Bollworm (Lepidoptera: Noctuidae) Behavior on Transgenic Cotton Expressing Cry1Ac and Cry1F Proteins[1]

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Abstract Bollworm, *Helicoverpa zea* (Boddie), larvae are known to move away from Bollgard™ (Monsanto Co., St. Louis, MO) cotton terminals. Bollworm larvae are also found more frequently on flower buds (squares) and bolls of Bollgard as compared with those of nontransgenic cotton. However, data are not available for bollworm behavior on commercially available transgenic cotton varieties expressing 2 *Bacillus thuringiensis* Berliner proteins. Thus, field studies were conducted in Stoneville, MS, during 2007 and 2008 to determine whether bollworm behavior differed among cotton expressing the Cry1Ac and Cry1F proteins (Widestrike®, Phytogen 485, PhytoGen Seed Co., LLC, Indianapolis, IN) and nonBt cotton (Phytogen 425, PhytoGen Seed Co., LLC, Indianapolis, IN). Two-day-old bollworm larvae were placed into terminals of either individual cotton plants or plants within 1-m plots during the flowering period. Comparison of larval movement away from cotton terminals between Widestrike and nonBt plants did not differ at 3, 6, 24, or 48 h after infestation. In addition, larval distribution on fruiting structures did not differ between Widestrike and nonBt cotton. These data indicate that different scouting methods for bollworm larvae should be used for the various Bt cotton technologies commercially available.

Key Words *Bacillus thuringiensis*, bollworm, behavior, resistance management, transgenic cotton

Transgenic insecticidal cotton technologies have been the standard for control of tobacco budworm, *Heliothis virescens* (F.), and bollworm, *Helicoverpa zea* (Boddie), since the introduction of Bollgard® (event MON 531, Monsanto Co., St. Louis, MO) cotton in 1996. These technologies eliminated the need for numerous foliar insecticide applications targeted at tobacco budworm, as commercially available cotton varieties that express the *Bacillus thuringiensis* Berliner (Bt) endotoxin, Cry1Ac, provide absolute control of tobacco budworm. Bollworms are inherently less susceptible to Bt cotton as compared with the tobacco budworm (Stone and Sims 1993). Because of this, bollworms can cause significant levels of boll damage to Bollgard cotton varieties, and supplemental insecticide applications are needed for adequate control (Mahaffey et al. 1995, Jackson et al. 2003).

Levels of Bt proteins in Bt cotton plants (MON 531) have been shown to differ among the various plant tissue types, such as terminals, squares, flowers, bolls, and leaves (Greenplate 1999). White flowers express lower levels of the Cry1Ac protein

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compared with other plant parts (Greenplate 1999). Bollworms have the ability to detect and avoid feeding sites containing Bt toxins (Greenplate et al. 1998, Akin et al. 2001) and have been shown to migrate away from infestation sites more rapidly on Bt cotton lines (MON 531) than on nonBt genotypes (Gore et al. 2002, Bommireddy et al. 2007). The larval behavior observed in these studies explained why bollworms are more often detected in white flowers of Bollgard cotton than nonBt cotton.

Dow AgroSciences LLC (Indianapolis, IN) introduced WideStrike™ in 2004. These varieties produce the Cry1Ac (from transformation event DAS-21Ø23 - 5) and Cry1F (from transformation event DAS-24236 - 5) Bt endotoxins and have increased efficacy against bollworms compared with Bollgard varieties (Huckaba et al. 2003, Jackson et al. 2005). Although bollworm larvae are commonly found feeding on WideStrike cotton, larval behavior appears to differ from other Bt technologies. Larvae are more commonly observed feeding in terminals of WideStrike cotton than other Bt cottons (Smith et al. 2005). Currently, no research has been conducted to investigate this phenomenon. Thus, field studies were conducted to compare bollworm larval behavior on WideStrike and nonBt cotton lines.

Materials and Methods

Field studies were conducted in Washington Co. near Stoneville, MS, during 2007 and 2008. Cotton varieties consisting of nonBt (PHY 425 R) and WideStrike (PHY 485 WR) expressing both Cry1Ac and Cry1F proteins were planted every 2 - 3 wks from May 1 to June 10 during 2007 and 2008. Cotton varieties were maintained according to recommendations for cotton production from the Mississippi State University Extension Service.

