LABORATORY AND FIELD PERFORMANCE OF COTTON CONTAINING CRY1AC, CRY1F, AND BOTH CRY1AC AND CRY1F (WIDESTRIKE®) AGAINST BEET ARMYWORM AND FALL ARMYWORM LARVAE (LEPIDOPTERA: NOCTUIDAE)

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LABORATORY AND FIELD PERFORMANCE OF COTTON CONTAINING CRY1AC, CRY1F, AND BOTH CRY1AC AND CRY1F (WIDESTRIKE®) AGAINST BEET ARMYWORM AND FALL ARMYWORM LARVAE (LEPIDOPTERA: NOCTUIDAE)

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ABSTRACT

The efficacy of transgenic cotton genotypes containing Cry1Ac, Cry1F, and Cry1Ac stacked with Cry1F (WideStrike®, Dow Agrosciences, Indianapolis, IN) were investigated during 2001-2003 against the beet armyworm, *Spodoptera exigua* (Hübner) (=BAW), and the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (=FAW), in laboratory bioassays and small experimental field plots. In all experiments, cotton containing Cry1F was more toxic to BAW and FAW larvae compared to cotton containing only Cry1Ac. In the majority of experiments, the addition of Cry1Ac to the Cry1F genotype had no increased effect on efficacy and certain biological parameters against BAW and FAW larvae compared to cotton containing only Cry1F. Furthermore, the presence or absence of an additive, synergistic, or antagonistic effect between Cry1Ac and Cry1F was not observed in these field and laboratory experiments.

Key Words: cotton, Cry1 genes, transgenic cotton, beet armyworm, fall armyworm, *Spodoptera* spp.

RESUMEN

La eficacia de los genotipos de algodón transgénicos que tienen Cry1Ac, Cry1F, y Cry1Ac combinados con Cry1F (WideStrike®, Dow Agrosciences, Indianapolis, IN) fueron investigados durante 2001-2003 contra del gusano trozador (BAW), *Spodoptera exigua* (Hübner), y el gusano cogollero (FAW), *Spodoptera frugiperda* (J. E. Smith), en bioensayos de laboratorio y en experimentos en parcelas pequeñas de campo. En todos los experimentos, el algodón que tenia Cry1F fue el más tóxico a las larvas de BAW y de FAW en comparación al algodón que tenia solamente Cry1Ac. En la mayoría de los experimentos, la adición de Cry1Ac al genotipo Cry1F no tuvo un incremento sobre la eficacia y ciertas parámetros biológicos contra las larvas de BAW y FAW comparado al algodón que tenia solamente Cry1F. Además, no se observó la presencia o ausensia de un efecto aditivo, sinergistico o antagónico entre el Cry1Ac y Cry1F en estos experimentos de campo y de laboratorio.

Since the first Cry1Ac *Bacillus thuringiensis* Berliner (Bt) cotton variety was commercialized in 1996 (Bollgard®, Monsanto Ag. Co., St. Louis, MO), there have been numerous advancements for insect control with transgenic technology. Current and experimental cotton varieties can contain Cry1Ac alone or they can be stacked with Cry2Ab (Bollgard® II, Monsanto Ag. Co.) or Cry1F (WideStrike®, Dow Agrosciences, Indianapolis, IN). Furthermore, a novel exotoxin from *B. thuringiensis* also is currently in development (VipCot®, Syngenta Crop Protection, Greensboro, NC).

The beet armyworm, *Spodoptera exigua* (Hübner) (=BAW), is an occasional but serious pest of various vegetable and row crops in the mid-southern United States of America (=Mid-South). Compared to other North American armyworm species, knowledge of the ecology of this pest in the Mid-South is limited. This pest has no known photoperiod or temperature induced diapause mechanism (Kim & Kim 1997), and it is able to overwinter by continuous generations in southern Florida and Texas. Therefore, initial populations of beet armyworms found throughout the Mid-South are believed to be the result of immigration from those areas (Mitchell 1979; Hendricks et al. 1995). Populations in the Mid-South are typically found in cotton after July 1, with higher populations on various wild hosts in the fall months (Adamczyk et al. 2003). Although larval feeding on cotton is primarily concentrated on foliage, larvae can cause devastating losses in yield (Hardee & Herzog 1997; Adamczyk et al. 1998).

