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Heterosis and Combining Ability in Diallel Crosses of Upland Cotton, *Gossypium hirsutum* L.[1]

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LODEN and Richmond (6) reviewed early work on heterosis in cotton, pointing out findings ranging from little or no hybrid vigor in certain crosses to rather substantial amounts in others. More recent investigations (1, 5, 10, 12) likewise indicate variable results from crosses among Upland cotton strains. Generally, in any group of material, certain crosses exhibit substantial heterosis for yield and certain component of yield as measured by a comparison of the F_1 with the average performance of the parental lines. When such F_1's are compared with the best of all the parents in the study or with standard commercial checks, however, there are very few instances of significantly superior performance of the hybrids. Heterosis seems to be of primary importance in yield, boll number, and boll size. Lint percent and fiber traits occasionally show small effects but are generally intermediate between the parents.

Rather meager and inconclusive information is available on the relative magnitudes of general and specific combining ability in Upland cotton. Turner (11), from an experiment comprised of diallel crosses of 7 inbred lines, reported specific combining ability to be more important than general combining ability for yield. Barnes and Staten (1) reported estimates for general and specific combining ability from diallel crosses of seven western Acala strains likewise indicating specific effects of greater magnitude than general effects. In another set of crosses involving Southeastern varieties, however, specific combining ability was not evident. White (12) from a diallel cross study among five primitive and foreign strains of *Gossypium hirsutum* reported a preponderance of general combining ability effects as compared to specific, although the latter were significant for yield.

At the present time pure F_1 seed in cotton can only be produced by laborious hand pollination procedures. This may account for the rather limited and inconclusive information available on heterosis and combining ability in cotton. The results of many studies involving different groups of material and different methods of experimentation will need to be accumulated before a clearer and more useful picture of the phenomena will begin to emerge. The present study was designed to provide some additional information which might contribute to a better understanding of the problem. Specific objectives were *(1)* to estimate amount of heterosis and inbreeding depression in a set of Upland cotton crosses and *(2)* to obtain estimates of variances of general and specific combining ability and examine their implications on breeding methods in cotton.

MATERIALS AND METHODS

At the initiation of the experiment an attempt was made to obtain a representative sample of American Upland cotton germplasm. Accordingly, 8 inbred lines, representing 8 different varietal sources, were chosen as follows:

Inbred line	*Source variety*
A-1	Deltapine 14
B-6	Cook 144
F-3	Stoneville 2B
G-4	Coker 100
L-3	Rowden 80
H-1	Acala 1517
K-2	Mexican Big Boll 128
M-8	Florida Green Seed

None of the source varieties listed above are grown today as commercial varieties. However, selections within or from crosses between these older varieties provide a substantial portion of the current commercial germplasm. The inbred lines were extracted by at least eight generations of continuous selfing of individual plants. Some visual selection was practiced during the inbreeding process; the main criterion, however, was to obtain relatively homozygous strains representative of their respective source varieties.

The 8 parental lines, together with all possible 28 F_1 crosses among them, the 28 F_2 populations, and a commercial check variety, Coker 100 Wilt, were evaluated at Clayton and Rocky Mount, N. C., in 1956. Reciprocal F_1 crosses were bulked. Three replications were grown at each location. Each plot consisted of 1 row, 15 feet long, with a spacing between rows of 42 inches at Clayton and 36 inches at Rocky Mount. Final stands averaged 3 plants per foot of row. Normal cultural practices were followed throughout the season.

Data were obtained on lint yield, line percent, and weight per boll from all plots at both locations. Percent yield at first pick as an index of earliness was measured only at the Clayton location. Fiber length (fibrograph, upper-half-mean in inches) and fiber strength (stelometer, T_1 index) values were obtained from two replicates of the Clayton test. A randomly selected sample of 25 bolls was harvested from each plot to obtain the information on lint percent and weight per boll. A 12-gram sample of lint was analyzed by the U. S. Department of Agriculture Fiber Laboratory at Knoxville, Tenn., for the fiber quality characteristics. Percent first pick was calculated by dividing the weight of seed cotton harvested at the first pick by the total weight of seed cotton per plot. Lint yield values were obtained by multiplying the total weight of seed cotton per plot by the lint percentage value for that plot.

