

# Boll Weevil *Anthonomus grandis* Boh. Oviposition Is Decreased in Cotton *Gossypium hirsutum* L. Lines Lower in Anther Monosaccharides and Gossypol

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Several cotton *Gossypium hirsutum* L. race stocks have been identified that possess resistance to the boll weevil *Anthonomus grandis* Boh. because oviposition in the bud is decreased. In three tests of 13 boll weevil resistant lines conducted over a 6 year period on average, boll weevil punctures were decreased by 37.2% as compared to two susceptible commercial lines, while anther sugars were decreased 34.3% and anther gossypol was decreased 19.6%. Sugars and gossypol in the petals and ovaries were not different, however. Gas-liquid chromatographic analyses via the alditol acetate procedure revealed that the major free sugars of both the boll weevil suppressant and commercial cotton lines were glucose, fructose, sucrose, and arabinose with lesser amounts of xylose, galactose, and erythritol. Efforts to incorporate genes for oviposition resistance into commercial lines based on their correlation with low anther sugar content may have some promise.

**Keywords:** *Boll weevil; oviposition; cotton plant; sugars; gossypol*

## INTRODUCTION

The entrance of the boll weevil (*Anthonomus grandis* Boh.) from Mexico to the United States in the early 1890s caused farmers to change from varieties of cotton (*Gossypium* spp.) that were grown from slow fruiting, late maturing, long staple types to earlier and more rapid-fruiting types of short staple cotton (*G. hirsutum* L.). A search for resistance was also initiated on the basis that it might be found in centers of origin where the plant and pest had coexisted for many years, perhaps centuries. Collections were made of primitive boll weevil resistant cotton plants from Mexico and Central America which were photoperiodic and did not flower during the long days of the growing season in the Cotton Belt.

Jenkins et al. (1978) tested 191 primitive *G. hirsutum* accessions and rated 69 as resistant to the boll weevil on the basis of oviposition suppression, but most were photoperiodic. A program was initiated to incorporate cotton with day-neutral genes into these photoperiodic primitive accessions (McCarty et al., 1979, 1982, 1987; McCarty and Jones, 1989). As a result, several lines were established on which weevils oviposited significantly less than on controls.

In an effort to identify compounds in cotton buds that might suppress or stimulate oviposition, Hedin and McCarty (1990) used several laboratory bioassay procedures to evaluate the effects of a number of known bud constituents. Although many had been reported to stimulate feeding (Hedin et al., 1968, 1977; McKibben et al., 1985), only sugars and gossypol stimulated oviposition in laboratory tests. Moreover, the somewhat lower concentrations of the sugars and gossypol in anthers of two suppressant lines (Hedin and McCarty, 1990) suggested that a relationship of content with resistance existed. Since additional boll weevil suppressant lines have been developed (McCarty, unpublished results), the objective of this work was to deter-

mine whether sugars and gossypol were consistently lower in anthers of lines that were suppressant.

## MATERIALS AND METHODS

**Cultivars, Race Stocks, and Agronomic Practices.** In 1987, day-neutral BC<sub>2</sub>F<sub>4</sub> lines T-326 and T-1180; a commercial cultivar, Stoneville 213 (ST213); and a breeding line, Stoneville 213 glandless (ST213 gl), were grown in field plots to produce flower buds for the various chemical analyses (Table 1). The day-neutral lines, T-326 DN and T-1180 DN, hereafter referred to without DN, previously were reported to carry resistance to boll weevil oviposition (McCarty et al., 1987). Stoneville 213 and Stoneville 213 glandless lines served as susceptible controls. Standard cultural practices were followed during the growing season. All plant material was collected from cotton plants of similar maturity.

In 1990, seven day-length-neutral primitive cotton lines (T-292F<sub>4</sub>, T-297F<sub>4</sub>, T<sub>1</sub>323F<sub>4</sub>, T-326B<sub>2</sub>F<sub>5</sub>, T-339F<sub>4</sub>, T-1134BC<sub>1</sub>F<sub>5</sub>, T-1180BC<sub>2</sub>F<sub>5</sub>) plus two cultivars (Deltapine 50, Stoneville 825) and one breeding line (Stoneville 213 glandless) (Table 1) were grown in field plots at the Plant Science Research Farm of the Mississippi Agricultural and Forestry Experiment Station located at Mississippi State University. The primitive lines in their original state are day length sensitive and have been reported to carry resistance to the boll weevil (Jenkins et al., 1978).

In 1993, advanced generations of the seven primitive lines grown in 1990 plus six additional day-neutral primitive lines (Table 2) and two commercial cultivars were grown in field plots. Standard cultural practices were followed throughout the growing seasons for 1987, 1990, and 1993.

