The Inheritance of Several Agronomic and Fiber Properties Among Selected Lines of Upland Cotton, *Gossypium hirsutum* L.[1]

Jerry L. Baker and Laval M. Verhalen[2]

ABSTRACT

A quantitative genetic study of lint yield, earliness, lint percent, 2.5 and 50% span length, uniformity index, fiber fineness, and fiber strength was conducted in upland cotton, *Gossypium hirsutum* L., utilizing the Jinks-Hayman diallel analysis. Ten selected lines and their 45 possible F_1 combinations in 1969 and 1970, plus the 45 corresponding F_2's in the second year, were included in randomized, replicated experiments at a single location.

Analyses of variance indicated highly significant differences among entries for all traits in both years. Partial failures of the diallel assumptions were noted for each trait, although some traits did more nearly comply with those assumptions than did others. Epistasis was not detected as a significant factor for any of the traits. A genotype by environment interaction for the additive components of variation was observed for lint yield, lint percent, and 2.5% span length. The dominance relationships among parents were not constant over years for earliness, lint percent, 2.5% span length, fiber fineness, or fiber strength. Multiple allelism was shown by all traits except fiber fineness; however, gene correlations and parental heterozygosity were not (or could not be) detected for any trait.

Overdominance governed lint yield, earliness, lint percent, 50% span length, and uniformity index. Partial dominance was operative for fiber fineness, and complete dominance was indicated for 2.5% span length and fiber strength. Narrow-sense heritabilities indicated that mass selection should be effective for improving 2.5% span length, fiber fineness, and fiber strength among lines in this material and somewhat less effective for improving earliness, lint percent, 50% span length, and uniformity index. Alternatives, such as pedigrees, sib tests, and progeny tests, must be considered to achieve genetic progress for lint yield in this material.

Additional index words: Lint yield, Earliness, Lint percent, Fiber length, Uniformity index, Fiber fineness, Fiber strength, Diallel analysis, Epistasis, Multiple alleles, Genotype by environment interaction, Dominance, Heritability.

COTTON (*Gossypium hirsutum* L.) producers in the High and Rolling Plains of Oklahoma and Texas are confronted in general with lower yields and poorer fiber quality than are producers in other sections of the Cotton Belt. Part of this problem is undoubtedly caused by the more severe environmental conditions common to the area (i.e., drouth, hail, early frost, etc.) and may never be completely resolved, but a portion of the problem can be mitigated by developing varieties better suited to withstanding (or avoiding) those environmental hazards.

Varieties with higher lint yield potentials would certainly be welcome as would those with higher lint percentages (a component of yield related to ginning costs). Increased earliness of maturity would minimize the drastic reductions in yield and fiber quality frequently caused by short growing seasons, particularly in the northern part of the Plains. As far as improved fiber properties are concerned, several years ago the textile mills increased their demands for high quality fiber and paid substantial premiums to obtain it. Although at present the incentive to produce a high quality fiber is not as great, over the long term quality cotton would appear desirable from an industry-wide standpoint.

The purpose of this research was to study the nature of gene action for lint yield, lint percent, earliness, and the more economically important fiber properties among selected lines of upland cotton. This information is required because the breeding methods employed for maximum genetic improvement of quantitative traits are dependent upon the types and relative amounts of genetic variability for those traits in the populations of interest. The diallel-cross technique was utilized herein since it allows the breeder to detect the kinds and to estimate the relative magnitudes of each possible source of genetic variability among a given set of parents. In addition, the diallel is a systematic method for identifying those parents and hybrids that have superior combinations of the characters of interest.

LITERATURE REVIEW

Gene action in cotton has been studied by numerous investigators, but their results have not been entirely consistent from experiment to experiment.

In a set of diallel crosses among seven inbred lines, Turner (22) reported specific combining ability (SCA) for seed cotton yield as being more important than general combining ability (GCA). Hayman (9) re-analyzed Turner's (22) data and found significant epistasis of the complementary type. Barnes and Staten (4) reported important SCA effects for lint yield, earliness, lint percent, fiber fineness, and fiber strength among hybrids of seven closely related 'Acala' strains. However, when 11 varieties were testcrossed on two strains of Acala, GCA predominated for all traits.

Miller and Marani (18) reported an appreciable amount of additive genetic variance for all of the traits they studied. There were indications in the F_2 of epistasis for lint yield, earliness, and fiber strength. Lee, Miller, and Rawlings (14) obtained significant estimates of additive variance for lint percent and all fiber properties. Both additive and nonadditive gene action was detected for lint yield; however, it was not possible to distinguish between dominance and epistasis or their combined effects. A significant additive by environment interaction component overshadowed the corresponding additive component, suggesting that little progress could be expected in selecting for stable fiber yields over the environments tested. Meredith, Bridge, and Chism (17) in the Mississippi Delta identified significant epistasis for only one trait, lint yield. Yield and its components showed considerable dominance effects, and fiber properties tended to be inherited in an additive fashion. They found that interactions with environments were small compared to the main effects for all traits.

Tabrah (21) investigated the backcross populations of 'Acala 44' $\times$ OK-86 and showed that most of the traits were influenced to a larger extent by additive effects than by dominance effects. Heritability estimates were generally low for lint yield and uniformity index, but they were medium to high for earliness, lint percent, and the fiber properties (other than uniformity index). In a cross between Acala and 'Hopi,' Stith (20) demonstrated partial dominance for higher lint percent and longer fiber; however, his material exhibited a lack of dominance for fiber fineness and strength. He found no evidence of transgressive segregation for any of the characteristics studied.

