

# Transgressive Segregation and the Nature of Gene Action for Yield in an Intervarietal Cross of Upland Cotton<sup>1</sup>

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## ABSTRACT

Two inbred parental lines, their  $F_1$ , and six inbred lines selected for high yield after three cycles of recurrent selection in this population were evaluated at three locations for two years. The  $F_1$  yielded 32.6% more than the midparent value and exceeded the higher parent by 13.3%. The  $F_1$  also exceeded the midparent values for several components of yield, including lint percentage, weight per boll, number of bolls per plot, lint index, and seed index.

The mean yield of the six selected lines exceeded that of the  $F_1$  by 5.5%. Each of the six lines was higher in lint yield and lint percentage than the higher parent of the original cross, which indicated that transgressive segregation for these traits had occurred.

Fifteen possible crosses among the six lines were compared with the above entries at three locations in the second year. These hybrids averaged 9.6% higher in yield than the mean of their parents. Significant heterosis was also detected for lint percentage, weight per boll, number of seed per boll, and lint index.

Estimates of general combining ability from the set of diallel crosses were significant for all traits except lint percentage, which demonstrated the importance of additive genetic effects for those traits. The variance for specific combining ability was significant only for lint percentage.

**Additional index words:** Heterosis, Combining ability, Recurrent selection, Hybrid cotton, Components of yield.

**H**ETEROISIS in cotton has been observed for yield with increases ranging from very small amounts up to 40% above midparent values. Loden and Richmond (1951) reviewed the early work on heterosis in *Gossypium* and presented evidence of significant increases in yield that resulted from interspecific, intervarietal, and intravarietal crosses. More recently, Al-Rawi and Koehl (1969), Miller and Marani (1963), White and Richmond (1963), and others have reported additional evidence of heterosis for yield.

However, the production of  $F_1$  hybrid seed on a commercial scale is not economically feasible at the present time due to lack of a fully satisfactory male-sterility mechanism and to the frequently low amounts of natural crossing in the major production areas. The question arises, therefore, whether it would be

possible to select strains from the segregating generations of superior  $F_1$ 's which would equal or exceed the performance of the  $F_1$  per se.

The genetic materials used in the present investigation included two inbred parental lines, their  $F_1$ , six inbred lines selected for high yield after three cycles of recurrent selection in this population, and the diallel set of 15 crosses among those six lines. Observations are reported on: (a) the amount of heterosis in the original cross, (b) the performance of the six selected lines compared with the  $F_1$  from which they were selected, and (c) the heterotic effects in the diallel cross.

## MATERIALS AND METHODS

### Genetic Material

Genetic materials used in this study included two inbred lines (G-4 and H-1), the  $F_1$  between them, six inbred lines selected for high lint yield after three cycles of recurrent selection (cycle-3 selections), and the diallel cross among those six lines. G-4 and H-1 are selections from a pedigree system of inbreeding in the 'Coker 100' and 'Acala 1517' varieties, respectively. The cycle-3 selections were maintained through more than six generations of bulk selfing of a 75-plant progeny row. Approximately equal numbers of selfed seed were harvested from each plant. These selections can be assumed to be relatively homozygous but not homogeneous. A more detailed description of the original parents and the technique used to derive the cycle-3 selections has been presented by Miller and Rawlings (1967). Reciprocal crosses were bulked to produce the seed of the diallel cross.

### Design of Experiments

The two inbreds, the  $F_1$ , and the six selections were evaluated at Rocky Mount, Lewiston, and Clayton, N. C. in 1967 and 1968. The 15 diallel crosses were included only in the 1968 tests. A randomized complete-block design with four replicates was grown at each location in each year.

### Cultural Practices and Data Collected

Plots were single rows 7.6 m long with row spacings of 1.0 m at Rocky Mount, 0.9 m at Lewiston, and 1.1 m at Clayton. An excess of seed was drilled in each plot; and following emergence, seedlings were thinned to a uniform stand approximating nine plants per meter of row. Fertilizer and insecticide applications were in accordance with recommended practices for each of the locations.

A randomly selected sample of 25 bolls was harvested from each plot in 1967 and at Rocky Mount in 1968. A 50-boll sample was harvested at the remaining two locations in 1968. These boll samples were used to determine lint percentage, weight per boll in grams, number of seed per boll, lint index (weight of the lint from 100 seeds in grams), and seed index (weight of 100 seeds in grams). Data were recorded for seed cotton yield within each plot. Lint yield values were calculated by multiplying total weight of seed cotton per plot by the lint percentage value for that plot. Values for number of bolls per plot were computed by dividing total seed cotton weight by the weight per boll (as determined from the boll sample).

