

# Heterosis and Inheritance of Quantitative Characters in Interspecific Crosses of Cotton<sup>1</sup>

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## ABSTRACT

Performance of the  $F_1$ ,  $F_2$  and backcross generations of nine interspecific crosses, between each of three varieties of *Gossypium hirsutum* L. ('Acala 4-42', 'Empire W,' and 'Coker 100A') and each of three varieties of *G. barbadense* L. ('Karnak,' 'Malaki,' and 'Giza 7'), in comparison with the parental varieties, was evaluated in three field trials in 1964 and 1965. Heterosis ( $F_1$  performance above mean of parents) was between 52% and 73% for lint yield and was associated with heterosis for boll number, flower number, and percentage of boll retention. Boll weight of  $F_1$  hybrids was intermediate and their lint percent and number of seeds per boll were lower than the parental mean. Heterosis was also significant for seed index, lint index and plant height.

$F_2$  deviation ( $F_2$  performance below mean of  $F_1$  and midparent) and backcross deviations (BC performance below mean of  $F_1$  and recurrent parent) were significant for almost all of the characters examined. Lint yield of the  $F_2$  was much lower than that of either parent, whereas lint yield of backcrosses was similar to that of the recurrent parents.

Heterosis was caused by dominance effects only (no epistasis) for seed index and in one trial for final plant height. Heterosis for yield of seed cotton, yield of lint, boll number, flower number, percentage of boll retention, lint index and plant height at flowering was caused by dominance in the presence of epistasis. Intermediate  $F_1$  performance (no heterosis), found for boll weight and for maturity, was caused by the estimates of dominance and additive  $\times$  additive epistasis parameters being of nearly equal magnitudes. The negative heterosis found for lint percent and number of seeds per boll was caused by the additive  $\times$  additive epistasis being larger than the dominance effects.

**Additional index words:** *Gossypium*, genetic parameters, backcrosses.

**H**ETEROISIS of a considerable magnitude was reported previously for lint yield and many other traits in crosses between two cotton species, *Gossypium hirsutum* L. and *G. barbadense* L. (5, 6, 7). Lint yield of these interspecific  $F_1$  hybrids was 64 to 93% above mean parental performance. Similar results or lower heterotic effects were reported by Fryxell et al. (3), Barnes and Staten (2), Stroman (8) and Ali and Lewis (1). Backcross performance was investigated by Ali and Lewis (1), who found that more than half of the heterotic effect was lost in the first backcross, and reduction in yield and boll weight was very severe in the backcross to the *G. barbadense* L. parent.

A large magnitude of heterosis in these crosses was also reported for yield of seed cotton, number of bolls, seed index, and lint index (5), and it was suggested that part of the genetic variance for these traits was nonadditive (dominance and epistatic effects). A more precise separation of epistatic and dominance effects from additive effects can be made by evaluating the performance of some additional generations (4).

The purpose of the experiments reported here was to study the performance of  $F_1$  and  $F_2$  generations of interspecific crosses as well as backcrosses to either parents, and to try to explain the genetic basis of heterosis for yield and components of yield in these crosses.

## MATERIALS AND METHODS

Three field trials were conducted on alluvial clay type soil in the coastal region of Israel: (a) in 1964, and (b) and (c) in 1965. Nine interspecific crossing combinations were included in these trials. Each of three varieties of upland cotton, *G. hirsutum* L. ('Acala 4-42', 'Empire W,' and 'Coker 100A'), was crossed with each of three varieties of Egyptian cotton, *G. barbadense* L. ('Karnak,' 'Malaki,' and 'Giza 7'). A split-plot randomized-blocks design was used, and the crossing combinations were assigned to the main plots. In trial (a) there were four subplots in each main plot and these included the two parental varieties (Ph, Pb) and the  $F_1$  and  $F_2$  of the cross between them. In trials (b) and (c) there were six subplots in each main plot and these included Ph, Pb,  $F_1$ , and  $F_2$  and also backcrosses (BC<sub>b</sub>, BC<sub>c</sub>) to both parental varieties. There were seven replications in trial (a), and six in trials (b) and (c). Each subplot consisted of one row 3 m long. Rows were spaced 1 m apart. The hills were spaced 25 cm apart in trial (a) and 20 cm apart in trials (b) and (c); there were one or two cotton plants in each hill.