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (=FAW), also is a destructive migratory pest of many crops in the Western Hemisphere (Sparks 1979; Young 1979). Like the BAW, this pest has the potential to damage both conventional cotton bolls and Bollgard® cotton bolls (Adamczyk et al. 1998).

Although certain lepidopterous pests of cotton are controlled by Bollgard® cotton [e.g., tobacco budworms and pink bollworms, *Pectinophora gossypiella* (Saunders)], the Cry1Ac δ-endotoxin in

Bollgard® cotton is ineffective for control of BAW and FAW (Adamczyk et al. 1998; Henneberry et al. 2001). Consequently, outbreaks of BAW and FAW on Bollgard® often need full application rates of foliar insecticide treatments to keep these populations below economic injury levels (Hood 1997; Smith 1997). Efficacy data for BAW and FAW feeding on Bollgard II® is mainly limited to laboratory bioassays and small experimental field plots. However, the addition of Cry2Ab along with Cry1Ac appears to have improved the efficacy of Bollgard II® against both BAW and FAW (Adamczyk et al. 2001; Stewart et al. 2001). The purpose of the study was to examine the efficacy of Cry1Ac, Cry1F, and Cry1Ac stacked with Cry1F against BAW and FAW in laboratory bioassays and small experimental field plots.

Materials and Methods

Field Plots

From 2001-2003, experimental transgenic cotton varieties (Dow Agrosciences, Indianapolis, IN) were planted in research plots near Elizabeth, MS under a yearly Experimental Use Permit (EUP) (Table 1). In 2001, cotton was planted on May 23 and plots consisted of 2 rows (1.0 m centers) × 10.67 m. In 2002 and 2003, cotton was planted on May 13 and June 10, respectively, and plots consisted of 4 rows (1.0 m centers) × 12.20 m. All plots were arranged in a randomized complete block design with each variety replicated 8 times (twice in each block). Plots were irrigated once in 2002 and twice in 2001 and 2003. Only insecticides not active on Lepidoptera were applied to all plots throughout the season as dictated by local management practices.

Insects

Colonies of fall armyworms (FAW) and beet armyworms (BAW) were established from local migratory populations found in the Mississippi Delta. In May 2001, larvae (ca. 500) of FAW were collected from whorl-stage field corn near Stoneville, MS. FAW egg masses (ca. 20) were collected in August 2003 from royal paulownia, *Paulownia tomentosa* (thumb.) (Sieb. & Zucc. ex Steud.). BAW larvae (ca. 500 each year) were collected from redroot pigweed, *Amaranthus retroflexus* L., in June 2001 and July 2002. Both species were reared for one complete generation in the laboratory as described by Adamczyk et al. (1998), and the subsequent generation was utilized in either bioassays or field inoculations.

Table 1. Experimental transgenic cotton genotypes evaluated in 2001-2003.

Genotype	Cry genes	Years evaluated
MXB-7 (Cry1Ac)	1Ac	2001, 2002
MXB-9 (Cry1F)	1F	2001, 2002
MXB-13 (Cry1Ac/Cry1F or Widestrike®)	1Ac and 1F	2001-2003
PSC355 (conventional cotton isoline)	None	2001-2003

Field Experiments

Inoculations of BAW egg masses to plants for all varieties were conducted in 2001 and 2002. In the laboratory, egg masses were deposited on nylon cloth placed on the top of adult rearing cages (3.79-liter cardboard containers). For each inoculation, an egg mass of equal size (ca. 200-300 eggs/2.54-cm^2 cloth sample) was stapled to the underside of a mature leaf in all plots. Egg masses were spaced ca. 0.5 m from each other. Each plot received a total of 42 egg masses on July 10-12, 2001 and 56 egg masses on August 1-2, 2002. Eight days after inoculations (DAI), BAW populations were estimated with a standard 1.2-m drop cloth placed in the center row per plot (3 samples/plot). All recovered larvae within a plot were placed in 232-ml plastic containers and transported to the laboratory and weighed within 1 h after arrival. Prior to analysis, the coefficient of variation for the mean weights and number of larvae among genotypes was substantially improved by a log transformation. Both mean weights and numbers of BAW were analyzed by REML-ANOVA and were separated according to Fisher's Protected LSD (Littell et al. 1996; PROC MIXED, SAS Institute 2001).

