Influence of Transgenic Corn Expressing Insecticidal Protein of *Bacillus thuringiensis* Berliner on Natural Populations of Corn Earworm (Lepidoptera: Noctuidae) and Southwestern Corn Borer (Lepidoptera: Crambidae)[1]

Kerry C. Allen and Henry N. Pitre[2]

Department of Entomology and Plant Pathology, Mississippi State University, Mississippi State, Mississippi 39762 USA

J. Entomol. Sci. 41(3): 221-231 (July 2006)

Abstract A 2-yr study was conducted to measure the influence of transgenic corn, *Zea mays* L., expressing the Cry1Ab endotoxin of *Bacillus thuringiensis* (Berliner) (Bt) by means of Event MON810 on natural populations of *Helicoverpa zea* (Boddie) and *Diatraea grandiosella* (Dyar). The studies were conducted at Leland and Morgan City, MS, in 1999 and at Morgan City in 2000. Although total numbers of *H. zea* larvae were not significantly different on transgenic corn hybrids compared with their near-isogenic parent lines, fewer large larvae were found on the transgenic hybrids. Differences in *H. zea* larval growth were noticeable when larvae fed on Bt corn vs non-Bt corn. The delay in larval growth for insects within a single generation, which could possibly result in asynchronous mating between insecticide resistant and susceptible insects, was observed for larvae feeding on plants expressing the Bt toxin. *Diatraea grandiosella* caused limited damage to the transgenic corn hybrids compared with their near-isogenic parent lines. Yields were not significantly greater for the Bt corn hybrids compared with their near-isogenic parent lines. Yields were not significantly greater for the Bt corn hybrids compared with the near-isogenic, non-Bt corn parents; however, there was a trend toward higher yields for Bt hybrids compared with their near-isogenic non-Bt parents.

Key words transgenic corn, *Diatraea grandiosella, Helicoverpa zea, Zea mays*

Transgenic plants offer a range of possibilities for insect control and have such advantages as reducing chemical pesticide spray drift and ground water contamination. Advances in plant transformation and gene expression have overcome previous obstacles limiting the commercialization of transgenic insect resistant crops (Gasser and Fraley 1989). *Bacillus thuringiensis* (Berliner) (Bt) has been successfully used in commercially developing transgenic crops for insect control.

Corn, *Zea mays* L., is one of the most widely grown crops in the United States, with over 24 million ha planted every year. Genetic engineers have given much attention to Bt-based transgenic corn (Bt corn) (Andow and Hutchinson 1998). The primary targeted pest of Bt corn is the European corn borer, *Ostrinia nubilalis* (Hübner), which is one of the most destructive pests of corn in the United States, with yield losses and control expenditures exceeding US$1 billion annually (Mason et al. 1996). Bt corn has

[1]Received 12 April 2005; accepted for publication 23 February 2006.
[2]Address inquiries (email: hpitre@entomology.msstate.edu).

activity against several other economically important pests. Survival and larval feeding by fall armyworm, *Spodoptera frugiperda* (J. E. Smith), and southwestern corn borer, *Diatraea grandiosella* (Dyar), are significantly reduced on Bt corn compared with conventional corn varieties (Williams et al. 1997, Archer et al. 2000, Buntin et al. 2004). Bt corn expressing toxin in ear tissues may provide some levels of control of the corn earworm, *Helicoverpa zea* (Boddie) (Andow and Hutchinson 1998, Storer et al. 2001).

Pests such as *H. zea* may be the first to develop resistance to the insecticide because they use multiple hosts over many generations and move among transgenic Bt crops (ILSI HESI 1998). The use of a refuge crop, where the pest can increase in number without exposure to Bt toxins, can assist in insecticide resistance management. The number of insect generations per season and proportion of total pest population feeding on transgenic crops affect the exposure of a given insect species to Bt toxins. There is need for greater measures in insecticide resistance management, such as increased refuge size, if exposure is high (Gould 1998).

Diatraea grandiosella is known to feed on only a few grass species including corn, sorghum, sugarcane, Sudangrass, and Johnsongrass (Wilbur et al. 1950). It has become a greater concern to farmers in Mississippi with the increased acreage planted to corn in recent years. Because a large part of the life cycle of *D. grandiosella* is spent inside the stalk, behind leaves or leaf collars, or in other protected sites, conventional insecticide sprays must be timed precisely to obtain adequate control of this insect. Bt corn provides an opportunity for farmers to protect their crops from damage by this insect without insecticide sprays.