Insects. Bollworm larvae were collected from crimson clover, *Trifolium incarnatum* L., from late April to early May during each year of the study. These larvae were used to establish a test colony each year, which was maintained on artificial diet in the laboratory for 1 - 2 generations prior to testing. Artificial diet was prepared using Stonefly *Heliothis* Diet (Ward's Natural Science, Rochester, NY). Larvae were maintained on diet in 29.5-ml clear plastic cups until pupation. Pupae were transferred into 3.9-L cardboard containers, and emerging adults were fed a 10% sucrose solution (w/v). Cheesecloth covered the tops of containers and served as an oviposition substrate. Once oviposition was initiated, cheesecloths were removed daily and placed into clear plastic bags until larval eclosion. Neonate bollworms were placed onto artificial diet for 48 h prior to being infested onto cotton plants.

Plant infestations. Individual plants of either nonBt or WideStrike cotton were isolated by removing adjacent plants within 1 m to eliminate interplant movement of bollworm larvae. Infestations occurred from 8 July to 20 August onto individual nonBt and WideStrike cotton plants during flowering growth stages in 2007 and 2008. Plants were examined prior to infestation for an existing heliothine infestation. Only non-infested plants were used in the study. A single 2-day-old bollworm larva was placed on the terminal of each plant using a small paintbrush. Infested plants were evaluated at 3, 6, and 24 h after infestation using whole-plant examination. The number of main stem nodes that each larva moved below the terminal and the plant structure (terminal, square, flower, boll) infested with a larva was recorded. The study consisted of 6 replications, which were represented by day of infestation. Fifty plants of each variety were infested on each day for a total of 300 infested plants of each variety over the 2-yr period.

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In addition to individual plant infestations, small plots (1 row m) of nonBt and WideStrike were established in randomized blocks during 2007 and 2008. Plants were thinned so that each plot contained 10 plants. Plant terminals within each plot were infested with 2-d-old bollworm larvae using a small paintbrush for a total of 20 larvae per plot. Small plots were infested from 8 July to 20 August, and a total of 10 plots of each variety were infested during the 2 yr experiment. Individual whole-plant inspections were made at 24 and 48 h after infestation. We again recorded the number of main stem nodes that each larva moved below the terminal and the plant structure (terminal, square, flower, boll) infested with a larva.

Statistical analyses. Both experiments were established as a split-plot randomized complete block design. The main plot unit was cotton variety, and the subplot unit was a repeated measure (evaluation time) over 2 or 3 time periods. Numbers of larvae infesting plant structures were converted to percentages based on the number of plants infested on a given day. All data were analyzed using repeated measures analysis of variance using PROC MIXED in SAS (Littell et al. 1996). The repeated measure subunit was best modeled by including replication x variety and replication x evaluation time as random effects. Several repeated measures covariance structures were evaluated using BIC fit statistics produced by PROC MIXED in SAS.

Results

For individual plant infestations, bollworm larval movement away from plant terminals did not differ among the nonBt and WideStrike cotton varieties evaluated (Fig. 1). The cotton variety by evaluation time interaction was not significant ($F = 0.16$; df = 2, 10; $P = 0.856$), nor was the cotton variety main effect ($F = 0.63$; df = 1, 5; $P = 0.463$). The average number of main stem nodes that bollworm larvae moved below plant terminals differed among evaluation times ($F = 32.74$; df = 2, 10; $P = 0.001$) when averaged across cotton varieties. Bollworm larvae migrated away from nonBt and

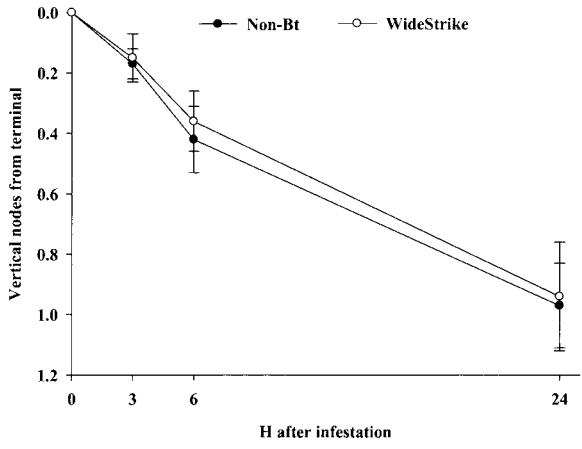

Fig. 1. Vertical distribution (± SE) of bollworm larvae on main stem nodes below terminals of individual flowering nonBt and Widestrike cotton plants.

