Heterosis and Gene Action in Cotton, *Gossypium hirsutum* L.[1]

William R. Meredith, Jr. and R. R. Bridge[2]

ABSTRACT

Heterosis (F_1 — MP), useful heterosis (F_1 — 'Deltapine 16'), and gene action estimates were obtained at four locations from the six groups of populations involving 'Deltapine 16' (*Gossypium hirsutum* L.) crossed with six cultivars ('Q_1,' 'Del Cerro 183,' 'FTA 263-20,' 'Acala 3080,' 'Mo277-396,' and 'Stoneville 603').

Heterosis for lint yield was detected in each cross. F_1 yields ranged from 92 to 115% of that of Deltapine 16, while F_2 yields ranged from 86 to 107%. Increases in boll size were partially responsible for the increased productivity of the hybrids. Parental lines originating from outside the Delta in general produced hybrid-by-location mean squares greater than those from Delta-derived parents. These interactions were related to the higher relative performance of Deltapine 16 at the locations with higher yield. The potential benefits from utilizing heterosis were especially evident when all traits were considered simultaneous. Four of the six F_1's produced yields equal to or greater than Deltapine 16 while also having longer, stronger, and finer fiber.

Heterosis for each of the nine traits studied was determined primarily by dominance gene action. Of the 54 possible tests additive-by-additive epistasis was significant in only four instances, and even in those four cases the mean squares for epistasis were much smaller than were those for additive or dominance effects.

Additive effects predominated for lint percentage, seed index, fiber strength, fiber elongation, and fiber fineness. However, dominance was greater for boll size. Both were involved for lint yield and fiber length. In every case there were some crosses that did not fit the general trend.

The interaction of additive effects with locations was usually of greater magnitude than the dominance-by-location interaction. There were 28, 13, and 1 instances of significant additive, dominance, and additive by additive epistatic by location interactions, respectively. Interactions with locations were the greatest practical limitation for lint yield selection and they were less important for the other traits. The interactions with locations were particularly large for the cross involving Acala 3080. Breeding implications are discussed.

Additional key words: Hybrids, Yield, Yield components, Variety improvement, Fiber traits, Genotype-environment interactions, Selection.

INTENSIVE cotton (*Gossypium hirsutum* L.) breeding programs have been conducted in the Mississippi Delta for at least 50 years to develop high-yielding, medium-staple commercial varieties. These varieties are now being planted on about half the cotton acreage in the United States (4). They have largely been produced by pedigree selection following the initial crosses, and few attempts to untilze heterosis have been reported from this area. So far, large-scale production of hybrid seed in the Delta has been impractical, since natural crossing is usually less than 1%.

Heterosis has often been observed in cotton, but to be of potential value, a hybrid should be more profitable than the best available commercial variety. This means that the hybrid would have to be higher yielding and probably possess superior fiber properties as well. There has been some question whether a hybrid would perform better than the current Delta varieties in their prime area of adaptation. In this study we investigated the potential value of heterosis in Delta environments utilizing one of the better Delta varieties as a common parent in each cross studied.

There has also been very little information reported on gene action from the Delta. Another objective in this study was to obtain estimates of additive, dominance, and epistatic effects for nine traits under four rather diverse Delta environments.

Numerous studies from other areas have shown significant heterosis for yield where heterosis was defined as F_1 — MP where MP denotes the midparent value. However, Jones and Loden (13) reported that the seed cotton yields from nine F_1's were from 17 to 47% higher than the better parent. Fryxell, Staten, and Porter (7) found that 17 of 36 interspecific F_1's exceeded their higher parent in lint yield. Several of the hybrids tended to combine the higher-yielding ability of *G. hirsutum* with the greater fiber quality of *G. barbadense* L. Crosses made by White and Richmond (29) among cottons of diverse origin exhibited heterosis for lint yield but did not produce hybrids exceeding the better check varieties. An average heterosis of 5.5% for lint yield was detected by Al-Rawi and Kohel (1). Ten other characters exhibited heterosis ranging from —3.9% for days to first flower to 9.7% for seed index.

Each of the above studies was conducted in a single environment, while the following were conducted in multiple environments. Turner (23) found that six of 21 hybrids produced seed cotton yields significantly higher than the higher parent in the 1st year's study, but only one of the six was superior the following year. Hawkins. Peacock, and Ballard (8) reported a 3-year average lint yield increase of 19% for six crosses over the better parent. On a yearly basis, the best F_1 hybrid 'Empire' × 'Pope,' ranged from 4.2 to 50.5% better than the highest-yielding parent.

F_2 yields tended to be lower than the parent varieties. Miller and Lee (20) found that top-cross hybrids generally had higher yields than the parents. Certain top-crosses were 15 to 20% superior in yield over the better varieties. Also, the magnitude of heterosis remained constant over a wide range of yield levels. Meredith, Bridge, and Chism (19) reported little "useful" heterosis for yield alone, but F_1 hybrids did possess better combinations of yield and fiber properties than the best commercial check. Lee, Miller, and Rawlings (14) reported an average heterosis of 26% for lint yield. Some parental lines tended to be good combiners at one location and poor at others and had an overall effect of 0 for combining ability. "Useful" amounts of heterosis for interspecific hybrids have been reported by Marani (15, 16, 18). The results by Miller and Marani (21) do point out that in some cases heterosis, although present, may not be of sufficient magnitude to be "useful."

