

Heritability and Combining Ability for Gossypol Content in Six Lines of Upland Cotton¹

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ABSTRACT

Six lines of upland cotton (*Gossypium hirsutum* L.), selected for different levels of gossypol and other terpenoids in flower buds, were intercrossed in all combinations, including reciprocals. Parents and F₁ hybrids were grown in a complete diallel set with three replications in one environment. Analysis of variance of gossypol level, using the methods of Griffing, revealed a large and highly significant component for general combining ability, and a small nonsignificant component for specific combining ability. There was also a very small, but significant, estimate for reciprocal effects. We concluded that gossypol in flower buds is inherited in an additive manner (94% narrow sense heritability) and should thus be readily selectable.

Analysis of the same materials using Hayman's technique confirms the highly significant and predominant additivity of inheritance, but also suggests that dominance cannot be completely ruled out as a source of significant variation.

Additional index words: Host-plant resistance, Polyphenolics, Diallel analysis.

THE desirability of having insect-resistant upland cotton (*Gossypium hirsutum* L.) has prompted a major effort to develop varieties with high gossypol concentrations in plant tissues, along with other insect-repelling characteristics (6).

The flower bud (square) is the preferred feeding site of early instar bollworm and budworm (*Heliothis* spp.) larvae in currently used upland cultivar cottons. The primary objective of this study was to determine the heritability of gossypol concentration in the squares of six strains of upland cotton that had been selected as primary source material in an insect-resistance breeding program.

Genetic transfer of high gossypol content from 'primitive' to more productive stocks has proved difficult because: 1) the inheritance of gossypol level is thought to be multigenic in nature and definite dominance-recessive expression has not been observed (5, 10); 2) the gossypol level must be estimated by a time-consuming chemical analysis; 3) the level of gossypol in square tissue changes with environments and during the development of the cotton plant (6); and 4) high gossypol level has been associated with inferior agronomic characters and low yield (7).

Several pairs of genes have been identified (3, 4) that concomitantly affect gossypol level and pigment gland expression. Other loci do not affect the action of the two major pairs (*G₁gl₂*, *G₁gl₃*) when they

are combined as homozygous recessives, although they may modify the expression of the dominant forms (9). Also, a number of allelic forms of *G₁gl₂* and *G₁gl₃* are variable in expression (11). Therefore, strains homozygous for the two major loci may contain highly variable levels of gossypol (10).

Lee et al. (5) studied the inheritance of seed gossypol in parents and hybrids in 'Coker' and 'Empire' backgrounds differing in the major gland determining alleles. They showed that most of the genetic variance was additive; epistasis and dominance, though significant, accounted for only 6% of the total variance. Singh and Weaver (10) found partially dominant gene action for low levels of gossypol in leaves and flower buds. Transgressive segregation in species crosses was also found, and individual segregates with high levels of gossypol were reported to be fixable.

MATERIALS AND METHODS

The experiment reported here was conducted in a greenhouse at New Mexico State University during 1973 with the progenies of all possible crosses of six selected strains with different levels of gossypol.

The six upland strains selected as parents were: 70-217-1 (217), a line selection from the densely glanded line; TH-149, derived from an early triple-hybrid of *G. hirsutum*, *G. arboreum* L., and *G. thurberi* Tod. (original material was obtained from J. A. Lee, North Carolina State University); 169-1 (169), selected from an Acala outcross of the high gossypol selection XG-15, obtained from M. J. Lukefahr, Brownsville, Tex.; 488, a strain from 'Acala 1517-BR-2' type-selected for 4 years; gossypol content is higher than in most commercial varieties and is quite stable in leaves and squares; 1230-15-3 (1230), selected from a cross between XIII-F, a high gossypol strain obtained from Lukefahr and Acala; plants were selected for high gossypol content and large bolls; 69-102 (102), originated as a single plant selection from 'Del Cerro 153', it was grown in the greenhouse from 1969 to 1971 and selected for trueness to type; 70-166-3-1 (166), derived from an outcross of Lukefahr's high gossypol 'TU-4' with an Acala type and selected for heavy glands for four generations, is distinctly different from the line 1230-15-3 which has a similar pedigree.

These selected lines contain several levels of bud gossypol. Because all the lines had been rigorously selected for four to five generations, they were believed to be homozygous for genes governing gossypol content.

Fifteen to 20 seeds of each cross along with a like number for reciprocals and each parent were sown in compacted peat pots. Ultimately three uniform plants of each type were selected and transferred to 20-cm pots. The 108 plants were arranged in three randomized blocks of 36 plants each in a compact group on greenhouse benches. A bank of fluorescent lamps was placed on the north side of the benches to increase the light in the greenhouse.

Because the first squares were delayed on plants from some crosses, the first three squares on all plants were removed and tagging began with the fourth square. Twenty-day-old squares from each plant were collected at 4 day intervals until five squares had been collected. Sample preparation and gossypol analysis followed the p-anisidine method (12). Diallel analyses were performed using mean percentage gossypol content (dry weight basis) of the squares from each plant, following the

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Table 1. Mean gossypol percent dry weight of five squares from each plant in the 6 × 6 diallel set.