In 2001, a minimum of 15 leaves (i.e., egg masses)/plot that showed evidence of successfully hatched neonates were visually examined after 9 DAI for BAW damage. Leaf damage was estimated with a categorical rating scale where 0% indicated no leaf damage while evidence of leaf consumption was given a value of 10%, 25%, or 50%. Prior to analysis, damage ratings appeared to be normally distributed, and a square-root transformation did not improve the coefficient of variation significantly among genotypes. Therefore, no transformation on this categorical data set was needed. Mean damage ratings were analyzed by REML-ANOVA, and means were separated according to Fisher's Protected LSD (Littell et al. 1996, PROC MIXED, SAS Institute 2001).

Bioassays

First-position flower buds (=squares) containing various transgenes (Table 1) were assayed in 2001 for bioactivity against BAW and FAW neonates. Individual squares were placed into a

Tight-Fit Lid sealing Petri dish (50 × 9 mm, BD Falcon® #351006, VWR International). For BAW, 3 larvae were placed in a dish containing a single square (5 dishes/plot) for a total of 120 larvae/genotype. For FAW, a single larva was placed in a dish containing a single square (10 dishes/plot) for a total of 40 larvae/genotype. Four days after exposure (DAE), larvae were prodded with a camel-hair brush and considered alive if coordinated movement was observed. Percent survival of neonates was analyzed by REML-ANOVA, and means were separated according to Fisher's Protected LSD (Littell et al. 1996; PROC MIXED, SAS Institute 2001).

In 2002, terminal leaves containing various transgenes (Table 1) were assayed for bioactivity against BAW neonates. Individual leaves were placed into a Tight-Fit Lid sealing Petri dish (50 × 9 mm, BD Falcon® #351006, VWR International). Three larvae were placed in a dish containing a single terminal leaf (5 dishes/plot) for a total of 120 larvae/genotype. At 3, 6, and 8 DAE, larvae were prodded with a camel-hair brush and considered alive if coordinated movement was observed. Percent survival of neonates was analyzed by REML-ANOVA, and means were separated according to Fisher's Protected LSD (Littell et al. 1996; PROC MIXED, SAS Institute 2001).

In 2003, terminal leaves containing only the Cry1Ac/Cry1F genotype (Table 1) were assayed for bioactivity against FAW neonates. A single larva was placed in a dish containing a single square or single terminal leaf (20 dishes/plot) for a total of 160 larvae/genotype. At 4 and 7 DAE, larvae were prodded with a camel-hair brush and considered alive if coordinated movement was observed. Percent survival of neonates was analyzed by REML-ANOVA, and means were separated according to Fisher's Protected LSD (Littell et al. 1996; PROC MIXED, SAS Institute 2001).

Results and Discussion

Field Experiments

Experimental cotton genotypes had differential affects on the survival of BAW larvae (Table 2). In 2001, the mean number of BAW larvae was significantly reduced in plots containing Cry1F and Cry1F stacked with Cry1Ac compared to the plots containing Cry1Ac alone or conventional cotton (PSC 355). The mean number of BAW larvae found in plots containing only Cry1Ac was not significantly different from the mean number of larvae found in conventional cotton. Therefore, the addition of Cry1Ac to cotton containing Cry1F had no significant effect in reducing the number of BAW larvae found in plots containing both these transgenes. However, in 2002 all transgenic cotton genotypes had significantly reduced mean BAW larval numbers as compared to the mean number of BAW larvae found in conventional cotton. Unlike 2001, cotton containing only Cry1Ac had significantly reduced BAW larval numbers as compared to the mean number of BAW larvae found in conventional cotton. In an adjacent experiment, higher parasitism rates of larvae from *Cotesia marginiventris* (Cresson) were observed in 2002 compared to 2001 (Adamczyk & Hardee 2002). This may have contributed to the lower numbers of recovered larvae in all plots in 2002 than in 2001. Sublethal affects of Cry1Ac (Henneberry et al. 2001) combined with increased parasitism may have resulted in the increased BAW mortality found in the Cry1Ac genotype in 2002 as compared to 2001. Another possibility is that different agronomic conditions (e.g., higher nitrogen levels) may have increased the level of Cry1Ac expressed in the plants which translated into the increased efficacy against BAW found in 2002 (Pierce et al. 1999).

Table 2. Number of BAW larvae found on various transgenic genotypes 8 days after egg inoculations in 2001 and 2002.