Flowers were counted every 3 to 5 days during the flowering season, and the total number of flowers per m<sup>2</sup> was calculated from these data. Plant height was determined by measuring three random plants in each plot. Seed cotton was harvested five times in trial (a), and a random sample of 10 bolls was taken from each plot at each harvest for determination of boll weight. Composite samples of 300 to 500 g of the first two harvests and of the last three harvests of each plot were ginned on a 40-cm (16") roller-gin for determination of lint percent. In trials (b) and (c) there were two harvests, and 20 random bolls were taken from each plot at each harvest date for determination of boll weight. Samples of approximately 300 g were ginned from each harvest of each plot.

Three samples of 100 seeds each were counted and weighed from each ginned sample for determination of seed index. The weighted means, with respect to yield of seed cotton at each harvest, were calculated for boll weight, lint percent and seed index. Lint index, number of seeds per boll, and number of bolls per m<sup>2</sup> were calculated from these data and the yield of seed-cotton. Percentage of boll retention was calculated from boll number and flower number data. Maturity was expressed in trial (a) as the mean date of maturity (7), and in trials (b) and (c) as percent of yield in first harvest.

Heterosis was calculated as the percentage increase of  $F_1$  performance above the mean performance of parental varieties.  $F_2$  deviation was calculated as the percentage decrease of  $F_2$  performance from the average of  $F_1$  and mid-parental performance. In trials (b) and (c) backcross deviation was calculated as the percentage decrease of BC performance from the average performance of  $F_1$  and the recurrent parent. F-tests were calculated, to test the significance of these effects, based on error-terms from analysis of variance. Effects of general and specific combining ability in the  $F_1$ ,  $F_2$ , BC<sub>b</sub>, and BC<sub>c</sub> generations were calculated as in a factorial arrangement.

Genetic parameters were calculated in experiments (b) and (c) by the method suggested by Hayman (4). These parameters are considered as summations over all genes by which the parental lines differ. Parameter  $d$  measures pooled additive effects and  $h$  measures pooled dominance effects. There are three parameters measuring epistasis:  $i$  measures pooled interaction between additive effects;  $j$  between additive and dominance effects; and  $l$  between dominance effects. The expectations of

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generation means ( $P$  and  $P'$  are the parental varieties,  $B$  and  $B'$  the respective backcrosses) may be expressed as

$$\begin{array}{rcl} P & = & m + d - \frac{1}{2}h + i - j + \frac{1}{4}l \\ P' & = & m - d - \frac{1}{2}h + i + j + \frac{1}{4}l \\ F_1 & = & m + \frac{1}{2}h \\ F_2 & = & m + \frac{1}{4}i \\ B & = & m + \frac{1}{2}d + \frac{1}{4}i \\ B' & = & m - \frac{1}{2}d + \frac{1}{4}i \end{array}$$

The estimates of the parameters may be calculated from these formulas as

$$\begin{array}{rcl} \hat{m} & = & F_2 \\ \hat{d} & = & B - B' \\ \hat{h} & = & -\frac{1}{2}P - \frac{1}{2}P' + F_1 - 4F_2 + 2B + 2B' \\ \hat{i} & = & -4F_2 + 2B + 2B' \\ \hat{j} & = & -\frac{1}{2}P + \frac{1}{2}P' + B - B' \\ \hat{l} & = & P + P' + 2F_1 + 4F_2 - 4B - 4B' \end{array}$$

## RESULTS AND DISCUSSION

### Heterosis

The average performance of the generations is given in Fig. 1. The magnitude of heterotic effects and  $F_2$  deviations for all characters measured are presented in Table 1. Heterosis for yield of seed cotton and yield of lint was of a very large magnitude.  $F_1$  yields were also considerably higher than those of the best parental varieties (by 50 to 66% for seed-cotton and 26 to 36% for lint). When these results are compared with those of previous trials (6, 8), it may be concluded that heterosis for lint yield in interspecific crosses is quite stable in different crossing combinations and for several years. It was associated, in all cases, with heterosis for the number of bolls produced, the number of flowers, and percentage of boll retention.

