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Glands, Gossypol Content, and Tobacco Budworm Development in Seedlings and Floral Parts of Cotton[1]

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ABSTRACT

Larvae of tobacco budworm, *Heliothis virescens* (F.), were placed on seedlings and fed on detached fresh flower buds (squares) of cotton, *Gossypium hirsutum* L. Cotton entries included four parents, carrying all true-breeding combinations of the duplicate gland-determining alleles Gl_2, gl_2, Gl_3^{rai}, and gl_3, and all 12 F_1 hybrids, including reciprocals. Data were obtained on larval preference for seedlings; weight of larvae fed on fresh squares; gland density in seedlings; stigmas; and bolls; and gossypol content of cotyledons, seedling leaves, and squares. Gland density and gossypol content were highly correlated with the number of gland-determining alleles present and with each other. Both were highly negatively correlated with larval seedling preference and larval weight. Gl_2, the "A" subgenome allele, was more expressive in seedlings, while Gl_3^{rai}, the "D" subgenome allele, transferred from *G. raimondii* Ulbr., was more expressive in stigma-gland density and square-gossypol content. In fact, the number of stigma glands was as high, and larval weights were as low, in the monomeric $gl_2gl_2Gl_3^{rai}Gl_3^{rai}$ as in the dimeric $Gl_2Gl_2Gl_3^{rai}Gl_3^{rai}$, thus suggesting the predictive value of stigma-gland counts in these cottons, and the possible practical value of the monomeric as a breeding stock. Diallel analyses showed that most of the genetic variance in gland density, gossypol content, and larval response was additive. Dominance was virtually absent. Epistasis varied considerably, but contributed substantially to the total genetic variance of gland density in seedlings, stigmas, and bolls. Reciprocal and maternal effects were generally small and nonsignificant.

Additional index words:* *Gossypium hirsutum* L., *Heliothis virescens* (F.), *Diallel analysis.

THIS paper is the third in a series dealing with the interrelationships of pigment-gland density and gossypol content in cotton, *Gossypium hirsutum* L., with feeding preferences of larvae of the tobacco budworm, *Heliothis virescens* (F.).

The two earlier reports discussed the response of *H. virescens* larvae to cotton seedlings differing in the duplicate gland-determining alleles Gl_2 and Gl_3 (Wilson, 1971), or in those bearing the substituted Gl_3^{rai} (Wilson and Lee, 1971). We now present previously unreported data on gossypol content of cotyledons and leaves of seedlings, and of flower buds (squares), on gland density in stigmas and bolls, and of growth of tobacco budworm larvae when fed fresh, detached squares from cottons carrying all combinations of Gl_2, gl_2, Gl_3^{rai}, and gl_3. We also present data from a seedling feeding test repeated to compare results with our first test (Wilson and Lee, 1971) and to relate to results obtained by feeding larvae on squares.

MATERIALS AND METHODS

J. A. Lee, USDA, North Carolina State University, Raleigh, made available seeds of four parental lines (in 'Empire' background), which included glandless and the three true-breeding lines carrying the gland-determining alleles Gl_2 (native allele in the "A" subgenome of the allotetraploid *G. hirsutum*) and/or Gl_3^{rai} [an allele in the "D" subgenome, transferred from the American diploid *G. raimondii* Ulbr. (Lee, 1965)], and of all 12 F_1 hybrids (including reciprocals) from diallel crosses between these lines.

We planted seeds of the four parents and six F_1 hybrids in expanded peat pellets in a greenhouse at College Station, Texas on March 26, 1971. We counted the number of glands on the cotyledonary petiole of 10 seedlings per entry April 19, 1971 and moved 20 seedlings per entry to the field April 22, 1971. We planted seeds of the parents and the six reciprocal F_1 combinations in the greenhouse April 23, 1971, counted seedling glands May 4, 1971, and moved 20 seedlings of each entry to the field May 7, 1971. A severe hailstorm on May 9, 1971 destroyed many seedlings, which necessitated transfer of remnant seedlings from the greenhouse to the field. As the individual plants flowered, we counted the number of glands on a single stigma face of one open flower per plant. As the plants set bolls, we counted the number of glands in an area 1 cm square immediately adjacent to a suture of one boll per plant. Preliminary counts had indicated that gland numbers were highly correlated within and among stigmas and bolls from the same plant.