**Harvesting and Processing of Buds.** Two hundred flower buds (squares), approximately 8 mm diameter, were collected at random from each cotton line in early August in 1990 and 1993. All plant material was collected from cotton plants of similar maturity. The boll weevil prefers to feed and lay eggs in 8 mm squares, and during early August they are very active in field plots. Once the squares were collected, they were transported to the laboratory, where they were dissected into parts in 1993 (anthers, petals, ovaries). The samples were then freeze-dried, ground, and held for analysis. In 1990 whole squares were freeze-dried and prepared for analysis.

**Procedures for Recording Oviposition and Feeding Punctures.** In 1990 the day-neutral lines of Lukefahr and

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**Table 1. Allelochemicals and Nutrients in Buds of Boll Weevil Oviposition Deterrent Lines, 1987 and 1990**

line	gossypol	flavonoids	anthocyanins	condensed tannins	amino acids	free sugars	oviposition punctures, <sup>a</sup> %	feeding punctures, <sup>a</sup> %
1987 (Anthers), %								
ST213gl	0.21	0.94	0.02	2.58	0.53	6.80		
ST213	1.00	0.98	0.02	2.48	0.33	12.30	68.4	
T-326 BC <sub>2</sub> F <sub>4</sub> <sup>b</sup>	0.77	0.94	0.02	2.07	0.50	9.40	39.0	
T-1180 BC <sub>2</sub> F <sub>4</sub> <sup>b</sup>	0.79	0.92	0.02	3.75	0.69	6.50	36.8	
1990 (Whole Buds), %								
T-292F <sub>4</sub>	1.21	1.36	0.02	7.27	1.10	4.08	32.0	17.8
T-297F <sub>4</sub>	1.43	1.62	0.02	6.98	0.72	2.07	18.8	10.0
T-323F <sub>4</sub>	0.97	1.21	0.02	7.86	0.93	4.41	25.0	10.6
T-326BC <sub>2</sub> F <sub>5</sub> <sup>b</sup>	1.10	1.23	0.01	4.83	0.58	5.51	29.2	10.2
T-339F <sub>4</sub>	0.99	1.17	0.01	6.47	0.54	5.51	25.8	12.8
T-1134BC <sub>1</sub> F <sub>5</sub>	0.98	1.20	0.01	7.71	1.24	6.31	32.8	14.2
T-1180BC <sub>2</sub> F <sub>5</sub> <sup>b</sup>	1.09	1.29	0.01	5.82	0.95	1.89	32.4	17.0
ST-213gl				6.45	0.79	4.45		
DPL-50	1.21	1.77	0.01	5.24	0.50	6.06		
ST-825	1.20	1.28	0.01	4.90	0.58	7.74		
DPL-16							55.8	19.8
ST-213							49.0	14.2
lsd 0.05	0.17					0.53	8.9	6.2

<sup>a</sup> Mean of seven weekly square collections, % of squares examined. Data collected by M. J. Lukefahr, Rio Farms, Ed Couch, TX (Lukefahr and Vieriera, 1986). <sup>b</sup> T-326 and T-1180 were day-neutral (DN) Lines.

**Table 2. Sugars and Gossypol in Anthers, Petals, and Ovaries of Boll Weevil Oviposition Deterrent Lines, 1993, Percent of Dry Weight**

line	anthers		petals		ovaries		oviposition punctures, <sup>a</sup> %
	sugars	gossypol	sugars	gossypol	sugars	gossypol	
T-292 F <sub>6</sub>	2.81	0.46	7.70	0.57	1.65	0.15	
T-297 F <sub>6</sub>	2.24	0.58	6.47	0.62	5.67	0.15	
T-323 F <sub>6</sub>	4.32	0.51	7.45	0.56	5.60	0.14	
T-326 BC <sub>2</sub> F <sub>7</sub>	3.31	0.57	6.96	0.62	4.25	0.16	
T-339 F <sub>6</sub>	4.43	0.51	6.55	0.58	4.99	0.14	
T-1134 BC <sub>1</sub> F <sub>7</sub>	4.37	0.54	5.46	0.61	3.61	0.15	
T-1180 BC <sub>2</sub> F <sub>7</sub>	3.83	0.53	7.33	0.55	4.62	0.14	
T-78 BC <sub>4</sub> F <sub>5</sub>	3.72	0.54	6.08	0.58	2.97	0.13	
T-140 BC <sub>4</sub> F <sub>5</sub>	3.86	0.44	7.94	0.49	9.93	0.11	53.2
T-267 F <sub>4</sub>	3.55	0.48	7.77	0.56	8.51	0.12	54.9
T-732 BC <sub>4</sub> F <sub>4</sub>	3.08	0.43	6.77	0.50	6.63	0.13	46.4
T-1149 BC <sub>4</sub> F <sub>5</sub>	4.37	0.44	5.92	0.70	8.11	0.13	51.2
T-1167 BC <sub>3</sub> F <sub>4</sub>	3.82	0.43	6.73	0.57	8.76	0.11	
DPL 50	5.91	0.57	6.81	0.85	8.69	0.14	68.9
ST-213	5.33	0.63	7.54	0.64	11.83	0.14	
ST-213gl	5.21	0.27	6.16	0.09	6.44	0.05	
lsd 0.05	1.10	0.08					8.2

