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Suppression of diamondback moth using Bt-transgenic plants as a trap crop

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Abstract

Several types of trap crops have been recommended for managing the diamondback moth, *Plutella xylostella*, including collards (*Brassica oleracea* var. *acephala*) and Indian mustard (*Brassica juncea* L.). However, results have been variable perhaps because populations of *P. xylostella* develop on these trap crops and spill over to the cash crop. To overcome this problem, we sought to develop "dead-end" trap crops that were more attractive for oviposition than the cash crop but on which *P. xylostella* larvae cannot survive. We have produced *Bacillus thuringiensis* (Bt)-transgenic collard and Indian mustard lines with a *cry1C* gene that have the potential to be used as a "dead-end" trap crop for *P. xylostella*. Greenhouse and small cage studies confirmed the control of *P. xylostella* larvae on the Bt crops. Furthermore, Indian mustard was significantly preferred over cabbage and collards for oviposition, regardless of whether the Indian mustard was Bt or non-Bt. The use of Bt Indian mustard as a trap crop significantly reduced the number of larvae that appeared on a cabbage cash crop, compared with using a non-Bt Indian mustard trap crop. However, this reduction also occurred when using Bt collards as a trap crop, despite collards being less preferred for oviposition. In fact, despite the overall increase in oviposition caused by the presence of Indian mustard compared with collards, the use of either Bt Indian mustard or Bt collards provided the same level of protection to the cash crop. Both plants also resulted in significant suppression of a *P. xylostella* population over 3 generations in the greenhouse test and 2 generations in the small cage experiment, suggesting that in places where immigration may be limited some long-term population suppression may occur. We suggest that Bt trap crops may be useful tools in situations where the cash crop may not be suitable or desirable for genetic engineering.

Keywords: *Bacillus thuringiensis*; *Brassica oleracea*; *Plutella xylostella*; Trap crop

1. Introduction

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is considered the most damaging insect pest of cruciferous crops worldwide, with an estimated control cost of nearly US$1 billion annually (Talekar and Shelton, 1993). Most of these control costs are due to the intense use of insecticides against this pest, but this has led to many populations that have developed resistance to many of the traditional insecticides (Talekar and Shelton, 1993). More recently, some populations of *P. xylostella* have developed resistance to newer active ingredients, including spinosad and indoxacarb (Zhao et al., 2006). Control failures of *P. xylostella* have become common in many parts of the world, especially in Southeast Asia, India, China, Central America, the Caribbean and the southeastern United States, and novel approaches are sorely needed. One such approach is the use of trap crops. There has been a recent resurgence of interest in trap cropping as an IPM tool because of concerns about the potential negative effects of pesticides on human health and the environment, pesticide resistance and general economic considerations of agricultural production.

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Trap crops are an alternative method of control in which plants are deployed to attract, intercept, retain and/or reduce targeted insects or the pathogens they vector in order to reduce damage to the main crop (Shelton and Badenes-Perez, 2006). This definition encompasses the inherent characteristics of the trap crops as well as their deployment in space and time. *P. xylostella* is the insect pest for which most attempts of control through trap cropping have been undertaken, but results have been variable (Shelton and Badenes-Perez, 2006). In India, Srinivasan and Moorthy (1992) tested and then promoted the use of Indian mustard, *Brassica juncea* (L.) Czern, as a trap crop when planted in 2-row strips every 15 rows of the cash crop. Others have found a trap crop of Indian mustard less effective (Pawar and Lawande, 1995; Luther et al., 1996; Bender et al., 1999). Collards, *Brassica oleracea* L., var. *acephala*, have also been promoted as a trap crop when planted as a border around a field (e.g. Mitchell et al., 2000), but other studies have indicated no effect (Shelton and Nault, 2004) or inconsistent results (Musser et al., 2005). It is not clear to us that either of these crops is effective or has been widely adopted as a trap crop. Some of the failings of these trap crops could be due to an insect population building on the trap crop and spilling over to the cash crop. To avoid this, the term "dead-end" trap crops was proposed to describe plants that are highly attractive to insects but on which they or their offspring cannot survive (Shelton and Nault, 2004). An example of such a plant for use against *P. xylostella* is yellow rocket, *Barbarea vulgaris* (R. Br.) var. *arcuata*, a biannual invasive weed that occurs in temperate regions worldwide (Uva et al., 1997). In trials conducted in a greenhouse and screenhouse and in small field experiments, such plants have proven successful in reducing damage to the cash crop (Badenes-Perez et al., 2004, 2005; Shelton and Nault, 2004; Lu et al., 2004). However, there are drawbacks to this plant since at least one other lepidopteran pest species, imported cabbageworm, *Pieris rapae* L., is not adversely affected by yellow rocket (unpublished data). Additionally, growers are reluctant to plant 10–20% of their land to a plant species that is not marketable, as is the case for yellow rocket (Badenes-Perez et al., 2005).