Boll weight of  $F_1$  hybrids was intermediate and did not contribute to heterosis in yield. Lint percent of

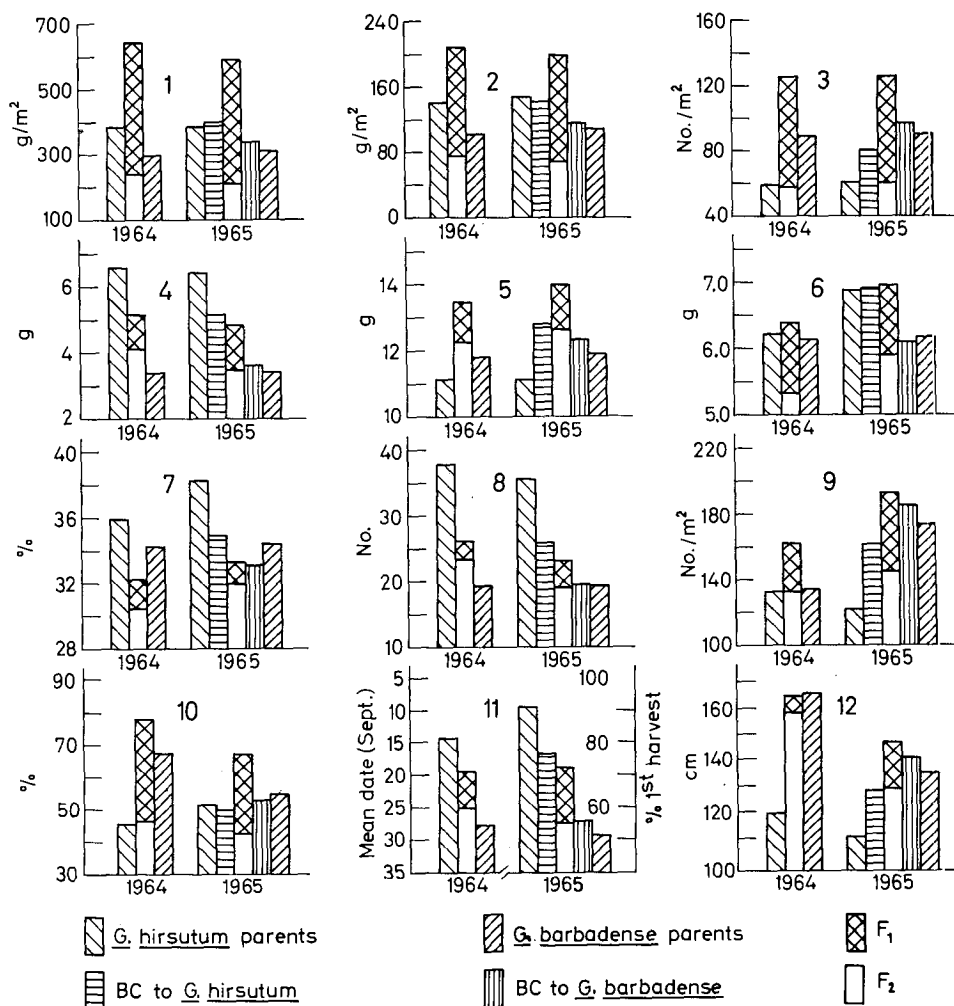


Fig. 1. Average performance of all interspecific crosses (1964 = experiment a, 1965 = average of experiments b and c). 1. Yield of seed-cotton; 2. yield of lint; 3. number of bolls; 4. boll weight; 5. seed index; 6. lint index; 7. lint percent; 8. number of seeds per boll; 9. number of flowers; 10. percentage of boll retention; 11. maturity; and 12. plant height.

**Table 1. Heterosis and  $F_2$  deviation in interspecific crosses of cotton.**

Character	Heterosis, %†			$F_2$ deviation, %‡		
	Exp. a	Exp. b	Exp. c	Exp. a	Exp. b	Exp. c
Seed cotton yld.	90.9**	67.7**	79.8**	51.9**	47.8**	63.2**
Lint yield	73.3**	51.8**	63.1**	56.1**	51.4**	65.6**
Lint percent	-8.5**	-9.0**	-8.5**	9.6**	7.9**	7.7**
Boll weight	3.5**	2.2	-8.1**	18.7**	24.0**	32.3**
Boll number	70.0**	52.5**	83.1**	41.2**	32.5**	47.3**
Seed index	17.3**	21.6**	22.6**	1.6	1.4*	1.9**
Lint index	2.8**	5.6**	7.2**	15.1**	12.3**	12.6**
Seeds per boll	-8.9**	-12.0**	-21.6**	13.9**	20.5**	27.8**
Flower number	21.8**	25.1**	36.1**	10.5**	12.7**	17.1**
Boll retention, %	38.6**	20.9**	33.0**	31.0**	22.4**	33.7**
Maturity	9.4**	11.0**	-6.2**	25.7**	22.7**	23.0**
Plant height						
At flowering	15.1**	18.2**	19.7**	7.0**	11.0**	6.5**
End of season	16.1**	15.5**	21.5**	-1.6	0.2	6.0**

