

A Diallel Analysis of Several Agronomic Traits in Upland Cotton (*Gossypium hirsutum* L.)¹

Laval M. Verhalen, Walter C. Morrison, Baha A. Al-Rawi, Kwee-Chong Fun, and Jay C. Murray²

ABSTRACT

Diallel analyses of seed cotton yield per plant, lint yield per plant, lint percent, and earliness were conducted on 10 selected varieties of upland cotton (*Gossypium hirsutum* L.) and the 45 F_1 crosses among them in 1965 and on the parents, F_1 's, and their 45 F_2 progenies in 1966 using the procedure developed by Jinks and Hayman. A partial failure of the assumptions was observed for each trait. However, lint percent more nearly fulfilled the assumptions than did the measurements for yield or earliness. Epistasis did not appear to be a factor in any of those failures. A genotype by environment interaction for the additive components of variation was noted for lint percent. A single interaction for the dominance components influenced earliness.

All traits appeared to be governed by a weighted overall degree of dominance in the overdominance range except for lint percent in the 1966 F_1 where partial dominance was indicated. The magnitudes of their heritability estimates indicated that mass selection on a plot mean basis when plots are small would not be very effective in altering any of these traits. Pedigrees, sib tests, or progeny tests (or various combinations among them) almost certainly will be required to improve seed cotton yield, lint yield, or earliness in this material and may be necessary to improve lint percent.

The reliability of F_1 diallel estimates from year to year at a single location was investigated. Comparisons between F_1 's and F_2 's were also made.

Additional index words: Seed cotton yield per plant, Lint yield per plant, Lint percent, Earliness, Epistasis, Genotype by environment interaction, Degree of dominance, Heritability.

GENETIC studies of several agronomic traits in upland cotton (*Gossypium hirsutum* L.) using the diallel analysis have recently been completed. This report, summarizing the results of those analyses, extends the information in the literature on these traits. These results are conceivably of theoretical interest to cotton geneticists and of practical use to cotton breeders. Diallel analyses of several fiber property traits in this material have been published previously (18, 19).

LITERATURE REVIEW

Manning (11) estimated a narrow-sense heritability for lint yield per plant of .10 to .15 on the basis of actual genetic advance over six generations of selection in 'BP 52'. Richmond and Ray (15) studied three "product-quantity" measures of earliness in all possible crosses among one early and two late parents. Their measure entitled "percentage of crop harvested" (PCH) was similar to the measure of earliness used in this paper. PCH exhibited dominance for earliness in the two crosses of early by late parents and for late-

ness in the cross between the two late parents. At the four harvest dates this trait was studied, broad-sense heritability estimates on a plant basis were greater than zero for two of the crosses at only one date; and they were low even in those instances, .14 and .03. Heritabilities in the other cross exceeded .20 at three of the four dates. Murray and Verhalen (13) obtained inconsistent narrow- and broad-sense heritabilities on a plant basis for lint yield and earliness in early generation materials of the cross they studied. However, progeny row analyses of the BC_2F_4 generation of that cross gave predicted genetic advances through selection which corresponded rather closely with observed selection responses. Broad-sense heritabilities on a plot basis for lint yield and earliness in the BC_2F_4 material were .45 and .73, respectively.

White and Kohel (21) in a diallel analysis among five widely different parents and their F_1 's detected significant additive genetic variation for lint yield per acre, lint percent, and earliness with significant dominance variation for only lint yield per acre. The degree of dominance for yield was in the partial dominance range, .91; and the direction of the dominance was toward higher yield. In further analyses of these parents and their F_1 's but also including the F_2 generation, White (20) detected no significant epistasis for lint yield per acre, lint percent, or earliness, although he did find multiple allelism to be operative in the two latter traits. He obtained an estimate of 1.32 for degree of dominance for lint yield, i.e., overdominance. Hayman (6, 7) found complementary epistasis and possibly multiple allelism in seed cotton yield per plot data supplied by Turner (17). Al-Rawi and Kohel (3) in a nine-parent diallel including parents, F_1 's, and F_2 's showed that lint yield per plant, lint percent, and earliness exhibited significant additive genetic variance and that yield and earliness also had significant dominance variance. Significant epistatic effects were found only for earliness. Both yield and earliness displayed partial dominance with estimates of .64 and .95, respectively; and both had narrow-sense heritability estimates of .41 on a plot mean basis.