Use of transgenic plants expressing one or more proteins from the common soil bacterium, *Bacillus thuringiensis* (Bt), may be an option for creating dead-end trap crops with suitable agronomic capabilities. Previous studies in our and other laboratories have demonstrated excellent direct control of *P. xylostella* by *B. oleracea* plants carrying a synthetic or fully modified *cry1* Bt gene (Metz et al., 1995; Cao et al., 1999; Jin et al., 2000; Bhattacharya et al., 2002; Zhao et al., 2005). Cao et al. (2005) developed transgenic collards expressing a *cry1Ac* or *cry1C* gene and proposed using them not only as a direct method of control, but also as a trap crop. Use of an effective Bt trap crop could not only help protect the non-transgenic cash crop but, if approved by regulatory agencies for human consumption, could also be a cash crop and thus be more economically attractive for producers. Additionally, if these dead-end trap crops were deployed against a resident population of insects, they may provide longer-term population suppression.

The goals of this study were to evaluate several potential Bt crucifers for their ability to act as dead-end trap crops and to assess their ability to suppress populations of *P. xylostella* over multiple generations.

2. Materials and methods

2.1. Plants

Experiments were conducted with the collard (*B. oleracea* L. var. *acephala*) variety "Champion", the Indian mustard (*B. juncea* (L.) Czern) variety "Green Wave" and the cabbage (*B. oleracea* L. var. *capitata*) variety "Fresco". Bt collards and Bt Indian mustard were produced by inserting a *cry1C* Bt gene, in association with the *hpt* gene for hygromycin resistance, into seedling explants by *Agrobacterium tumefaciens*-mediated transformation (Cao et al., 2005). "Champion" collards and "Green Wave" Indian mustard were used as the parental lines for Bt and non-Bt trap crops and the cabbage variety "Fresco" was used as the cash crop.

2.2. Greenhouse experiments

Experiments were conducted in greenhouses at Cornell University's New York State Agricultural Experiment Station in Geneva, NY, in 2005. A total of 20 cages were placed in greenhouses in a randomized complete block design with 5 treatments and 4 replications. Each cage was 1.8 m long × 0.9 m wide × 1.7 m high and constructed of nylon netting. The 5 treatments were as follows: 10 Bt Indian mustard plants surrounding 40 cabbage plants; 10 non-Bt Indian mustard plants surrounding 40 cabbage plants; 10 Bt collard plants surrounding 40 cabbage plants; 10 non-Bt collard plants surrounding 40 cabbage plants; and 50 cabbage plants (control). Pots containing the trap crops (Bt and non-Bt collards and Indian mustard) were placed in a single row surrounding the block of cabbage plants. All plants were individually potted in 15 cm diameter pots containing Cornell artificial soil. Plants had 6 true leaves when they were placed into the cages and the distance between all pots was 3 cm. At the beginning of the experiment, we introduced 10 female and 10 male *P. xylostella* adults into each of the 20 cages. The insect colony was <3 generations removed from the field and had no evidence of being resistant to the Cry1C protein when tested in a leaf-dip bioassay (Zhao et al., 2005). After 3 days, the majority of eggs were laid, and the first egg count was made by randomly selecting and examining 5 plants from the border (trap crops) and 5 from the interior (cash crop). Twelve days later, when the majority of the eggs had developed into larvae or pupae, another insect count was made for the first generation. At the end of the first