Sublethal exposure to Bt crops has been found to slow insect development and prolong the duration of immature stages (Luttrell et al. 1982, Mascarenhas and Luttrell 1997). Insects that survive on Bt crops take longer to develop to the adult stage than insects on conventional crops and may result in asynchronous mating. The potential difference in development on Bt crops versus non-Bt crops may have a significant, positive effect on resistance development (Gould 1998).

This study compares naturally-occurring infestations of *H. zea* and *D. grandiosella* larvae on Bt corn hybrids with their near-isogenic parent lines in the field in Mississippi.

Materials and Methods

Large corn plots were planted at Morgan City (Leflore Co.) and Leland (Washington Co.) in 1999, and at Morgan City in 2000 in Mississippi. Corn hybrids used during both seasons were Pioneer brand 31B13 (Bt), Pioneer 3223 (near-isogenic parent line of 31B13), Pioneer brand 33V08 (Bt), and Pioneer 3394 (near-isogenic parent line of 33V08). The Bt corn nybrids used were provided by Pioneer Hi-Bred International, Des Moines, IA) and express Cry1Ab endotoxin derived by event MON810.

Each hybrid was planted with four replications in a randomized complete block design. Planting date, row spacing, number and length of rows, and plot size for each year and location are presented in Table 1. Plots were maintained using agronomic practices of production farms in the two locations. Insecticide was not applied on the plots with the exception of an early-season pyrethroid spray application targeting cutworms at early whorl stage at Morgan City in 2000.

Plots were sampled weekly to determine infestations of lepidopteran pests using a destructive whole plant sampling technique. Five consecutive plants were cut at the

Table 1. Corn planting date, plot areas, number of rows and row spacing for studies at Leland, MS in 1999 and Morgan City, MS in 1999 and 2000

Location	Planting date	Row spacing (cm)	No. of rows	Plot area (ha)
Leland	11 Apr 99	76.2	20	0.44
Morgan City	11 Apr 99	96.5	24	0.90
Morgan City	27 Apr 00	96.5	20	0.75

soil surface at two locations in each plot on each sample date for plant examination. Reproductive plant stages (R1-R6) were recorded according to Ritchie et al. (1996). Each test was sampled 9-10 times. Leaves were examined and then removed from each sampled plant to search for larvae behind leaf collars. Once reproductive structures began to form, ears were carefully shucked to search husks, silks and kernels for larvae. Stalks with holes were split lengthwise using a knife and searched for corn borer larvae. Numbers of live *H. zea* and *D. grandiosella* larvae per ten plants were recorded. Larvae were identified as small (<0.64 cm), medium (0.64-1.90 cm), or large (>1.90 cm). Each larva was identified and individually placed in a 30-ml plastic cup on wheat-germ casein diet (King et al. 1985). Cups were placed in a refrigerated box and transported to the laboratory. Neonates were reared to mid-instars for positive identification.

Damage by *D. grandiosella* was estimated at the end of the growing season at Morgan City in both years. Five consecutive plants were cut at the soil surface at four random locations in each plot. Stalks were split, as described above, and the length of corn borer tunnels in each stalk was measured. Data were recorded on numbers of plants with tunnels and tunnel length for each of 20 plants in each plot.

Yield estimates were obtained after plant maturity by mechanically harvesting whole plots at Leland using a John Deere 9,600 harvester equipped with a yield monitor. Partial plots (0.19 ha) were harvested for yield estimates at Morgan City and weighed using a weigh wagon with digital scales. Moisture was tested using a Dole 400 moisture tester (Seedburo Equipment Co., Chicage, IL), and yield estimates are reported at standard moisture of 15.5%.

Data were analyzed using analysis of variance (ANOVA) with means separated using Fisher's protected least significant difference (LSD, $P = 0.05$) test (SAS Institute 1989).

Results

Although the corn crops were monitored during the growing season to obtain information on several lepidopterous pests, *H. zea* was the only species encountered in sufficient numbers to justify statistical analysis. End of the season damage caused by *D. grandiosella* also was analyzed.