White and Kohel (27), in a diallel analysis of five widely diverse parents and their F_1's, detected significant additive variation for lint yield, earliness, and lint percent. In addition, dominance was operative for lint yield. The degree of dominance for yield was in the partial dominance range, 0.91, and most of the dominant genes had positive (i.e., toward higher yield) effects. White (26) in the same diallel, but including F_2's as well as parents and F_1's, obtained an estimate of 1.32 for degree of dominance for yield, which indicates overdominance. He detected no significant epistasis for yield, earliness, or lint percent although multiple allelism was detected for the two latter traits. Al-Rawi and Kohel (2, 3) reported epistasis for earliness but none for lint yield, lint percent, or the fiber properties. Multiple allelism and possibly correlated gene distribution appeared operable for yield and lint percent. Yield, earliness, and all fiber properties, except for fiber fineness (overdominance), were within the partial dominance range. Heritability estimates

were relatively high for all fiber properties measured except fineness.

Verhalen et al. (25) in a 10-parent diallel noted that lint yield, seed cotton yield, earliness, and lint percent were controlled by overdominant gene action, except for lint percent in 1 year when partial dominance was estimated. Epistasis was not detected for any of these traits. A single genotype by environment interaction for the dominance components influenced earliness. An interaction for the additive components of variation was noted for lint percent. Verhalen and Murray (23, 24) found that overdominant gene action governed fiber fineness, long fibers were partially dominant over short fibers, and additive gene action conditioned fiber strength. No evidence of epistasis was detected for any of these fiber traits. Significant interactions of additive and dominance effects with environment did occur for fiber fineness. Meredith and Bridge (16) testcrossed six diverse cultivars and strains on 'Deltapine 16' and found additive effects predominated for lint percent, fiber fineness, and fiber strength. Both additive and dominance effects were involved in the inheritance of lint yield and fiber length. Additive by additive epistasis was very small relative to additive and dominance effects for all traits. The dominance effects tended to interact less with environments than did the additive effects.

MATERIALS AND METHODS

The varieties and lines of upland cotton selected for use as parents were 'Deltapine 16,' 'Mo-Del,' 'Stoneville 7A,' 'Tamcot 788,' 'Westburn,' 'Lockett 4789A,' 'Quapaw,' 'Dunn 56C,' S65-391, and S65-396. Except for the last two, each entry was or is a commercial variety of upland cotton. After this experiment was initiated, the S65-391 and S65-396 strains were bulked in a 1:1 mixture and released in 1970 as the variety 'Delcot 277' by the Missouri Agricultural Experiment Station. The parents used herein were specifically chosen (primarily on their diversity for yield, plant type, fiber properties, and resistance to major diseases) and do not represent a random sample of all upland varieties. Thus, inferences derived from the data apply in the strict sense to the parents, crosses, and generations studied. The degree to which the conclusions may be extended to the species as a whole is unknown.

Diallel crosses among the parents, ignoring reciprocals, were made at Iguala, Mexico, in the winter of 1968-69 and 1969-70. The 10 parents and their 45 F_1's were grown in 1969 and 1970 at Perkins, Oklahoma. The 45 F_2 progenies were included in the second year. The experiment was conducted in a randomized complete-block design with four replications. Plots were single rows 7.6 m long and 1.0 m apart. Plants within plots were spaced at a distance of approximately 0.5 m with one plant per hill. To partially compensate for differential spacing between plants caused by missing hills, 'De Ridder Red' (a variety with the dominant marker gene, R_1) was planted as soon as such hills were detected.

Two harvests were made on the material each year with seven plants from each plot chosen at random for analyses. The following characters were measured: 1) lint yield over both harvests in g/plant; 2) earliness as the ratio of lint yield from the first harvest to total lint yield expressed as a percentage; 3) lint percent as the ratio of lint:seed cotton expressed as a percentage; 4) 2.5% span length in inches as measured on the digital fibrograph; 5) 50% span length in inches also measured on the fibrograph; 6) uniformity index as the ratio of 50 to 2.5% span length expressed as a percentage; 7) fiber fineness as measured on the micronaire and expressed in $\mu g/$ inch; and 8) fiber strength as measured on the stelometer with the jaws of the machine separated by a 1/8-inch spacer (i.e., T_1) and expressed in g/grex. Fiber samples from each plant in each harvest were obtained and analyzed separately. Then, weighted averages for lint percent and each fiber measurement over the two harvests were calculated for each plant based on the percentage of total lint yield per harvest of that plant. All

subsequent calculations were based on those weighted averages.

The diallel procedure, as developed by Jinks and Hayman (7, 8, 9, 10, 11, 12), was used to analyze the above traits. This method partitions phenotypic variation into genotypic and environmental components and further subdivides the genotypic variation into additive and dominance components. In addition to a detailed description of the various genetic properties and parameters operating among a given set of lines, the analysis can be used to detect epistasis and test whether certain other assumptions of the diallel analysis have been fulfilled. Such estimates are of theoretical interest because they provide information on the genetic mechanisms by which traits are inherited. They are also of practical interest since such estimates in large measure influence breeding procedures.

The Jinks-Hayman analysis is based on the assumptions of diploid segregation, no reciprocal differences, homozygous parents, no genotype-environment interactions within locations and years, no epistasis, no multiple alleles, and uncorrelated gene distributions (5). Based on past experience in upland cotton, the first two assumptions may be considered valid with some degree of confidence (6, 13, 28). Assumption three (i.e., homozygous parents) is likely not fulfilled in the strict sense. Specific tests are available for the remaining assumptions. The last three were investigated for each trait using the procedures devised by Hayman (8, 9). Because those tests require F_1 and F_2 data, only the 1970 information could be used for that purpose. Epistasis was tested by chi-square (8). A detailed analysis of variance of the second-degree statistics was calculated to provide a test for multiple allelism (in the absence of epistasis); when both epistasis and multiple allelism were absent, parental heterozygosity and gene correlation could be tested (9). The definitions, procedures, and formulas for these tests are described in Hayman's (8, 9) papers and need not be repeated here. In addition, the processes have been discussed in more recent literature (2, 3, 26). The assumption of no genotype-environment interactions within locations and years was partially tested for each trait using the procedure outlined by Allard (1) for the additive and dominance components of variation. Since this study was conducted at only one location over 2 years, a location effect is confounded in the results, making them somewhat less sensitive than they would have been had an additional location been included.

