

# Gene Action in the Inheritance of Fiber Properties in Intervarietal Diallel Crosses of Upland Cotton, *Gossypium hirsutum* L.<sup>1</sup>

K. M. Al-Rawi and R. J. Kohel<sup>2</sup>

## ABSTRACT

We grew nine selected cotton varieties, all possible  $F_1$  hybrid combinations among these varieties, and their corresponding  $F_2$ 's in a split-plot design with four replications. Heterosis, when measured as the departure from the average midparent value, was manifested at a low level for 50% span length (4.0%), 2.5% span length (2.8%), fiber strength (5.6%) and fiber elongation (8.5%). Heterosis was not observed for fiber fineness. Inbreeding depression, measured as a reduction in  $F_2$  below  $F_1$  performance, was not significant for any of the fiber properties measured. General and specific combining ability were both highly significant for all fiber properties.

Jinks-Hayman's method of diallel cross analysis showed that all fiber properties were within the range of partial dominance (except fiber fineness, which showed overdominance, possibly caused by repulsion linkage) and that all are polygenically inherited characters.

Heritability, as the ratio of the additive, or additive  $\times$  additive epistatic variance, or both, to the total phenotypic variance, was relatively high for all fiber properties measured, except fiber fineness. This result suggested that a major part of the total phenotypic variance was additive.

**Additional Index Words:** Diallel analysis, Heterosis, Inbreeding depression, Combining ability.

THE purpose of our experiment was to obtain information on the genetic basis of heterosis, and to investigate the nature of the genetic systems controlling fiber properties.

Relatively few studies exist concerning the genetic systems that control fiber properties in cotton. Ware and Harrell (1944) found that fiber length was partially dominant in a cross between two lines of upland cotton. Ware and Harrell (1963) and Self and Hen-

derson (1954) reported that lint strength was inherited in a partially dominant fashion, and was controlled by many genes. Fryxell et al. (1958) found heterosis for fiber elongation in hybrids between *Gossypium hirsutum* and *G. barbadense*. Miller and Lee (1964) found that various fiber properties of hybrids were similar to the midparent values. Lee, Miller, and Rawlings (1967) found small but significant levels of heterosis for fiber properties and they obtained significant general combining ability estimates for all the fiber properties measured. Verhalen and Murray (1967 and 1969) noted that overdominant gene action governed fiber fineness, long fibers were partially dominant over short fibers, and additive gene action governed fiber strength.

## MATERIALS AND METHODS

The parental cotton varieties used in this study were: (1) 'Acala 4447,' (2) 'Deltapine TPSA,' (3) 'Stoneville 213,' (4) 'Deltapine Smooth Leaf,' (5) 'Lankart Sel. 57,' (6) 'Acala 1517D,' (7) 'Carolina Queen,' (8) 'Paymaster 101A,' and (9) 'Stoneville 7A.' Hereafter, entries will be identified by numbers 1 through 9, as indicated, while their  $F_1$  and  $F_2$  hybrids will be designated by appropriate number combinations. All possible crosses, including reciprocals, were made among these nine lines.  $F_1$  plants from each cross were self-pollinated to obtain  $F_2$  generation material. These plant populations were grown at the Texas A&M cotton genetics nursery in 1967.

The experimental design was a split-plot randomized block with four replications. Each replication consisted of nine whole plots. Each whole plot contained the maternal parent, the  $F_1$  array, the reciprocal  $F_1$ 's, and their corresponding  $F_2$ 's. Each subplot contained 10 plants.

Fiber samples were taken on a total plot basis and analyzed by the U.S. Department of Agriculture Fiber Testing Laboratory at Knoxville, Tenn., to obtain information on the following fiber properties: (1) 50% span length: length in inches, at which 50% of the fibers are this length or longer; (2) 2.5% span length: length in inches, at which 2.5% of fibers are this length or longer; (3) strength expressed in terms of force (g per tex) necessary to break the fiber bundle with the two jaws of the testing instrument 3.2 mm apart; (4) percentage elongation before breakage of the fiber bundle measured for strength; and (5) fineness of the sample measured by the Micronaire and expressed in standard Micronaire units.

We used Griffing's (1956) combining ability analysis and Hayman's (1954) diallel cross techniques to obtain estimates of the genetic parameters.