Genotype	Mean number of larvae ± SEM	
	2001	2002
PSC 355	37.8 ± 13.16 a	17.8 ± 9.44 a
Cry1Ac	31.0 ± 10.73 a	5.3 ± 1.70 b
Cry1F	4.8 ± 1.11 b	1.5 ± 0.50 c
Cry1Ac/Cry1F	6.3 ± 1.75 b	3.0 ± 0.71 bc
df	3, 9	3, 9
F value	16.20	13.43
($P > F$) ANOVA	<0.001	0.001

Means in a column followed by the same letter are not significantly different ($\alpha = 0.05$); Fisher's Protected LSD option of PROC MIXED (Littell et al. 1996; SAS Institute 2001). Means were log-transformed prior to analysis.

BAW larvae collected from all transgenic cotton genotypes had significantly lower mean weights as compared to BAW larvae collected from conventional cotton in 2001 and 2002 (Table 3). In addition, mean weights of BAW larvae were significantly lower when collected on cotton containing Cry1F as compared to BAW larvae collected from cotton containing only Cry1Ac. As with BAW larval numbers (Table 2), mean weights of BAW larvae collected from cotton containing both Cry1Ac and Cry1F were not significantly different from mean weights of BAW larvae collected from cotton containing only Cry1F for both years.

Leaf damage caused by BAW larvae was significantly lower in all transgenic cotton genotypes compared to conventional cotton in 2001 (Table 4). As with BAW larval weights (Table 3), larval damage was significantly lower in cotton containing Cry1F compared to cotton containing only Cry1Ac. Furthermore, BAW larval damage was

TABLE 3. WEIGHT OF BAW LARVAE 8 DAYS AFTER EGG INOCULATIONS ON VARIOUS TRANSGENIC GENOTYPES IN 2001 AND 2002.

	Mean weight of larvae (mg) ± SEM			
Genotype	No. weighed	2001	No. weighed	2002
PSC 355	94	17.4 ± 4.07 a	45	7.4 ± 1.40 a
Cry1Ac	114	6.5 ± 0.71 b	38	2.6 ± 0.36 b
Cry1F	19	3.3 ± 0.21 c	16	0.6 ± 0.23 c
Cry1Ac/Cry1F	21	2.3 ± 0.27 c	19	1.2 ± 0.18 c
df		3, 12		3, 9
F value		43.28		34.93
(*P* > *F*) ANOVA		<0.001		<0.001

Means in a column followed by the same letter are not significantly different ($\alpha = 0.05$); Fisher's Protected LSD option of PROC MIXED (Littell et al. 1996; SAS Institute 2001). Means were log-transformed prior to analysis.

not significantly different among the genotypes with Cry1F alone and Cry1F stacked with Cry1Ac.

Bioassays

Similar trends in larval survival on the various cotton structures from the different genotypes (Table 1) were found in the laboratory. The addition of Cry1Ac to the Cry1F genotype did not significantly reduce BAW or FAW larval survivorship when fed cotton squares compared to squares containing only Cry1F (Table 5). For both BAW and FAW, only squares that contained Cry1F significantly decreased larval survivorship compared to conventional cotton. This same trend was observed for BAW neonates fed cotton terminal leaves (Table 6). Survival of FAW larvae in 2003 was significantly lower when fed squares and terminal leaves of cotton containing both Cry1Ac and Cry1F than conventional cotton (note that Cry1Ac and Cry1F alone genotypes were not tested in 2003) (Table 7).

The *Cry1F* transgene apparently contributed more to total toxicity than the *cry1Ac* transgene in the Cry1Ac/Cry1F genotype (=WideStrike®) against BAW and FAW larvae. Luo et al. (1999) used a diet bioassay containing purified Cry1Ac or Cry1F and showed that Cry1F was >10× more toxic than Cry1Ac against BAW and FAW larvae. In Bollgard II®, the *cry2Ab* transgene is expressed throughout the plant at much higher levels than Cry1Ac (Greenplate et al. 2003). However, on an equal dose basis, Cry2Ab is more toxic against the soybean looper, *Pseudoplusia includens* (Walker), than Cry1Ac, while Cry1Ac is more toxic against the bollworm, *H. zea* (Sims 1997). Therefore, differences between toxicity of *cry1Ac* and *Cry1F* transgenes to BAW and FAW could be due to a higher titer of Cry1F in the plant compared to Cry1Ac, inherent toxicity differences between the two transgenes, or possibly a combination of both. However, the presence or absence of an additive, synergistic, or antagonistic effect between Cry1Ac and Cry1F was not observed in

TABLE 4. LEAF DAMAGE CAUSED BY BAW LARVAE 9 DAYS AFTER EGG INOCULATIONS ON VARIOUS TRANSGENIC GENOTYPES IN 2001.