MATERIALS AND METHODS

'Paymaster 101,' 'Gregg,' 'Western Stormproof,' 'Lankart 57,' '6-77,' 'Deltapine 45,' 'Coker 100A WR,' 'Acala 44,' 'Stoneville 7,' and 'Auburn M' were used as parents in this experiment. With the exception of 6-77, all are, or were until recently, commercial varieties of cotton grown over extensive areas in the United States. Line 6-77 is the result of selection for increased resistance to bacterial blight [*Xanthomonas malvacearum* (E. F. Sm.) Dows.] within the variety 'Stormproof No. 1.' The 10 parents were chosen on the basis of their individual characteristics and do not represent a random sample of all upland cotton varieties. Thus, inferences derived from the data apply, in the strict sense, only to the material studied.

In 1965 the 10 parents and the 45 F_1 hybrids, ignoring reciprocals, were planted in a 7×8 rectangular lattice design with three replications at Perkins, Okla. A dummy entry, '8948,' was used to increase the number of entries to 56 as required by the design. Plots were single rows 7.5 m long, and plants within plots were spaced approximately 50 cm apart. Single

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² Assistant Professor, Graduate Research Assistant, Former Graduate Student (now on the Faculty of the College of Agriculture and Veterinary Medicine, University of Baghdad, Iraq), Graduate Student, and Professor in the Department of Agronomy, Oklahoma State University, Stillwater, Oklahoma 74074.

border rows of the variety 'Kemp' were planted between adjacent plots to equalize border effects between plots. Seedling disease reduced stands considerably. To partially compensate for the differential spacing between plants which occurred, 'De Ridder Red,' a variety with the dominant marker gene, R_L , was planted in the blank hills as soon as they were detected. Cultural practices, including irrigation, were conducted as needed. Six plants within each plot were chosen for harvest using a table of random digits (16). However, seven plots had four to six plants, and within those plots all plants were taken.

In 1966 the 10 parents, the 45 F_1 crosses, and their 45 F_2 progenies were planted in a 10×10 triple lattice design. All other variables under experimental control such as test location, number of replications, plot size, plant spacing, etc., were the same as in 1965. Seedling disease was not as severe as in the previous year, although 10 plots did have between three and six plants. In those plots all plants were taken.

Each year two harvests were made. Acala 44 was used as a reference point for the time of first harvest, that being when approximately half of its bolls had opened. Second harvests were conducted each year several weeks after the first killing frost when the remaining bolls had been given an opportunity to open. After each harvest, data were recorded on a plant basis for seed cotton yield measured in grams, lint yield in grams, and lint percent calculated as lint yield divided by seed cotton yield and expressed as a percentage. Earliness was calculated for each plant as the percentage lint yield from the first of two harvests. Data used in the analyses were seed cotton yield per plant (summed over both harvests), lint yield per plant (summed over both harvests), a weighted average of lint percent over the two harvests calculated for each plant based on the percentage of total lint yield per harvest of that plant, and earliness as described above. The analysis of the data followed the diallel procedure developed by Jinks and Hayman (5, 9, 10).

RESULTS AND DISCUSSION

Analyses of variance were conducted on a plot mean basis for each trait in 1965 and in 1966. Plants within plots were weighted equally in the determination of those plot means. Highly significant differences among entries were obtained in each analysis. After it was determined that observed differences were indeed significant, diallel analyses were conducted on values unadjusted for block effects in three sets of data: the F_1 (and parental) data in 1965, F_1 (and parental) data in 1966, and F_2 (and parental) data in 1966. Varietal means for the characters studied are listed in Table 1.

General Tests of the Assumptions

Assumptions of the diallel analysis are diploid segregation, no reciprocal differences, homozygous parents, no multiple alleles, uncorrelated gene distribution, no genotype-environment interaction within locations and years, and no epistasis (4). Failure of any one or any combination of the assumptions invalidates to some degree the inferences derived by means of the analysis. Therefore, three general tests of the assumptions were employed to screen the traits for such failures. In the discussions of those tests which follow, V_r is the variance of the members of the r th array; W_r is the covariance of the members of the r th array with their nonrecurrent parents; and W_r' is the covariance of the members of the r th array with the array means of their nonrecurrent parents. The r th array includes all crosses involving the r th parent as well as the r th parent itself.