RESULTS

Heterosis and Inbreeding Depression

There were significant differences among the parents for all characters measured. The inbred parental lines ranged in yield from 297 to 756 pounds of lint per acre, with only one of the lines exceeding the commercial check. Parental lines were also generally lower in lint percent and fiber length than the commercial check.

Comparisons of average parent, F_1, and F_2 generations are given in Table 1. Heterosis, expressed as percent increase of the F_1 hybrids above the average of the parents, was significant for all characters measured. The F_1 hybrids had higher lint yields, higher lint percent, larger bolls, longer and stronger lint, and were earlier than the average of the parental lines. The magnitude of the average heterotic effects was greatest for yield, medium for boll weight and earliness, and relatively small for the remaining traits.

Inbreeding depression, measured as the average percent decrease of the F_2 from the F_1, was observed for all characters measured, although it was not statistically significant for either fiber strength or earliness. Those characters which

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evidenced the greatest amount of heterosis, likewise showed the most inbreeding depression. Analysis of the variance associated with the regression of mean values on generations indicated the inbreeding depression was largely of the linear order, although small but significant deviations were noted for 4 traits (Table 1). Observed F_2 means for lint yield and weight per boll were less than expected from the linear regression on generations, while fiber strength and percent first pick were higher than expected.

Since the primary interest in heterosis in cotton is centered on lint yield, a more detailed examination of heterosis and inbreeding depression for this trait in the eight inbred lines is presented in Figure 1. The first bar indicates the performance of each parent. The second bar indicates the average of the 7 midparent values involving the parent and the other 7 lines to which it was crossed. The solid bar represents the average of the 7 F_1 hybrids between the parent and the other 7 inbreds, and the last bar indicates the average F_2 performance of the 7 corresponding crosses. For each common parent, the average yield of its F_1 hybrids was substantially higher than the corresponding midparent value. The F_2 populations generally gave yields intermediate between F_1 and midparent averages. The parental inbreds are located in Figure 1 in the order of descending yield from left to right. There was a tendency for the average yield of the F_1 hybrids involving a common parent to likewise decrease in yield as the yield of the common parent decreased. It should be noted, however, that the absolute amount of heterosis (difference between the F_1 hybrids and their average midparent value on a pounds of lint per acre basis) tended to remain constant, regardless of the common parent yield. If expressed on a percentage basis, heterosis was thus substantially greater in crosses involving low yielding lines (40–45%) than in crosses between high yielding parents (20–39%).

Table 1—Average performance of parental, F_1, and F_2 generations and average percent heterosis, inbreeding depression, and F_2 deviation from linear regression for agronomic and fiber traits in cotton.

Character	Generation			Check variety	Heterosis, %†	Depression, %‡	F_2 deviation, %§
	Parent	F_1	F_2				
Lint yield, lb./A.	505	644	532	603	27.5**	17.4**	-7.4*
Lint %	33.7	34.2	33.8	35.8	1.5**	1.2**	-0.4
Weight per boll, g.	7.11	7.74	7.33	6.93	8.9**	5.3**	-1.3*
Fiber length, U.H.M., in.	1.12	1.16	1.14	1.17	3.6**	1.7**	0.0
Fiber strength, T_1	1.81	1.87	1.86	1.84	3.3**	0.5	+1.1*
Earliness, % 1st. pick	66.3	74.2	72.0	65.0	11.9**	3.0	+2.5*

*, ** Significant differences from zero at 5% and 1% levels. † $(F_1 - MP)/MP$
‡ $(F_1 - F_2)/F_1$. § [observed $F_2 - (F_1 + MP)/2]/[(F_1 + MP)/2]$.

Considering the 28 individual F_1 crosses, all but 1 exceeded the midparent value for that cross in yield, and all but 6 exceeded the best parent involved in the cross. In the entire group of F_1 hybrids, however, none were significantly higher yielding than the best parental line, G-4, although 4 crosses exceeded the G-4 line by small amounts.

An examination of the individual F_1 hybrids for the traits other than yield revealed that even though there was significant heterosis as measured from the midparent value in a majority of the crosses, many of the hybrids did not exceed the value of the high parent of the cross. As with yield, the highest F_1 values for any trait were generally only equal or slightly superior to the best of the eight parents for that particular character. Individual F_2 generation values for all traits tended to be intermediate between the midparent value and the corresponding F_1.