These same plants were used as a source of squares for gossypol analysis and for larval feeding tests. We collected pooled samples of squares from each of the four parents and 12 hybrids on June 23, 1971 and again on July 26, 1971 (one square per plant per entry, collected from the first position on a fruiting branch four nodes from the plant apex). These squares were shipped on dry ice to Brownsville, Texas, where we determined gossypol content, using Smith's (1967) method.

Tobacco budworm eggs were shipped to College Station July 6, 1971 for larval feeding tests. The larvae were transferred to an artificial wheatgerm diet as they hatched on July 9, 1971. On July 12, larvae of a uniform size were placed singly in 1-oz clear plastic cups to which single, fresh cotton squares had been added. Squares were changed every other day through July 20 and larvae were weighed to the nearest mg on July 21. Because of an unanticipated shortage of fresh squares (caused by a shortage of plants in some entries as an aftermath of the hailstorm), only five larvae per entry were used in each of three replications of the 12 hybrid combinations and in each of six replications of the four parental lines.

Wilson and Lee (1971) reported 1970 results from feeding tobacco budworm larvae on cotton seedlings of the same genotypes as used in the test reported in the present paper. The same methods were also used for these tests in 1971. Appropriate dates for the 1971 test are as follows: cotton seeds planted May 21; tobacco budworm eggs received May 26, transferred to wheatgerm media May 28, moved to seedlings (two larvae per seedling; four seedlings/entry/replication; six replications) June 3, after having been starved 17 to 18 hours; seedling damage rated and number of larvae per seedling counted on June 4, 5, and 10.

We raised another set of seedlings at Brownsville, including the four parents and six hybrids, but not the reciprocal hybrids. We planted the seeds in five randomized blocks and grew seedlings to the two leaf stage. We determined gossypol percentages from pooled samples of cotyledons, and first and second true leaves.

Data for gossypol content of seedlings and squares, larval weights, estimates of seedling damage, and number of larvae left on seedlings were subjected to randomized block analyses

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and means were separated using Duncan's New Multiple Range Test. Genetic (additive, dominance, and epistasis) and maternal and reciprocal effects were estimated, using the diallel analysis proposed for a two locus model by Lee, Cockerham, and Smith (1968). Gland counts, on the other hand, had been made in unreplicated plots and were therefore subjected to a completely randomized analysis. Means were separated using Kramer's (1956) adaptation of Duncan's New Multiple Range Test to unequal subclass numbers. For the diallel analysis of gland-count data, the subclass numbers were equalized, depending upon the minimum number of plants that had been counted (n=7, 8, and 10 for number of stigma glands, boll glands, and seedling glands, respectively). Gland- and larval-count data were transformed ($\sqrt{x+0.5}$) before they were analyzed.

To simplify the discussion, the four true-breeding genotypes will be referred to as follows: $Gl_3Gl_2Gl_3^{rai}Gl_3^{rai}$ = dimeric; $Gl_2Gl_2gl_3gl_3$ = the Gl_2 monomeric; $gl_2gl_2Gl_3^{rai}Gl_3^{rai}$ = the Gl_3^{rai} monomeric; $gl_2gl_2gl_3gl_3$ = glandless. In the tables these four genotypes are designated as A, B, C, and D, respectively, the F_1 hybrids are designated as AB, AC, AD, etc., and the reciprocal F_1 hybrids are designated as BA, CA, DA, etc., with the pistillate parent listed first, as is customary.

RESULTS

In Table 1 are presented data on gossypol content in cotyledons and first two true leaves, seedling damage ratings (1=least damage to 5=most damage), and the number of larvae left on seedlings. The number of glands on the cotyledonary petiole (Table 2) and gossypol content in seedling organs are highly positively correlated (for example, r=.94 between number of seedling glands and percent gossypol, second true leaf). On the other hand, number of seedling glands and seedling-gossypol content are highly negatively correlated with seedling damage ratings and number of larvae left on seedlings (for example, r=—.95 between percent gossypol and larval damage to the second leaf).