generation, the stems of the plants in each cage were cut and 40% of the foliage containing *P. xylostella* larvae was randomly selected and placed on the floor of the cage so that adult *P. xylostella* could emerge. The remaining foliage and larvae on it were removed from the cages because of higher than anticipated populations in the non-Bt treatments. Removal of an equal percentage of insects in each cage simulated a density-independent event and allowed us to continue the experiment for more generations. At the first emergence of the second generation of adults in the cage, another set of the appropriate plants was introduced into each cage and these plants were subjected to oviposition by the *P. xylostella* in the cage. Egg and larval counts were made on this second generation of insects using the same methods as for the first generation. After the second generation had developed, the stems of the plants were cut and all the foliage was placed on the floor of the cage. The third generation of adults emerged and laid their eggs on a new set of plants that had been introduced, and oviposition and larval counts were performed as before. For each generation, data on oviposition and larval plus pupal counts were analyzed using ANOVA and Tukey–Kramer's HSD mean separation test ($P<0.05$).

2.3. Small cage experiments

A total of 15 cages were placed in greenhouses in a randomized complete block design with 5 treatments and 3 replications. Each cage was 0.6 m long × 0.45 m wide-0.6 m high and constructed of nylon netting. The 5 treatments were as follows: 3 Bt Indian mustard plants and 3 cabbage plants; 3 non-Bt Indian mustard plants and 3 cabbage plants; 3 Bt collard plants and 3 cabbage plants; 3 non-Bt collard plants and 3 cabbage plants; and 6 cabbage plants (control). Pots containing the 6 plants were placed randomly in a cage. All plants were potted in 15 cm diameter pots containing Cornell artificial soil. Plants had 6 true leaves when they were placed into the cages. At the beginning of the experiment, we introduced 3 female and 3 male *P. xylostella* adults into each of the 15 cages. The insect colony was the same one used in the greenhouse studies and <4 generations removed from the field. After 3 days, the majority of eggs were laid, and the first egg count was made by examining all 6 plants from each cage. Eight days later, when the majority of the eggs had developed into larvae, another insect count was made for the first generation. At the end of the first generation, the stems of the plants in each cage were cut and all the foliage was placed on the floor of the cage so adult *P. xylostella* could emerge. At the first emergence of the second generation of adults in the cage, another set of the appropriate plants was introduced into each cage and these plants were subjected to oviposition by *P. xylostella*. Egg and larval counts were made on this second generation of insects using the same methods as for the first generation. The experiment was terminated after the larval count in the second generation. For each generation, data on oviposition and larval counts were analyzed using ANOVA and Tukey–Kramer's HSD mean separation test ($P<0.05$).

3. Results

3.1. Greenhouse experiments

In the first generation, Indian mustard was significantly preferred ($F=14.82$, df = 9, $P<0.001$) over cabbage and collards for oviposition, regardless of whether the Indian mustard was Bt or non-Bt (Fig. 1A). There were no significant differences between the number of eggs on cabbage or on Bt collards or on non-Bt collards. The number of larvae and pupae developing on Bt Indian mustard was significantly lower ($F=19.42$, df = 9, $P<0.001$) than on non-Bt Indian mustard (Fig. 1B). The number of larvae plus pupae on Bt collards was also significantly lower than on non-Bt collards. The number of larvae and pupae on the cash crop was lowest in the presence of Bt Indian mustard (Fig. 1B), despite the high oviposition on Indian mustard (Fig. 1A). Similar trends were seen for both oviposition and larval plus pupal counts in the second generation (data not shown).