The statistics estimated and the symbols used in this paper are those employed by Jinks and Hayman (7, 12). V_r is the variance of the members of the rth array, and W_r is the covariance of the members of the rth array with their nonrecurrent parents. The rth array includes the rth parent and all crosses involving that parent. The population parameters estimated were E_0, E_1, E_2, D, F, H_1, and H_2. The E_0, E_1, and E_2 parameters are estimates of parental, F_1, and F_2 environmental variances, respectively, which were obtained from between plot-within plot analyses of variance of the parental, F_1, and F_2 entries (as the case might be) within each block. Because the other parameters were estimated on a plot-mean basis, it was necessary to convert the estimates of environmental variance to an equivalent basis by dividing the within plot mean square by the mean number of plants per plot within that block, i.e., seven. The genetic parameters (i.e., D, F, H_1, and H_2) were calculated using Hayman's (9) formulas. D is the additive genetic variance, F is an indicator of the relative frequency of dominant vs recessive alleles in the parents, and H_1 and H_2 are dominance genetic variances. An estimate of each parameter was obtained in each replication of the three data sets. Here, we had the option of combining F_1 and F_2 data in 1970 to obtain parameter estimates; however, this was not done since differences between generations (if present) would have been obscured in a combined analysis. Tests for significance among

parameter estimates were made using the standard error estimation technique suggested by Nelder (19).

Estimators and ratios were calculated in each replication using the above genetic parameters to provide information about the genetic systems operating for each trait. Then, means over replications and standard errors of those means, used for setting confidence limits, were calculated for each estimate as was done earlier for the parameters. Those estimators and ratios were:

$(H_1/D)^{1/2}$ and $(H_1/4D)^{1/2}$ = weighted overall measures of the average degree of dominance at each locus in the F_1 and F_2, respectively;

$H_2/4H_1 = \overline{uv}$ is an estimator of the average frequency of negative vs positive alleles (at loci exhibiting dominance) in the parents (7) and has a maximum value of 0.25;

$K_D/K_R = [(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F]$ is the ratio of the total number of dominant to recessive alleles in the parents;

$K_{(F)_1} = (\overline{F_1} - \overline{P})^2/(1/4 \ H_2)$ and $K_{(F)_2} = (\overline{F_2} - \overline{P})^2/(1/16 \ H_2)$ are estimates of the number of groups of closely linked genes, or at the lower limit a single gene, in the F_1 and F_2, respectively, which control the trait and exhibit dominance to some degree;

$(1/4 \ D)/(1/4 \ D + 1/4 \ H_1 - 1/4 \ F + E)$ = heritability in the F_1 using the formula defined by Crumpacker and Allard (5) and $(1/4 \ D)/(1/4 \ D + 1/16 \ H_1 - 1/8 \ F + E)$ = heritability in the F_2 as modified by Verhalen and Murray (24); and

$(\overline{F} - \overline{P})$ = an estimate of the direction of dominance over all crosses where F refers to F_1's or F_2's (as the case may be).

RESULTS AND DISCUSSION

In 1969 and 1970, the analyses of variance on a plot-mean basis revealed highly significant differences among entries for each trait. This implied that there were genetic differences for these traits in this material and that detailed analyses of gene action could be conducted. Parental means for the characters studied are listed in Table 1.

Tests of the Assumptions

The failure of one or more assumptions influences (and presumably invalidates to some extent) the inferences derived from using the diallel analysis. Therefore, the three broad, general tests described previously by Verhalen and Murray (23, 24) were employed to determine whether the traits fulfilled the assumptions of the analysis as a whole. In summary, the three tests were conducted on three populations (the F_1 in 1969 and 1970 and the F_2 in 1970). The results showed that none of the traits completely fulfilled the assumptions although some more nearly complied than did others. The two fiber length traits were the most satisfactory, lint yield and lint percent the least so, and the remaining traits were intermediate in compliance.

Table 1. Mean performance of parents over 1969 and 1970.

| | Lint yield,* g/plant | | Earliness, % | Lint percent* | | Fiber length | | | | | |
| | | | | | | 2.5% span* | | 50% span | Unif. index | Micronaire | 1/8-inch gauge stelometer |
Parent	1969	1970		1969	1970	1969	1970				
Deltapine 16	34	18	41.7	38.7	35.3	1.056	1.057	0.483	45.7	4.5	2.13
Mo-Del	27	18	63.4	36.5	33.2	1.039	1.085	0.483	45.5	4.4	2.29
Stoneville 7A	10	16	41.5	39.7	36.7	1.063	1.056	0.476	44.9	4.4	1.89
Tamcot 788	34	13	74.0	37.4	33.5	1.038	1.002	0.466	45.7	3.8	2.18
Westburn	33	15	66.0	35.5	32.5	0.979	0.957	0.445	46.0	3.6	2.01
Lockett 4789A	35	21	75.2	36.5	33.5	1.032	1.012	0.475	46.4	3.9	2.02
Quapaw	33	19	79.2	36.5	33.8	1.006	0.976	0.480	48.5	4.6	2.18
Dunn 56C	30	11	62.5	35.3	34.2	1.035	1.024	0.489	47.5	3.8	2.32
S65-391	31	19	69.3	36.2	34.8	1.072	1.098	0.489	45.9	3.6	2.32
S65-396	34	19	63.2	36.7	36.5	1.087	1.049	0.500	46.8	3.9	2.44

* Because the parents exhibited a significant years by parents interaction for these traits (Table 3), the means for each year are listed separately.