\*, \*\* Significant at the 0.05 and 0.01 levels, respectively.

†  $(F_1 - MP)/MP$  (where MP = mid-parent). ‡  $[1/2(F_1 + MP) - F_2] / 1/2(F_1 + MP)$ .

$F_1$  hybrids was lower than that of either parent, because heterosis for seed index was larger than heterosis for lint index. The number of seeds per boll of  $F_1$  hybrids was lower than that of the parental mean. Maturity of  $F_1$  plants was intermediate, but there was a significant heterosis for plant height.

### $F_2$ Performance

$F_2$  performance was at a very low level for most of the traits examined. Yields of seed-cotton and of lint were much lower (by 25 to 39% and 29 to 44%, respectively) than the lowest yielding parental variety.  $F_2$  performance for boll number, lint percent, lint index and percentage of boll retention was also lower than that of the lowest parent.

When no epistasis is effective,  $F_2$  performance would be expected to be near the average of  $F_1$  and mean parental performance. It was shown by Robinson and Cockerham (9) that a significant  $F_2$  deviation from this average indicates epistatic gene action. All the traits that were examined in the present study, with the exception of seed index and final plant height, showed significant  $F_2$  deviations in all the experiments.

Boll weight of  $F_2$  plants was lower than that of the  $F_1$ , and the same was also true for the number of seeds per boll.  $F_2$  performance for the number of flowers and for plant height at flowering was near the average of the parental varieties.  $F_2$  plants were rather late, being similar in maturity to the *G. barbadense* L. parental varieties.

### Backcross Performance

Yields of the backcrosses and their lint index were very close to those of the recurrent parents, but backcross performance for boll number, seed index, flower number and plant height was higher than that of the recurrent parents. Lint percent and percentage of boll retention of the backcrosses were lower than those of the recurrent parents.

When no effects of epistasis are assumed, backcross performance would be expected to be near the average of  $F_1$  and recurrent parent performance. The deviations of backcross performance from this expected value are given in Table 2. These backcross deviations were rather large for yields of seed-cotton and of lint, boll number, boll weight, number of seeds per boll, percentage of boll retention, and maturity. Smaller backcross deviations were found for lint percent, seed index, and lint index, and there were no

significant backcross deviations for flower number and plant height.

### General and Specific Combining Ability

The generations and trials in which significant effects of general and specific combining ability were found are given in Table 3. General combining ability (g.c.a.) was detected for many characters, whereas specific combining ability was significant in only a few cases. Similar results were also found in previous experiments (8). In many cases significant effects of g.c.a. were detected in the  $F_2$  and BC generations as well as in the  $F_1$ .

Effects of g.c.a. of upland and Egyptian varieties in all generations, as compared to parental performance, are given for some of the traits in Fig. 2. The magnitude of g.c.a. effects in all the generations was generally in accordance with the performance of the parental varieties themselves. This indicates that the selection of parental varieties for use in crossing may be based on their own performance. This may also be an indication of the presence of additive genetic effects.

There were more cases of consistent g.c.a. effects of the *G. hirsutum* L. parental varieties than of the *G. barbadense* L. ones. Progeny of Coker 100A produced higher yields of seed-cotton and of lint and more bolls than progeny of the other *G. hirsutum* L.