At the beginning of the third generation, the mean number of eggs on the non-Bt Indian mustard was 55.5 per plant compared with <10 per plant on all other plants (Fig. 2A), including the Bt Indian mustard. At the conclusion of the third generation, the mean number of larvae plus pupae on the non-Bt Indian mustard was 11.3 per plant, while the density on the Bt Indian mustard was significantly lower at 0.8 (Fig. 2B). The density on non-Bt collards was 20.6, which was significantly higher than the 1.1 density on the Bt collards. Both the Bt Indian mustard and Bt collard treatments significantly suppressed the population of *P. xylostella* on the cash crop, compared with non-Bt Indian mustard and collard treatments, respectively, and there was no significance difference in the number of larvae plus pupae on the cash crop in the Bt Indian mustard and Bt collard treatments (Fig. 2B).

3.2. Small cage experiments

As in the greenhouse trials, in the first-generation Indian mustard was significantly preferred over cabbage and collards for oviposition, regardless of whether the Indian mustard was Bt or non-Bt ($F=23.53$, df = 9, $P<0.001$) (Table 1). Interestingly, the total number of eggs laid in the cages containing Bt and non-Bt Indian mustard was 130 and 110, respectively, which was at least 3.5-fold higher than in those cages that did not contain any Indian mustard ($F=15.38$, df = 4, $P<0.001$). The mean number of larvae per plant on the non-Bt trap plants was at least 11 while the number on Bt Indian mustard and Bt collards was 0.1 and 0.3, respectively (the presence of larvae on the Bt plants was likely to have been the result of larvae moving from the non-Bt plants in the cage) ($F=10.23$,