Table 2. Analyses of variance of the second-degree statistics.

| Source | df | Lint yield, g/plant | Earliness, % | Lint percent | Fiber length | | | Micronaire (× 10⁻²) | 1/8-inch gauge stel. (× 10⁻⁴) |
					2.5% span (× 10⁻⁶)	50% span (× 10⁻⁴)	Unif. index		
Components	22	272.43**	48,029.47**	5.5236**	8.7000**	0.3291**	2.9794**	5.8904**	28.4427**
Interaction and multiple allelism	58	23.37**	4,862.56**	0.5484**	0.1986**	0.0193**	0.2176**	0.1058	0.6071**
L, m.a., parental heterozygosity, and gene correlation	9	25.59	2,679.34	0.4884*	0.0711	0.0000	0.0414	0.0602	0.3983*
Reps by components	66	30.41	7,557.03	0.7413	0.4892	0.0144	0.2656	0.1673	1.0430
Reps by l. and m.a.	174	13.96	2,085.83	0.2672	0.0876	0.0069	0.0840	0.0877	0.3315
Reps by l., m.a., p.h., and g.c.	27	17.03	1,816.33	0.1698	0.0837	0.0100	0.0839	0.1110	0.1709

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

Table 3. Genotype by year analyses of the additive components of variation.

| Source | df | Lint yield, g/plant | Earliness, % | Lint percent | Fiber length | | | Micronaire | 1/8-inch gauge stelometer |
					2.5% span	50% span	Unif. index		
Years	1	5,362.8**	6,310.13**	124.25**	0.001647	0.008467**	45.30**	0.02	0.4531**
Reps within years	6	21.9	611.00**	2.12	0.000927	0.000639**	3.14**	0.20**	0.0263
Parents	9	44.7	1,332.76**	12.54*	0.010849**	0.002029**	8.83**	1.19**	0.2301**
Years by parents	9	39.3**	226.65	2.83*	0.001493**	0.000187	0.96	0.09	0.0095
Error	54	10.7	109.96	1.08	0.000485	0.000170	0.59	0.06	0.0137

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

Chi-square tests for epistasis (8) were conducted for each trait. None of the calculated values were significant at the 0.05 probability level which suggests that epistasis was either absent in or made a negligible contribution to the expression of these traits in 1970. A detailed analysis of variance of the second-degree statistics was then calculated for all characters (9). The components mean squares (Table 2) were significant for all traits. The interaction-multiple allelism mean squares were significant in all instances, except for fiber fineness. Because epistasis has been previously ruled out for all traits, the significance of the interaction-multiple allelism mean squares must be caused by multiple allelism. Since multiple allelism was present for these traits, independent tests for parental heterozygosity and gene correlation could not be conducted. Apparently, all four assumptions involved in this test were fulfilled by fiber fineness.

The results of the analyses of variance for the additive components are summarized for each trait in Table 3. The test is founded on the basis that heritable differences between homozygous parents, in the absence of epistasis, result from the additive effects of genes (1). Hence, parental lines differing significantly from each other must carry genes with different additive effects. The significance of the years mean square has no specific genetical interpretation, because any of a large number of environmental factors could have caused the observed differences between seasons. The significance of the parents mean square, however, is direct evidence that for each of the traits, except lint yield, at least some of the parents carry alleles with different additive effects. Nonsignificance of the years by parents mean squares suggests that these additive effects were constant over years for earliness, 50% span length, uniformity index, fiber fineness, and fiber

strength. The significant interaction terms for lint yield, lint percent, and 2.5% span length indicate that the additive effects for those traits were not consistent from year to year.

The results of the analyses of variance of the dominance components are given in Table 4. The interpretation here again follows Allard's (1) reasoning when epistasis is not a complicating factor. The years mean square was significant for all characters except 50% span length, indicating that the rescaling used in this test was at least partially ineffective. Significance of the dominance mean square for each trait suggests that the mean degree of dominance was in the partial dominance or overdominance range in every case. The significance of the years by dominance interaction for lint yield, earliness, lint percent, fiber fineness, and fiber strength suggests that mean degree of dominance for those traits differed between the two seasons, whereas it was consistent for the other traits. The significance of the arrays component of variation for earliness, lint percent, uniformity index, fiber fineness, and fiber strength indicates that at least some of the parents differed in dominance effects. Such differences were not evident for lint yield or for 2.5 and 50% span length. The significance of the years by arrays item for earliness, lint percent, 2.5% span length, fiber fineness, and fiber strength shows that the parents did not maintain the same dominance relationships among themselves over the 2 years for those traits. This relationship was constant for lint yield, 50% span length, and uniformity index. The lack of significance of the dominance by arrays and the years by dominance by arrays mean squares for each character provides additional evidence that epistasis was not important in these characters in this material.