<sup>a</sup> Mean of five sampling dates, % of squares examined. Data collected by M. J. Lukefahr, Rio Farms, Ed Couch, TX (Lukefahr and Vieriera, 1986).

Vieriera (1986) that were grown at Mississippi State were also grown in field plots by M. J. Lukefahr at Rio Farms, Ed Couch, TX for boll weevil resistance evaluation. Replicated field plots (five replications) of each cotton line plus commercial cultivars, to be used as checks, were planted in early March. Beginning June 6, weekly infestation counts were made for 7 consecutive weeks by collecting 33 squares from each plot. The squares were separated into groups that had either egg or feeding punctures. In 1993 four additional lines were evaluated (Table 2); however, only five sampling dates were used in evaluating boll weevil resistance. Field design and sampling procedures were as in the 1990 test.

**Analyses of Water-Soluble Total Sugars in Buds.** Samples that had been freeze-dried were weighed and ground in distilled, deionized water (0.1 g in 20 mL) with a high-speed blender. After centrifugation, an aliquot was reacted with the anthrone reagent (Horwitz, 1975) and compared spectrophotometrically at 620 nm with the chromophore obtained from reaction of the anthrone reagent with glucose.

**Chromatographic Analyses of Bud Sugars by Gas Chromatography (GLC).** Total sugars were determined on freeze-dried powders before and after hydrolysis with 2 M trifluoroacetic acid, by derivatization to form their alditol acetates, and subsequently analyzed by GLC, all as described by York et al. (1985) and Sturgeon (1990). Standards were analyzed to confirm the GLC data.

**Analysis of Sugars by Thin Layer Chromatography (TLC).** To confirm the presence of mono- and disaccharides and to search for oligosaccharides, aqueous and aqueous-alcoholic extractions of anthers were analyzed by silica gel TLC using 1-butanol/acetic acid/water (2/1/1 and 8/1/1) and propyl acetate/formic acid/water (11/5/3) (Bieleski, 1993). Visualization was with the naphthoresorcinol-H<sub>3</sub>PO<sub>4</sub> reagent.

**Analysis of Allelochemicals and Amino Acids.** Analyses for gossypol and related terpenoid aldehydes were performed on cyclohexane/ethyl acetate/acetic acid (500:500:1; CHEA) extracts of plant (whole bud or bud parts) tissue by the phloroglucinol reaction [2% in absolute EtOH/concentrated HCl (1:1); stand 1 h] with subsequent spectrometric analysis at 550 nm. The concentration was determined by comparison with data obtained from authentic gossypol and is expressed as gossypol equivalents. Condensed tannin analyses were performed on 70% aqueous methanol (MW) extracts of tissue. The anthocyanidin chromophore was developed from the tannin by boiling for 1 h with 1-butanol/HCl (95:5) (Hedin et al., 1982). The concentration was determined by comparison with the color obtained at 550 nm from a purified cotton condensed tannin sample, the structure of which was elucidated by Collum et al. (1981). The anthocyanin content was determined by measuring the absorbency at 540 nm of an

extract of freeze-dried tissue extracted with methanol/water/HCl (79:19:3), using the molar extinction coefficient ( $E$ ) of cyanidin 3- $\beta$ -glucoside (Hedin et al., 1967). Flavonoids were determined after extraction of freeze-dehydrated tissue with 70% aqueous acetone. Diphenylboric acid-ethanolamine complex (Natural Product Reagent A, Aldrich Chemical Co., 1%) in methanol was added, and the chromophore absorptivity at 440 nm was determined and compared to that obtained from a purified sample of isoquercitrin, the most prevalent flavonoid in cotton. Amino acids were determined by HPLC analysis after hydrolysis of anther tissue by employing their phenylthiocarbonyl derivatives (Cohen et al., 1986).