Components of Variance

The F_1 data from the two locations were analyzed as outlined by Rojas and Sprague (8) and estimates obtained of the appropriate components of variance. The significance of the estimates of variances of general combining ability was determined by an approximate F-test, according to

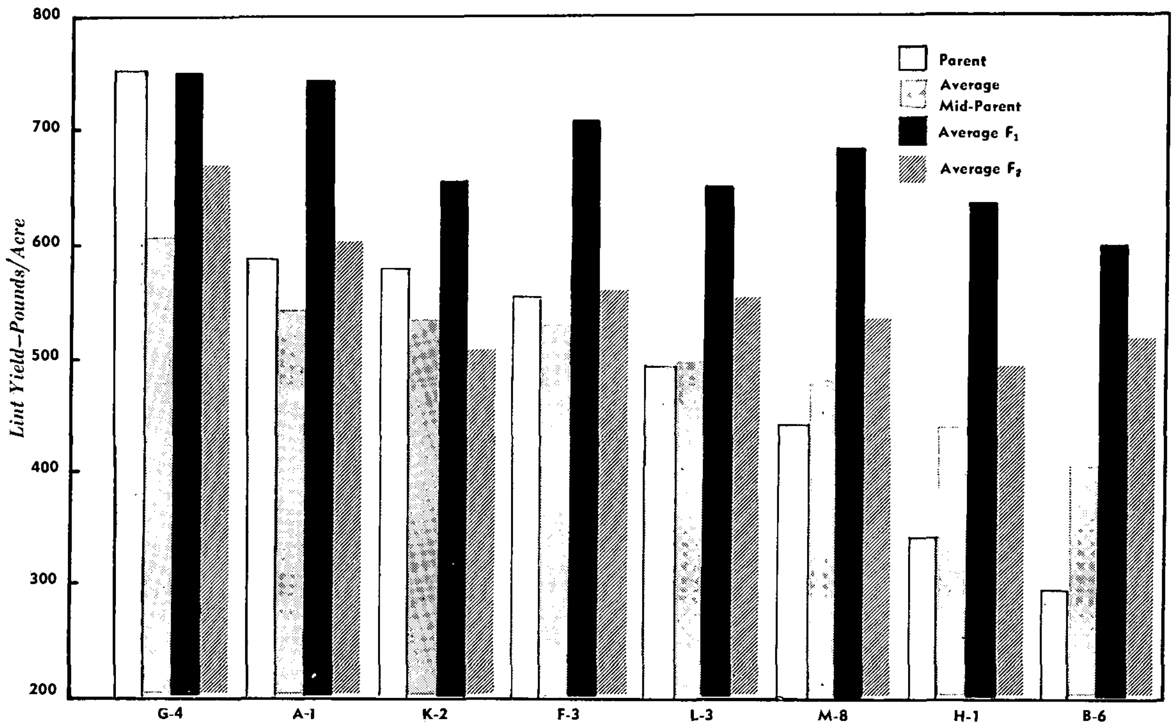

Figure 1—Parent, midparent, F_1 and F_2 means for lint yield in cotton (Explanation in text).

Cochran (2). A similar analysis was made on the F_2 generation. Estimated components of variance from each generation and for all characters studied are presented in Table 2.

Variances of general combining ability (σ^2_g) were relatively large in magnitude and significant for all characters studied. In contrast, variances of specific combining ability (σ^2_s) were much smaller in magnitude and significant in only three cases; for weight per boll in the F_1 generation, and for lint yield and lint percent in the F_2 generation. Variances of the interactions of general and specific effects with locations were generally small and nonsignificant. Only 1 of the 12 interaction estimates, lint percent in the F_2 generation, was significant at the 5% level of probability.

General Combining Ability of Individual Parents

Estimates of the general combining ability (g_i) of each line, relative to the others in the set of parents, were calculated by method 4, model 1, of Griffing (4). These, together with the performance of the parental lines themselves, are given in Tables 3 and 4 for lint yield and weight per boll, respectively. Tests of significance were made by Duncan's (3) multiple range test.

There is very close agreement between the estimates of general combining ability from the F_1 and F_2 generations, as well as a marked tendency for the ranking of the lines for general combining ability effects to be the same as the ranking based on parental performance *per se*. Although not presented here, similar calculations for the remaining traits followed this same general pattern.