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<sup>2</sup>Formerly Graduate Student, Soil & Crop Sciences Department, Texas A&M University, (now, Department of Field Crops, Faculty of Agriculture and Veterinary Medicine, University of Mosul, Mosul, Iraq); and Research Geneticist, Crops Research Division, ARS, USDA, College Station, Texas, 77843.

## RESULTS AND DISCUSSION

### Heterosis and Inbreeding Depression

Heterosis and inbreeding depression results are summarized in Table 1. The  $F_1$  hybrids had higher means, on average, than the midparents and  $F_1$  means were very close to  $F_2$  means for all fiber properties. No reciprocal differences were found for any of these characters (Table 2), and the means were calculated by pooling the reciprocal hybrids. The range of variability among the parents for each character was expressed as the ratio of the mean of the highest parent to that of the lowest parent.

Heterosis, calculated as the percent increase of the  $F_1$  hybrids above the average of the parents, was significant for all fiber properties except for fiber fineness. The range of superiority of  $F_1$  over midparent values was from 2.8% for 2.5% span length to 8.5% for fiber elongation. Inbreeding depression calculated as the percent reduction of  $F_2$  below  $F_1$  performance, was not significant for any of the fiber properties.

Individual heterosis and inbreeding depression effects were calculated for each cross. The number of crosses showing significant heterotic and inbreeding effects at the .05 level are presented in Table 1. The low level of heterosis and the absence of inbreeding depression suggest that a major portion of the genetic effects in the crosses between these varieties are additive.

### Combining Ability

We analyzed mean performance of the parental lines and the  $F_1$  for combining ability as outlined by John (1963), based on Griffing's (1956) method 1 of model 1 (Table 2). General (G.C.A.) and specific (S.C.A.) combining ability effects were highly significant for all fiber properties.

We estimated G.C.A. and S.C.A. effects and used them to calculate the estimates of G.C.A. and S.C.A. variances associated with each parent,  $\sigma_g^2$  and  $\sigma_s^2$ , respectively, (Griffing, 1956). These individual variances, together with the environmental variance ( $\sigma_e^2$ ), based on means, are given in Table 3. Comparison between  $\sigma_g^2$  and  $\sigma_s^2$  is very instructive; e.g., for fiber strength, parents No. 1 and 6 both exhibited high G.C.A. effects, but they attained their high average performance in entirely different ways. The relatively low S.C.A. variance associated with parent 1 indicated that it transmitted its high performance uniformly to all of its  $F_1$ 's. However, the relatively high S.C.A. variance associated with parent 6 indicated that there were specific combinations of parent 6 with certain inbreds that gave higher or lower performance than expected on the basis of parental performance. In addition to the comparison of  $\sigma_g^2$  and  $\sigma_s^2$  among different lines, comparison of the relative magnitudes of  $\sigma_g^2$  and  $\sigma_s^2$  to  $\sigma_e^2$  will give some idea of the precision of the estimates of the effects and their variances.

### The Diallel Cross

Hayman's (1954) diallel cross analysis is based on several assumptions. These assumptions are tested as

Table 1. Average performance of  $F_0$ ,  $F_1$ , and  $F_2$  generations, and overall heterosis and inbreeding depression of fiber properties.

Character	Generation mean			Highest parent	Lowest parent	Heterosis	Inbreeding depression	No. of crosses significant, .05	
	$F_0$	$F_1$	$F_2$					Heterosis	Inbreeding depression
50% span length	0.466	0.484	0.476	1.23	4.0*	1.6	9	0	0
2.5% span length	1.022	1.051	1.036	1.27	2.8*	1.4	8	0	0
Strength	19.187	20.269	20.249	2.15	5.6**	0.1	7	0	0
Elongation	6.341	6.882	6.866	2.33	8.5**	0	8	0	0
Fineness	4.154	4.214	4.215	1.28	1.4	0	1	0	0

\*, \*\* Significant at .05 and .01 levels, respectively.

Table 2. Analysis of variance for combining ability and reciprocal effects.

