Baseline Susceptibility of the Fall Armyworm (Lepidoptera: Noctuidae) to Cry1Ab Toxin: 1998-2000[1]

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Abstract 'Attribute' sweet corn containing a *cry1Ab* gene (Bt11 Event) from *Bacillus thuringiensis* Berliner was registered for commercial use in 1998. A requirement of registration was to conduct baseline susceptibility studies to Cry1Ab toxin in fall armyworm populations collected from sweet corn growing areas in south Texas and south Florida. In addition, fall armyworm populations collected in sweet corn growing areas must be annually monitored for changes in susceptibility to the Cry1Ab protein. Fall armyworm larvae were collected near Belle Glade, FL, Homestead, FL, Weslaco, TX, and Corpus Christi, TX, in 1998 through 2000 and evaluated for susceptibility to Cry1Ab toxin. The Tifton Laboratory colony of fall armyworm that has been in culture for more than 10 yrs was used as the susceptible control. Comparison of the calculated LC_{50}s for the various colonies did not indicate an appreciable change in susceptibility during the period 1998-2000. These data provide baseline information as to the susceptibility of the fall armyworm to Cry1Ab protein produced in insect-resistant transgenic corn.

Key Words Fall armyworm, transgenic corn, *Bt* gene, Cry1Ab

Current reliance on pesticides for control of insects and plant pathogens has created concern for environmental impacts and sustainability of agricultural production systems (Weeks et al. 1999). This concern has led to a greater emphasis on the development and use of alternative pest control measures to be used in concert with more traditional methods to provide growers with the degree of pest control needed to meet the quality standards demanded by consumers. Novartis Seeds, Inc. (currently Syngenta Seeds, Inc.) developed transgenic sweet corn containing a modified *cry1Ab* gene (Bt11 Event) that confers a high level of resistance to European corn borer, *Ostrinia nubilalis* (Hübner), and corn earworm, *Helicoverpa zea* (Boddie), and a moderately high level of resistance to the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lynch et al. 1999a, 1999b, Wiseman et al. 1999). The Environmental Protection Agency (EPA) approved registration of Novartis' *Bt* sweet corn, 'Attribute,' in 1998.

One of the primary concerns of large commercial plantings transgenic crops containing a gene for *Bacillus thuringiensis* (Bt) toxin production is the potential for insects to develop resistance to the plant-produced toxins. This potential becomes even more significant when one considers that primary pests could be exposed to

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similar Bt toxins in more than one crop. Indeed, resistance to Cry proteins has been reported in the field for the diamondback moth, *Plutella xylostella* (L.) (Tabashnik et al. 1990, Shelton et al. 1993) and in laboratory colonies of the tobacco budworm, *Heliothis virescens* (F.) (Stone et al. 1989, Gould and Anderson 1991, MacIntosh et al. 1991, Gould et al. 1992, Marrone and McIntosh 1993, Gould et al. 1995, Lee et al. 1995), European corn borer (Bolin et al. 1995, Huang et al. 1997), beet armyworm, *Spodoptera exigua* (Hübner) (Moar et al. 1995), African armyworm, *S. littoralis* (Boisduval) (Müller-Cohn et al. 1996), and the cabbage looper, *Trichoplusia ni* (Hübner) (Estada and Ferre 1994). Furthermore, cross resistance to the Bt toxins also has been reported (Gould et al. 1992, Frutos et al. 1999).

The EPA met with Bt corn-registrants, academic and government scientists, and public interest groups in several meetings from 1992 through 1999 to discuss methods to delay the development of target pest resistance to the Bt toxins (EPA 1999). These discussions resulted in the development of an industry-insect resistance management (IRM) plan for Bt field corn that was implemented in the 2000 growing season. Among the major components of the plan is a high dose expression of the toxin in Bt plants, a structured non-Bt corn refuge, grower education, and insect monitoring for resistance. We report here the development of baseline data for susceptibility and the results of annual monitoring for sensitivity in the fall armyworm to Cry1Ab protein for fall armyworm collected in 1998 through 2000.