The first general test of the assumptions is an analysis of variance of the quantity $(W_r - V_r)$. This value is expected to be constant over arrays if the assumptions are valid (8, 10). The quantity was obtained for each array in each replication and then analyses of

Table 1. Mean performance of parental varieties over 1965 and 1966.

Variety	Yield of seed cotton, g/plant	Yield of lint, g/plant	Lint percent		Earliness, %
			1965	1966	
Paymaster 101	111	38	34.7	33.5	67.0
Gregg	113	37	32.7	32.0	59.3
Western Stormproof	75	28	38.6	34.7	42.3
Lankart 57	122	44	37.9	33.9	46.5
6-77	113	36	33.4	30.5	53.5
Deltapine 45	107	37	35.1	33.2	40.7
Coker 100A WR	106	37	35.9	34.4	38.5
Acala 44	75	25	34.4	33.0	45.9
Stoneville 7	117	41	35.7	32.8	38.8
Auburn M	149	51	36.3	32.5	52.8

* Since the parents exhibited a significant years \times parents interaction for this trait (see Table 5), the means for each year are listed separately.

Table 2. Analyses of variance of $(W_r - V_r)$ values.

Source	df	Mean squares					
		F_1 (1965)	F_1 (1966)	F_2 (1966)	F_1 (1965)	F_1 (1966)	F_2 (1966)
		Yield of seed cotton, g/plant			Yield of lint, g/plant		
Arrays	9	72,356	554,528	118,678	1,375	7,639	2,767
Reps	2	61,140	2,963,239*	855,839*	1,506	31,565**	4,767
Error	18	67,694	354,201	236,758	1,101	4,585	3,184
		Lint percent			Earliness, %		
		F_1 (1965)	F_1 (1966)	F_2 (1966)	F_1 (1965)	F_1 (1966)	F_2 (1966)
		Yield of seed cotton, g/plant			Yield of lint, g/plant		
Arrays	9	.4809	.2945	.4979	7,214	1,441	575
Reps	2	.4264	.2584	.5715	4,890	1,871	5,426*
Error	18	.5666	.2015	.5863	9,504	1,026	1,367

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

Table 3. (W_r, W_r') regression coefficients.

Measurement	Generation	Coefficient	95% confidence limits
Yield of seed cotton, g/plant	F_1 (1965)	.319	.168---.470
	F_1 (1966)	.155	(-.046)---.356
	F_2 (1966)	.266	(-.025)---.557
Yield of lint, g/plant	F_1 (1965)	.331	.179---.483
	F_1 (1966)	.081	(-.123)---.285
	F_2 (1966)	.266	.069---.463
Lint percent	F_1 (1965)	.476	.325---.627
	F_1 (1966)	.364	.150---.578
	F_2 (1966)	.492	.227---.757
Earliness, %	F_1 (1965)	.342	.244---.440
	F_1 (1966)	.393	.215---.571
	F_2 (1966)	.119	(-.085)---.323

variance were conducted upon the 30 values obtained in each set of data for each trait. The results of these analyses are presented in Table 2. The mean squares attributable to arrays were not significant at the 0.05 probability level for any trait in any set of data. Therefore, no failures of the assumptions were detected within this test. Results were comparable from F_1 to F_1 grown in different years and from either F_1 to the F_2 . These comparisons were also true in the fiber data, except for fiber length between the F_1 and F_2 generations (19). Using this test, White and Kohel (21) calculated array mean squares for lint yield per acre, lint percent, and earliness which were not significant. However, Al-Rawi and Kohel (3) obtained significant array mean squares for lint yield per plant, lint percent, and earliness in their study.

The second general test of the assumptions is an analysis of the (W_r, W_r') regression. Like V_r and W_r , estimates of W_r' are available for each array in each replication. The estimates of W_r in the 1965 F_1 data were averaged over replications as were the estimates of W_r' . Regression coefficients were then calculated using those means. The same procedure was followed for the 1966 F_1 and F_2 data. In this test the regression coefficient should be significantly different from zero but not from 0.5 if the assumptions are fulfilled (1). The regression estimates and their 95% confidence limits may be found in Table 3. Yield of seed cotton and of lint failed one or both criteria of this test in each set of data examined, while lint percent conformed to both requirements in every instance. Earli-

Table 4. (V_r , W_r) regression coefficients.