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WideStrike plant terminals at a similar rate at all evaluation times. The average number of main stem nodes that larvae moved below the terminal increased at each subsequent evaluation time. At 3, 6, and 24 h after infestation, the average number of main stem nodes that bollworm larvae moved below plant terminals was 0.16, 0.40, and 0.95, respectively.

As with larval movement, the proportion of plant structures infested with bollworm larvae did not differ among the cotton varieties tested (Fig. 2). No significant cotton variety main effect was observed for the proportion of bollworm larvae infesting terminals ($F = 3.70$; df = 1, 5; $P = 0.113$), squares ($F = 0.92$; df = 1, 5; $P = 0.353$), flowers ($F = 0.08$; df = 1, 5; $P = 0.794$), or bolls ($F = 1.00$; df = 1, 5; $P = 0.341$). There was a significant evaluation time effect for the proportion of bollworm larvae infesting terminals ($F = 84.09$; df = 2, 10; $P = 0.001$) and squares ($F = 27.55$; df = 2, 10; $P = 0.001$), but not for flowers ($F = 1.83$; df = 2, 10; $P = 0.187$) or bolls ($F = 1.00$; df = 2, 10; $P = 0.402$). The percentages of larvae found in terminals at 3, 6, and 24 h were 84.5, 68.9, and 34.6, respectively; whereas, 9.2, 25.3, and 50.1% of bollworm larvae were found infesting squares at 3, 6, and 24 h, respectively. Few larvae were found infesting flowers and bolls during the 24 h evaluation period. No larvae were found in flowers at the 3 h evaluation time. Larvae were found on bolls during only the 24 h evaluation time.

In the small plots, no difference was observed between nonBt and WideStrike varieties with regard to the average number of main stem nodes that bollworm larvae moved away from the terminal (Fig. 3). There was no significant cotton variety main effect ($F = 1.82$; df = 1, 9; $P = 0.210$), but a significant evaluation time effect ($F = 67.93$; df = 1, 9; $P = 0.001$) was evident. As with individual plants, the rate of bollworm larval movement away from plant terminals was similar between nonBt and WideStrike varieties although larval movement away from terminals increased from 24 - 48 h. The average number of main stem nodes that bollworm larvae moved below plant terminals was 1.03 at 24 h and 1.48 at 48 h.

The proportions of bollworm larvae infesting various plant structures did not differ between nonBt and WideStrike cotton varieties in small plots (Fig. 4). Cotton variety had no significant effect on the proportion of larvae found in terminals ($F = 2.16$; df = 1, 9; $P = 0.176$), squares ($F = 0.04$; df = 1, 9; $P = 0.855$), flowers ($F = 2.80$; df = 1, 9; $P = 0.129$), or bolls ($F = 0.02$; df = 1, 9; $P = 0.893$). There was a significant evaluation time effect on the proportion of larvae infesting terminals ($F = 12.33$; df = 1, 9; $P = 0.003$) and bolls ($F = 10.87$; df = 1, 9; $P = 0.009$), but not for squares ($F = 0.17$; df = 1, 9; $P = 0.689$) or flowers ($F = 2.80$; df = 1, 9; $P = 0.129$). The percentages of larvae found in terminals decreased from 24 - 48 h, with 41.6% found in terminals at 24 h and 32.0% at 48h. The proportions of larvae infesting bolls increased over the rating period; the proportion of larvae infesting bolls was 3.4% at 24 h and 10.5% at 48 h.