Larval preference is not shown as clearly as in seedling tests reported earlier (Wilson, 1971; Wilson and Lee, 1971); nevertheless, the trend of increased seedling damage and number of larvae left on seedlings with lower gland density is still evident.

Gossypol percentages of cotyledons and the second true leaf are practically identical, but that of the first true leaf is consistently lower (except in glandless or near-glandless entries). The reason for the lower level in the first leaf is unknown, but is suspected to be a consequence of the rapid expansion of this organ prior to sampling.

Table 2 presents data on gland density in seedlings, stigmas, and bolls; on gossypol content in squares; and on weight of tobacco budworm larvae fed on fresh, detached squares. Gland density and gossypol content in seedlings and floral parts are positively correlated with the number of gland-determining alleles present. Three separate patterns of gene effects emerge, however, as follows: (i) Gl_2 is more expressive than Gl_3^{rai} in the seedling; (ii) Gl_3^{rai} is more expressive than Gl_2 in affecting number of stigma glands and in square-gossypol content; and (iii) both alleles are approximately equal in their effects upon boll-gland density.

An effect observed earlier, in which one allele acting alone produces a minimum number of seedling glands, but two alleles acting in concert effect a large increase (Wilson and Lee, 1971), was manifested conspicuously in number of stigma and boll glands and to a lesser extent in gossypol content of seedlings and squares.

Table 1. Gossypol content and damage to cotton seedlings by tobacco budworm larvae and number of larvae left on seedlings (two larvae placed on each seedling June 3, 1971).

Genotype*	% gossypol, cotyledons	% gossypol 1st leaf	% gossypol 2nd leaf	Damage (1-5) Cotyledon, June 10	Damage (1-5) First leaf June 5	Damage (1-5) Second leaf June 5	No. larvae on plants June 10
A	.72 a†	.46 a	.73 a	3.17 ab	2.42 a	2.21 a	1.21 ab
B	.49 c	.23 c	.42 c	3.75 abc	2.95 ab	3.33 bc	1.21 ab
C	.34 d	.23 c	.28 d	4.00 bc	3.08 ab	3.47 bc	1.21 ab
D	.06 f	.16 d	.09 c	4.33 c	4.13 c	4.20 c	1.67 bc
AB	.61 b	.39 b	.57 b	3.08 a	2.75 ab	3.00 ab	1.00 a
AC	.60 b	.40 ab	.60 b	3.17 ab	2.70 ab	2.95 ab	1.08 a
AD	.46 c	.23 c	.38 c	3.50 ab	3.01 ab	3.79 bc	1.04 a
BC	.50 c	.28 c	.29 d	3.63 abc	2.79 ab	3.58 bc	1.21 ab
BD	.16 e	.12 d	.13 e	3.83 abc	3.72 bc	4.19 c	1.63 bc
CD	.13 c	.10 d	.11 e	3.71 abc	3.43 abc	4.00 c	1.79 c

* A = $Gl_2Gl_2Gl_3^{rai}Gl_3^{rai}$; B = $Gl_2Gl_2gl_3gl_3$; C = $gl_2gl_2Gl_3^{rai}Gl_3^{rai}$; D = $gl_2gl_2gl_3gl_3$. AB, AC, AD, etc. are F_1 hybrids. † Means with letters in common within a column not significantly different according to Duncan's New Multiple Range Test, 5% level.

Table 2. Gland density in seedlings and floral parts, gossypol content of squares, and weights of larvae fed on fresh squares.