Only a few *H. zea* larvae were found on corn before ears began to develop during both years at both locations. Numbers of *H. zea* found on developing ears on four sample dates at Leland, MS, in 1999 are reported in Table 2. No significant differences were observed for number of small, medium, or large *H. zea* larvae at 74 (R1-R2), 81(R3), or 87(R4) days after planting. Pioneer 31B13 (Bt) had significantly

Table 2. Mean number of *H. zea* larvae on corn at Leland, MS in 1999

	No. larvae* per 10 plants on sampling date (±SEM)															
	24 June				1 Jule				7 July				15 July			
Variety	S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T
3223	1.0 (0.4) a	1.5 (0.9) a	0.5 (0.3) a	3.0 (1.1) a	0.5 (0.3) a	3.3 (0.3) a	2.0 (0.7) a	5.8 (1.0) a	0.3 (0.3) a	0.3 (0.3) a	1.5 (0.7) a	2.0 (0.7) a	—	0.5 (0.3) b	0.8 (0.5) a	1.3 (0.5) b
31B13 Bt	2.0 (0.4) a	1.3 (0.6) a	0.0 (0.0) a	3.3 (0.8) a	1.5 (0.7) a	3.8 (0.5) a	0.5 (0.5) a	5.8 (1.0) a	0.0 (0.0) a	2.0 (0.6) a	0.5 (0.3) a	2.5 (0.7) a	—	2.3 (0.5) a	0.8 (0.5) a	3.0 (0.4) a
3394	1.5 (0.5) a)	3.0 (0.6) a	0.0 (0.0) a	4.5 (0.5) a	0.3 (0.3) a	2.0 (0.4) a	1.0 (0.7) a	3.3 (0.9) a	0.0 (0.0) a	1.3 (0.6) a	2.5 (0.7) a	3.8 (1.3) a	—	0.0 (0.0) b	0.5 (0.3) a	0.5 (0.3) b
33V08 Bt	2.5 (0.3) a	0.5 (0.3) a	0.0 (0.0) a	3.0 (0.4) a	0.8 (0.5) a	2.5 (0.5) a	0.0 (0.0) a	3.3 (0.5) a	0.3 (0.3) a	1.3 (0.5) a	0.5 (0.5) a	2.0 (0.4) a	—	0.3 (0.3) b	0.3 (0.3) a	0.5 (0.3) b

Means (±SEM) within a column not followed by a common letter are significantly different ($P \leq 0.05$, LSD).

* Larval size: S = small (<0.64 cm), M = medium (0.64-1.90 cm), L = large (>1.90 cm), T = total larvae.

more medium ($F = 15.0$; df = 3, 9; $P < 0.001$) and total *H. zea* larvae 95 days (R5) after planting ($F = 8.3$; df = 3, 9; $P = 0.006$) than the other hybrids tested.

At Morgan City in 1999 (Table 3), no differences in numbers of small, medium or large *H. zea* larvae found on developing ears were detected among hybrids 73 (R1-R2) or 94 (R4-R5) days after planting. However, greater numbers of small *H. zea* larvae were found on the Bt hybrids Pioneer 31B13 and Pioneer 33V08 than their respective near-isogenic parent lines ($F = 12.2$; df = 3, 9; $P = 0.002$) 80 days (R3) after planting. Also, at 80 days after planting, Pioneer 3,394 had a greater number of large larvae than its Bt line, Pioneer 33V08 or Pioneer 31B13 (Bt) ($F = 2.8$; df = 3, 9; $P = 0.010$). Pioneer 31B13 (Bt) and Pioneer 33V08 (Bt) had significantly greater numbers of medium larvae than their near-isogenic parent lines, Pioneer 3223 and Pioneer 3394, respectively ($F = 12.9$; df = 3, 9; $P = 0.001$) 86 days (R3-R4) after planting. Pioneer 31B13 (Bt) and Pioneer 3223 had greater numbers of total *H. zea* larvae than Pioneer 33V08 (Bt) and Pioneer 3394 at 86 days after planting ($F = 15.3$; df = 3, 9; $P = 0.001$).