Table 4. Genotype by year analyses of the dominance components of variation.

| Source | df | Lint yield, g/plant | Earliness, % | Lint percent | Fiber length | | | Micronaire | 1/8-inch gauge stelometer |
					2.5% span	50% span	Unif. index		
Years	1	15.5813**	0.3115*	0.1981*	0.2023*	0.0951	0.6363**	0.3349**	0.9734**
Reps within years	6	14.6759**	0.1640*	0.2658**	0.1843*	0.8506**	0.3209**	0.0415	0.1248**
Dominance	1	63.1643**	4.0450**	2.2302**	0.2984**	4.1365**	2.8329**	0.2161**	0.5929**
Years by dominance	1	10.8004**	1.0433**	0.6877**	0.1108	0.1188	0.0328	0.2512**	0.4223**
Arrays	9	0.5940	0.3795**	0.2099**	0.0575	0.1517	0.1078*	0.1795**	0.1224**
Years by arrays	9	0.7047	0.1841**	0.1317**	0.1078**	0.1827	0.0419	0.0709**	0.1371**
Dominance by arrays	9	0.4658	0.0335	0.0544	0.0215	0.0734	0.0361	0.0123	0.0244
Years by dominance by arrays	9	0.3171	0.0114	0.0421	0.0195	0.0316	0.0443	0.0101	0.0191
Error	114	1.0485	0.0609	0.0385	0.0362	0.0981	0.0472	0.0241	0.0371

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

Table 5. Mean estimates of genetic and environmental components from the F_1-parental data in 1969.

Parameter	Lint yield, g/plant	Earliness, %	Lint percent	Fiber length 2.5% span (× 10⁻²)	50% span (× 10⁻²)	Unif. Index	Micronaire	1/8-inch gauge stelometer
E_0	9.4**	48.08**	0.33**	0.133**	0.078**	0.30**	0.0235**	0.0030**
E_1	9.5**	40.07**	0.26**	0.126**	0.052**	0.25**	0.0168**	0.0027**
D	8.9	245.87**	2.12**	1.067**	0.260	1.03	0.1439*	0.0274**
F	7.5	64.12	1.59*	−0.059	0.063	0.39	0.0719	0.0060
H_1	36.3**	259.11**	2.15**	0.748*	0.345*	1.45	0.0667*	0.0438**
H_2	34.0**	225.21**	1.52*	0.652*	0.286**	1.30*	0.0467	0.0379**

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

Parameters and Genetic Systems

When partial failures of the assumptions have been demonstrated, Hayman (7) postulates a more complex genetical system than the simple theory describes. However, he does state that it is still possible to make estimates of the population parameters and genetic components for such a trait, although it should be realized that such estimates are probably less reliable than they would have been had all the assumptions been fulfilled. With this in mind, those parameters were estimated and listed in Tables 5 and 6.

All estimates of environmental variance were significantly different from zero at the 0.01 level of probability. The mean of E_0 exceeded that of E_1 for all characters except lint yield in both years. In 1970 the estimates of E_2 were also larger than E_0 for all traits except earliness, 50% span length, and fiber strength. D was significant in both years for earliness, lint percent, 2.5% span length, fiber fineness, and fiber strength but only in 1970 for lint yield, 50% span length, and uniformity index. The F values were consistently positive over all three sets of data for each trait except in one instance for 2.5% span length and that estimate was not significantly different from zero. In fact, F was significant only for lint percent in 1969, for fiber fineness only in the 1970 F_1, and for earliness and uniformity index in the 1970 F_1 and F_2 data. The positive and significant estimates suggest a greater frequency of dominant alleles in the parents for those traits. However, conclusive statements would be hazardous because of the lack of uniformity between sets of data.

H_1, H_2, or both were significantly different from zero in at least one set of data for each character. In fact, both were significant in every instance for lint yield, earliness, 2.5 and 50% span length, and fiber strength. H_2 was smaller than H_1 in every case, but this was not totally unexpected since, theoretically, H_2 should be equal to or less than H_1 (7). H_1 greater than H_2 indicates that the positive and negative alleles at the loci for the trait in question are not equal in proportion in the parents. Estimates of H_1 were also generally greater in the F_1 than the estimates of D and F obtained in the same year. Estimates of F, H_1, and H_2 were larger in the F_2 than in the 1970 F_1. This is to be expected because the F_2 is a segregating

generation, whereas the F_1 is not. Since H_1 was greater than D in most instances, this suggests that dominant genetic variance is more important for most traits in this material than is additive genetic variance.

Estimators and ratios were calculated using the genetic parameters obtained for Tables 5 and 6 to provide further information about the genetic systems operating for each trait. The mean values of those estimates and their 95% confidence limits are presented in Table 7. All estimates of degree of dominance for lint yield, earliness, lint percent, 50% span length, and uniformity index were in the overdominance range though in most cases the estimates were not significantly different from one. However, the consistency of those estimates between sets of data would suggest overdominance for the five traits. Two of three estimates for 2.5% span length were barely in the overdominance range and not significantly different from one. The 0.84 estimate in the 1969 F_1 was significantly different from one and therefore would suggest partial dominance. However, taking into consideration the mean data from both years, 0.98, one could probably suggest complete dominance for this trait in this material with some degree of confidence. Two of the three estimates for fiber fineness were in the partial dominance range, and none of the three were significantly different from one. However, a 0.81 mean over the 2 years suggests partial dominance. Two of three estimates for fiber strength were greater than one. Even though the overdominance estimate for the 1969 F_1 did not include one within its confidence limits, the mean from the three sets of data was 1.05 so complete dominance is likely the most reasonable interpretation for this character. However, since the above estimates for degree of dominance were calculated for a fixed set of parents, all estimates may be biased upwards to some degree (10), and caution should be used in their interpretation.

Fiber fineness was the only trait in which no estimate of the quantity $\overline{uv}$ was significantly different from 0.25. One may then reasonably conclude that for all traits except fineness some doubt exists whether the parents had an equal distribution of alleles. Estimates of the ratio of dominant to recessive alleles in the parents, K_D/K_R, were greater than one for all traits except 2.5% span length in one data set. This

Table 6. Mean estimates of genetic and environmental components from the F_1, F_2, and parental data in 1970.