Materials and Methods

Fall armyworm larvae were collected from field and sweet corn or sorghum at Homestead, FL, Belle Glade, FL, Weslaco, TX, and Corpus Christi, TX, in May of 1998, April-June of 1999 and August-September of 2000 to establish laboratory colonies. Approximately 300 to 500 fall armyworm larvae were collected from each location, placed individually on pinto bean diet (Perkins 1979), and shipped to the Crop Protection and Management Research Laboratory, Tifton, GA. Upon receipt, the cups containing larvae were placed in an incubator operated at 26.7°C, 75% RH, and a 16:8 h light:dark photoperiod. Larvae were checked each Monday, Wednesday, and Friday for pupation and adult emergence. Upon emergence, adults were held in a 15.6°C room until sufficient numbers of moths had emerged for mating. Approximately 25 to 40 pairs of moths were then placed in a 3.8-L carton lined with waxed paper and with a paper towel over the top for oviposition. The oviposition containers were placed in the 26.7°C incubator as described above. Moths were fed a 10% sugar solution and the waxed paper and paper towel containing eggs were changed each Monday, Wednesday, and Friday. Upon hatching, 2 to 4 neonate larvae were placed in a cup containing pinto bean diet (Perkins 1979) and the cup was capped, labeled with the fall armyworm strain and date, and returned to the 26.7°C incubator to maintain the individual colonies. Colonies were maintained in the laboratory for 3 to 8 generations before completion of the bioassays.

The Cry1Ab toxin was provided by Novartis Seeds, Inc./Syngenta Seeds, Inc. Bioassays were conducted with larvae from colonies collected from the four locations noted above and compared with that of the Tifton Laboratory Colony. On the day prior to the bioassay, 10 to 15 neonate fall armyworm were placed on pinto bean diet (Perkins 1979) in 29.6-ml jelly cups. Thirty cups with caps were prepared for each of the five colonies and placed in the 26.7°C incubator. The bioassay was designed in a randomized complete block with four replications, 9 to 10 concentrations of Cry1Ab,

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and 24 observations per concentration per replication, i.e., the 24 wells in the tissue culture plate [Nunclon® (A. Diagger & Co., Inc., 620 Lakeview Parkway, Vernon Hills, IL), 12 mm diam wells, 1.9 cm^2 surface area] for a total of 96 observations per concentration. For the bioassay, approximately 3.0 mL of pinto bean diet was dispensed into each of the 24 wells of a tissue culture plate and the diet was allowed to solidify. The Cry1Ab toxin was serially diluted in sterile deionized water and 0.1 mL applied to the surface of bean diet. The toxin solution was spread over the surface of the diet by rocking the tissue culture plate from side to side several times and then allowed to dry for approximately 2 h. Concentrations evaluated were 0, 0.08, 0.16, 0.31, 0.63, 1.25, 2.5, 5.0, 10.0, and 20.0 $\mu g/cm^2$ surface area in 1998, and 0, 0.06, 0.18, 0.51, 1.62, 4.87, 14.62, and 43.86 $\mu g/cm^2$ surface area in 1999 and 2000. After infesting each well of the 24-well plate with 1 one-day-old fall armyworm, a 10.2 × 15.2 cm piece of parafilm (A. Diagger & Co., Inc., 620 Lakeview Parkway, Vernon Hills, IL) was placed over the wells before the lid was placed on the tissue culture plate. A hole had previously been burned in the top of the culture plate with a no. 2 insect pin for each of the 24 cells. A No. 00 insect pin was then used to punch a hole through the parafilm by inserting the pin through each hole in the lid, which allowed for air/moisture exchange. The lids to the tissue culture plates were secured with 4 size-10 clip binders to prevent movement of larvae between cells. All plates with larvae were placed in an incubator operated at 26.7 C, 75% RH, and a 16:8 h (light:dark) photoperiod. Mortality data were recorded at 7 d after treatment. The concentration-mortality response data were analyzed by probit analysis using the POLO-PC program (LeOra Software 1987). The POLO-PC program evaluates parallelism of the regressions for the different insect colonies to a standard, i.e., the Tifton Laboratory colony, using Chi-square to test the goodness of fit.