Measurement	Generation	Coefficient	95% confidence limits
Yield of seed cotton, g/plant	F_1 (1965)	.274	(-.300)--0.848
	F_1 (1966)	-.105	(-.609)--0.399
	F_2 (1966)	.472	.139--0.805
Yield of lint, g/plant	F_1 (1965)	.225	(-.240)--0.690
	F_1 (1966)	-.042	(-.561)--0.477
	F_2 (1966)	.429	(-.106)--0.964
Lint percent	F_1 (1965)	.527	.044--1.010
	F_1 (1966)	.562	(-.125)--1.249
	F_2 (1966)	.221	(-.281)--0.723
Earliness, %	F_1 (1965)	.634	.107--1.161
	F_1 (1966)	.361	(-.594)--1.316
	F_2 (1966)	.640	.307--0.973

ness was intermediate in that its 1966 F_1 regression corresponded to expectations, whereas its 1965 F_1 and 1966 F_2 regressions did not. As previously shown when studying the fiber traits (19), this test was not consistent in the F_1 from year to year or from the F_1 to the F_2 . Thus, with this test each generation should be tested each year.

The third general test of the assumptions is an analysis of the (V_r , W_r) regression. Mean estimates of V_r were obtained in the same manner as were the W_r and W_r' means in the previous test. Using those means, regressions between V_r and W_r were calculated for each trait in each set of data. The coefficients in this test are expected to be significantly different from zero but not from 1.0 if all of the assumptions are correct (10). These regressions and their 95% confidence limits are presented in Table 4. Yield of seed cotton and of lint again failed the assumptions in all three sets of data, while lint percent and earliness complied with expectations only in the 1965 F_1 . As before (19), this test did not give consistent results from year to year or from generation to generation; and therefore, each generation should be tested in each year.

Summarizing the general tests of the assumptions, three tests were conducted on three sets of data for each trait. Out of those nine tests, yield of seed cotton failed six, yield of lint six, earliness four, and lint percent two. Therefore, none of these traits strictly complied with the assumptions of the analysis although some more closely fulfilled them than did others.

Specific Tests of the Assumptions

The only specific assumptions tested were those of no epistasis and of no genotype-environment interaction within locations and years. The latter assumption was partially tested since only one location was involved in these experiments.

The assumption of no epistasis was investigated for each trait using the chi-square test derived by Hayman (6). Since parental, F_1 , and F_2 data are required for this test, it was conducted only on the 1966 data. The observed chi-square values with 45 degrees of freedom were 20.8, 19.8, 34.9, and 22.1 for seed cotton yield, lint yield, lint percent, and earliness, respectively. None of these values were significant at the 0.05 probability level which in turn implies that epistasis did not make a significant contribution to the expression of these traits in 1966. Results of this test in other materials (3, 6, 7, 20) were discussed in the literature review section.

The assumption of no genotype-environment interaction within locations and years was tested for each

Table 5. Genotype by year analyses of the additive components of variation.

Source	df	Mean squares			
		Yield of seed cotton, g/plant	Yield of lint, g/plant	Lint percent	Earliness, %
Years	1	859	411*	87.85**	499.36
Reps within years	4	367	39	7.12**	278.66
Parents	9	2,786	320	12.32**	538.37*
Years \times parents	9	908	102	2.30*	143.98
Error	36	709	83	1.05	141.62

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

trait using the analyses devised by Allard (2) for the additive and dominance components of variation. Since a single location was used in these experiments, a location effect is confounded in the results rendering them less sensitive than they would have been had an additional location been used.

The test for additive components is based on the assumption that heritable differences between homozygous parents, in the absence of epistasis, are determined by the additive effects of genes (2). Estimates of plot means for each trait were obtained for each parent in each replication in 1965 and 1966, and analyses of variance were then conducted among those 60 means. The form of the analysis and the results for each variable are given in Table 5. Since no significant epistasis was detected for these traits, Allard's (2) interpretations assuming no epistasis were followed. The years mean square has no specific genetical interpretation since any of a large number of environmental factors can cause significant differences in this source of variation. Years were considered to be random; and as a consequence, the years by parents mean square was used to test parents mean square. The significance versus nonsignificance of the parents mean squares indicates that certain parents carried alleles with different additive effects for lint percent, and earliness, whereas they did not for seed cotton and lint yield. The significant interaction term for lint percent suggests that those additive effects were not constant relative to one another from year to year. Those for earliness appeared to be constant. The yield variables did not exhibit significant interactions of additive variation with years.