Param-eter	Lint yield, g/plant F₁	F₂	Earliness, % F₁	F₂	Lint percent F₁	F₂	2.5% span length (× 10⁻²) F₁	F₂	50% span length (× 10⁻²) F₁	F₂	Unif. Index F₁	F₂	Micronaire F₁	F₂	1/8-inch gauge stelometer F₁	F₂
E_0	4.7**	--	54.58**	--	0.89**	--	0.249**	--	0.083**	--	0.49**	--	0.0367**	--	0.0050**	--
E_1	5.4**	--	40.20**	--	0.70**	--	0.235**	--	0.063**	--	0.35**	--	0.0341**	--	0.0037**	--
E_2	--	6.1**	--	53.39**	--	1.00**	--	0.295**	--	0.077**	--	0.54**	--	0.0425**	--	0.0049**
D	14.7*	--	206.16**	--	2.13*	--	2.363*	--	0.388*	--	1.51**	--	0.2020**	--	0.0451**	--
F	23.4	33.8	291.23**	537.40**	2.03	4.79	1.310	1.331	0.149	0.345	1.03	2.34*	0.0809*	0.1705	0.0186	0.0344
H_1	41.0*	127.1*	551.72**	1,933.38*	3.57**	18.02	2.504*	9.022*	0.741*	2.802**	2.13*	8.60*	0.2260**	0.4641	0.0330**	0.1745**
H_2	25.3**	92.5*	424.72**	1,472.68*	2.44**	14.39*	1.866*	7.185**	0.631*	2.212**	1.65*	5.65	0.1882**	0.3204	0.0251**	0.1423**

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

implies an excess of dominant genes in the parents for each trait. The number of effective factors, K, has been described by Mather (15) as the smallest unit of hereditary material that is capable of being recognized by the methods of biometrical genetics. The value of K will be underestimated unless the dominance effects of all genes are equal in sign and magnitude of effects and the distribution of genes is uncorrelated (11, 15). Estimates for lint yield, earliness, and 2.5% span length were relatively high; however, none of them were significantly different from zero. Estimates for the remaining traits were small and fairly uniform or were erratic both within and between sets of data.

The direction of dominance can be estimated by the quantity $(\bar{F} - \bar{P})$. From a comparison of the $(\bar{F}_1 - \bar{P})$ and $(\bar{F}_2 - \bar{P})$ results in 1970, it is obvious that a portion of the positive hybrid vigor observed in the F_1 was lost in the F_2 for lint yield, earliness, lint percent, 2.5 and 50% span length, and fiber strength. Negative heterosis was observed in the F_1 for uniformity index and fiber fineness, but their means regressed toward the midparent in the F_2. The variation was such that in most sets of data the differences between offspring and midparent values were not significantly different from zero. Perhaps, a more meaningful estimate of the direction of dominance is obtained by $(V_r + W_r)$ correlations with parental means. This estimate is obtained by computing a linear correlation coefficient between the mean values of $(V_r + W_r)$ of each array averaged over blocks and the corresponding parental means averaged over blocks. The calculated coefficients are given in Table 8. A high correlation indicates that most dominant alleles act in one direction and most recessive alleles act in the opposite direction (7). Only three coefficients (one for lint yield and two for earliness) were significantly different from zero at the 0.05 or 0.01 probability levels. All coefficients for lint yield and earliness were negative in sign. Because parents with a preponderance of dominant alleles have a lower array variance and covariance than highly recessive parents (5), the negative coefficients indicate that the dominant alleles are positive in direction, i.e., operating in the direction of higher lint yield and increased earliness. The correlations for the other traits except fiber fineness were erratic in magnitude, direction, or

Table 7. Mean ratios estimating the genetic characteristics of the population.