Results

Bioassay of fall armyworm larvae on a diet surface treated with Cry1Ab protein in 1998 showed less than a 2-fold difference in the LC_{50} values (Table 1). In addition, the 95% confidence interval (CI) for the LC_{50} values overlapped for all colonies indicating

Table 1. Bioassay of Cry1Ab against one-day-old larvae of *Spodoptera frugiperda* from colonies collected at five locations in 1998

	Mortality at 7 days*			
	LC_{50}		LC_{90}	
Colony	$\mu g/cm^2$	95% CI	$\mu g/cm^2$	95% CI
Tifton Laboratory	1.74a	1.24-2.49	21.10a	11.96-48.47
Belle Glade, FL	1.11a	0.69-1.61	8.58ab	5.52-16.39
Homestead, FL	1.29a	0.93-1.78	13.12ab	8.01-26.37
Corpus Christi, TX	1.50a	1.04-2.13	14.50ab	8.79-29.85
Weslaco, TX	0.90a	0.60-1.26	6.13b	4.08-10.83

* Means in a column followed by the same letter are not significantly different ($P \leq 0.05$).

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that there was no difference in susceptibility to Cry1Ab among the colonies established from larvae collected in the field or the Tifton Lab colony. Similarly, only a 3-fold difference was noted for the LC_{90} values; however, 95% CI suggests the larvae from the Weslaco colony were more susceptible to Cry1Ab protein than were larvae from the Tifton Lab colony. The tests of the hypotheses that the slopes for the five colonies were the same were rejected, and the tests for parallelism were rejected (Fig. 1A).

LC_{50} values for the bioassay of fall armyworm colonies collected in 1999 were higher and more variable (4.8-fold difference) than values for the previous year (Table 2). In 1999, larvae from the Corpus Christi colony had the highest LC_{50}, significantly higher than the LC_{50} ($P \leq 0.05$) for the Homestead fall armyworm colony. However, none of the LC_{50} values were significantly higher than the Tifton Lab colony, and there were no differences among the LC_{90} values of the colonies. The tests of the hypotheses that the slopes for the regressions for the various 1999 colonies were the same were rejected and the tests for parallelism also were rejected (Fig. 1B).

Bioassay of fall armyworm larvae collected in 2000 showed that the LC_{50} for the Tifton Lab colony was significantly higher ($P \leq 0.05$) than those for all colonies with the exception of the Corpus Christi colony, and that the LC_{50} for the Corpus Christi colony was significantly higher than that for the Homestead and Weslaco Colonies (Table 3). However, there were no significant differences in the LC_{90} values among colonies. A test of the hypothesis that the slopes for the regressions for the various 2000 colonies was the same was rejected, but the test for parallelism was accepted (Fig. 1C).

Discussion

LC_{50} variation among fall armyworm colonies was 1.9-fold in 1998, 4.7-fold in 1999, and 2.9-fold in 2000. These differences in susceptibility to the Cry1Ab protein probably reflect natural variation in susceptibility among fall armyworm populations. LC_{50} variation within a fall armyworm colony collected in a given locality across years ranged from 4.9-fold for fall armyworm collected at Homestead, FL, to 15.4-fold for fall armyworm collected at Weslaco, TX, and probably reflected both natural variation in fall armyworm populations and slight variation in toxin concentration of the different Cry1Ab preparations. In addition, none of the field-collected fall armyworm populations were less susceptible to the Bt protein than were fall armyworm from the Tifton Lab colony which had never been exposed to the protein. These data suggest those fall armyworm populations from these different geographical areas are susceptible to the Cry1Ab protein and that there have been no changes in susceptibility, as measured by a significant increase in the LC_{50} in fall armyworm collected from these locations in 1998-2000.