**Procurement of Chemicals.** All commercially available chemicals were obtained from Sigma Chemical Co., St. Louis, MO. Gossypol was a gift from the Southern Regional Research Center, USDA, New Orleans, LA.

**Statistical Procedures.** Standard statistical procedures were followed for data analysis. Means were calculated, and LSD 0.05 was used for comparison of significance.

## RESULTS AND DISCUSSION

Data obtained from the analyses of cotton bud anthers collected in 1987 and of whole buds in 1990 for sugars, amino acids, gossypol, flavonoids, anthocyanins, and condensed tannins are given in Table 1. Oviposition and feeding punctures were also recorded. The data from the 1987 test were published by us in 1990 (Hedin and McCarty, 1990).

In the 1987 test (Table 1), free (water-extractable) sugars were higher in anthers of ST-213 (but not in the glandless isolate) than in the two boll weevil suppressant lines. Gossypol was about 20% higher in ST-213 than in the boll weevil suppressant lines. Oviposition punctures were approximately 2-fold higher in ST-213. Differences in the other analyses were either minimal or did not show helpful informative trends. Seven additional boll weevil suppressant lines available for 1990 testing (Table 1) tended to be lower in bud sugars than the three commercial cultivars (3.67% vs 5.48%). Oviposition punctures in the 1990 test were on average 43% lower (statistically significant) in the boll weevil suppressant lines than in the standard lines. Two different but comparable pairs of commercial cultivars were used for the sugar and oviposition puncture tests. Gossypol again tended to be lower in several, but not all, of the boll weevil suppressant lines. Amino acids and condensed tannins tended to be slightly higher in the boll weevil suppressant lines.

In 1993, free (water-extractable) sugars and gossypol contents of anthers, petals, and ovaries were analyzed on 13 boll weevil suppressant lines. The results were compared with those of two commercial glanded cultivars and a nonglanded isolate (Table 2). Sugars tended to be higher in the anthers of the 3 commercial cultivars than in 10 suppressant lines (6.08% vs 4.25%). They were about the same in petals of the suppressant lines and cultivars but also tended to be higher in the ovaries of the commercial cultivars as compared with several suppressant lines. Gossypol was about the same in both the anthers and petals of the commercial cultivars and the suppressant lines, but lower than in 1987 and 1993. Gossypol was low in ovaries of all cotton lines tested. Boll weevil punctures were reduced in the suppressant lines by about 25%.

The data on oviposition punctures listed in Tables 1-3 were obtained using the day-neutral lines of Lukefahr and Vieriera (1986). These cottons were grown in 1990 in field plots in Texas (see Materials and Methods). The same lines were grown at Mississippi

**Table 3. Boll Weevil Oviposition Punctures and Anther Sugars, Gossypol, and Flavonoids Found in 13 Experimental Boll Weevil Lines, Expressed as Percent of Susceptible Controls (Averages for 1987, 1990, and 1993)<sup>a</sup>**

line	% of susceptible controls			
	oviposition punctures	sugars	gossypol	flavonoids
ST-213	100.0	100.0	100.0	100.0
ST-213gl		97.7		53.0
DPL-50	100.0	110.8	90.4	86.9
T-78		69.7	85.7	102.5
T-140	77.2	72.4	69.8	107.9
T-267	79.6	66.6	76.1	92.0
T-292	65.3	53.0	86.5	114.4
T-297	38.4	34.4	105.1	118.0
T-323	51.0	69.0	80.5	106.0
T-326	58.3	69.9	86.1	102.8
T-339	52.7	77.1	81.4	101.3
T-732	67.3	57.7	68.2	84.7
T-1134	66.9	81.7	83.3	94.0
T-1149	74.3	87.9	69.8	103.4
T-1167		71.6	68.2	91.4
T-1180	60.0	49.7	84.4	100.2
av	62.8	65.7	80.4	101.4

<sup>a</sup> See Tables 1 and 2 for statistics.

State for chemical evaluations. There was the concern that the lines would give different results because of being grown at two geographical locations. However, informal observations on oviposition punctures conducted at Mississippi State substantiated the data obtained on the Texas lines.

Table 3 is a summary table in which boll weevil punctures and the sugar, gossypol, and flavonoid contents of the 13 experimental lines that were analyzed on one or more occasions during the 3 test years were averaged and are expressed as a percent of the susceptible ST-213 line. Boll weevil oviposition punctures were decreased in the boll weevil suppressant lines by an average of 37.2%, while anther sugars were decreased by an average of 34.3% and anther gossypol was decreased by 19.6%. Anther flavonoids were essentially unchanged. No statistical treatments beyond those presented in Tables 1 and 2 were carried out. Nevertheless, a general trend relating decreased boll weevil oviposition to lower anther sugars and gossypol is apparent.