Discussion

Bollworm larvae and associated feeding injury in nonBt cotton is typically concentrated in the upper portion of the plant canopy (Fye 1972). Because bollworm moths target the upper one-third of the plant canopy for oviposition (Farrar and Bradley 1985), neonate bollworms focus on the palatable tissues of young foliage and small squares. As larval age increases along with consumption levels, larvae tend to move lower into the canopy in search of larger squares, flowers, or bolls. In this study, the presence of Cry1Ac and Cry1F Bt proteins in the WideStrike cotton variety had no measurable impact on the rate of larval movement away from plant terminals

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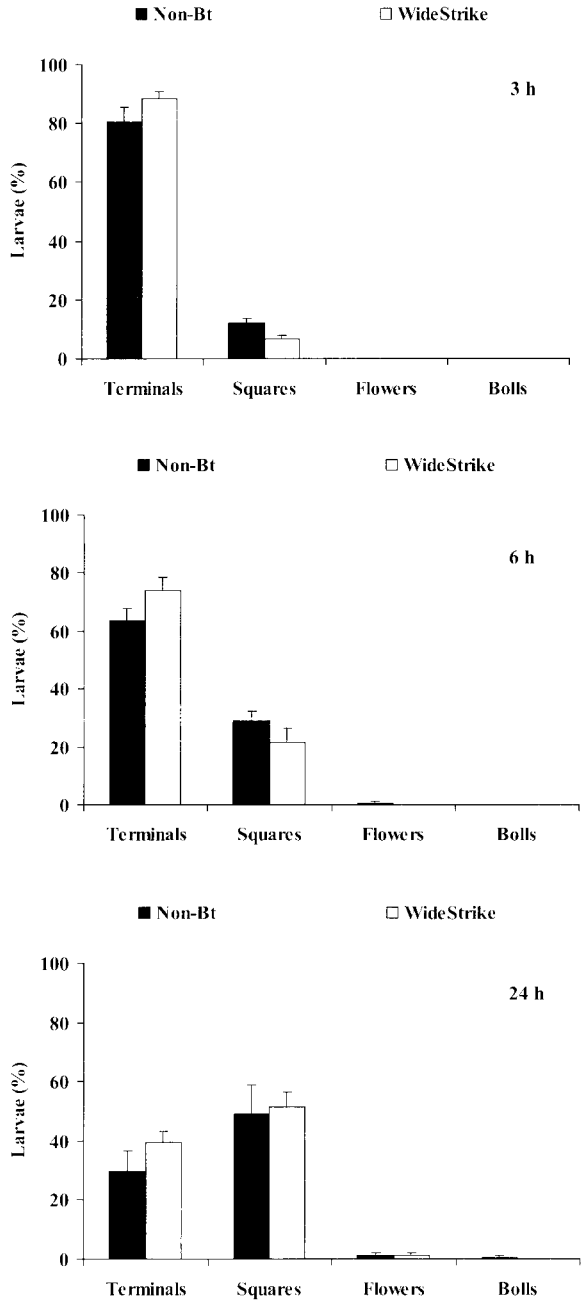

Fig. 2. Percentage (± SE) of bollworm larvae infesting various plant structures of individual flowering nonBt and Widestrike cotton plants.

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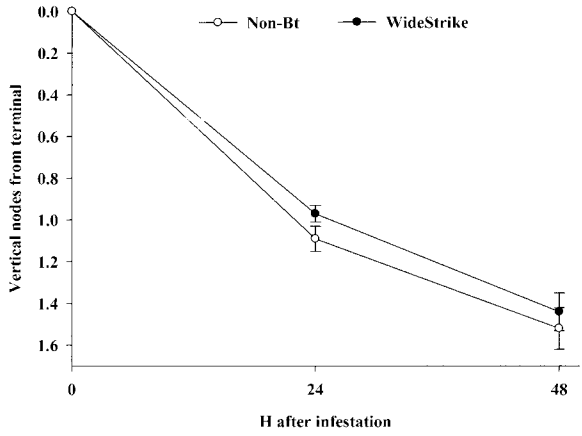

Fig. 3. Vertical distribution (± SE) of bollworm larvae on main stem nodes below terminals of flowering nonBt and Widestrike cotton plants in small plots.

when compared with a nonBt variety. After 24 h on individual plants, larvae moved an average of one node below the terminal on both WideStrike and nonBt plants, and 51 and 49% of larvae, respectively, infested squares at this time. These data are contrary to reports on larval movement with other Bt cotton technologies. Gore et al. (2002) demonstrated that the rate of larval movement below plant terminals of Bollgard cotton was higher than that of nonBt cotton. In addition, more larvae infested flowers and bolls of Bollgard cotton after 24 h as compared with the nonBt variety. Similarly, Parker and Luttrell (1999) found that higher proportions of tobacco budworm larvae dispersed from terminals in Bollgard cotton compared with nonBt cotton.