Significant differences in size and total number of *H. zea* larvae on developing ears were observed on only one (July 11; 75 d) of four sampling dates at Morgan City during 2000 (Table 4). A significantly larger number of small larvae were found on 31B13 (Bt) than on the other hybrids ($F = 9.6$; df = 3, 9; $P = 0.004$), and Pioneer 3223 had a greater number of large *H. zea* larvae than its Bt line.

The cumulative total of *H. zea* larvae per 10 plants at Morgan City in 1999 revealed significantly greater numbers of small *H. zea* larvae ($F = 6.35$; df = 3, 9; $P = 0.0133$) on the Bt hybrids compared with their near-isogenic parent lines. The total number of medium larvae at Leland in 1999 was significantly greater ($F = 5.37$; df = 3, 9; $P = 0.0214$) on Pioneer 31B13 (Bt) than on Pioneer 3223, its near-isogenic parent line. This trend was observed for the Bt versus non-Bt comparisons at Morgan City in 1999. Pioneer 3394 and Pioneer 3223 had a greater number of large *H. zea* larvae than their Bt lines ($F = 7.49$; df = 3, 9; $P = 0.0081$) at Morgan City in 1999. At Morgan City in 2000, both conventional hybrids had greater total number of large *H. zea* larvae than their respective Bt counterparts for combined sampling dates ($F = 10.15$; df = 3, 9; $P < 0.0030$).

Both non-Bt corn hybrids had a greater number of stalks with *D. grandiosella* tunnels, greater total tunnel length, and greater average tunnel length per plant than the Bt hybrids in 1999 ($F = 16.8$; df = 3, 9; $P < 0.001$) and 2000 ($F = 25.7$; df = 3, 9; $P < 0.001$) at Morgan City (Table 5). However, the Bt corn hybrids did not yield more than their near-isogenic parents (Table 6). Pioneer 31B13 (Bt) had greater yield than Pioneer 3394 or Pioneer 33V08 (Bt), but was not significantly greater than its near-isogenic parent line ($F = 4.18$; df = 3, 9; $P = 0.0612$) at Leland in 1999 (Table 6). Pioneer 31B13 (Bt) and Pioneer 3223 had significantly greater yields ($F = 12.6$; df = 3, 9; $P = 0.0014$) than Pioneer 3394 or Pioneer 33V08 (Bt) at Morgan City in 2000 (Table 6). No significant differences for mean yield were detected among treatments at Morgan City in 1999.

Discussion

The differences observed among corn hybrids in the number and size of *H. zea* larvae can be related to sample date during 1999 and 2000. Significant differences in larval size and total number of larvae were observed after corn plants began producing silks, as this was the time with the greatest populations of *H. zea* larvae. Once

Table 3. Mean number of *H. zea* larvae on corn at Morgan City, MS in 1999

	No. larvae* per 10 plants on sampling date (±SEM)															
	23 June				30 June				6 July				14 July			
Variety	S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	T
3223	2.0 (1.0) a	1.0 (1.0) a	0	3.0 (2.0) a	0.0 (0.0) b	2.8 (0.8) a	1.5 (0.7) ab	4.3 (0.5) a	0.8 (0.5) a	1.3 (0.6) bc	3.0 (0.4) a	5.0 (0.7) a	0.3 (0.3) a	1.0 (0.4) a	1.3 (0.3) a	2.5 (0.9) a
31B13 Bt	2.5 (0.5) a	1.0 (1.0) a	0	3.5 (0.5) a	3.5 (0.5) a	3.5 (1.0) a	0.8 (0.5) b	7.8 (1.3) a	0.8 (0.5) a	4.3 (0.9) a	1.3 (0.6) a	6.3 (0.8) a	0.3 (0.3) a	0.8 (0.5) a	1.3 (0.3) a	2.3 (0.8) a
3394	4.0 (2.0) a	1.5 (1.5) a	0	5.5 (0.5) a	0.8 (0.5) b	2.0 (0.6) a	2.3 (0.8) a	5.0 (1.3) a	0.3 (0.3) a	0.3 (0.3) c	2.3 (0.5) a	2.8 (0.5) b	0.0 (0.0) a	0.3 (0.3) a	0.3 (0.3) a	0.5 (0.3) a
33V08 Bt	4.0 (0.0) a	0.5 (0.5) a	0	4.5 (0.5) a	2.8 (0.5) a	3.3 (0.6) a	0.8 (0.5) b	6.8 (1.1) a	0.3 (0.3) a	2.0 (0.4) b	1.3 (0.3) a	3.5 (0.7) b	0.0 (0.0) a	0.8 (0.8) a	0.8 (0.5) a	1.5 (1.2) a

Means (±SEM) within a column not followed by a common letter are significantly different ($P \leq 0.05$, LSD).