The test for dominance components (2) is an analysis of variance of the 60 V_r and 60 W_r estimates for each trait from the 10 arrays, three replications, and two years in which the F_1 was studied. Individual V_r and W_r terms within each replication were divided by the variance among the parents in that replication before analysis to minimize the additive components in the test and, in doing so, to increase the test's sensitivity to dominance interaction terms. This rescaling also tends to minimize the fluctuation of basic variability between environments which is likely to mask between-environment comparisons in genetic systems (2). The form of the analysis and the results for each trait are listed in Table 6. The interpretations again follow Allard's (2) reasoning where epistasis is not a complicating factor. The years mean square was significant for earliness indicating that rescaling was at least partially ineffective for that character. Significance of the dominance mean square suggests that the mean degree of dominance for each trait was either partial dominance or overdominance. Reference to Table 8 shows the latter alternative to be correct for each trait. The significance of the years by dominance

Table 6. Genotype by year analyses of the dominance components of variation.

Source	df	Mean squares			
		Yield of seed cotton, g/plant	Yield of lint, g/plant	Lint percent	Earliness, %
Years	1	0.0385	0.3922	0.0264	0.5590*
Reps within years	4	4.5038**	4.3214**	0.2263**	0.0629
Dominance	1	31.5085**	36.7635**	1.6054**	9.2686**
Years \times dominance	1	0.6796	0.6049	0.0048	1.5209**
Arrays	9	0.5045	0.4712	0.1422*	0.1841
Years \times arrays	9	0.0988	0.1911	0.0207	0.1486
Dominance \times arrays	9	0.5245	0.5116	0.0171	0.0622
Years \times dominance \times arrays	9	0.2130	0.2597	0.0250	0.0399
Error	76	0.5460	0.5560	0.0347	0.1099

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

interaction for earliness indicates that mean dominance for that trait was significantly different in the two years, whereas the nonsignificance of this interaction for the other characters shows the reverse. The arrays mean square was significant for lint percent, suggesting differences in dominance among the parents for that trait. Such differences were not in evidence for the yield variables or earliness. No significant years by arrays interaction was obtained, signifying that the dominance relationships among the parents were constant from year to year. The lack of significance of the dominance by arrays and the years by dominance by arrays mean squares for each trait provides additional evidence for the lack of epistasis in this material.

Parameter Estimates

Estimates of population parameters for a trait are feasible even when that trait has exhibited partial failures of the assumptions (5). However, such estimates are not as reliable as they would be had all of the assumptions been fulfilled. Individual estimates for each parameter were obtained in each replicate as suggested by Nelder (14); and standard errors of the mean, used in the tests of significance, were estimated by the variation of block values around the overall mean. The mean parameter estimates and their significance levels are listed in Table 7. E_0 , E_1 , and E_2 are estimates of parental, F_1 , and F_2 environmental variances, respectively. Estimates of E_0 were obtained for each trait from a between plot-within plot analysis of variance of the parental entries within each replication. Since the other parameters were estimated on a plot mean basis, it was essential to put the estimates of E_0 on an equivalent basis; and this was accomplished by dividing the within plot mean square by the average number of plants per plot for the parental entries in that replication. E_1 and E_2 were obtained in the same manner using F_1 and F_2 entries, respectively. The other parameters (D , F , H_1 , and H_2) are as defined by Jinks and Hayman (10) using the notation of Mather (12) and were calculated using Hayman's (7) formulas. D is the additive genetic variance, F is an indicator of the relative frequency of dominant versus recessive alleles in the parents, and H_1 and H_2 are dominance genetic variances.

All estimates of environmental variation were significantly different from zero. As was true for the fiber traits (18, 19), E_0 was larger than the corresponding E_1 for lint percent and earliness in both years. This trend was reversed in the yield variables. D was significant in both years for lint percent and earliness,

Table 7. Mean parameter estimates of the agronomic traits studied.

