANOVA and PROC GLM) (SAS Institute 1989). If there was a significant ($P \leq 0.05$) interaction between treatment and replication, the interaction was tested as an error term. Percent egg hatch, number of larvae emerged, number of F_1 sterile larvae, number of F_1 normal larvae, and percentage of F_1 sterile larvae were the dependent variables. When the statistical model indicated significant treatment effects, differences between means were separated by the Tukey-Kramer statistic ($P \leq 0.05$) for multiple comparisons.

To ascertain whether assortative mating was taking place inside the field cages, the frequency of each type of mating within each treatment was calculated based on the number of eggsticks identified as originating from different parental crosses. The "expected" mating frequency was calculated from the ratio of insect types (U or T) within each treatment. The "observed" mating frequency was compared with the "expected" mating frequency using the χ^2 statistic (PROC FREQ, goodness of fit test; SAS Institute 1989).

Finally, the release-recapture data from the six different release dates were pooled, and the 10 virgin female-baited traps located at the release site were treated as replications. Data collected from the three

Table 3. Comparison of mean \pm SD percentage egg hatch, no. larvae emerging and no. F₁ sterile and F₁ normal larvae produced by *C. cactorum*

Treatment	Mean no. eggsticks per cage \pm SD	Mean no. eggs per eggstick \pm SD	Percent egg hatch \pm SD	No. larvae emerged \pm SD	No. F ₁ sterile larvae \pm SD	No. F ₁ normal larvae \pm SD
N ^a	11 \pm 4.8	37 \pm 8.4	85 \pm 17.7a	34 \pm 19.8a	0b	34 \pm 19.8a
N + 5:1 T♂	15 \pm 9.7	35 \pm 6.9	45 \pm 30.9b	16 \pm 14.5b	5 \pm 6.5a	11 \pm 16.8b
N + 5:1 T♂♀	32 \pm 20.9	37 \pm 4.1	7 \pm 16.3c	2 \pm 4.9bc	2 \pm 4.8b	0.2 \pm 1.6b
N + 10:1 T♂	15 \pm 7.4	42 \pm 10.6	24 \pm 15.7b	10 \pm 9.1b	9 \pm 7.8a	2 \pm 7.2b
N + 10:1 T♂♀	83 \pm 30.2	32 \pm 3.0	4 \pm 13.2c	1 \pm 4.8c	1 \pm 3.1b	0.5 \pm 3.7b

Treatments in cages included a 5:1 or 10:1 overflooding ratio of treated (200 Gy) males or of treated males and females. Means within each column followed by the same letter are not significantly different ($P > 0.05$).
^a Untreated "population" of 10 male and 10 female adult *C. cactorum*.

traps along the Jekyll Island causeway were not included in the statistical analysis. Treatment means were compared using the Student's *t*-test statistic.

Results and Discussion

Field Cage Experiments. Eggsticks were found in each cage for \approx 10 d. In control cages (N) where only fertile moths (10♂ and 10♀) were released, the mean number of eggsticks per cage was 11 (range, 6–17; Table 3). This mean number increased to 15 (range, 8–29) and 15 (range, 4–20) (Table 3) eggsticks in cages receiving N + 5:1 T♂ and N + 10:1 T♂, respectively, even though no additional female *C. cactorum* were added with these treatments. However, in cages receiving N + 5:1 T♂♀ and N + 10:1 T♂♀, the mean number of eggsticks per cage increased to 32 (range, 7–58) and 83 (range, 51–119; Table 3), respectively, because of the release/presence of 50 or 100 additional sterile females in these treatments. It is worth noting that the mean number of eggsticks laid per female did not differ in the different treatments. Females laid an average of 2.2 eggsticks in the control (N), 3.0 eggsticks in cages receiving treated males (both N + 5:1 T♂ and N + 10:1 T♂), and 2.2 and 3.0 eggsticks in cages receiving treated males and females (N + 5:1 T♂♀ and N + 10:1 T♂♀). It should also be kept in mind that in cages where the treatment included the release of treated males and females (T♂♀), either at a 5:1 or a 10:1 overflooding ratio, 100% of the treated females were completely sterile. Fully sterile female *C. cactorum* will lay eggsticks, but none of the eggs will

hatch. Finally, the mean number of eggs per eggstick was similar in all treatments (Table 3).

The different treatments significantly ($F = 69.06$; $df = 19,605$; $P < 0.0001$) affected the mean percentage of eggs hatching from all eggsticks collected in each field cage (Table 3). The percentage of eggs that hatched in control (N) cages (85%) was significantly higher than that found in any of the cages that received treated moths. Even though the percent hatch in cages that received a 10:1 overflooding ratio of either T♂ (24%) or T♂♀ (4%) was approximately one-half of the percent egg hatch in cages that received a 5:1 ratio (45% for T♂ and 7% for T♂♀), these differences were not significant. Nevertheless, for both overflooding ratios (5:1 and 10:1), the percent egg hatch was significantly lower (7% for 5:1 and 4% for 10:1) in cages where both genders (T♂ and T♀) were released together.