Related experiments have also been conducted with Bt cotton that expresses insecticidal toxins that differ from the Cry1Ac protein in Bollgard. Bommireddy et al. (2007) reported that both bollworm and tobacco budworm larvae were detected farther down the plant on Vip3A-expressing plants and plants expressing the Vip3A and Cry1Ab Bt proteins as compared with nonBt cotton plants. Larvae began to avoid feeding after 3 h on the Vip3A or VipCot™ (Syngenta Crop Protection, Greensboro, NC) plant tissues and increased their rate of movement down the plant. In addition, studies with Bollgard and VipCot showed that a higher proportion of larvae infested squares of the nonBt variety compared with Bt plants.

In the current experiment, larvae remained relatively close to terminals in both varieties for up to 48 h. Larvae in WideStrike cotton moved an average of 1.5 nodes below the terminal compared with 1.4 nodes on nonBt. Larval distribution among fruiting structures also was similar between varieties. The proportion of larvae remaining in terminals or squares at 48 h was 78% for nonBt cotton and 74% for WideStrike. Conversely, reports from Gore et al. (2002) showed higher proportions of larvae infesting terminals and squares of nonBt cotton at 24 and 48 h after infestation as compared with Bollgard. Also, both flowers and bolls of Bollgard plants were infested with higher proportions of larvae compared with nonBt plants.

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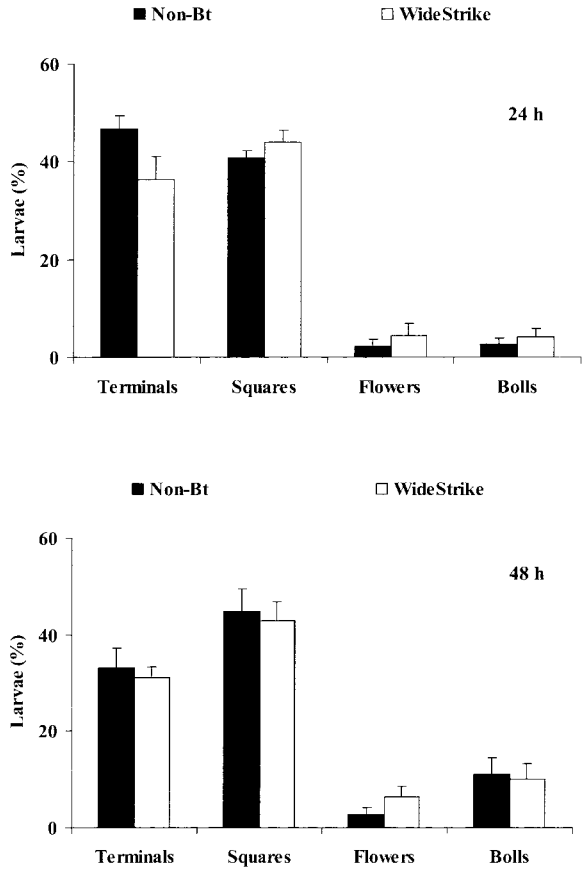

Fig. 4. Percentage (± SE) of bollworm larvae infesting various plant structures of flowering nonBt and Widestrike cotton plants in small plots.

Differences observed in larval movement patterns and larval distribution among feeding sites in previous studies with Bt cotton were presumably caused by larval avoidance measures. This avoidance behavior in bollworm larvae was previously demonstrated with Bt foliar sprays (Jyoti et al. 1996) and Bt toxins incorporated into artificial diet (Gore et al. 2005). In addition, Gould et al. (1991) found that tobacco budworm larvae avoided artificial diet containing a Bt protein when given a choice between toxic and nontoxic diet. This behavioral characteristic, however, is not limited to Bt toxins. Two-spotted spider mites, *Tetranychus urticae* Koch, were deterred by pyrethroid residues on leaf surfaces (Hall 1979, Iftner and Hall 1983, Penman and Chapman 1982). Over 30 pesticides have been reported to cause behavioral effects on arthropods (Lockwood et al. 1984).