Genotype	No. glands, cotyledonary petiole	No. glands, stigma face	No. glands /cm² boll	% gossypol, squares	Larval wt, mg
A*	100.2 a†	42.50 a	50.5 a	.73 a	50.67 d-f
B	82.3 b	28.00 e	24.8 cd	.19 e	139.13 ab
C	38.8 e	42.60 a	25.8 c	.51 c	42.90 f
D	0.0 f	0.0 d	0.0 e	.07 f	163.30 a
AB	73.3 bc	37.10 b	43.9 ab	.53 bc	85.70 b-f
BA	103.7 a	35.90 b	41.1 ab	.56 bc	87.50 b-f
AC	56.8 d	44.70 a	47.5 ab	.60 b	45.57 ef
CA	54.7 d	44.10 a	40.3 b	.71 a	78.33 b-f
AD	55.7 d	32.70 b	22.4 cd	.32 d	129.00 a-c
DA	66.3 cd	37.10 b	28.7 c	.29 d	117.30 a-d
BC	40.4 e	34.80 b	15.3 d	.30 d	64.23 c-f
CB	58.0 d	35.10 b	20.8 cd	.29 d	100.90 a-f
BD	3.7 f	0.23 d	1.0 e	.05 f	124.73 a-c
DB	3.0 f	0.09 d	0.1 e	.10 f	118.77 a-d
CD	1.4 f	1.27 d	0.1 e	.08 f	115.23 a-c
DC	2.5 f	1.72 d	0.2 e	.09 f	160.13 a

* See Table 1. † Means with letter in common within a column not significantly different, Duncan's New Multiple Range Test, 5% level.

Table 3. Simple correlation coefficients between larval weights and gland density, gossypol content, and plant damage.

Parameter	Larval weight
No. seedling glands	-.597
% gossypol, second leaf	-.639*
Larval damage to second leaf	.723*
No. stigma glands	-.806**
No. boll glands	-.700*
% gossypol, squares	-.879**

* P < .05. ** P < .01

For example, compare BD ($Gl_2gl_2gl_3gl_3$) with B ($Gl_2Gl_2gl_3gl_3$), or CD ($gl_2gl_2Gl_3^{rai}gl_3$) with C ($gl_2gl_2Gl_3^{rai}Gl_3^{rai}$).

Even though the test for differences in larval weights was not very precise, differences were nevertheless obviously related to differences in gland density and gossypol content of squares. The most conspicuous result was that larvae weighed no more after having been fed fresh squares from the Gl_3^{rai} monomeric genotype than they did after having been fed on squares from the dimeric genotype.

Table 3 presents simple coefficients of correlation between larval weight and gland density, gossypol content, and seedling damage. The highest negative correlation, as might have been expected, is that between larval weight and square gossypol content. The linear regression equation from these data (Y=151.96 — 150.14X, where Y=larval weight, and X=percent square gossypol) shows a decrease in larval weight of 15.01 mg for each .1% increment in gossypol in the square. The correlation between larval weight and number of stigma glands is also negative and highly significant.

Table 4. Diallel analysis summary for gland density.

		Number of glands					
		Seedling		Stigma		Boll	
Source	df	M.S.	Var.‡	M.S.	Var.	M.S.	Var.
General	3	458.69**		171.76**		219.04**	
Additive Gl_2	1	976.22**	3.049	190.15**	0.847	314.97**	1.224
Additive Gl_3^{rai}	1	388.17**	1.212	305.37**	1.363	340.86**	1.334
Add. × add.	1	11.67**	0.035	19.77**	0.087	1.30	-.001
Specific	6	44.23**		26.08**		15.10**	
Dominance Gl_2	1	0.05	-.001†	8.89**	0.078	0.09	-.006
Dominance Gl_3^{rai}	1	24.42**	0.151	6.96**	0.061	0.60	-.002
Add./add.	1	47.88**	0.148	20.78**	0.091	17.55**	.062
Epistatic	3	64.34**	1.071	39.96**	0.863	24.11**	.377
Maternal	3	5.54**		0.31		0.17	
Reciprocal	3	2.25**		0.11		0.63	
Error	*	0.22		0.16		0.80	

*144 for seedling glands, 96 for stigma glands, 112 for boll glands. ** P <.01
† See Lee, Cockerham, and Smith (1968) for explanation of negative genetic variance estimates. ‡ Variance component for source of variation indicated.