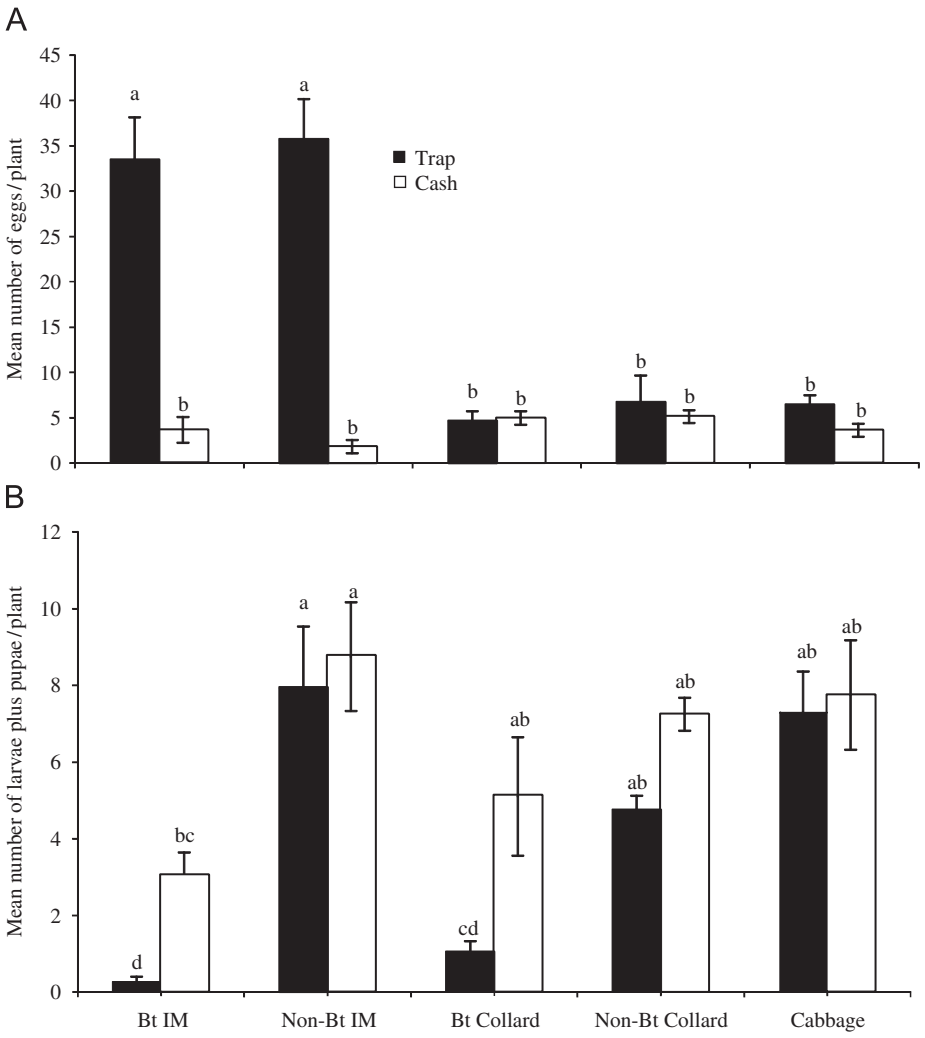

Fig. 1. Mean number of *Plutella xylostella* eggs (A) or larvae plus pupae (B) per plant in the first generation of a trap cropping experiment. The term trap crop refers to plants that are intended to reduce insects on the cash crop. IM refers to Indian mustard and Bt refers to plants that have been engineered to express Cry1C proteins from *Bacillus thuringiensis*.

df = 9, $P<0.001$). The number of larvae on the cash crop was lowest in the Bt Indian mustard treatment; however, this was similar to that on the non-Bt Indian mustard.

In the second generation, the non-Bt Indian mustard had nearly 300 eggs per plant, which was 80-fold higher than in the Bt Indian mustard treatment, and at least 7-fold higher than the next highest treatment (non-Bt collard) ($F = 15.38$, df = 9, $P<0.001$). The high number of larvae produced in the first generation in the non-Bt Indian mustard treatment resulted in an extremely high number of eggs laid per cage in the second generation. This in turn led to the highest number of larvae on the cash crop (mean per plant of 53.4) in the second generation, compared to only 0.1 on the cash crop in the Bt Indian mustard treatment ($F = 6.37$, df = 9, $P<0.001$).

4. Discussion

Bt cotton and Bt corn plants are the only 2 genetically engineered insecticidal plants presently commercialized and they were grown on 32.1 million hectares in 2006 (James, 2006). They have provided excellent control of targeted pests (Shelton et al., 2002), enhanced biological control (Romeis et al., 2006) and economic and environmental benefits (Brookes and Barfoot, 2006). They have been used as a direct method of insect control, but have provided some unexpected benefits such as in the case of Bt cotton, which has led to long-term suppression of the pink bollworm, *Pectinophora gossypiella,* in the field (Carriere et al., 2003). A 10-year study over 15 regions across Arizona demonstrated that Bt cotton suppressed this major pest far more effectively than insecticide sprays, and the authors suggest that Bt plants may be used for regional pest suppression and reduce the need for traditional insecticide sprays. Bt plants may also be used as a trap crop, as was demonstrated for control of the Colorado potato beetle, *Leptinotarsa decemlineata*. When Bt potatoes were planted early in the season to attract immigrating Colorado potato beetle adults, they acted as an early season, dead-end trap crop and reduced colonization of the