DISCUSSION

Nature of Gene Action

One of the major interests from the study of heterosis for this material is its implications on the nature of gene action in cotton. The eight parental lines used in this study were chosen as a sample of available germplasm in American Upland. Matzinger and Kempthorne (7) have shown that the estimates of variance of general combining ability (σ^2_g) and specific combining ability (σ^2_s) from the diallel set of crosses of such parents relate to estimates of genetic variance for the population of which the parental lines are a sample. The expectations are as follows:

$$\sigma^2_g = (1/2)\,\sigma^2_A + (1/4)\,\sigma^2_{AA} + (1/8)\,\sigma^2_{AAA} + \ldots.$$

$$\sigma^2_s = \sigma^2_D + (1/2)\,\sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD} + (3/4)\,\sigma^2_{AAA} + \sigma^2_{AAD} + \sigma^2_{ADD} + \sigma^2_{DDD} + \ldots.$$

where σ^2_A = additive genetic variance, σ^2_D = dominance variance, σ^2_{AA} = additive $\times$ additive epistatic interaction, etc.

The sizeable magnitudes of the estimates of σ^2_g in this material thus suggest that a major portion of the genetic variance in the base population is additive in nature. On the other hand, the presence of small but statistically significant estimates of σ^2_s for boll weight in the F_1 generation and for lint yield and lint percent in the F_2 generation do suggest that at least some of the genetic variance in the population is nonadditive (dominance and epistasis). The small but significant deviations of the F_2 mean values from the linear regression of lint yield, boll weight, fiber strength, and earliness on generations, suggest the presence of epistasis for these traits. Such deviations can not be accounted for by either additive or dominance effects (9).

It is difficult to reconcile the rather large magnitudes of heterosis and inbreeding depression observed for yield with the very small estimates of σ^2_s. Such heterosis and inbreeding depression effects can only be explained through the presence of some type of nonadditive gene effects. It may be that the nonadditive effects, although quite small as compared to the additive ones, are still sufficient to account for rather sizeable amounts of heterosis and inbreeding depression. It should be emphasized that the estimates of σ^2_g and σ^2_s are only relative values and depend upon the specific sample of parents studied. There was a very wide range in the yield performance of the 8 parents as inbreds (297 to 756 lbs./A.), and the average performance of each parent in crosses was rather closely correlated with the performance of the selfed parental lines. These observations suggest the presence of very sizeable variances for additive effects in the base population. Although nonadditive variances may also be present and very real in their effects, their magnitudes in this study could only be measured in relative terms and thus they appeared quite small.

The present results are in general accord with those

Table 2—Estimates of variance of general (σ^2_g) and specific (σ^2_s) combining ability and interactions with locations, (σ^2_{gl} and σ^2_{sl}).

Variance components	Lint yield	Lint, %	Weight per boll	Fiber length	Fiber strength	Earliness
			F_1 generation			
σ^2_g	3894**	1.500**	0.229**	0.002**	0.008**	19.47**
σ^2_s	-441	0.047	0.068**	0.000	0.001	0.25
σ^2_{gl}	-276	-0.006	0.009	-	-	-
σ^2_{sl}	1201	-0.032	-0.018	-	-	-
			F_2 *generation*			
σ^2_g	3481**	1.282**	0.239**	0.002**	0.004**	22.92**
σ^2_s	1735*	0.187*	-0.011	0.000	0.003	7.14
σ^2_{gl}	732	0.055*	0.008	-	-	-
σ^2_{sl}	683	-0.094	0.018	-	-	-

*, ** Significant differences from zero at 5% and 1% levels.

Table 3—Estimates of the relative general combining ability (g_i) of the parental lines in the F_1 and F_2 generations and the performance of the lines, *per se*, in respect to lint yield.

Parental line	g_i† F_1	g_i† F_2	Yield of parental line†, lb./A.
G-4	552 a	763 a	756 a
A-1	440 a	343 b	587 b
F-3	250 ab	81 bc	562 b
M-8	17 abc	-204 cd	436 bc
K-2	-172 bc	-293 cd	571 b
L-3	-191 bc	15 bc	493 b
H-1	-355 bc	-459 d	339 c
B-6	-536 c	-247 cd	297 c

† Results followed by the same letter are not significantly different at the 5% level.