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## Statistical Analyses

Entries, locations, and years were considered as random variables constituting representative samples of their populations. A combined analysis of variance over the three locations in two years was computed for the two inbreds, the  $F_1$ , and the six selections. A combined analysis over the three locations in 1968 was computed for the same entries including the 15 diallel cross entries. The form of the analysis of variance, the expectations of the mean squares, and the approximate F-test for entries were as outlined by Cochran and Cox (p. 565-567, 1957). Differences among entries were significant at the 0.01 level of probability for all traits in both analyses. The following comparisons between specific entries or groups of entries were made: (a)  $F_1$  versus midparent and  $F_1$  versus the higher parent; (b) the mean of the six selections versus the  $F_1$ ; and (c) the mean of the 15 diallel crosses versus the mean of their six parents. The first two comparisons were made from the combined two-year data while the latter comparison could only be obtained from the 1968 data. Tests of significance were made utilizing the variance of the difference between two means ( $s^2_d$ ) which was estimated as  $s^2/rn_1 + s^2/rn_2$ , where  $s^2$  is the appropriate error variance,  $r$  is the number of replications, and  $n_1$  and  $n_2$  were the number of entries involved in estimating the respective means. For the combined two-year analysis, the entry by location and entry by year interaction were small and statistically nonsignificant for all traits except line percentage, which exhibited a significant entry by year interaction; but even then, this component was smaller than the second-order interaction component. The second-order interaction was generally large and statistically significant. Thus, this mean square was used as the appropriate error term for the planned comparisons among means from the combined two-year data. For comparisons involving the 15 diallel crosses grown only in 1968, the entry by location interaction mean square was used as the appropriate error term. It is recognized that the variance component for entries in the entry mean square is confounded with the entry by year interaction since the material was grown in one year.

A diallel analysis of the 15  $F_1$ 's grown at the three locations in 1968 provided estimates of general combining ability ( $\sigma^2_g$ ), specific combining ability ( $\sigma^2_s$ ), and the interactions of those effects with locations. The expectations of mean squares followed those described by Matzinger and Kempthorne (1956). F-tests of both general and specific combining abilities were approximated as suggested by Cochran and Cox (1957).

## RESULTS

### Heterosis in the Original Cross

The performance of the parents and their  $F_1$  from the test data combined over years and locations is presented in Table 1. The  $F_1$  consistently exceeded the midparent with the differences being statistically significant for all traits except number of seed per boll. Lint yield of the  $F_1$  was 32.6% higher than the midparent value. This increased yield appears to result from the production of more and larger bolls per plant in combination with a higher lint index. The  $F_1$  yielded 13.3% more than its higher yielding parent.

### Transgressive Segregation

Performance of the cycle-3 selections in comparison with the  $F_1$  is presented in Table 2. The selections ranged in yield from 731 to 836 kg/ha as compared to 748 kg/ha for the  $F_1$  from which they were derived. The six selections averaged 5.5% higher in yield than the  $F_1$ , although this difference was not statistically significant. For components of yield, the selections averaged higher in lint percentage and number of bolls per plot but had smaller seed and smaller bolls than the  $F_1$ . Each selection was higher in lint yield and lint percentage than the higher parent of the original cross, indicating transgressive segregation for these traits. These results are in agreement with the

Table 1. Means and heterosis in the original cross estimated from data combined over years and locations.

Trait	Means				Heterosis	
	Parents		Mid-parent	$F_1$	Mid-parent, %†	High parent, %†
	G-4	H-1				
Lint yield, kg/ha	660	468	564	748	32.6**	13.3*
Lint, %	34.5	29.9	32.2	33.4	3.7**	-3.2*
Weight per boll, g	5.71	6.79	6.25	6.93	10.9**	2.1
No. of bolls/plot	252	169	210	242	15.2*	-4.0
No. of seed/boll	33.7	36.9	35.3	36.3	2.8	-1.6
Lint index	5.82	5.49	5.66	6.39	12.9**	9.8**
Seed index	11.2	12.9	12.0	12.8	6.7**	-0.8

\*, \*\* Significant at the 0.05 and 0.01 levels of probability, respectively. † Measured as 100 ( $F_1$  - Midparent)/Midparent. ‡ Measured as 100 ( $F_1$  - High parent)/High parent.

Table 2. Comparisons of the cycle-3 selections with the original  $F_1$  from data combined over years and locations.