Genotype	No. evaluated	Mean % leaf damage ± SEM
PSC 355	91	39.0 ± 1.79 a
Cry1Ac	95	32.2 ± 3.21 b
Cry1F	74	17.4 ± 1.76 c
Cry1Ac/Cry1F	76	18.5 ± 4.06 c
df		3, 9
F value		31.65
(*P* > *F*) ANOVA		<0.001

Means in a column followed by the same letter are not significantly different ($\alpha = 0.05$); Fisher's Protected LSD option of PROC MIXED (Littell et al. 1996;SAS Institute 2001).

TABLE 5. SURVIVAL OF BAW AND FAW LARVAE AT 4 DAE WHEN FED COTTON SQUARES FROM VARIOUS TRANSGENIC GENOTYPES IN 2001.

	Mean % survival ± SEM	
Genotype	BAW	FAW
PSC 355	76.7 ± 6.78 a	52.5 ± 4.79 a
Cry1Ac	70.0 ± 4.88 a	55.0 ± 8.66 a
Cry1F	44.2 ± 8.06 b	20.0 ± 10.80 b
Cry1Ac/Cry1F	43.3 ± 7.77 b	25.0 ± 9.57 b
df	3, 21	3, 12
F value	9.95	4.32
(*P* > *F*) ANOVA	<0.001	0.028

Means in a column followed by the same letter are not significantly different ($\alpha = 0.05$); Fisher's Protected LSD option of PROC MIXED (Littell et al. 1996; SAS Institute 2001).

TABLE 6. SURVIVAL OF BAW NEONATES WHEN FED COTTON TERMINAL LEAVES FROM VARIOUS TRANSGENIC GENOTYPES IN 2002.

	Mean % survival ± SEM		
Genotype	3 DAE[1]	6 DAE	8 DAE
PSC 355	83.3 ± 0.06 a	81.7 ± 0.08 a	78.3 ± 0.09 a
Cry1Ac	90.0 ± 0.04 a	86.7 ± 0.05 a	78.3 ± 0.03 a
Cry1F	80.0 ± 0.05 a	56.7 ± 0.10 b	48.3 ± 0.10 b
Cry1Ac/Cry1F	80.0 ± 0.03 a	55.0 ± 0.02 b	53.3 ± 0.03 b
df	3, 9	3, 9	3, 9
F value	0.92	7.35	6.90
(*P* > *F*) ANOVA	0.468	0.010	0.010

Means in a column followed by the same letter are not significantly different ($\alpha = 0.05$); Fisher's Protected LSD option of PROC MIXED (Littell et al. 1996; SAS Institute 2001).
[1]Days after exposure to leaves.

TABLE 7. SURVIVAL OF FAW NEONATES WHEN FED COTTON SQUARES AND TERMINAL LEAVES FROM VARIOUS TRANSGENIC GENOTYPES IN 2003.

	Mean % survival ± SEM			
	Squares		Leaves	
Genotype	4 DAE[1]	7 DAE	4 DAE	7 DAE
PSC 355	61.9 ± 3.44 a	50.0 ± 4.79 a	75.0 ± 7.14 a	71.9 ± 5.34 a
Cry1Ac/Cry1F	25.0 ± 3.54 b	8.1 ± 1.57 b	65.0 ± 5.68 b	25.6 ± 3.71 b
df	1, 6	1, 3	1, 3	1, 3
F value	55.84	147.99	19.20	50.70
(*P* > *F*) ANOVA	<0.001	0.001	0.022	0.006

Means in a column followed by the same letter are not significantly different ($\alpha = 0.05$); Fisher's Protected LSD option of PROC MIXED (Littell et al. 1996; SAS Institute 2001).
[1]Days after exposure to squares or leaves.

these field and laboratory experiments. Insuring that both transgenes provide dual protection against key lepidopterous pests is crucial for resistance management to transgenic crops (Gould & Tabashnik 1998).

DISCLAIMER

Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

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