In general, *Spodoptera* spp. larvae are not very susceptible to the Cry toxins (Strizhov et al. 1996). Prior to the advent of transgenic plants, control of the fall armyworm with conventional Bt-based insecticides has been low to moderately effective (Gardner and Fuxa 1980, Krieg and Langenbruch 1981, Teague 1993, All et al. 1996). Transgenic corn hybrids expressing Cry1Ab protein (i.e., Bt11 and MON810 events) have significantly reduced fall armyworm leaf feeding damage in both field and sweet corn (Williams et al. 1997, 1998, 1999, Buntin et al. 2001, Lynch et al. 1999a). These authors reported substantial reductions in leaf-feeding damage by the fall armyworm on the transgenic hybrids. However, Williams et al. (1997) reported only 50% or less reduced survival and reduced weight gain when larvae were fed

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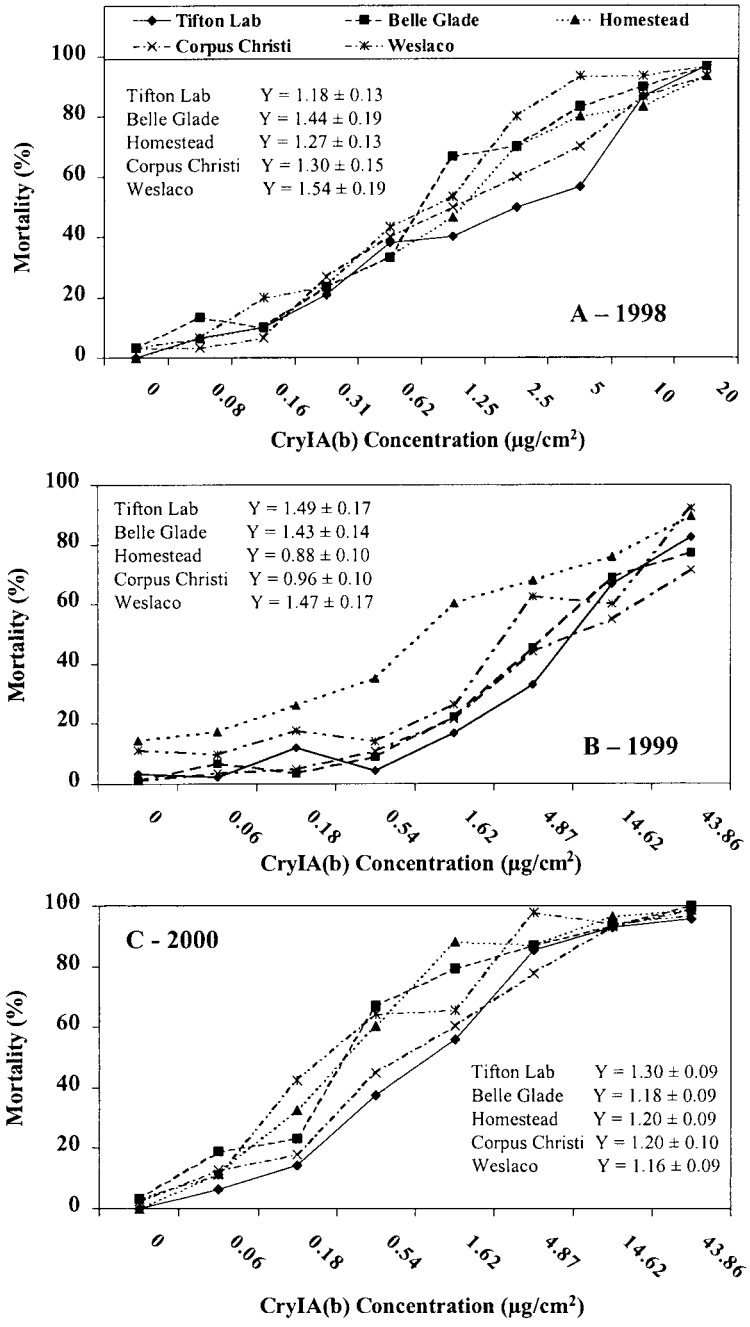

Fig. 1. Relative susceptibility of fall armyworm populations collected from five different locations in 1998-2000 to Cry1A(b).