Trait	$F_1$	Mean of selections	Mean of sel. vs. $F_1$ , %†	Range of indiv. sel.
Lint yield, kg/ha	748	789	5.5	731-836
Lint, %	33.4	36.4	9.0**	35.9-37.1
Weight per boll, g	6.93	6.18	-10.8**	5.58-6.65
No. of bolls/plot	242	262	8.3*	239-277
No. of seed/boll	36.3	35.7	-1.7	34.4-36.9
Lint index	6.39	6.31	-1.3	5.48-6.92
Seed index	12.8	11.1	-13.3**	9.6-12.4

\*, \*\* Significant at the 0.05 and 0.01 levels of probability, respectively. † Measured as 100 (Mean of selections -  $F_1$ )/ $F_1$ .

Table 3. Comparisons of the 15 diallel crosses with their six parental cycle-3 selections from 1968 data over locations.

Trait	Mean of sel.	Mean of diallel crosses	Heterosis %†	Range of indiv. sel.	Range of crosses
Lint yield, kg/ha	795	871	9.6**	769-833	771-957
Lint, %	37.4	37.9	1.3*	36.4-38.3	36.9-39.0
Weight per boll, g	5.57	5.77	3.6**	5.02-5.91	5.26-6.01
No. of bolls/plot	292	304	4.1	274-315	255-357
No. of seed/boll	34.4	35.1	2.0**	32.5-35.6	33.7-37.2
Lint index	6.09	6.26	2.8**	5.27-6.71	5.79-6.62
Seed index	10.2	10.3	1.0	8.0-11.5	9.1-11.1

\*, \*\* Significant at the 0.05 and 0.01 levels of probability, respectively. † Measured as 100 (Crosses - Sel)/Sel.

previous work by Miller and Rawlings (1967) which also indicated the effectiveness of recurrent selection for high yield in this population.

### Heterosis in the Diallel Crosses

The means and ranges of the 15 diallel crosses compared with their six parents in 1968 are presented in Table 3. Individual hybrids ranged in yield from 771 to 957 kg/ha compared to a range of 769 to 833 kg/ha for their parents. The hybrids averaged 9.6% higher in lint yield than the mean of their parents. This comparison was significant at the 0.01 probability level. Significant mean heterosis was also detected for lint percentage, weight per boll, number of seed per boll, and lint index. Thus, despite the fact that the cycle-3 selections averaged higher in yield than the original  $F_1$  from which they were derived, hybrids among these selections showed even further heterosis. It should be noted, however, that for all traits the percentage of heterosis was less within the diallel crosses than observed in the original G-4  $\times$  H-1 hybrid.

### General and Specific Combining Ability

Estimates of variance components from the diallel cross are presented in Table 4. Estimates of  $\sigma^2_g$  were significant for all traits except lint percentage. This latter trait, however, was the only one with a significant estimate of  $\sigma^2_s$ . Variances of interaction of general effects by locations ( $\sigma^2_{gl}$ ) were significant for lint

Table 4. Estimates of variance components for general combining ability ( $\sigma_g^2$ ), specific combining ability, ( $\sigma_s^2$ ), general combining ability effects by locations ( $\sigma_{gl}^2$ ), and specific combining ability effects by locations ( $\sigma_{sl}^2$ ) from 1968 data over locations.†

Trait	Variance components			
	$\sigma_g^2$	$\sigma_s^2$	$\sigma_{gl}^2$	$\sigma_{sl}^2$
Lint yield, kg/ha	3,393*	-484	-347	2,589*
Lint, %	0.005	0.144*	0.164**	0.022
Weight per boll, g	0.051*	0.006	-0.006	0.012
No. of bolls/plot	920*	54	61	166
No. of seed/boll	1.25*	0.19	-0.15	0.25
Lint index	0.031**	0.001	0.006*	0.005
Seed index	0.571**	0.008	0.008	0.008

\*, \*\* Significant at the 0.05 and 0.01 levels of probability, respectively. † Since these experiments were conducted within a single year,  $\sigma_g^2$  and  $\sigma_s^2$  are in reality confounded estimates of ( $\sigma_g^2 + \sigma_{sy}^2$ ) and ( $\sigma_s^2 + \sigma_{sy}^2$ ), respectively, while  $\sigma_{gl}^2$  and  $\sigma_{sl}^2$  are estimates of ( $\sigma_{gl}^2 + \sigma_{gly}^2$ ) and ( $\sigma_{sl}^2 + \sigma_{sly}^2$ ), respectively.

percentages and lint index and of specific effects by locations ( $\sigma_{sl}^2$ ) for lint yield. For all traits except lint percentage, the variance component for general combining ability was substantially larger than the other three.