The presence of large numbers of unhatched eggs in treatments that received fully sterile females (N + 5:1 T♂♀ and N + 10:1 T♂♀) made the reduction in the percent egg hatch in these treatments seem artificially high compared with the control. Therefore, it is more appropriate in this experimental design to evaluate treatment effects by comparing the actual number of larvae that emerged from all treatments. Furthermore, because of the marked difference in the percent egg hatch when fertile females (U♀) are mated to fertile (U♂) or to treated (T♂) males, we were able to effectively identify the eggsticks produced by each type of cross. This, in turn, allowed us

Table 4. Comparison of expected versus observed percentage of matings in field cages containing *C. cactorum*

Treatment	Percentage of matings ^a					
	U♀ × U♂		U♀ × T♂		T♀ × U♂ and T♀ × T♂	
	Expected	Observed	Expected	Observed	Expected	Observed
Control (N)	100	100	0	0	0	0
5:1 ratio males	16.67	33.5	83.3	66.5	0	0
5:1 ratio male and female	2.67	1.00	13.88	30.97	69.4	67.30
10:1 ratio males	9.09	8.88	90.9	91.12	0	0
10:1 ratio male and female	0.83	1.55	8.27	32.92*	90.07	65.53*

Treatments in cages included a 5:1 or a 10:1 overflooding ratio of treated (200 Gy) males or treated males and females.

^a Observed values for a treatment and cross that are followed by an asterisk are significantly different ($P > 0.05$) from the expected value for that treatment and cross.

to determine the number of F_1 normal and F_1 sterile larvae produced per treatment (Table 3).

The "overall" number of F_1 larvae that emerged from each eggstick was significantly ($F = 45.17$; $df = 19,605$; $P < 0.0001$) affected by treatment. In control cages (N), the number of emerged larvae (34) was significantly higher than in any of the cages receiving treated moths. Even though the number of emerged larvae in cages that received $N + 10:1 T\delta$ (10) or $N + 10:1 T\delta\varphi$ (1) was lower than in cages that received $N + 5:1 T\delta$ and $N + 5:1 T\delta\varphi$ (16 and 2), the differences were not significant. However, when the overflooding ratio was 10:1, significantly fewer larvae emerged from cages that had received $T\delta$ and $T\varphi$. As expected, of the F_1 larvae that did emerge, the number that were categorized as F_1 sterile larvae was significantly greater in cages that received $T\delta$ only compared with those emerging in the control or in cages that received both $T\delta$ and $T\varphi$ ($F = 11.88$; $df = 19,605$; $P < 0.0001$; Table 3). All of the matings taking place in cages that received $T\delta$ only ($N + 5:1 T\delta$ and $N + 10:1 T\delta$) would have involved only fertile females ($N = 10 U\delta + 10 U\varphi$), whereas in cages receiving $T\delta$ and $T\varphi$, the possible matings would have involved fertile ($U\varphi$) and released sterile ($T\varphi$) females. Only matings between a fertile female ($U\varphi$) and a treated male ($T\delta$) can give rise to F_1 sterile larvae. Finally, the number of larvae categorized as F_1 fertile was significantly ($F = 47.38$; $df = 19,605$; $P < 0.0001$) higher in the control cages than in any of the cages that received treated moths.

In this experiment, reduction in percent egg hatch and number of F_1 larvae produced were used to assess the effectiveness of releasing different ratios and gender combinations of *C. cactorum* treated with 200 Gy on population suppression under semifield conditions. Our results show that an overflooding ratio as low as 5:1 (treated:fertile) is sufficient to bring about a significant reduction in the "wild" population inside field cages and that a ratio of 10:1 is even more effective. This was true for both ratios, irrespective of whether treated males only or treated males and females were used in the release. Nevertheless, for both ratios, the suppressive effect was much greater when treated males and treated females were released together.