	Male parents						Hybrid-array means
	217	169	488	1230	102	166	
Female parents							
217	1.38	1.22	1.38	1.25	1.16	1.17	1.26
169	1.14	0.91	0.91	0.90	0.75	0.98	0.93
488	1.14	0.83	0.83	1.03	0.91	1.05	0.96
1230	1.35	1.03	1.00	0.95	0.89	1.25	1.08
102	1.14	0.80	0.79	0.97	0.91	1.06	0.95
166	1.44	1.11	1.27	1.11	1.03	1.18	1.19
L.S.D., 0.05 =	0.189						

Table 2. Analysis of variance of gossypol level for general combining ability (GCA), specific combining ability (SCA), and reciprocal effects in a 6 × 6 diallel set.

Source of variation	df	Mean squares
GCA	5	0.186**
SCA	15	0.006
Reciprocals	15	0.010*
Error	70	0.004

*,** Significant at the 0.05 and 0.01 level of probability, respectively.

methods of Griffing (1) and Hayman (2, 8). Certain comparisons have been made on data collected in 1972 from several of the experimental lines used in this experiment (12).

In order to test the adequacy of the diallel model the V_r , W_r statistics were calculated. In an additive-dominance model where the parent-progeny covariance is symbolized by W_r , and the progeny variance by V_r , an analysis of variance of W_r - V_r will be non-significant for lines if the model holds (8). Further indication of the adequacy of the model can be obtained by a graphical representation of W_r vs. V_r , which should result in a regression line of unit slope if the model holds.

RESULTS AND DISCUSSION

The parent and progeny means as listed in Table 1 were used for the diallel analysis. An analysis of variance revealed a highly significant entry effect but a non-significant block effect. The common environmental component of variation, E , was estimated by block × line interaction.

The hybrid arrays of high gossypol parents 217 and 166 had gossypol levels consistently higher than those from the low gossypol parents (Table 1). Medium gossypol lines 1230 and 488, particularly the latter, also produced F_1 progenies averaging higher than the midparent.

The differences in gossypol content obtained in these fully glanded parental lines and crosses may have been caused by segregation at the major gland determining loci, gl_2 and gl_3 , or may be due to background genes. Our experiment did not allow us to differentiate among these possibilities. However, it seems likely that the selections derived from the high gossypol lines XG-15, XIIIIF, and IU-4 carry the special allele at the gl_3 locus identified by Lee (4) in related material. Strain 217 could possibly carry alleles from *G. arboreum* or *G. thurberi*. Lines 102 and 488 trace back to *G. barbadense* L. crosses and may carry some genes from that species.

Gossypol percentage of the common parents in 1972, grown both in the greenhouse (1.55) and in the field (1.59), were higher than those grown in the greenhouse

Table 3. Reciprocal effects for gossypol level, among F_1 's of a 6 × 6 diallel set.

Female parents	Male parents					
	217	169	488	1230	102	166
217	--					
169	-0.044	--				
488	-0.121**	-0.041	--			
1230	0.049	0.070*	-0.015	--		
102	-0.009	0.023	-0.061*	0.042	--	
166	0.135**	0.064*	0.110**	-0.070*	-0.018	--

*,** Significant at the 0.05 and 0.01 levels of probability, respectively.

Table 4. GCA effects, GCA, and SCA variances of the six parental lines taken from a 6 × 6 diallel set.

Parent	GCA effects	GCA variance	SCA variance
217	0.200	0.0399	0.00122
169	-0.104	0.0105	-0.00054
488	-0.065	0.0040	0.00244
1230	-0.005	-0.003	0.00066
102	-0.118	0.0137	0.00038
166	0.091	0.0081	0.00047

in 1973 (1.04). An analysis of variance using the means of the parents common in the three trials showed a significant difference in gossypol content due to environment. We had shown previously, however, that the interaction between lines and environments was non-significant (12). Thus the relative value of the lines may be determined in a single test when they are compared to well-known, stable checks.

An analysis of variance for W_r — V_r substantiates the validity of the assumptions undergirding the interpretation of the diallel analysis. The difference between arrays was not significant, which indicates that these assumptions are valid for the strains and hybrids that we studied.

Analysis of the data using Griffing's method showed that general combining ability (GCA) was highly significant, reciprocal effects were small but significant, while specific combining ability (SCA) was not significant (Table 2). The results indicated that the additive component was highly predominant in the parental population used in the analysis.

Table 3 reveals that reciprocal effects were significant in a number of combinations. Previously, Wilson and Shaver (11) had not found significant maternal effects for square gossypol content in *G. hirsutum*.

The estimates of GCA and SCA effects and variances are listed in Table 4. Both 217 and 166, the high gossypol lines, are ranked highest in positive GCA effects. The other four lines contributed very little to GCA. Line 488 possesses the largest SCA variance and useful agronomical traits worth transferring, while the other lines seem to have little value in an improvement program.

Supplemental analysis by Hayman's V_r vs. W_r graphical method (not shown) indicated that partial dominance may contribute a small amount. This dominance component is so small as to border on the limits of detection and of no real consequence in breeding strategy.

The values for heritability in the broad and the narrow sense were 0.96 and 0.94, respectively.

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