Source	df	Mean squares				
		50% span length	2.5% span length	Strength	Elongation	Fineness
Reps.	3	.1068	.1282	16.0300	5.2085	.2544
G.C.A.	8	.0110**	.0575**	97.7696**	11.6374**	.8502**
E (a)	24	.0007	.0016	6.3152	0.6448	.2771
S.C.A.	36	.0014**	.0050**	9.7600**	1.2060**	.3758**
Reciprocal	36	.0010	.0021	4.2536	0.4526	.3530
E (b)	216	.0008	.0016	4.3871	0.5185	.2053

\*\* Significant at .01 level.

Table 3. Estimates of general and specific combining ability variances associated with each parent together with the environmental variance based on means.

Parent number	Individual variances	50% span length	2.5% span length	Strength	Elongation	Fineness
1	$\sigma_g^2$	.112	.005	1.4989	.0138	-.0024
	$\sigma_s^2$	.015	.0198	-.0933	.0106	.0098
	$\sigma_e^2$	.0186	.0400	1.1440	.1328	.0531
2	$\sigma_g^2$	.055	-.0004	0.0312	.1520	-.0012
	$\sigma_s^2$	.069	.0117	-.02487	.0008	.0321
3	$\sigma_g^2$	.055	-.0011	0.7242	-.0064	.0017
	$\sigma_s^2$	.009	.0050	-.01132	-.0323	.0684
4	$\sigma_g^2$	.135	-.0020	0.3258	.2128	-.0027
	$\sigma_s^2$	.136	.0206	0.0625	.0279	.0504
5	$\sigma_g^2$	.000	.0205	0.3072	.2175	-.0029
	$\sigma_s^2$	.002	-.0031	0.1504	-.0223	.0360
6	$\sigma_g^2$	.667	.2189	5.9217	-.0013	-.0018
	$\sigma_s^2$	.043	.0231	0.3119	-.0188	-.0070
7	$\sigma_g^2$	.016	.0196	1.5595	.2975	.0019
	$\sigma_s^2$	.059	.0541	0.7106	.0784	.0620
8	$\sigma_g^2$	.072	.2896	-.0479	.0312	.0561
	$\sigma_s^2$	.120	.0082	-.0853	.0014	.0194
9	$\sigma_g^2$	.040	.0821	-.0412	.3008	-.0028
	$\sigma_s^2$	-.017	-.0038	-.01077	.0032	.0844

follows: (1) *diploid segregation* — *G. hirsutum* is an amphidiploid that segregates in a diploid manner (Endrizzi 1962, Kimber 1961); (2) *homozygous parents* — the parental lines have been maintained by controlled self-fertilization for at least five generations and were assumed homozygous; (3) *no reciprocal differences* — even though no significant reciprocal differences were detected (Table 2), the  $F_1$  entries in the diallel table were replaced by the mean of their reciprocals for all fiber properties prior to the analysis; (4) *no genotypic-environmental interaction within locations and years* — Bartlett's test was used to test homogeneity of the variances computed over replica-

tions. Fiber strength showed a significant chi-square deviation (.05 level), but the other fiber properties showed nonsignificant chi-square homogeneity deviations.

The assumptions of: (5) *no epistasis*, (6) *no multiple alleles*, and (7) *uncorrelated gene distribution* were tested by the analysis of variance of (Wr-Vr). This value was expected to be constant over arrays if all the assumptions were valid. The results of this analysis are presented in Table 4. There were no significant variations of (Wr-Vr) among the arrays for any of the fiber properties; this indicated that assumptions 5, 6, and 7 were valid.

Least squares estimators of genetic variance components are presented in Table 5. D = component of variation due to additive effects of genes, F = covariance of additive and non-additive effects, H<sub>1</sub> = component of variation due to non-additive effects, H<sub>2</sub> = component of variation due to non-additive effects corrected for gene distribution, and h<sup>2</sup> = overall dominance effects of heterozygous loci. All the genetic parameters were significantly different from zero. The magnitude of the additive genetic component (D) was larger than the dominance component (H<sub>1</sub>) for all characters except fineness. The parameter F was positive and significantly different from zero for all characters. This result indicates that the parents carried an excess of dominant genes.