Ratio	F_1 (1969)	95% confidence limits	F_1 (1970)	95% confidence limits	F_2 (1970)	95% confidence limits
Lint yield, g/plant						
Dominance	1.87†	1.15 - 2.59†	1.81	1.11 - 2.51	1.66	0.58 - 2.74
$\overline{uv}$	0.24	0.16 - 0.32	0.16	0.12 - 0.20	0.18	0.13 - 0.23
K_D/K_R	1.99†	0.88 - 3.10†	2.75	1.19 - 4.31	2.49	0.61 - 4.37
K	1.60	(-0.15) - 3.35	2.79	(-0.20) - 5.70	1.59	(-0.70) - 3.90
$(\bar{F} - \bar{P})$*	3.20	(-0.30) - 6.70	3.80	2.30 - 5.30	2.60	0.90 - 4.30
Heritability	0.12	(-0.03) - 0.27	0.27	0.01 - 0.54	0.29	0.06 - 0.51
Earliness, %						
Dominance	1.07	0.66 - 1.48	1.65	1.20 - 2.09	1.51	1.16 - 1.86
$\overline{uv}$	0.22	0.17 - 0.26	0.19	0.15 - 0.23	0.19	0.16 - 0.21
K_D/K_R	1.31	0.56 - 2.06	2.64	1.65 - 3.63	2.65	1.73 - 3.57
K	2.25	(-1.39) - 5.89	1.19	(-0.59) - 2.97	0.53	(-0.49) - 1.55
$(\bar{F} - \bar{P})$*	10.10	(-1.77) - 21.98	9.86	(-2.45) - 22.17	4.37	(-6.89) - 15.63
Heritability	0.40	0.15 - 0.65	0.34	0.11 - 0.57	0.33	0.23 - 0.43
Lint percent						
Dominance	1.01	0.70 - 1.32	1.41	0.93 - 1.89	1.67	0.49 - 2.85
$\overline{uv}$	0.18	0.15 - 0.21	0.18	0.10 - 0.25	0.21	0.16 - 0.25
K_D/K_R	2.30	1.00 - 3.60	2.77	0.07 - 4.47	2.28	0.75 - 3.81
K	1.93	1.57 - 2.27	0.25	0.03 - 0.47	0.33	(-0.31) - 0.87
$(\bar{F} - \bar{P})$*	0.85	0.57 - 1.13	0.27	(-0.27) - 0.81	0.00	(-0.83) - 0.84
Heritability	0.57	0.28 - 0.86	0.31	0.06 - 0.55	0.28	0.06 - 0.50
2.5% span length						
Dominance	0.84	0.73 - 0.95	1.07	0.59 - 1.55	1.02	0.80 - 1.24
$\overline{uv}$	0.22	0.13 - 0.30	0.18	0.15 - 0.22	0.21	0.16 - 0.26
K_D/K_R	0.95	0.35 - 1.55	1.71	0.75 - 2.67	1.30	0.00 - 2.60
K	1.66	(-0.98) - 4.30	1.52	(-0.20) - 3.24	0.66	(-0.83) - 2.15
$(\bar{F} - \bar{P})$*	0.014	(-0.004) - 0.032	0.026	0.005 - 0.047	0.013	(-0.002) - 0.029
Heritability	0.45	0.28 - 0.62	0.51	0.14 - 0.89	0.46	0.09 - 0.83
50% span length						
Dominance	1.27	0.70 - 1.84	1.49	0.53 - 2.44	1.48	0.56 - 2.40
$\overline{uv}$	0.23	0.10 - 0.36	0.21	0.17 - 0.25	0.20	0.15 - 0.24
K_D/K_R	1.00	0.85 - 1.15	1.37	0.61 - 2.13	1.41	0.55 - 2.27
K	0.70	(-0.41) - 1.81	0.63	(-0.83) - 2.09	0.31	(-0.33) - 0.95
$(\bar{F} - \bar{P})$*	0.006	0.002 - 0.010	0.009	(-0.005) - 0.022	0.004	(-0.008) - 0.015
Heritability	0.31	0.03 - 0.59	0.33	0.06 - 0.60	0.33	0.08 - 0.57
Uniformity Index						
Dominance	1.23	0.92 - 1.54	1.17	0.91 - 1.42	1.20	0.63 - 1.77
$\overline{uv}$	0.25	0.17 - 0.32	0.19	0.15 - 0.24	0.15	0.09 - 0.22
K_D/K_R	1.19	(-0.26) - 2.64	1.80	1.48 - 2.12	2.02	1.19 - 2.85
K	0.25	(-0.29) - 0.80	0.43	(-0.56) - 1.42	1.23	(-2.65) - 5.11
$(\bar{F} - \bar{P})$*	-0.03	(-0.38) - 0.44	-0.34	(-1.04) - 0.36	-0.23	(-1.09) - 0.63
Heritability	0.30	0.04 - 0.56	0.35	0.29 - 0.41	0.34	0.17 - 0.51
Micronaire						
Dominance	0.69	0.33 - 1.05	1.05	0.95 - 1.15	0.71	0.30 - 1.12
$\overline{uv}$	0.16	0.08 - 0.25	0.21	0.16 - 0.26	0.19	0.08 - 0.31
K_D/K_R	2.60	(-0.37) - 5.57	1.46	1.11 - 1.81	1.76	1.15 - 2.36
K	1.25	0.18 - 2.32	0.31	(-0.39) - 1.01	0.71	(-0.25) - 1.66
$(\bar{F} - \bar{P})$*	0.11	(-0.04) - 0.26	-0.09	(-0.25) - 0.07	-0.02	(-0.18) - 0.14
Heritability	0.66	0.22 - 1.10	0.41	0.37 - 0.46	0.52	0.50 - 0.54
1/8-inch gauge stelometer						
Dominance	1.27	1.08 - 1.46	0.87	0.71 - 1.03	1.01	0.75 - 1.26
$\overline{uv}$	0.22	0.20 - 0.24	0.19	0.14 - 0.24	0.20	0.16 - 0.24
K_D/K_R	1.17	0.57 - 1.77	1.73	0.65 - 2.81	1.61	0.81 - 2.41
K	0.18	(-0.12) - 0.47	0.38	(-0.41) - 1.17	0.24	(-0.24) - 0.72
$(\bar{F} - \bar{P})$*	-0.001	(-0.082) - 0.081	0.023	(-0.060) - 0.106	0.012	(-0.071) - 0.095
Heritability	0.35	0.25 - 0.45	0.60	0.28 - 0.92	0.52	0.24 - 0.80

* Mean of the 45 F_1 (or F_2) versus midparent comparisons within each replication.   † Means based on three replications. Because of a zero estimate of D in replication two, the estimates of $(H_1/D)^{1/2}$ and $[(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F]$ were undefined therein and could not be used.

Table 8. $(V_r + W_r)$ correlations with the parental means.

Trait	Generation and year		
	F_1 (1969)	F_1 (1970)	F_2 (1970)
Lint yield, g/plant	-0.369	-0.961**	-0.216
Earliness, %	-0.904**	-0.754*	-0.477
Lint percent	-0.402	0.579	0.024
2.5% span length	0.261	0.025	0.441
50% span length	0.059	0.374	0.242
Uniformity index	-0.491	0.473	0.485
Micronaire	0.433	0.440	0.433
1/8-inch gauge steL	0.213	-0.069	0.528

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

both. The consistent and positive coefficients for fineness would suggest that dominant alleles are operating in the direction of increased fiber fineness, i.e., lower micronaire values.