Table 5. Diallel analysis summary for gossypol content and larval weight.

		% gossypol					
		Cotyledons		Squares		Larval weight	
Source	df	M.S.	Var.†	M.S.	Var.	M.S.	Var.
General	3	1.050**		.515**		16,842.5**	
Additive Gl_2	1	1.923**	.0240	.397	.0124	5,271.8	82.24
Additive Gl_3^{rai}	1	1.215**	.0152	1.145**	.0358	40,458.9**	815.38
Add. × add.	1	.012	.0001	.004	.0001	4,796.9	72.39
Specific	6	.041**		.021**		1,538.2	
Dominance Gl_2	1	.037**	.0005	.002	.0001	810.2	-10.69
Dominance Gl_3^{rai}	1	.021**	.0003	.031**	.0010	1,749.7	8.90
Add./add.	1	.001	.0001	.002	.0001	809.0	-7.60
Epistatic	3	.062**	.0023	.031**	.0029	1,920.1	37.26
Maternal	3	--		.002		337.7	
Reciprocal	3	--		.003		1,967.3	
Error	*	.002		.001		1,323.9	

* 36 for % gossypol, cotyledons; 15 for % gossypol, squares; 30 for larval weight.
** P <.01. † Variance component for source of variation indicated.

Table 6. Percent additive, dominance, and epistatic genetic variances.

	Number of glands			% gossypol		Larval wt, mg fresh squares
Source	Seedling	Stigma	Boll	Cotyledon	Square	
Additive Gl_2	55.6	26.4	41.7	56.8	23.8	8.8
Additive Gl_3^{rai}	22.1	42.4	45.5	35.9	68.5	87.3
Dominance Gl_2	0.0	2.4	0.0	1.1	0.2	0.0
Dominance Gl_3^{rai}	2.8	1.9	0.0	0.8	1.9	0.0
Epistasis	19.5	26.9	12.8	5.4	5.6	3.9

Summaries of the diallel analyses appear in Tables 4 and 5. Table 6 presents the percentages of additive, dominance, and epistatic genetic variances calculated from these analyses.

Additive effects are all highly significant, except for the effects of Gl_2 on larval weight. Additive genetic variances make up from 68.8% of the total genetic variances for number of stigma glands to 96.1% of the total for larval weight. Dominance effects are sometimes significant, but never account for more than 4.3% of the total genetic variance. Epistatic effects are also sometimes significant. Epistatic genetic variances contribute from 3.9% of the total genetic variance in larval weight, to 26.9% of the total variance in number of stigma glands. Maternal and reciprocal effects are generally small and nonsignificant (the one exception is in number of seedling glands, where both of these effects are statistically sigificant, but small compared to genetic effects).

Additive × additive interaction effects are generally significant for number of glands and nonsignificant for gossypol content and larval weight. In one instance the two double heterozygotes (AD and BC) differ significantly in number of glands on the cotyledonary petiole.

DISCUSSION

The cotton genotypes used in this study represent all combinations of the presence or absence of the duplicate gland-determining alleles Gl_2 and Gl_3^{rai} in a common genetic background. They are thus of value as components of a model system in which to demonstrate the interrelationships of gland density, gossypol content, and insect response.

Gossypol content in squares of these cottons ranges from approximately the "normal" level (amount found in fully glanded, present commercial varieties) to almost none (glandless varieties), and therefore below the level considered to impart effective resistance to *Heliothis* (Lukefahr and Houghtaling, 1969). Lukefahr, Noble, and Houghtaling (1966) demonstrated that larvae of *Heliothis* spp. grew larger on diets made from six glandless varieties than on their six glanded counterparts of cotton. Oliver, Maxwell, and Jenkins (1971 obtained similar results, but showed that this effect was noticeably influenced by varietal background. The latter workers also infested caged glanded and glandless plants with larvae, and obtained similar results when they weighed the larvae after 6 days on the plants. In the stocks that we used in the present study, tobacco budworm larvae responded positively as gland density and thus gossypol content decreased. This positive response was demonstrated in the amount of seedling damage, in numbers of larvae remaining on seedlings, and in growth of larvae fed on fresh squares.