Genetic ratios and estimators were calculated (Table 6). The average degree of dominance (H<sub>1</sub>/D)<sup>1/2</sup> showed that all fiber properties were within the partial dominance range except fiber fineness which showed overdominance. The estimate of the average frequency of negative vs. positive alleles at loci exhibiting dominance ( $\bar{p} \bar{q}$ ), showed that the positive and negative alleles were not distributed equally among the parents in all fiber measurements. The ratio of dominant to recessive genes, <sup>K</sup>D/<sup>K</sup>R, showed an excess of dominant alleles in the parents. An estimate of the number of effective factors, K, that control the character and exhibit dominance to some degree, showed that at least two effective factors control each character. However, K is underestimated when the gene effects are not equal.

Heritability, defined as the ratio of the additive, or additive × additive epistatic variance, or both, to the total phenotypic variance (Crumpacker and Allard 1962), was relatively high for 2.5% span length, fiber strength, and fiber elongation; low for 50% span length; and very low for fiber fineness. Comparison of the order of dominance of the parents with their mean performance is informative. For 2.5% span length, for example, the order of dominance of the parents was 645319287 and the rank of the mean performance was 693152487. Thus parent number 6 had the longest 2.5% span length and exhibited the most dominance.

Results showed that 50% span length, 2.5% span length, fiber strength, and fiber elongation exhibited partial dominance; and that fiber fineness exhibited overdominance (which might have been caused by close repulsion linkage); and also that all fiber measurements were inherited polygenically. Also, heterosis in those characters was caused by dominance only, since H<sub>1</sub> was significant and epistasis was not detected.

Table 4. Analysis of variance of (W<sub>r</sub>-V<sub>r</sub>) for fiber properties.

Source	df	Mean square			
		50% span length × 10 <sup>-4</sup>	2.5% span length × 10 <sup>-4</sup>	Strength	Elongation
Reps.	3	.0013	.0963	7.1991	.0106
Arrays	8	.0014	.0088	8.1486	.0459
Error	24	.0008	.0056	4.7834	.0587

Table 5. Mean estimates of genetic variance components together with the environmental variance for fiber properties.

	50% span length	2.5% span length	Strength	Elongation	Fineness
D	.000883**	.0061**	24.4791**	2.6193**	.0930**
F	.000440*	.0051**	30.0239**	3.2434**	.0961*
H <sub>1</sub>	.000460**	.0036**	15.7490**	1.8822**	.1081**
H <sub>2</sub>	.000316**	.0015*	4.4121*	0.6026*	.0426*
h <sup>2</sup>	.001075**	.0025**	6.8023**	1.9172**	.0632**
E	.000743	.0016	4.5799	0.5311	.2125

\*, \*\* Significant at .05 and .01 levels, respectively.

Table 6. Ratios of components, heritability estimators, and the order of dominance of the parents for fiber properties.

Ratios	50% span length	2.5% span length	Strength	Elongation	Fineness
$\frac{(H_1)^{1/2}}{(D)^{1/2}}$	0.72	0.77	0.80	0.84	1.08
$\bar{p} \bar{q} = \frac{(H_1)}{(4H_1)}$	0.1718	0.1065	0.0700	0.0800	0.0986
$\frac{K_D}{K_R} = \frac{(4DH_1)^{1/2} + F}{(4DH_1)^{1/2} - F}$	2.05	3.40	7.49	6.42	2.84
$K = \frac{h^2}{H_1}$	3.4	1.6	1.6	3.2	1.4
Heritability = $\frac{1}{2} D$	0.23	0.56	0.86	0.77	0.08
$\frac{1}{2} D - \frac{1}{4} F + \frac{1}{4} H_1 + E$					
Order of dominance of the parents dominant — recessive	613598427	645319287	165342897	589631247	619827453
Order of the parents based on their mean performance high — low	961523847	693142487	691825347	256431987	871496235

The results of this study and those of Verhalen and Murray (1967 and 1969) are in close agreement for the characters evaluated by both sets of investigators. Environments at the two locations are quite different, but the varietal selections in both investigations represented a similar array of genetic backgrounds.

The first step in any breeding program involves the selection of good parents; the diallel cross analysis provides a tool in identifying parents whose hybrids are most likely to respond to selection.

The preponderance of additive genetic variance and low level of heterosis for fiber properties in the diallel cross evaluated, are evidence that mass selection and full-sib family selection should be considered preferable to a program utilizing first generation hybrids for fiber property improvement.

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