Table 4—Estimates of the relative general combining ability (g_i) of the parental lines in the F_1 and F_2 generations and the performance of the lines, *per se*, for weight per boll.

Parental line	g_i† F_1	g_i† F_2	Weight per boll†, g.
L-3	4.44 a	4.53 a	8.73 a
H-1	2.60 b	1.41 b	7.37 ab
F-3	1.98 b	2.06 b	8.11 a
K-2	1.50 b	2.41 b	8.12 a
M-8	-1.77 c	-1.75 c	6.31 b
B-6	-1.99 c	-2.21 c	6.11 b
G-4	-3.00 cd	-2.47 cd	6.38 b
A-1	-3.82 d	-3.99 d	5.76 b

† Results followed by the same letter are not significantly different at the 5% level.

reported by Ramey.[3] Ramey found in an analysis of the genetic variance of two F_2 populations of Upland cotton that the nonadditive genetic variances were generally small relative to the additive genetic variances. The average degree of dominance in his material appeared to be in the partial to complete range.

Implications on Breeding Methodology

There was little or no "useful" heterosis observed in this set of material, since even the best F_1 hybrids generally were not significantly superior to the best of the 8 parental lines. It should be pointed out, however, that only one of the parental lines has a yield performance at a commercially acceptable level. Thus in this set of material it was not possible to study crosses among parents of high level performance *per se*. Such crosses might be expected to show heterosis of potentially greater usefulness.

The estimates of sizeable amounts of additive genetic variance in the base population certainly suggest that significant advancements can be made through the use of selection procedures which increase the frequency of favorable genes showing primarily additive effects. On the other hand, the magnitude of the heterosis and inbreeding depression for traits such as lint yield, definitely indicate the presence of nonadditive variance in the base population. The greatest ultimate advance, therefore, would depend upon breeding procedures which utilize both types of genetic variance.

It would appear most feasible to first proceed with selection which would increase the frequency of favorable genes with additive effects. Certainly the data from the present set of material indicate there is little to be gained from testing F_1 crosses among parental lines of poor performance *per se*. The data likewise suggest that selection based on the performance of the selections *per se*, would also be effective in improving general combining ability. Ultimately, as a major portion of these favorable genes with additive effects become fixed or homozygous, breeding procedures which can utilize the nonadditive variation might prove profitable.

It has been generally observed in many plant species that crosses between genetically diverse parents exhibit more heterosis than crosses between more closely related strains. This suggests that it would be desirable to proceed with selection for favorable genes with additive effects in separate and diverse populations. Maximum usefnl heterosis might thus be obtained ultimately through crosses between high yielding strains isolated from genetically diverse populations.

SUMMARY

Eight inbred lines of Upland cotton and all possible F_1 hybrids and F_2 populations were evaluated at 2 locations. The characters studied included lint yield, lint percent, and weight per boll. In addition, earliness, fiber length, and fiber strength were measured at one of the locations.

Heterosis, expressed as percent increase of the F_1 hybrids above the average of the parents, was significant for all characters measured. The magnitude of the heterotic effects was greatest for lint yield (27.5%), medium for boll weight and earliness, and relatively small for the remaining traits. Inbreeding depression in the F_2 generation was observed for all characters, although it was not statistically significant for either fiber strength or earliness.

A diallel analysis of variance of the F_1 and F_2 generations suggested an appreciable amount of variance due to general combining ability for all characters. In contrast, variances of specific combining ability were much smaller in magnitude and significant only in 3 cases; boll weight in the F_1 generation, and lint yield and lint percent in the F_2 generation. Variances of the interactions of general and specific effects with locations were generally small in magnitude and nonsignificant. Estimates of the relative general combining ability of the individual parental lines indicated a rather good agreement between the ranking of the lines for such effects and the ranking based on parental performance *per se*.

If reference is made to a base genetic population, the results of the diallel analysis suggest that the major portion of the genetic variance resulted from genes with additive effects. The observed heterosis and inbreeding depression of rather sizeable magnitudes for yield, however, indicate the presence of some type of nonadditive gene effects. Although inbreeding depression was largely of the linear order, small but significant deviations were noted for 4 of the 6 traits, suggesting the presence of some epistatic effects.

No "useful" heterosis was observed in this set of material since even the best F_1 hybrids were not significantly superior to the best of the eight parental lines.

Implications of these findings on breeding procedures are discussed.

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