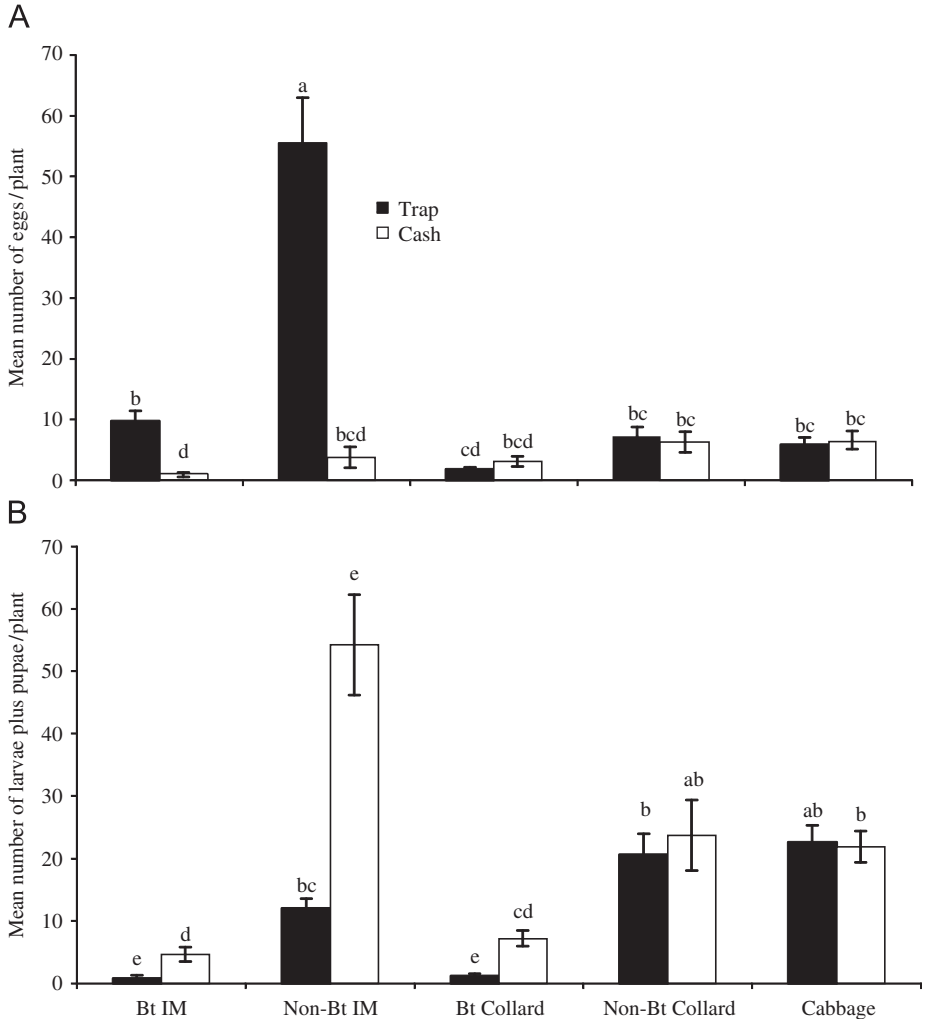

Fig. 2. Mean number of *Plutella xylostella* eggs (A) or larvae plus pupae (B) per plant in the third generation of a trap cropping experiment. The term trap crop refers to plants that are intended to reduce insects on the cash crop. IM refers to Indian mustard and Bt refers to plants that have been engineered to express Cry1C proteins from *Bacillus thuringiensis*.

Table 1
Mean number of *Plutella xylostella* eggs and larvae per plant by generation on trap plants and cash plants, and the total per cage