* Larval size: S = small (<0.64 cm), M = medium (0.64-1.90 cm), L = large (>1.90 cm), T = total larvae.

Table 4. Mean number of *H. zea* larvae on corn in Morgan City, MS in 2000

	No. larvae* per 10 plants on sampling date (±SEM)															
	30 June				6 July				11 July				20 July			
Variety	S	M	L	T	S	M	L	T	S	M	L	T	S	M	L	L
3223	1.8 (0.9) a	0.0 (0.0) a	0	1.8 (0.9) a	6.8 (1.7) a	3.5 (1.6) a	0.0 (0.0) a	6.8 (1.7) a	3.3 (1.1) b	4.5 (0.9) a	3.8 (0.5) a	11.5 (0.5) a	0.3 (0.3) a	2.3 (1.0) a	2.8 (0.5) a	5.3 (1.1) a
31B13 Bt	0.8 (0.5) a	0.0 (0.0) a	0	0.8 (0.5) a	5.5 (0.5) a	0.5 (0.3) a	0.0 (0.0) a	6.0 (0.7) a	7.3 (1.9) a	2.3 (1.0) a	0.3 (0.3) c	9.8 (1.8) a	0.8 (0.3) a	3.0 (1.0) a	2.0 (0.4) a	5.8 (0.9) a
3394	3.0 (0.4) a	0.8 (0.5) a	0	3.8 (0.9) a	4.5 (0.9) a	3.0 (1.4) a	0.3 (0.3) a	7.8 (2.1) a	1.5 (0.7) b	1.8 (0.8) a	2.3 (0.6) ab	5.5 (0.5) b	0.5 (0.5) a	0.8 (0.5) a	2.5 (1.0) a	3.8 (1.0) a
33V08 Bt	0.5 (0.5) b	0.0 (0.0) a	0	0.5 (0.5) a	4.8 (0.9) a	0.8 (0.8) a	0.3 (0.3) a	5.8 (1.1) a	2.3 (0.5) b	2.0 (0.4) a	0.8 (0.5) bc	5.0 (0.4) b	0.0 (0.0) a	3.8 (0.5) a	1.5 (0.3) a	5.3 (0.7) a

Means (±SEM) within a column not followed by a common letter are significantly different ($P \leq 0.05$, LSD).
* Larval size: S = small (<0.64 cm), M = medium (0.64-1.90 cm), L = large (>1.90 cm), T = total larvae.

Table 5. Mean number of corn plants with *D. grandiosella* tunnels (PWT), total tunnel length (TTL), and average tunnel length (ATL) of stalks at Morgan City, MS in 1999 and 2000

	Corn borer tunnels per 20 plants* (±SEM)					
	1999			2000		
Variety	PWT	TTL	ATL	PWT	TTL	ATL
3223	10.3 (2.2) a	172.1 (42.6) a	8.6 (2.1) a	7.3 (1.0) a	94.2 (18.2) a	4.7 (0.9) a
31B13 Bt	0.5 (0.3) b	3.1 (2.2) b	0.2 (0.1) b	0.0 (0.0) b	0.0 (0.0) b	0.0 (0.0) b
3394	9.3 (1.3) a	119.5 (35.1) a	6.0 (1.8) a	5.5 (1.2) a	61.3 (17.1) a	3.1 (0.9) a
33V08 Bt	0.0 (0.0) b	0.0 (0.0) b	0.0 (0.0) b	0.3 (0.3) b	3.6 (3.6) b	0.2 (0.2) b

Means (±SEM) within a column not followed by a common letter are significantly different ($P \leq 0.05$, LSD).

* PWT = no. plants with tunnels, TTL = total tunnel length (cm) per 20 plants, ATL = avg. tunnel length (cm) per plant.