Whether it is more beneficial/economical to release mixed genders or male only strains is a long-standing question in SIT programs. In SIT programs for Diptera, the release of sterile females can have serious detrimental consequences. For example, sterilized female fruit flies (i.e., Mediterranean fruit fly, *Ceratitidis capitata*; Mexican fruit fly, *Anastrepha ludens*) still puncture the fruit to lay sterile eggs, which causes fruit scarring and facilitates pathogen entry into fruit. As a consequence, genetic sexing strains have been developed for Mediterranean fruit fly (Franz and Kerremans 1993), and male-only releases are routinely used in areawide suppression programs. However, experimental evidence strongly suggests that sterile females are beneficial in SIT programs against pestiferous Lepidoptera. Field cage experiments conducted by Hussein and Madsen (1964) on navel orange worm

(*Amyelois transitiella*; Lepidoptera: Pyralidae), by Guerra et al. (1974) on tobacco budworm [*Heliothis virescens* (F.) Lepidoptera: Noctuidae], and by Van Steenwyk et al. (1979) on pink bollworm have shown that sterile females have a significant (and in some cases the only) positive contribution in population suppression in all of these species. Furthermore, season-long field releases of males alone, females alone, and mixed genders of codling moths conducted by White et al. (1976) in apple orchards resulted in population suppression figures of 88.5, 89.7% and 91.5%, respectively, suggesting that sterile females play an important role in the mating dynamics of a wild population under SIT. The results presented herein suggest that sterile female *C. cactorum* played a critical role in population suppression inside field cages, possibly through their action as a sperm sink (i.e., competing with fertile females for mates and, as such, removing the limited fertile sperm from the system). The most effective treatments in our experiments, both in terms of reduction in egg hatch and reduction in number of F_1 fertile larvae produced, were invariably those that included the release of sterile female *C. cactorum*. Our results contribute to the mounting body of evidence that suggests that sterile females play a pivotal role in the suppression of pestiferous Lepidoptera when SIT is used (Bloem and Carpenter 2001).

A comparison of the observed and expected mating frequency within the field cages revealed that the observed frequency of each mating type was not significantly different from the expected frequency except in the cages where a 10:1 overflooding ratio of $T\delta$ and $T\varphi$ were released together (Table 4). In this treatment, a higher percentage of observed matings occurred between $U\varphi$ and $T\delta$ than was expected. However, because the $U\varphi \times U\delta$ cross did not participate in more mating events than was expected in any of the treatment cages, the data indicate that the competitiveness of the treated moths was not reduced as a result of the radiation treatment. In other words, there was no evidence for assortative mating between the U and T moths in this experiment.

Release-Recapture of Treated and Untreated Male Cactus Moths. There was no significant difference between the mean \pm SD number of treated (10.83 ± 11.3) and untreated (8.67 ± 5.6) males captured during the release-recapture study. In general, males were recaptured within 3 d after release. Also, most of the released males that were recaptured were caught in the 10 traps located at the release site (Fig. 1). Nevertheless, a few males were recaptured in traps that were 1.4, 1.5, and 2.5 km away from the release site (Fig. 1).

These results represent a valuable contribution toward the initiation of a SIT/ F_1 sterility program to prevent the westward spread of *C. cactorum* into areas of the western United States and Mexico. Our data suggest that male and female *C. cactorum* treated with 200 Gy of gamma radiation are highly competitive. Based on the data from the release recapture study, a program should aim to release treated *C. cactorum* at

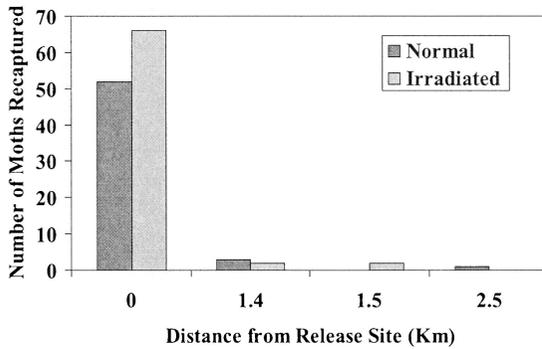


Fig. 1. Comparison of normal and irradiated (200 Gy) male *C. cactorum* moths with respect to the number of males recaptured in female-baited sticky traps and the distance from the release site in which males were captured. A total of 1,222 males were released (611 of each treatment type) over the 15-d period of 17–31 October 2003.

least twice per week. Furthermore, our data suggest that releasing mixed genders should bring about control of the population sooner than releases of males only. Target overflooding ratios in current SIT area-wide suppression programs for Lepidoptera vary between 40:1 (for codling moth, *Cydia pomonella*) and 60:1 [for pink bollworm, *Pectinophora gossypiella* (Saunders) Lepidoptera: Gelechiidae] (Staten et al. 1993, Bloem and Bloem 2000). However, field cage studies by Proverbs and Newton (1962) and Bloem et al. (1999a) reported that overflooding ratios as low as 20:1 and 10:1 brought about effective control of “wild” codling moth populations in field cages when fully sterile or partially sterile moths were released. In practical terms, an SIT program for *C. cactorum* should probably aim for a target overflooding ratio between 10:1 and 20:1. Future field research will test the information presented here under true season-long and areawide conditions.

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