Feeding behavior in the present study was not affected by the Bt toxins present in the WideStrike plants when compared with the nonBt cotton. The nonavoidance observed here has also been demonstrated with other insect species. Colorado potato

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beetle, *Leptinotarsa decemlineata* Say, feeding behavior was not affected by potato plants expressing the Bt protein Cry3B (Arpaia et al. 2000). Similarly, CO potato beetle larvae and larvae of the diamond back moth, *Plutella xylostella* L., did not avoid potato leaf disks treated with Bt as a foliar spray (Ferro and Lyon 1991, Arpaia and Ricchiuto 1993, Hoy and Hall 1993). With regard to synthetic insecticides, various pyrethroids had no effects on feeding behavior of *P. xylostella* larvae (Adams et al. 1992, Hoy and Hall 1993).

Because the avoidance behavior of bollworm differs among these various Bt technologies, there may be differences in protein expression levels in various plant parts among these technologies. Previous studies have reported differences in secondary plant metabolites among structures of an individual plant (McKey 1979, Metcalf et al. 1982), in addition to the Bt proteins expressed in transgenic cotton plants (MON 531) (Greenplate 1999, Greenplate et al. 2000). Cry1Ac and Cry1F protein expression in WideStrike cotton tissues were recently described by Siebert et al. (2009). Cry1F concentrations in terminal leaf tissues increased with leaf age; whereas, Cry1Ac concentrations in terminal leaves decreased over time. Larval survival also has been shown to differ among WideStrike plant parts. Adamczyk et al. (2008) found that beet armyworm, *Spodoptera exigua* (Hübner), larval survival was higher on leaves from the upper canopy of WideStrike cotton plants compared with leaves from the middle portion of the plant canopy. In addition, feeding damage to cotton leaves caused by beet armyworm and fall armyworm, *Spodoptera frugiperda* (J. E. Smith), was 2.7 and 11.1 times greater, respectively, on leaves from the upper portions of WideStrike cotton plants than leaves from the middle portion of the plant canopy. Adamczyk et al. (2008) suggested that the increased survival and damage observed in the terminal portion of WideStrike cotton plants was caused by low levels of Cry1F in the new foliage compared with fully-expanded leaves.

Both WideStrike and Bollgard cottons express the Cry1Ac protein, which might suggest that bollworm avoidance behavior would be similar between the Bt technologies. Although these 2 transformation events produce the same protein, these events use different promoters that may influence the variability in protein expression and larval survival between the technologies. Differences in protein expression may also be explained by gene insertion disparities (Sachs et al. 1998), parental background (Adamczyk and Meredith 2004), and environment (Greenplate 1999). Although it is difficult to identify the direct cause of the observed variability in protein expression and subsequent larval survival on Bt plants, it is evident that differences exist among the commercially available Bt technologies.

Our results suggest that scouting protocols and insecticide treatment initiation recommendations should differ based on the Bt technology that is being evaluated. Currently, scouting methods for bollworm in Bt cotton focus on sampling fruiting structures, particularly blooms and bolls lower in the plant canopy. Our results further suggest that larvae infesting the terminal portions of WideStrike cotton plants must also be considered to make appropriate management decisions with this technology.

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References Cited

Adamczyk Jr., J. J. and W. R. Meredith Jr. 2004. Genetic basis for variability of Cry1Ac expression among commercial transgenic *Bacillus thuringiensis* (Bt) cotton cultivars in the United States. J. Cotton Sci. 8: 17-23. http://www.cotton.org/journal/2004-08/1/upload/jcs08-017.pdf.

Adamczyk, J. J., S. Greenberg, S. Armstrong, J. W. Mullins, L. B. Braxton, R. B. Lassiter and M. W. Siebert. 2008. Evaluations of Bollgard, Bollgard II, and WideStrike technologies against beet and fall armyworm larvae (Lepidoptera: Noctuidae). Fla. Entomol. 91: 531-536.

Adams, A. J., C. W. Hoy, F. R. Hall and S. Y. Nettleton. 1992. Larval feeding and movement in two *Plutella xylostella* (Lepidoptera: Plutellidae) populations exposed to discrete deposits of permethrin. Pestic. Sci. 35: 243-247.