**Table 2. Backcross deviations in interspecific crosses of cotton backcrossed to both parental species.**

Character	BCb deviation, %†		BCb deviation, %‡	
	Exp. b	Exp. c	Exp. b	Exp. c
Seed cotton yld.	14.6**	21.1**	21.8**	28.1**
Lint yield	15.4**	20.6**	23.1**	28.5**
Lint percent	1.3*	1.3*	2.1**	1.7**
Boll weight	8.2**	10.5**	12.0**	14.9**
Boll number	10.4**	17.8**	9.2**	12.7**
Seed index	-0.4	-3.6**	4.4**	5.6**
Lint index	2.8**	-2.4*	7.1**	7.8**
Seeds per boll	8.8**	15.0**	6.5**	8.7**
Flower number	1.0	-6.6*	-1.6	-1.4
Boll retention, %	8.0**	21.3**	10.9**	14.5**
Maturity (% 1st harvest)	9.4**	4.2**	11.3**	8.9**
Plant height,				
At flowering	2.7	-1.0	1.8	1.4
End of season	0.1	0.2	-0.2	-1.3

\*, \*\* Significant at the 0.05 and 0.01 levels, respectively.

† Deviation of backcrosses to *G. hirsutum* L. parental varieties, calculated as  $[1/2(F_1 + Ph) - BCb] / 1/2(F_1 + Ph)$ .‡ Deviation of backcrosses to *G. barbadense* L. parental varieties, calculated as  $[1/2(F_1 + Ph) - BCb] / 1/2(F_1 + Ph)$ .**Table 3. The generations and experiments in which significant (at the 0.05 level) effects of general or specific combining ability have been found.**

Character	General combining ability effects of:		Specific combining ability effects
	<i>G. hirsutum</i> L. parental varieties	<i>G. barbadense</i> L. parental varieties	
Seed cotton yld.	$F_1$ (abc), BCb(bc)	BCb(c)	BCb(c)
Lint yield	$F_1$ (abc), BCb(bc)		$F_2$ (b)
Lint percent	$F_1$ (abc), $F_2$ (abc), BCb(bc)	$F_1$ (b), $F_2$ (ab), BCb(b), BCb(b)	
Boll weight	BCb(c)	$F_1$ (b)	
Boll number	$F_1$ (abc), BCb(bc)	$F_1$ (abc), BCb(bc)	BCb(bc)
Seed index	$F_1$ (abc), $F_2$ (abc), BCb(bc), BCb(bc)	$F_1$ (bc), $F_2$ (bc), BCb(bc)	$F_2$ (c)
Lint index	$F_1$ (abc), $F_2$ (a), BCb(bc)	$F_2$ (a)	$F_1$ (a), BCb(b)
Seeds per boll	$F_1$ (abc), $F_2$ (ac), BCb(b)		
Flower number	$F_1$ (abc), $F_2$ (abc), BCb(bc), BCb(b)	$F_1$ (abc), $F_2$ (c), BCb(bc)	
Boll retention, %	$F_1$ (ac)	BCb(c)	BCb(b)
Maturity	$F_1$ (c), $F_2$ (a), BCb(bc)	$F_1$ (ac), $F_2$ (bc), BCb(b), BCb(c)	$F_1$ (a), BCb(c)
Plant height,			
At flowering	$F_1$ (a), $F_2$ (a)	BCb(b)	
End of season	$F_1$ (a), $F_2$ (ac), BCb(b), BCb(b)	$F_1$ (b), $F_2$ (c), BCb(b)	

\* BCb and Cb are backcrosses to *G. hirsutum* L. and *G. barbadense* L. parental varieties, respectively. a, b or c in parentheses after the generation designate the experiment in which a significant effect was found.