Parameter	F ₁ (1965) F ₁ (1966) F ₂ (1966)			F ₁ (1965) F ₁ (1966) F ₂ (1966)		
	Yield of seed cotton, g/plant			Yield of lint, g/plant		
E_0	213**	375*	--	30*	44*	--
E_1	239**	510**	--	35**	64**	--
E_2	--	--	499**	--	--	61**
D	395	1,194	--	50	127	--
F	-29	1,025	2,059	-16	128	196
H_1	957	3,197*	6,048*	129*	357**	578
H_2	988	2,715	3,952	136*	296*	437
	Lint percent			Earliness, %		
E_0	0.61*	0.79*	--	58.61**	48.47*	---
E_1	0.44**	0.67*	--	55.17**	47.15*	---
E_2	--	--	0.86*	--	--	52.55**
D	3.35*	1.52*	--	259.49*	49.71*	---
F	2.28	0.84	2.00*	53.00	-4.36	130.85*
H_1	5.23	1.32	8.27	466.96*	167.95*	576.96
H_2	4.16*	0.72	6.45	445.41**	161.09*	442.08

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

but not in either year for yield of seed cotton or lint. F was not significant for any trait in the F_1 , and it was consistent in sign over all three sets of data only for lint percent. It was positive and significant in the F_2 for lint percent and earliness, suggesting a predominance of dominant alleles in the parents for those traits in that generation. H_1 and H_2 or both were significant in at least one instance for each trait. Both were larger than D in every case except for lint percent in the 1966 F_1 . The exhibition of significance or non-significance for each character was consistent for D as it was for the fiber traits with the exception of fiber length (19). F was consistent in this regard only in the F_1 from year to year while H_1 and H_2 were not consistent at all.

Several ratios were obtained using the estimates calculated for Table 7 to provide further information about each trait. Each ratio was estimated in each replication (14), and means of those estimates and their 95% confidence limits are shown in Table 8. Standard errors of the mean were again estimated by the variation of block values around the overall mean.

Three estimates of degree of dominance are listed in Table 8 with the formulas for their calculation provided in a footnote to that table. All estimates except those for lint percent in the 1966 F_1 were in the over-dominance range. Lint percent in that instance exhibited estimates in the range between 0 and 1, indicating partial dominance. Some mention should be made of dominance estimator three. In the 1966 F_1 for seed cotton yield and lint yield and in the F_2 for earliness, mean values were obtained which were conspicuously different from the others. Investigating further, it was found that each of those mean estimates was markedly influenced by an estimate from a single replication, and those single estimates were apparently due to pronounced underestimates of W_{0L01} and W_{0L02} . Ignoring the obviously dissimilar estimate in each case, dominance estimator three over the other two replications averaged 2.34, 2.75, and 1.81 for yield of seed cotton, yield of lint, and earliness, respectively. Each of these values is more realistic than the means obtained over all three replications, and each corresponds much more closely with the mean values obtained using dominance estimators one and two.

K estimates the number of effective factors as defined by Mather (12), and it measures only those factors showing some degree of dominance. The formula for its estimation in the F_1 is described by Jinks (9)

Table 8. Mean estimator ratios of the agronomic traits studied.

Estimator	F ₁ (1965)	95% confidence limits	F ₁ (1966)	95% confidence limits	F ₂ (1966)	95% confidence limits	F ₁ (1965)	95% confidence limits	F ₁ (1966)	95% confidence limits	F ₂ (1966)	95% confidence limits
	Yield of seed cotton, g/plant						Yield of lint, g/plant					
Dominance 1*	5.13	(-8.55)-18.81	11.85	(-28.43)-52.13	4.64	(-10.98)-20.26	6.39	(-10.99)-23.77	11.07	(-24.01)-46.16	2.80	0.39 - 5.21
Dominance 2*	2.07	(-0.81)-4.95	2.84	(-3.10)-8.78	1.82	(-1.71)-5.35	2.27	(-1.17)-5.71	2.82	(-2.56)-8.20	1.52	(-0.65)-3.69
Dominance 3*	2.03	(-0.08)-4.14	46.99	(-145.18)-239.16	2.57	(-2.89)-8.03	2.14	(-0.14)-4.42	-5.11	(-28.92)-39.14	1.70	(-0.07)-3.47
K	3.12	(-2.73)-8.97	2.58	1.72 - 3.44	1.78	(-1.45)-5.01	3.41	(-1.80)-8.62	2.73	1.95 - 3.51	1.76	(-1.24)-4.76
1/4 (H ₂ /H ₁)	0.26	0.24 - 0.28	0.20	0.11 - 0.29	0.16	0.12 - 0.20	0.26	0.24 - 0.28	0.20	0.08 - 0.32	0.20	0.10 - 0.30
Heritability	0.15	(-0.17)-0.47	0.26	(-0.51)-1.03	0.34	(-0.43)-1.11	0.14	(-0.18)-0.46	0.25	(-0.51)-1.01	0.31	(-0.47)-1.09
	Lint percent						Earliness, %					
Dominance 1*	1.55	1.38 - 1.72	0.82	0.17 - 1.47	1.40	(-0.75)-3.55	1.85	0.53 - 2.38	3.68	(-1.16)-8.52	3.01	(-3.23)-9.25
Dominance 2*	1.23	1.06 - 1.40	0.90	0.56 - 1.24	1.15	0.29 - 2.01	1.35	0.87 - 1.83	1.86	0.45 - 3.27	1.63	(-0.18)-3.44
Dominance 3*	1.40	0.54 - 2.26	0.80	0.50 - 1.10	1.34	(-0.38)-3.06	1.45	0.67 - 2.13	2.81	(-0.93)-6.53	31.92	(-97.67)-161.51
K	1.73	(-2.49)-5.95	8.12	(-11.72)-27.96	0.57	(-0.72)-1.86	1.45	0.32 - 2.58	1.30	(-0.89)-3.49	2.70	(-8.30)-13.70
1/4 (H ₂ /H ₁)	0.21	0.19 - 0.23	0.12	(-0.01)-0.25	0.18	0.14 - 0.22	0.24	0.19 - 0.29	0.25	0.17 - 0.33	0.17	0.06 - 0.28
Heritability	0.40	0.03 - 0.77	0.32	0.02 - 0.62	0.26	0.00 - 0.52	0.29	0.15 - 0.43	0.12	0.08 - 0.16	0.15	0.04 - 0.26