The response is largely linear, as shown by the preponderance of additive genetic variance, but shows some interesting variations that may have both practical and evolutionary implications.

Of the native gland-determining alleles in *G. hirsutum*, Gl_2 is more expressive than Gl_3 in determining gland patterns of cotyledons, leaves, and carpel walls (Lee, 1962; 1965), in seed-gossypol content (Lee, Cockerham, and Smith, 1968), and in the preference of tobacco budworm larvae for cotton seedlings (Wilson, 1971). Gl_2 is also more expressive than the substituted Gl_3^{rai} in seedling-gland-density, in larval preference for seedlings, and seed-gossypol content (Wilson and Lee, 1971), and in seedling gossypol content, as reported in the present paper.

The Gl_2-Gl_3 and Gl_2-Gl_3^{rai} relationships are different, however, in floral parts from those in seedling parts. Our data (unpublished) show that in the Gl_2-Gl_3 stocks in 'Empire' background, both monomerics have about the same number of stigma glands, but the Gl_3 monomeric has a much lower number of boll glands than the Gl_2 monomeric. Shaver and Garcia (1972), however, showed that gossypol content was significantly higher in the Gl_3 monomeric in each of the following flower-bud components: petals, sepals, stamens, stigma + style (but not in ovaries, where gossypol content was extremely low in both monomerics and in the glandless entry). Thus, Gl_3 in Empire background is more expressive than Gl_2 in its effect upon gossypol content of squares. The effect of Gl_3 on larval growth on fresh squares has not been studied.

The substituted Gl_3^{rai} is also more expressive than Gl_2 in its effects upon gossypol content of squares, on stigma-gland density, and in larval weight. In fact, stigma-gland density is as high, and larval weights are as low, in the Gl_3^{rai} monomeric as in the dimeric geno-

type. These results suggest that (i) stigma-gland counts are of high value in predicting larval performance in this set of cottons, and (ii) Gl_3^{rai} is of potential value in a breeding program designed to impart resistance to the tobacco budworm. Furthermore, the Gl_3^{rai} monomeric combines a relatively low seed-gossypol level [ca. one-half that of the dimeric (Wilson and Lee, 1971)] with a somewhat higher square-gossypol level (ca. three-fourths of that of the dimeric). Whether this favorable combination is of sufficient magnitude to be of importance in a breeding program remains to be seen. Also, the behavior of Gl_3^{rai} in lines with a high gossypol content (i.e., in the *Heliothis*-resistance range) is an unknown quantity.

These results suggest two possibilities in breeding for *Heliothis* resistant cotton, as follows: (i) use of a monomeric genotype, providing that it gives resistance without elevating seed-gossypol level; and (ii) use of gland-determining alleles transferred into cultivars from exotic sources, either alone or in combination with native alleles. Lee and Smith (1970) reported the successful cross between *G. davidsonii* Kell., with the highest seed-gossypol content among the "D" genome diploid species (El-Nockrashy, Simmons, and Frampton, 1969) and the tetraploid cultivated species *G. barbadense* L. Lee (pers. comm.) is attempting to move the major gland-determining allele (or alleles) from *G. davidsonii* into *G. hirsutum*. Singh and Weaver (1972) extracted transgressive segregants for high square-gossypol content from a *G. hirsutum* (high gossypol)-*G. barbadense* ('Pima S-4', also high gossypol) F_2 population.

Our results may help to explain a problem discussed by Lee (1962, 1965). He logically concluded from his observations that Gl_2 is a "relatively strong" allele and that Gl_3 is a "relatively weak" one. The problem is how this difference in expressivity developed in the allotetraploid derivative of two diploid species in which the major gland-determining genes possessed the potential for full expression. The solution to this problem seems to be that Gl_3 may have suffered greater loss of some functions than Gl_2 but now excels in others. Thus, even though both of these alleles act in concert to impart the fully glanded condition throughout the life of the plant, each has a specific major sphere of influence upon which natural selection could act independently.