Akin, D. S., S. D. Stewart and K. S. Knighten. 2001. Behavioral response of lepidopteran pests on cotton expressing insecticidal proteins of *Bacillus thuringiensis*, Pp. 828-830. *In* P. Dugger and D. Richter (eds.), Proc., 2001 Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

Arpaia, S. and B. Ricchiuto. 1993. Effects of *Bacillus thuringiensis* toxin extracts on feeding behavior and development of Colorado potato beetle (Coleoptera: Chrysomelidae) larvae. Environ. Entomol. 22: 334-338.

Arpaia, S., L. D. Marzo, G. M. Di Leo, M. E. Santoro, G. Mennella and J. J. A. van Loon. 2000. Feeding behaviour and reproductive biology of Colorado potato beetle adults fed transgenic potatoes expressing the *Bacillus thuringiensis* Cry3B endotoxin. Entomol. Exp. Appl. 95: 31-37.

Bommireddy, P. L., B. R. Leonard and K. Emfinger. 2007. Heliothine larval behavior on transgenic cotton expressing a *Bacillus thuringiensis* insecticidal exotoxin, Vip3A. J. Cotton Sci. 11: 199-207.

Farrar, R. R. and J. R. Bradley Jr. 1985. Within-plant distribution of *Heliothis* spp. (Lepidoptera: Noctuidae) eggs and larvae on cotton in North Carolina. Environ. Entomol. 14: 205-209.

Ferro, D. N. and S. M. Lyon. 1991. Colorado potato beetle (Coleoptera: Chrysomelidae) larval mortality: operative effects of *Bacillus thuringiensis* subsp. San Diego. J. Econ. Entomol. 84: 806-809.

Fye, R. E. 1972. Preliminary investigation of vertical distributions of fruiting forms and insects on cotton plants. J. Econ. Entomol. 54: 1410-1414.

Gore, J., B. R. Leonard, G. E. Church and D. R. Cook. 2002. Behavior of bollworm (Lepidoptera: Noctuidae) larvae on genetically engineered cotton. J. Econ. Entomol. 95: 763-769.

Gore, J., J. J. Adamczyk Jr. and C. A. Blanco. 2005. Selective feeding of bollworm and tobacco budworm (Lepidoptera: Noctuidae) on diet treated with different concentrations of Cry1Ac and Cry2Ab proteins from *Bacillus thuringiensis kurstaki* Berliner. J. Econ. Entomol. 98: 88-94.

Gould, F., A. Anderson, D. Landis and H. Van Mellaert. 1991. Feeding behavior and growth of *Heliothis virescens* larvae on diets containing *Bacillus thuringiensis* formulations or endotoxins. Entomol. Exp. Appl. 58: 199-210.

Greenplate, J. T., G. P. Head, S. R. Penn and V. T. Kabuye. 1998. Factors potentially influencing the survival of *Helicoverpa zea* on Bollgard® cotton, Pp. 1030-1033. *In* Proc. Beltwide Cotton Conf., San Diego, CA. 5-9 Jan. 1998. Natl. Cotton Counc. Am., Memphis, TN.

Greenplate, J. T. 1999. Quantification of *Bacillus thuringiensis* insect control protein cry1Ac over time in Bollgard cotton fruit and terminals. J. Econ. Entomol. 92: 1377-1383.

Greenplate, J. T., S. R. Penn, J. W. Mullins and M. Oppenhuizen. 2000. Seasonal Cry1Ac levels in DP50B: the "Bollgard basis" for Bollgard II, Pp. 1039-1040. *In* P. Dugger and D. Richter (eds.), Proc., 2000 Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

Hall, F. R. 1979. Effects of synthetic pyrethroids on major insect and mite pests of apple. J. Econ. Entomol. 72: 441-446.

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Hoy, C. W. and F. R. Hall. 1993. Feeding behavior of *Plutella xylostella* and *Leptinotarsa decemlineata* on leaves treated with *Bacillus thuringiensis* and esfenvalerate. Pestic. Sci. 38: 335-340.