* Dominance estimators one, two, and three in the F₁ were obtained with the formulas H_2/D , $(H_2/D)^{1/2}$, and $(V_{2L2}-E)/(W_{0L02}-E/n)$, respectively. These formulas in the F₂ were modified into $\frac{1}{2}(H_1/D)$, $\frac{1}{4}(H_2/D)$, and $(V_{2L2}-E)/(W_{0L02}-E/n)$, respectively. The interpretations of the symbols, V_{1L1} , V_{2L2} , W_{0L01} , W_{0L02} , and n , can be obtained from Jinks and Hayman's papers (5, 7, 9, 10).

while that for the F₂ has been described previously (19). K is underestimated if the dominance effects of the genes affecting that trait are not equal in size and direction or if the distribution of the genes is correlated (9, 12). Estimates for the yield variables and earliness were fairly uniform from year to year in the F₁ and from the F₁ to the F₂. Each had one estimate significantly different from zero. The estimates for lint percent were highly erratic between sets of data ranging from .57 to 8.12 and were also erratic within each set, as evidenced by the fact that none of its estimates were significantly different from zero.

The ratio $1/4 (H_2/H_1)$, estimates the average frequency of negative versus positive alleles in the parents (4). If distribution is equal, the ratio should be 0.25; if unequal, it will be smaller. Only the 1965 F₁ estimate for lint percent and the F₂ estimates for lint percent and yield of seed cotton were significantly different from 0.25. The 1966 F₁ lint percent was also low and almost did not include 0.25 in its confidence interval. One may reasonably conclude that the parents probably did not have an equal distribution of such alleles for lint percent. The same conclusion applies to yield of seed cotton in the F₂.

Narrow-sense heritability estimates on a plot mean basis were calculated in the F₁ using the formula devised by Crumpacker and Allard (4). The formula used in the F₂ may be found in a previous paper (19). None of the heritabilities for yield were significantly different from zero. The F₂ estimate for lint percent was also not significant. Letting "<" represent a mean heritability difference of about .10 units, these characters may be ranked on the basis of their heritabilities as follows: (earliness, yield of lint, yield of seed cotton) < lint percent. Should one desire to combine this hierarchy with the one constructed for the fiber properties (19), the average values for lint percent and micronaire were of similar magnitude, with the latter averaging some .05 units lower. The heritabilities averaged over the three sets of data reveal that about one-fifth of the variance exhibited by earliness, one-fourth that by yield, and one-third of that by lint percent is additive in nature. Mass selection on a plot mean basis when plots are small should be relatively ineffective for these traits compared to selection for fiber length or strength (19). Some emphasis on pedigrees, sib tests, or progeny tests (or combinations of them) may be necessary to make adequate improvement in lint percent and almost certainly will be required for the other three traits.

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