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Table 2. Bioassay of Cry1Ab against one-day-old larvae of *Spodoptera frugiperda* from colonies collected at five locations in 1999

Colony	Mortality at 7 days*			
	LC_{50}		LC_{90}	
	µg/cm^2	95% CI	µg/cm^2	95% CI
Tifton Laboratory	9.71a	6.35-14.41	70.46a	39.52-202
Belle Glade, FL	6.59a	4.75-8.95	52.04a	33.07-102
Homestead, FL	2.14b	0.78-4.52	60.22a	23.87-311
Corpus Christi, TX	10.22a	5.83-20.22	219a	79.26-1500
Weslaco, TX	5.53ab	2.75-9.16	41.47a	22.08-148

* Means in a column followed by the same letter are not significantly different ($P \leq 0.05$).

tissue from Bt-transgenic field corn plants in the laboratory. Buntin et al. (2001) reported that the Bt-transgenic field corn did not reduce the percentage of infested ears in the field, but that fall armyworm larvae developed much slower and caused less kernel damage on the Bt corn than on susceptible corn. Similarly, Lynch et al. (1999a, b) reported reduced survival and weight gain for fall armyworm larvae fed on excised whorl leaves and silks of Bt sweet corn in the laboratory and significantly less leaf feeding and ear damage on Bt sweet corn in the field.

The IRM plan for Bt field corn initiated by the EPA to prevent the development of insect resistance relies on four basic principles: high dose expression, non-Bt corn refugia, monitoring for resistance and grower education. The EPA Scientific Advisory Panel (1999) defined high dose as 25 times the toxin needed to kill susceptible larvae. While the protein in YieldGard (Bt11 and MON810 events) field corn may constitute a high dose for the European corn borer, and Attribute sweet corn may express a high

Table 3. Bioassay of Cry1Ab against one-day-old larvae of *Spodoptera frugiperda* from colonies collected at five locations in 2000

Colony	Mortality at 7 days*			
	LC_{50}		LC_{90}	
	µg/cm^2	95% CI	µg/cm^2	95% CI
Tifton Laboratory	1.03a	0.76-1.37	9.90a	6.57-16.85
Belle Glade, FL	0.44bc	0.28-0.66	5.44a	3.37-10.45
Homestead, FL	0.44c	0.33-0.56	5.07a	3.62-7.73
Corpus Christi, TX	0.94ab	0.61-1.37	11.02a	6.97-20.45
Weslaco, TX	0.36c	0.22-0.54	4.54a	2.75-9.10

* Means in a column followed by the same letter are not significantly different ($P \leq 0.05$).

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dose for the European corn borer and corn earworm, it is questionable that either Bt 11 or MON8 10 are high dose for the fall armyworm. Thus, the survival of fall armyworm on YieldGard field corn (Buntin et al. 2001), even with delayed development, poses a potential threat for the development of resistance to Cry1Ab, especially if surviving insects experience further selection pressure as they move to Bt cotton. Attribute sweet corn, on the other hand, is less likely to contribute to the development of resistance. Few, if any, fall armyworm larvae survive and their development is greatly delayed on Attribute sweet corn (Lynch et al. 1999a), and the phenology of sweet corn production greatly diminishes the probability that surviving larvae will complete development. Sweet corn for both the fresh and processing markets is harvested at about 18 to 21 days after silking. The development of any fall armyworm larvae that might survive on ears of *Bt* sweet corn would be greatly delayed and all ears would be removed and either placed in cold storage prior to shipment to fresh sweet corn markets, or processed immediately. In either instance, the early harvest would effectively prevent any larvae that might survive in the ear of the *Bt* sweet corn from completing development. Furthermore, shortly after harvest, Attribute growers are required to destroy any ears and stalks remaining in the field, thereby limiting the potential for insects surviving on Bt sweet corn to pupate, emerge, and contribute to the next generation.

The three most important lepidopteran pests of field corn and sweet corn in the U.S. are the European corn borer, corn earworm, and fall armyworm. Baseline susceptibility to Cry1Ab based on LC_{50} values ranged from 2.22 to 7.89 ng/cm^2 for the European corn borer (Marçon et al. 1999) and from 70.3 to 221.3 ng/cm^2 for the corn earworm (Siegfried et al. 2000). The present study has determined that the Cry1Ab baseline susceptibility of fall armyworm populations collected in south Texas and south Florida ranges from 0.36 to 10.22 μg/cm^2, considerably higher than those for the European corn borer and corn earworm. Further, these baseline data will provide the tool necessary to identify changes in susceptibility to Cry1Ab in fall armyworm populations.

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