Table 6. Mean (±SEM) corn yield (15.5% moisture) in kg per ha

	Location and year		
Variety	Leland, 1999	Morgan City, 1999	Morgan City, 2000
3223	8,524 (106.5) ab	11,411 (363.03) a	10,107 (415.0) a
31B13 Bt	8,763 (254.9) a	10,635 (520.75) a	10,894 (429.2) a
3394	8,156 (106.5) b	11,066 (197.37) a	8,812 (279.1) b
33V08 Bt	8,357 (99.1) b	11,179 (237.34) a	9,169 (323.8) b

Means (±SEM) within a column not followed by a common letter are significantly different ($P \leq 0.05$, LSD).

plants began producing ears, *H. zea* larvae were concentrated almost exclusively on developing kernels or silks. During each year at Morgan City, *H. zea* data from one sample date (day 80 in 1999, day 75 in 2000) showed greater numbers of small larvae but fewer large larvae were on one Bt hybrid compared with its near-isogenic parent line. Although total numbers of larvae were not different between Bt and non-Bt varieties, there were indications of differences in larval growth between these materials. Observations on larval development suggest that the delay in larval growth is a consequence of *H. zea* larvae feeding on plants expressing Bt toxin. Slower larval growth on Bt corn could have implications on the development of resistance to Bt corns. One assumption of the high dose/refuge strategy for resistance management is that surviving, resistant individuals emerging from transgenic plants expressing Bt toxins will have a greater probability of mating with individuals emerging from a refuge (non-Bt expressing plants). A possible delay in the development of surviving, resistant individuals on Bt corn compared with the development of susceptible individuals in a refuge may cause an asynchronous mating pattern. The effectiveness of a refuge may deteriorate because resistant individuals emerging from Bt corn will have a greater probability of mating with one another than mating with susceptible individuals emerging from the refuge.

The reduction in cumulative number of large *H. zea* larvae on the Bt hybrids in this study is the best indication that corn expressing the Cry1Ab endotoxin, by means of event MON810, can reduce the population of *H. zea* emerging from these plants. This study dealt only with larval development of *H. zea* and did not quantify numbers or timing of adult emergence from Bt corn versus conventional corn. Our data suggest that larval growth was inhibited, and the number of large larvae was reduced on the Bt hybrids. The reduction of *H. zea* larvae may benefit corn producers by minimizing damage by this insect and reducing the number of *H. zea* adults that may infest other hosts such as cotton.

Finding *H. zea* larvae on Bt corn plants, or conventional plants, does not ensure that they fed exclusively on the plant's tissues. The cannibalistic behavior of *H. zea* larvae is a possible contributing factor in the survival and growth of an unknown percentage of larvae. Cannibalism has been shown to be beneficial to *H. zea* larvae reared under stressful conditions (Joyner and Gould 1985). Barber (1936) reared *H. zea* larvae exclusively on other *H. zea* larvae and although they took a week longer to develop, there was no size or vigor loss in the larvae. The results from the present study might suggest that *H. zea* larvae fed Bt corn exhibit modifications in feeding behavior and possibly behavioral differences that influence larval development.

Although only a small number of *D. grandiosella* larvae were recorded on the Bt and conventional corn varieties in this study, destructive sampling of stalks at plant maturity indicated that there was sufficient damage (stalk tunnels) for comparison of varieties. The number of stalks with tunnels is considered a cumulative measurement of damage due to corn borers over a large part of the growing season. These data show that Bt corn containing the Cry1Ab endotoxin provide excellent control of *D. grandiosella* larvae. Only three plants were found with tunnels in the Bt hybrids in both years, which could have been the result of non-expressing plants in the Bt plots.

Rice and Pilcher (1998) reviewed recent reports of yield protection by Bt corn against corn borers. They cite references that showed from 0-203 bushels per ha greater yields of Bt compared with conventional corn. Although there were no significant differences in yield between the Bt hybrids and their near-isogenic parent lines in the present study, there was a trend toward greater yields in Bt hybrids in 1999 at Leland and in 2000 in Morgan City compared with yield of respective near-isogenic non-Bt parent lines. Additional testing, in a variety of environments, should elucidate the potential economic benefit of Bt corn to agricultural communities in Mississippi and elsewhere.

Acknowledgments

The authors thank A. Harris, R. Luttrell, S. Stewart and J. Reed for their reviews of this manuscript. This is journal number J-10699 of the journal series of the Mississippi Agricultural and Forestry Experiment Station.