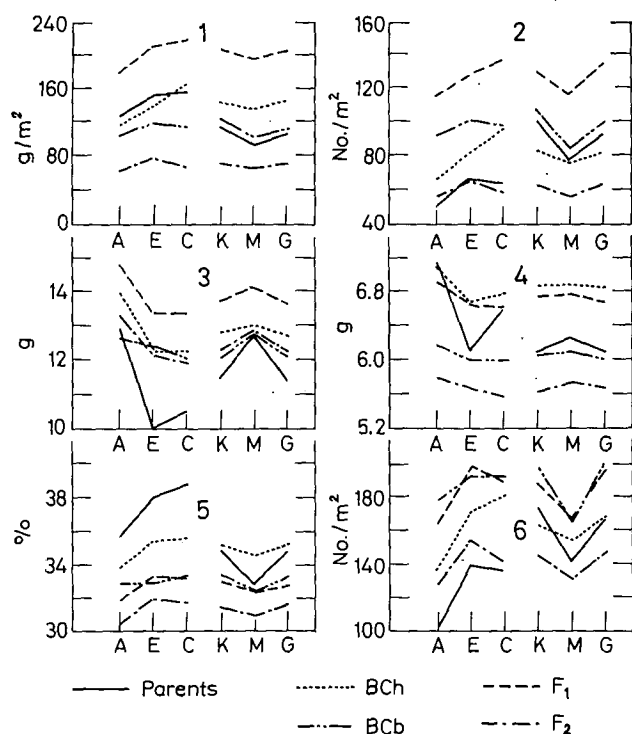


Fig. 2. Performance of parental varieties and their general combining ability effects in the  $F_1$ ,  $F_2$ ,  $BC_b$ , and  $BC_b$  generations (average of experiments b and c). *G. hirsutum* L. varieties: A = Acala 4-42, E = Empire W, C = Coker 100A. *G. barbadense* L. varieties: K = Karnak, M = Malaki, G = Giza 7. 1. Yield of lint; 2. number of bolls; 3. seed index; 4. lint index; 5. lint percent; and 6. number of flowers.

varieties. Progeny of Acala 4-42 had a higher seed index and lint index, a lower lint percent, fewer seeds per boll, and fewer flowers, whereas progeny of Empire W had a lower plant height. Progeny of Malaki produced lower yields of seed-cotton and of lint, fewer bolls, and fewer flowers than those of the other *G. barbadense* L. varieties. Progeny of Giza 7 had a lower plant height. No significant effects of g.c.a. were found for boll weight or percentage of boll retention.

It may be concluded that the  $F_1$  hybrids of Coker 100A with either Karnak or Giza 7 would be expected to produce high yields of lint under environmental conditions similar to those of our experiments. The tendency of most of the  $F_1$  crosses between *G. hirsutum* L. and *G. barbadense* L. varieties to produce excessively tall plants is undesirable for agronomic reasons; the g.c.a. of Empire W and of Giza 7 for producing lower plants is therefore of considerable importance.

### Genetic Parameters

Estimates of the genetic parameters for trials (b) and (c) are given in Table 4. Significant values of  $\hat{h}$  and  $\hat{i}$  were found for many of the characters, whereas  $\hat{l}$  was significant for some of them and  $\hat{j}$  for only a few traits.

Several assumptions underlie the estimation of these parameters. One assumption is that the parents are inbred lines. All the varieties that were used in our

study are fairly closely bred varieties, and they were selfed for at least three generations before the crosses were made for this study. They may therefore be considered as inbred lines. The model of Hayman (4) assumes an absence of linkage. However, linkage may have important effects in interspecific crosses. Van Der Veen (11) pointed out that the presence of linkage causes some bias in the estimates of parameters that are derived from the  $F_2$  and  $BC$  generations. However, estimators derived from nonsegregating generations (i.e., parents and  $F_1$ ) are unbiased by linkage.

Heterosis was defined in this study as the difference between  $F_1$  performance and the mean of parental varieties. Its expectation, in terms of the parameters of Hayman (4), is

$$F_1 - \frac{1}{2}(P+P') = h - i.$$

This estimate is unbiased by linkage.

The expectation of  $F_2$  deviation is

$$\frac{1}{2}[F_1 + \frac{1}{2}(P+P')] - F_2 = \frac{1}{2}i + \frac{1}{4}l$$

and the expectations of backcross deviations are

$$\frac{1}{2}(F_1+P) - B = \frac{1}{4}i + \frac{1}{4}l - \frac{1}{2}j$$

and  $\frac{1}{2}(F_1+P') - B' = \frac{1}{4}i + \frac{1}{4}l + \frac{1}{2}j$ .

These are estimates that may be biased by linkage. Significant and large  $F_2$  or  $BC$  deviations are probably an indication of the presence of epistatic effects, even in the presence of linkage. However, the estimates made for each of the components of epistasis ( $i$ ,  $j$ , or  $l$ ) may be considerably biased by linkage.

The parameters that were used in our study were defined against the  $F_2$  background population,  $m$  being equal to the mean performance of the  $F_2$  generation. Hayman (5) has shown that parameters  $d$  and  $h$  are defined uniquely only in the absence of any epistasis. When epistatic effects are present, however, the values of all the genetic parameters are dependent on the background population against which they are defined. In this case, the effect of heterosis cannot

Table 4. Estimates of genetic parameters, mean values for all interspecific crossing combinations.