## DISCUSSION

The degree of heterosis observed for yield and yield components in the cross between G-4 and H-1 was in general agreement with that reported by the investigators cited in the introduction. However, these are the first data of which we are aware that compare the performance of selected inbred cotton lines with the  $F_1$  from which they were derived. The ability to produce inbreds with lint yield equal or superior to the original  $F_1$  has important implications on cotton breeding methods.

Each of the six cycle-3 selections grown in this experiment traces to self-pollinated seed of an individual heterozygous plant. The lines were then maintained through more than six generations of bulk selfing. Each line was expected to be composed of a mixture of different, but relatively homozygous, genotypes. Therefore, the possibility existed that the high yield of these lines was due in part to overcompensatory competitive effects between genotypes within each line, as has been reported in soybeans by Brim and Shutz (1968). It is also possible that the heterogeneity *per se* resulted in greater yields over the range of environments than might be expected from homogeneous entries. On the other hand, Richmond and Lewis (1951) evaluated varietal mixtures of upland cotton for a three-year period and reported that the yields of the mixtures were not significantly different from the average yield of the component pure stocks. Unpublished data from the North Carolina Agricultural Experiment Station likewise do not show any yield advantage for mixtures of genotypes as compared to their component stocks. Thus, on the basis of the available information, it appears that the isolation of strains with lint yield equal or superior to the original  $F_1$  is indicative of transgressive segregation in this material. Studies with tobacco (Smith, 1952) and tomatoes (Williams, 1959) likewise report the isolation of pure breeding lines superior in yield to both parents and the  $F_1$  from which they were derived.

Additional heterosis for lint yield was observed in the diallel crosses among the cycle-3 selections; although in this case the heterosis was less than that often reported for upland cotton. Since the six strains

were all derived from the same cross, they would probably be more similar genetically than the types of parental materials usually chosen for such studies. In the original  $F_1$ , all loci by which the two parents differed were heterozygous so that maximum heterosis was observed. Any manipulation of this population, either by selection or random drift, will shift gene frequency from one half and thus reduce the number of heterozygous loci in the diallel population.

Estimates of  $\sigma_g^2$  from the diallel cross analysis were relatively large and statistically significant for all traits except lint percentage. This latter trait, however, was the only one for which we obtained a significant estimate of  $\sigma_s^2$ . The genetic expectations of the two variances (Matzinger, 1963) are:

$$\sigma_g^2 = 1/2 \sigma_A^2 + 1/4 \sigma_{AA}^2 + 1/8 \sigma_{AAA}^2 + \dots$$

$$\sigma_s^2 = \sigma_D^2 + 1/2 \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + 3/4 \sigma_{AAA}^2 + \sigma_{AAD}^2 + \sigma_{ADD}^2 + \sigma_{DDD}^2 + \dots$$

in which  $\sigma_A^2$  is the additive genetic variance,  $\sigma_D^2$  is the dominance variance, and the remaining terms are epistatic variances. Additive genetic effects thus appear to predominate in this material for all traits studied except lint percentage. However, the genetic determination of these traits in the diallel population is not completely clear since the superiority of the hybrids over their parents indicates at least some non-additive effects.

The fairly large amounts of heterosis observed in this material support the hybrid approach for cotton improvement. The present data suggest that  $F_1$ 's between the better lines available to a breeder at a certain point in time would be the superior yielding types. Currently, however, we do not have fully satisfactory male-sterility and fertility-restoration mechanisms available for the commercial production of hybrids. Furthermore, Koehl and Richmond (1962) have reported that the seed yield of male sterile plants as compared with fertile plants was reduced by 25 to 80% depending on the amount of natural crossing in the seed production area. Thus, the production of  $F_1$  hybrids for planting seed in cotton does not appear to be economically feasible at this time. The high performance of these cycle-3 lines, however, suggests that significant improvement may be realized through the use of intrapopulation selection procedures. The predominance of additive genetic effects for yield and yield components in the present material lend further support to this approach. The greatest improvement would probably result from a combination of the two approaches. Intrapopulation selection might be used in the earlier stages to exploit the additive and a portion of the additive by additive epistatic effects, followed by a hybrid program to utilize the remaining nonadditive genetic effects.

The cycle-3 selections were also compared with 'Coker 201', a widely grown commercial variety. Three of the lines outyielded Coker 201, although the differences were not statistically significant. However, the selections were unacceptable commercially since their seed cotton tends to "string out" and fall to the ground shortly after boll opening. Selection in this material was only for lint yield and traits other than lint yield should obviously be included in any applied selection program. Selecting for those additional traits would tend to reduce the selection

pressure which could then be applied to yield and, as a result, would possibly necessitate a greater number of recurrent cycles to bring yield levels up to or beyond that of the  $F_1$ .

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