Treatment	Eggs			Larvae		
	Trap	Cash	Total/cage	Trap	Cash	Total/cage
Gen 1						
Bt IM	43.1±8.2 aA	0.2±0.1 bBC	130±26.7 A	0.1±0.1 bCD	5.3±1.2 aBC	16.3±2.3 CD
Non-Bt IM	36.0±5.2 aAB	0.7±0.4 bBC	110±4.4 AB	22.6±3.4 aA	6.7±1.7 bBC	87.7±25.5 A
Bt collard	3.6±1.8 aC	1.3±0.6 aBC	14.7±8.7 C	0.3±0.2 bC	10.6±2.3 aAB	32.7±8.17 BC
Non-Bt collard	2.2±0.9 aC	1.7±0.8 aB	11.7±7.4 C	11.4±3.0 aB	15.0±2.7 aA	79.3±22.8 AB
Cabbage	4.0±1.9 aC	5.7±2.1 aA	29±13.1 C	11.1±1.6 aB	9.0±2.0 aBC	60.3±11.7 ABC
Gen 2						
Bt IM	7.3±1.7 aB	0.4±0.3 bCD	23.3±7.5 BC	0 aC	0.1±0.1 aCD	0.3±0.3 CD
Non-Bt IM	299.0±75.2 aA	36.0±11.7 bA	1005±425.4 A	30.2±6.6 aA	53.4±18.8 aA	251±131.5 A
Bt collard	3.7±1.2 aB	3.4±1.8 aCD	21.3±13.8 CD	0.1±0.1 bC	3.8±1.4 aBC	11.7±4.3 BC
Non-Bt collard	42.2±17.1 aB	29.8±10.8 aAB	216±99.4 AB	16.6±3.7 aB	14.9±4.6 aB	94.3±29.2 AB
Cabbage	26.8±10.9 aB	19.8±5.9 aABC	139.7±9.0 AB	11.6±2.7 aB	8.7±1.8 aB	60.7±8.8 AB

Mean number (±SE) of eggs or larvae followed by different lower-case letters within a row or different capital letters within a column are significantly different (Tukey–Kramer honestly significant difference test, $P<0.05$).IM, Indian mustard.

interior of the field that was planted to non-Bt potatoes (Hoy, 1999). Using non-Bt genetically engineered trap crops was also effective for control of the papaya ringspot virus (PRSV), which is transmitted by many aphid species in a non-persistent manner, making it difficult to control with insecticides (Gonsalves, 1998). In Hawaii, PRSV-resistant papaya is grown commercially and has been deregulated for US consumers, but they have not been approved by the Hawaiian's traditional high-value export market, i.e., Japan (Shelton and Badenes-Perez, 2006). However, some growers in Hawaii are using borders of PRSV-resistant papaya as a trap crop to reduce the movement of PRSV into the interior of the field where non-genetically engineered papaya are grown. This successful tactic allows the production of both non-genetically engineered papaya and genetically engineered papaya (Gonsalves and Ferreira, 2003), and is another example of how genetic engineering can be used in novel ways for pest management.

In our study, genetically engineering Indian mustard and collards to express Cry1C enabled both to be more effective trap crops because they reduced populations of *P. xylostella* on the cash crop. Both plants also resulted in significant suppression of a *P. xylostella* population over 3 generations in the greenhouse test and 2 generations in the small cage experiment, suggesting that in places where immigration may be limited some long-term population suppression may occur, as was the case with pink bollworm noted above. Furthermore, if a plant is highly attractive for oviposition but functions as a dead-end trap crop, long-term suppression may be achieved with a small area planted to the dead-end trap crop.

However, the choice of whether to use Bt Indian mustard or Bt collards as the trap crop for *P. xylostella* is complicated by the synovigenic nature of *P. xylostella*. Synovigenic insects mature eggs throughout their adult life whereas pro-ovigenic species emerge with a fixed number of eggs. Our data indicate that the presence of Indian mustard elicits more eggs to be laid by *P. xylostella* over their reproductive lives, a situation similar to the 23% increased oviposition by *P. xylostella* in the presence of *B. vulgaris* (Badenes-Perez et al., 2006). Non-Bt Indian mustard has been recommended as a trap crop (Srinivasan and Moorthy, 1992) but our data indicate that it can cause a greater threat to the cash crop unless it is treated in some fashion. As in our previous study (Shelton and Nault, 2004), we found no benefit of using non-Bt collards as a trap crop. We suggest that Bt trap crops may be useful tools in situations where the cash crop may not be suitable or desirable for genetic engineering to express Bt or other insecticidal proteins.

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