Character	Exp.	$\hat{d}$	$\hat{h}$	$\hat{i}$	$\hat{j}$	$\hat{l}$
Seed cotton, g/m <sup>2</sup>	b	51.0*	750.5*	526.0*	27.5	-205.0*
	c	74.0*	1039.0*	760.0*	21.0	-282.0*
Lint yield, g/m <sup>2</sup>	b	24.7*	255.6*	193.8*	8.4	-79.5*
	c	32.6*	363.6*	282.0*	7.4	-117.1*
Lint percent	b	2.07*	4.27*	7.50*	-0.28	-4.16*
	c	1.83*	5.56*	8.66*	0.11	-6.52*
Boll weight, g	b	1.39*	2.84*	2.74*	0.05	-0.85
	c	1.60*	3.40*	3.80*	0.01	-1.44
Bolls per m <sup>2</sup>	b	-15.9*	125.2*	85.8*	0.4	-48.8*
	c	-16.6*	201.0*	136.0*	-3.4	-73.3*
Seed index, g	b	0.17	2.11*	-0.34	0.61*	1.38
	c	0.82*	3.11*	0.48	1.19*	0.06
Lint index, g	b	0.65*	2.25*	1.90*	0.26*	-0.66
	c	0.97*	3.27*	2.78*	0.70*	-2.05*
Seeds per boll	b	6.60*	9.50*	12.30*	-1.20	-4.60
	c	6.30*	9.95*	15.30*	-2.65*	-3.50
Flowers per m <sup>2</sup>	b	-42.0*	131.0*	92.0*	-5.0	-94.0*
	c	-7.0	189.5*	138.0*	7.5	-163.0*
Boll retention, %	b	3.0	38.8*	28.4*	1.4	-7.6
	c	-8.1*	58.7*	40.0*	-3.5	4.7
Maturity, % 1st harvest	b	25.6*	37.7*	31.4*	-1.7	-6.1
	c	15.7*	48.2*	53.4*	2.9	-32.9*
Plant ht, cm At flowering	b	-1.9	31.6*	21.4*	-0.5	-16.0
	c	-1.0	31.1*	18.6*	1.8	-17.3
End of season	b	-14.4*	19.2*	1.2	-0.4	-1.5
	c	-12.7*	65.1*	37.4*	-2.3	-40.5*

\* Significantly different from zero, at the 0.05 level.

be partitioned uniquely into the additive, dominance and epistatic components.

Hayman (5) suggested a classification of the simpler genetic system into three groups, according to the relative importance of epistasis. Seed index and final plant height (in experiment b) belong to the first group under this classification. No significant epistasis was detected for these traits, and it is presumed that heterosis is caused by dominance effects ( $h$  parameter) only. The deviation of  $F_2$  from the mean of parental and  $F_1$  generations was very small for these traits. Significant, though small BC deviations were associated with a significant estimate of  $j$  for seed index, but the genetical meaning of this is rather doubtful.

All the other traits that were studied may be classified as belonging to the third group of Hayman (5). In this group there is a significant epistasis which is at least as important as the other modes of gene action.

Relatively high values of  $\hat{h}$  and  $\hat{i}$  were found for these traits, when the parameters were defined against the  $F_2$  generation background. The estimates of each of these parameters depend on the background population and are affected by linkage, but their difference ( $\hat{h} - \hat{i}$ ) is unique. The presence of epistasis is, however, indicated by the strong  $F_2$  deviation.

A large ( $\hat{h} - \hat{i}$ ) difference, which is associated with a strong effect of heterosis, was found for yield of seed-cotton, yield of lint, number of bolls, number of flowers, and percentage of boll retention. Backcross deviations were significant for all of these traits, except for the number of flowers.

The difference ( $\hat{h} - \hat{i}$ ) was rather small for lint index and plant height at flowering, and this was associated with a small effect of heterosis.  $F_2$  and

BC deviations were, however, rather large for these traits.

The magnitude of  $\hat{a}$  exceeded that of  $\hat{h}$  for lint percent and the number of seeds per boll, and this was associated with a negative heterosis.  $F_1$  and  $F_2$  performances for these traits were low in comparison with those of the parental varieties.

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