Huckaba, R. M., R. B. Lassiter, X. Huang, C. A. Blanco, V. B. Langston, L. B. Braxton, F. J. Haile, J. M. Richardson and J. Pellow. 2003. Field efficacy of Dow AgroSciences MXB-13 transgenic cotton for control of cotton bollworm and tobacco budworm, Pp. 1293-1298. *In* P. Dugger and D. Richter (eds.), Proc., 2003 Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

Iftner, D. C. and F. R. Hall. 1983. Effects of fenvalerate and permethrin on *Tetranychus urticae* Koch (Acari: Tetranychidae) dispersal behavior. Environ. Entomol. 12: 1782-1786.

Jackson, R. E., J. R. Bradley Jr. and J. W. Van Duyn. 2003. Field performance of transgenic cottons expressing one or two *Bacillus thuringiensis* endotoxins against bollworm, *Helicoverpa zea* (Boddie). J. Cotton Sci. 7: 57-64.

Jackson, R. E., J. R. Bradley and J. W. Van Duyn. 2005. Comparative efficacy of Bt technologies against bollworm in North Carolina, Pp. 1373-1378. *In* P. Dugger and D. Richter (eds.), Proc., 2005 Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

Jyoti, J. L., S. Y. Young, D. T. Johnson and R. W. McNew. 1996. *Helicoverpa zea* (Lepidoptera: Noctuidae): larval location, mortality, and leaf area consumption on *Bacillus thuringiensis*-treated cotton. Environ. Entomol. 25: 1438-1443.

Littell, R. C., G. A. Milliken, W. W. Stroup and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, NC.

Lockwood, J. A., T. C. Sparks and R. N. Story. 1984. Evolution of insect resistance to insecticides: a reevaluation of the roles of physiology and behavior. Bull. Entomol. Soc. Am. 30: 41-51.

Mahaffey, J. S., J. R. Bradley Jr. and J. W. Van Duyn. 1995. B. T. cotton: field performance in North Carolina under conditions of unusually high bollworm populations, Pp. 796-798. *In* P. Dugger and D. Richter (eds.), Proc., 1995 Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

McKey, D. 1979. The distribution of secondary compounds within plants, Pp. 55-133. *In* G. A. Rosenthal and D. H. Janzen (eds.), Herbivores. Their interaction with secondary plant metabolites. Academic Press, NY.

Metcalf, R. L., A. M. Rhodes, R. A. Metcalf, J. Ferguson, E. R. Metcalf and P. Y. Lu. 1982. Cucurbitacin contents and diabroticite (Coleoptera: Chrysomelidae) feeding upon *Cucurbita* spp. Environ. Entomol. 11: 931-937.

Parker Jr., C. D. and R. G. Luttrell. 1999. Interplant movement of *Heliothis virescens* (Lepidoptera: Noctuidae) larvae in pure and mixed plantings of cotton with and without expression of the Cry1Ac δ-endotoxin protein of *Bacillus thuringiensis* Berliner. J. Econ. Entomol. 92: 837-845.

Penman, D. R. and R. B. Chapman. 1982. Fenvalerate-induced distributional imbalances on two-spotted spider mite on bean plants. Entomol. Exp. Appl. 31: 71-78.

Sachs, E. S., J. H. Benedict, D. M. Stelly, J. F. Taylor, D. W. Altman, S. A. Berberich and S. K. Davis. 1998. Expression and segregation of genes encoding Cry1A insecticidal proteins in cotton. Crop Sci. 38: 1-11.

Siebert, M. W., T. G. Patterson, G. J. Gilles, S. P. Nolting, L. B. Braxton, B. R. Leonard, J. W. Van Duyn and R. B. Lassiter. 2009. Quantification of Cry1Ac and Cry1F *Bacillus thuringiensis* insecticidal proteins in selected transgenic cotton plant tissue types. J. Econ. Entomol. 102: 1301-1308.

Smith, R. H., D. P. Moore, R. A. Haygood, L. B. Braxton and A. R. Parker. 2005. Performance of Widestrike insect protection for control of lepidopteran pests in Alabama from 2001-2004, Pp. 1330-1335. *In* Proc. 1995 Beltwide Cotton Conference. National Cotton Council, Memphis, TN. (www.cotton.org/beltwide).

Stone, T. B. and S. R. Sims. 1993. Geographic susceptibility of *Heliothis virescens* and *Helicoverpa zea* (Lepidoptera: Noctuidae) to *Bacillus thuringiensis.* J. Econ. Entomol. 86: 989-994.

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