Water extracts were utilized to assay for anther sugars in a manner that reflected the most physiologically natural environment. However, to quantitatively analyze for total sugars, the alditol acetates of the sugars in the freeze-dried powders were prepared and analyzed by GLC and GLC-MS. In the previous analysis of water-extractable bud sugars in which HPLC was employed (Hedin and McCarty, 1990), only fructose, glucose, sucrose, and maltose were reported. In the present work in which total sugars of freeze-dried anther powders were analyzed by GLC of their alditol acetates (Table 4), no maltose was found, although a maltose-alditol acetate standard was successfully chromatographed. In addition to glucose, fructose, and sucrose, small quantities of erythritol, arabinose, xylose, and galactose, together accounting for about 20% of total sugars, were also found. The total sugar content of both commercial and suppressant lines was about 4.8%. When the samples were hydrolyzed with 2 M trifluoroacetic acid before analysis, the total anther sugar content increased to 10.4%, presumably because of the hydrolysis of complex carbohydrates to glucose and lesser amounts of galactose, xylose, and arabinose. The free sugar contents in anthers were similar for the

**Table 4. Cotton Bud Constituent Sugars in Boll Weevil Oviposition Deterrent and Nondeterrent Lines, Percent of Dry Weight**

line <sup>a</sup>	erythritol	arabinose	xylose	fructose	glucose	galactose	sucrose	total
				Anthers				
S	0.12	0.42	0.16	0.76	2.40	0.30	0.65	4.81
SH	0.42	1.10	0.80	0.59	6.50	0.97	tr	10.37
R	0.20	0.27	0.14	1.00	2.80	0	0.43	4.84
RH	0.14	1.30	0.63	0.60	6.60	1.20	tr	10.48
lsd 0.05 <sup>b</sup>	0.06	0.09	0.13	0.11	0.38	0.23	0.16	
				Ovaries				
S	0.20	0.24	0.10	0.42	1.70	0	1.70	4.36
SH	0.24	3.00	1.20	0.43	3.70	2.30	0.16	11.03
R	0.22	0.24	0.16	0.96	2.90	0	0.46	4.94
RH	0.22	4.10	1.30	0.62	4.30	2.50	tr	13.04
				Petals				
S	0.15	0.22	0.26	0.38	1.80	0.36	0.15	3.32
SH	0.16	2.40	0.81	0.36	3.30	2.40	0.20	9.63
R	0.16	0.11	0.25	0.58	2.90	0	0.13	4.99
RH	0.16	2.52	0.81	0.62	4.20	2.60	0.22	13.52

<sup>a</sup> S, susceptible; SH, susceptible hydrolyzed; R, resistant, RH, resistant hydrolyzed. S = ST-213. R = T-326 BC<sub>2</sub> F<sub>7</sub>. <sup>b</sup> lsd 0.05 values not calculated for ovaries and petals.

anthrone and alditol acetate procedures, when all lines were compared [4.80% (1990, whole bud) and 6.39% (1993), vs 4.82%], but the latter procedure did not give a lower analysis for the boll weevil suppressant line. Individual sugars were not noticeably different when the commercial and boll weevil suppressant lines were compared except that galactose was absent from the resistant line (before hydrolysis). A TLC system able to separate monosaccharides from di-, tri-, and tetrasaccharides (Bielecki, 1993) was employed to determine if the water-extractable sugar extracts contained significant amounts of oligosaccharides that conceivably could be making significant contributions to oviposition activity hitherto attributed to the mono- and disaccharides. However, no oligosaccharides seemed to be present. By inference, the mono- and disaccharides would be presumed to be responsible for any major behavioral activities of the sugar extracts.

We have studied arrestant responses of the southwestern corn borer *Diatraea grandiosella* Dyar (SWCB) to sugars (Hedin et al., 1993). The only structural relationship to be identified was the conformation at the C-2 position in which the hydroxyls of mannose and arabinose were in the axial position, whereas the C-2 hydroxyls of all the other sugars were in the equatorial position. Analogously, there may be subtle differences in the stereochemistry of the boll weevil line sugars that could suppress oviposition.

Alternatively, the absence of galactose or the lower quantities of sugars in the boll weevil suppressant lines may also be related to the lower oviposition. Gossypol tended to be generally lower in the boll weevil suppressant lines. It has been shown to be an oviposition stimulant in laboratory tests (Hedin and McCarty, 1990), but high-gossypol lines have not been reported previously to stimulate boll weevil oviposition in field tests.

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