References Cited

Andow, D. A. and W. D. Hutchison. 1998. Bt-corn resistance management, Pp. 19-66. *In* M. Mellon and J. Rissler [eds.], Now or Never: Serious New Plans to Save a Natural Pest Control, Union of Concerned Scientists, Cambridge, MA.

Archer, T. L., G. Schuster, C. Patrick, G. Cronholm, E. D. Bynum Jr. and W. P. Morrison. 2000. Whorl and stalk damage by European and southwestern corn borers to four events of *Bacillus thuringiensis* transgenic maize. Crop Prot. 19: 181-190.

Barber, G. W. 1936. The cannibalistic habits of the corn earworm. U.S. Dep. Agric. Tech. Bull. 49: 1-19.

Buntin, G. D., J. N. All, R. D. Lee and D. M. Wilson. 2004. Plant-incorporated *Bacillus thuringiensis* resistance for control of fall armyworm and corn earworm (Lepidoptera: Noctuidae) in corn. J. Econ. Entomol. 97: 1603-1611.

Gasser, C. S. and R. T. Fraley. 1989. Genetically engineering plants for crop improvement. Science 244: 1293-1299.

Gould, F. 1998. Sustainability of transgenic insecticidal cultivars: integration of pest genetics and ecology. Annu. Rev. Entomol. 43: 701-726.

ILSI Health and Environmental Sciences Institute (ILSI HESI). 1998. An evaluation of insect resistance management in Bt field corn: A science-based framework for risk assessment and risk management. Report of an expert panel. ILSI Press, Washington DC.

Joyner, K. and F. Gould. 1985. Developmental consequences of cannibalism in *Heliothis zea* (Lepidoptera: Noctuidae). Ann. Entomol. Soc. Am. 78: 24-28.

King, E. G., G. G. Hartley, D. F. Martin and M. L. Laster. 1985. Large-scale rearing of sterile backcross of the tobacco budworm (Lepidoptera: Noctuidae). J. Econ. Entomol. 78: 454-460.

Luttrell, R. G., S. Y. Young, W. C. Yearian and D. L. Horton. 1982. Evaluation of *Bacillus thuringiensis*-spray adjuvant-viral insecticide combinations against *Heliothis* spp. (Lepidoptera: Noctuidae). Environ. Entomol. 11: 783-787.

Mascarenhas, V. J. and R. G. Luttrell. 1997. Combined effect of sublethal exposure to cotton expressing the endotoxin protein of *Bacillus thuringiensis* and natural enemies on survival of bollworm (Lepidoptera: Noctuidae) larvae. Environ. Entomol. 26: 939-945.

Mason, C. E., M. E. Rice, D. D. Calvin, J. W. Van Duyn and W. B. Showers. W. D. Hutchininson, J. F. Witkowski, R. A. Higgins, D. W. Onstad and G. P. Dively. 1996. European corn borer ecology and management. North Central Region Publ. 327. Iowa State Univ., Ames.

Rice, M. E. and C. D. Pilcher. 1998. Potential benefits and limitations of transgenic Bt corn for management of the European corn borer (Lepidoptera: Crambidae). Am. Entomol. 44: 36-44.

Ritchie, S. W., J. J. Hanway and G. O. Benson. 1996. How a corn plant develops. Tech. Bull. No. 48, Coop. Ext. Ser., Ames, IA.

SAS Institute. 1989. SAS/STAT user's guide, version 6, fourth ed., vol. 1. SAS Institute, Cary, NC.

Storer, N. P., J. W. van Duyn and G. G. Kennedy. 2001. Life history traits of *Helicoverpa zea* (Lepidoptera: Noctuidae) on non-Bt and Bt transgenic corn hybrids in eastern North Carolina. J. Econ. Entomol. 94: 1268-1279.

Wilbur, D. A., H. R. Bryson and R. H. Painter. 1950. Southwestern corn borer in Kansas. Kansas Agr. Exp. Sta. Bull. 339, 46 pp.

Williams, W. P., J. B. Sagers, J. A. Hanten, F. M. Davis and P. M. Buckley. 1997. Transgenic corn evaluated for resistance to fall armyworm and southwestern corn borer. Crop Sci. 37: 957-996.