All heritabilities (Table 7), except for lint yield in the 1969 F_1, were significantly different from zero. Estimates were medium-to-high for all characters except yield. This suggests that a substantial proportion of the phenotypic variance for those traits was additive. The heritabilities averaged over the three sets of data reveal that about one-fifth of the variance exhibited by yield, one-third that by 50% span length and uniformity index, two-fifths that by earliness and lint percent, and one-half of that by 2.5% span length, fiber fineness, and fiber strength was additive in nature. This suggests that an effective breeding method within this material for improving 2.5% span length, fiber fineness, and fiber strength would be one leading toward the production of varieties rather than hybrids. Therefore, mass selection on a plot mean basis when plots are small should be relatively effective. On the other hand, such selection would be somewhat less effective for 50% span length, uniformity index, earliness, and lint percent, and it would be a great deal less effective for lint yield. In fact, alternatives such as half- or full-sib family selection, pedigrees, or progeny tests would probably be necessary to achieve genetic progress for lint yield in this material. The information obtained in regard to H_1 and degree of dominance suggests that a substantial potential exists for obtaining lint yield, earliness, lint percent, 50% span length, and uniformity index improvements in this material through the use of breeding programs utilizing F_1 hybrids.

REFERENCES

1. Allard, R. W. 1956. The analysis of genetic-environmental interactions by means of diallel crosses. Genetics 41:305-318.
2. Al-Rawi, K. M., and R. J. Kohel. 1969. Diallel analyses of yield and other agronomic characters in Gossypium hirsutum L. Crop Sci. 9:779-783.
3. ————, and ————. 1970. Gene action in the inheritance of fiber properties in intervarietal diallel crosses of upland cotton, Gossypium hirsutum L. Crop Sci. 10:82-85.
4. Barnes, C. E., and G. Staten. 1961. The combining ability of some varieties and strains of Gossypium hirsutum. New Mexico Agr. Exp. Sta. Bull. 457.
5. Crumpacker, D. W., and R. W. Allard. 1962. A diallel cross analysis of heading date in wheat. Hilgardia 32:275-318.
6. Endrizzi, J. E. 1962. The diploid-like cytological behavior of tetraploid cotton. Evolution 16:325-329.
7. Hayman, B. I. 1954. The theory and analysis of diallel crosses. Genetics 39:789-809.
8. ————. 1957. Interaction, heterosis, and diallel crosses. Genetics 42:336-355.
9. ————. 1958. The theory and analysis of diallel crosses. II. Genetics 43:63-85.
10. ————. 1960. The theory and analysis of diallel crosses. III. Genetics 45:155-172.
11. Jinks, J. L. 1954. The analysis of continuous variation in a diallel cross of Nicotiana rustica varieties. Genetics 39: 767-788.
12. ————, and B. I. Hayman. 1953. The analysis of diallel crosses. Maize Genetics Co-op. Newsletter 27:48-54.
13. Kimber, G. 1961. Basis of the diploid-like meiotic behaviour of polyploid cotton. Nature 191:98-100.
14. Lee, J. A., P. A. Miller, and J. O. Rawlings. 1967. Interaction of combining ability effects with environments in diallel crosses of upland cotton (Gossypium hirsutum L.). Crop Sci. 7:477-481.
15. Mather, K. 1949. Biometrical genetics. Dover Publications, Inc., London.
16. Meredith, W. R., Jr., and R. R. Bridge. 1972. Heterosis and gene action in cotton, Gossypium hirsutum L. Crop Sci. 12:304-310.
17. ————, ————, and J. F. Chism. 1970. Relative performance of F_1 and F_2 hybrids from doubled haploids and their parent varieties in upland cotton, Gossypium hirsutum L. Crop Sci. 10:295-298.
18. Miller, P. A., and A. Marani. 1963. Heterosis and combining ability in diallel crosses of upland cotton, Gossypium hirsutum L. Crop Sci. 3:441-444.
19. Nelder, J. A. 1953. Statistical models in biometrical genetics. Heredity 7:111-119.
20. Stith, L. S. 1956. Heritability and interrelationship of some quantitative characters in a cross between two varieties of Gossypium hirsutum. Iowa State College J. Sci. 30:439-440. (Abstr.)
21. Tabrah, T. A. 1970. Estimating genetic parameters in cotton (Gossypium hirsutum L.) using Comstock and Robinson's Design III. Ph.D. Thesis. Oklahoma State Univ.
22. Turner, J. H., Jr. 1953. A study of heterosis in upland cotton. I. Yield of hybrids compared with varieties. II. Combining ability and inbreeding effects. Agron. J. 45: 484-490.
23. Verhalen, L. M., and J. C. Murray. 1967. A diallel analysis of several fiber property traits in upland cotton (Gossypium hirsutum L.). Crop Sci. 7:501-505.
24. ————, and ————. 1969. A diallel analysis of several fiber property traits in upland cotton (Gossypium hirsutum L.). II. Crop Sci. 9:311-315.
25. ————, W. C. Morrison, B. A. Al-Rawi, K. C. Fun, and J. C. Murray. 1971. A diallel analysis of several agronomic traits in upland cotton (Gossypium hirsutum L.). Crop Sci. 11:92-96.
26. White, T. G. 1966. Diallel analyses of quantitatively inherited characters in Gossypium hirsutum L. Crop Sci. 6: 253-255.
27. ————, and R. J. Kohel. 1964. A diallel analysis of agronomic characters in selected lines of cotton, Gossypium hirsutum L. Crop Sci. 4:254-257.
28. ————, and T. R. Richmond. 1963. Heterosis and combining ability in top and diallel crosses among primitive, foreign, and cultivated American upland cottons. Crop Sci. 3:58-63.