It is interesting that Gl_3 (and Gl_3^{rai}) has a major influence on gland expression, and thus gossypol content, in squares and flowers. If we assume that the function of gossypol is to protect the plant from its insect enemies, then it seems possible that Gl_3 might continue to respond mainly to selective pressures applied by insects that normally attack floral parts, and Gl_2 to those applied by insects that attack foliar organs.

Although gene action is predominantly additive for each allele, and dominance is practically absent, as expected from earlier studies (Lee, Cockerham, and Smith, 1968; Wilson and Lee, 1971), there are some epistatic effects that deserve comment. In both seedlings and stigmas, the number of glands in the dimeric genotype is lower than expected on the basis of the gland-producing potential of the two alleles acting independently. The most conspicuous instance, alluded to earlier, is that number of stigma glands is as high in the Gl_3^{rai} monomeric as in the dimeric genotype. This phenomenon is not shown in boll-gland number or in square-gossypol content, where the two alleles apparently act additively in the dimeric stock.

Perhaps the largest source of interallelic interaction in number of glands is the concerted action of the two alleles when present in the double heterozygote, compared to an almost lack of expression in the genotypes that contain a single Gl_2 or Gl_3^{rai}. In the diallel analysis this effect is reflected in the dominance $\times$ dominance interaction component (not presented as separate variance components in Tables 4 and 5 because the epistatic effects are pooled). For example, the dominance $\times$ dominance interaction variance component represents 58, 77, and 88% of the total epistatic variance in number of boll glands, stigma glands, and seedling glands, respectively. This component, however, represents smaller percentages of total epistatic variance in other parameters.

REFERENCES

El-Nockrashy, A. S., J. G. Simmons, and V. L. Frampton. 1969. A chemical survey of seeds of the genus *Gossypium*. Phytochemistry 8:1949-1958.

Kramer, C. Y. 1956. Extension of multiple range tests to group means with unequal numbers of replications. Biometrics 12: 307-310.

Lee, J. A. 1962. Genetical studies concerning the distribution of pigment glands in the cotyledons and leaves of Upland cotton. Genetics 47:131-142.

———. 1965. The genomic allocation of the principal foliar-gland loci in *Gossypium hirsutum* and *Gossypium barbadense*. Evolution 19:182-188.

———, C. C. Cockerham, and F. H. Smith. 1968. The inheritance of gossypol level in *Gossypium*. I. Additive, dominance, epistatic, and maternal effects associated with seed gossypol in two varieties of *Gossypium hirsutum* L. Genetics 59:285-298.

———, and F. H. Smith. 1970. Some chemical properties of hybrid seed from a cross between *Gossypium barbadense* L. and *G. davidsonii* Kell. Crop Sci. 10:379-380.

Lukefahr, M. J., L. W. Noble, and J. E. Houghtaling. 1966. Growth and infestation of bollworm and other insects on glanded and glandless strains of cotton. J. Econ. Entomol. 59:817-820.

———, and J. E. Houghtaling. 1969. Resistance of cotton strains with high gossypol content to *Heliothis* spp. J. Econ. Entomol. 62:588-591.

Oliver, B. F., F. G. Maxwell, and J. N. Jenkins. 1971. Growth of the bollworm on glanded and glandless cottons. J. Econ. Entomol. 64:397-398.

Shaver, T. N., and J. A. Garcia. 1973. Gossypol content of cotton flower buds. J. Econ. Entomol. 66. (In Press).

Singh, I. D., and J. B. Weaver, Jr. 1972. Studies on the heritability of gossypol in leaves and flower buds of *Gossypium*. Crop Sci. 12:294-296.

Smith, F. H. 1967. Determination of gossypol in leaves and flower buds of *Gossypium*. J. Amer. Oil Chem. Soc. 44:267-269.

Wilson, F. D. 1971. Response of tobacco budworm larvae to cotton seedlings carrying various combinations of gland-determining alleles. Crop Sci. 11:268-270.

———, and J. A. Lee. 1971. Genetic relationship between tobacco budworm feeding response and gland number in cotton seedlings. Crop Sci. 11:419-421.