Previous research by others has shown inconsistent results for gene effects. Lee et al. (14) reported high estimates of additive variance for lint percentage, boll size, and fiber properties. Nonadditive gene action for yield was operable, but they (14) were unable to discriminate between dominance and epistasis or their combined effects as being the cause of the heterosis observed. Interaction components of additive by environmental effects were significant and larger than additive effects alone, suggesting the difficulty in selecting for yield under one environment. Miller and Marani (21) reported that the major portion of genetic variability for the traits they studied was additive in nature. Small, but significant, F_2 deviations from linear regression for lint yield, boll size, fiber strength, and earliness on their generation means suggested the presence of epistasis for those traits. Meredith et al. (19) found significant epistasis in the Mississippi Delta for only one trait, lint yield. Interactions with environments were small for all traits and usually not significant. They found evidence for dominance in lint yield and boll size, but the other yield components and fiber properties tended to be inherited in an additive manner.

Verhalen et al. (26) found that lint yield per plant, seed cotton yield per plant, lint percent, and earliness appeared to be governed by a weighted over-all degree of dominance in the overdominance range, except for lint percent in 1 year when partial dominance was observed. No evidence of epistasis was detected. A genotype-by-environment interaction for the additive components of variation was found for lint percent. Also, an interaction of dominance effects with environments was detected for earliness. Verhalen and Murray (25) found that fiber length and strength were conditioned by partial dominance and fiber fineness was governed by overdominance. Fiber fineness exhibited significant interactions of additive and dominance effects with environment. Epistasis was not detected for any of their fiber characteristics. In a diallel analysis of five diverse parents White and Kohel (28) concluded that additive effects were important for all agronomic traits measured but that dominance effects appeared to be operating for yield, boll size, bolls per plant, and seedling height. No evidence for epistasis was detected. They reported partial dominance for yield and boll size. Individual epistatic deviations were not detected, but overall epistasis was significant for boll size and seed index (27). In diallel analyses involving nine commercial varieties Al-Rawi and Kohel (1) reported epistasis for plant height, earliness, boll size, and number of bolls per plant. Heterosis for yield was due to dominance effects or epistasis or both. However, they (2) found essentially no evidence of epistasis in fiber properties. The small amount of heterosis detected was explainable on the basis of partial dominance. The major portion of genetic variability for all fiber properties appeared to be additive gene action.

Marani (17), working with intraspecific crosses of *G. hirsutum* and *G. barbadense*, generally found more dominance and epistasis in the *G. barbadense* crosses. Fiber length showed small dominance effects in both crosses and probably some epistasis for *G. barbadense*. Some dominance for fiber strength in *G. barbadense* was indicated with fineness appearing to be mostly due to additive effects. A large interaction of fineness with environments was noted.

With interspecific crosses Marani (18) found a high level of heterosis for lint yield, boll number, flower number, percent boll retention, and lint index, which was probably caused by both dominance and epistatic gene action. Boll size had approximately equal magnitudes of dominance and additive-by-additive epistasis. Since each had opposite signs, this caused the F_1 to approximate the average of its parents.

The significant specific combining ability for seed cotton yield observed by Turner (24) was reevaluated by Hayman (9, 11). He found epistasis to be a major contributing factor to the high estimates reported. Ramey (22) found dominant gene action to be involved for lint index in populations resulting from high $\times$ high and low $\times$ low lines. Epistasis was noted in populations resulting from crosses of high $\times$ low lines, and he suggests that dominance was probably also operative in this group.

MATERIALS AND METHODS

We crossed six inbred lines (two of which were developed in and four outside the Delta) with a currently popular Delta variety, 'Deltapine 16.' These parental strains were selected primarily on the basis of their diversity for yield components and fiber properties. The general genetic background and designation for each parent is as follows:

(DPL) 'Deltapine 16' — A high-performance, commercial variety developed in the Delta. It has medium fiber length and strength and a *G. hirsutum* background.

(Q) 'Q,' — A line developed by introgression of *G. barbadense* germplasm into 'Auburn 56' (*G. hirsutum*) by D. C. Harrel of the Pee Dee Experiment Station, Florence, S. C.

(DC) 'Del Cerro 183' — A strain developed by James Meyer, Stoneville, Miss., from a 'Del Cerro' bulk. Del Cerro has a very complex parentage involving *G. turberi* Tod., *G. arboreum* L., *G. barbadense*, and *G. hirsutum* var. *punctartum* (Schum & Thonn) Roberty introgressed into several *G. hirsutum* types. This strain is considered to have been developed outside of the Delta.

(FTA) 'FTA 263-20' — Another strain developed by D. C. Harrel from triple hybrid (*G. arboreum*, *G. thurberi* $\times$ *G. hirsutum*) interbreeding with *G. hirsutum*.

(A) 'Acala 3080' — Variety developed by the New Mexico Agr. Exp. Sta. (3), *G. hirsutum* background.

(Mo) 'Mo 277-396' — A component line of the variety 'Delcot 277' released by the Missouri Agr. Exp. Sta. (5). It has a complex background involving the triple hybrid and 'Tanguis' (*G. barbadense*) introgressed into *G. hirsutum*.

(Stv) 'Stoneville 603' — A commercial variety of *G. hirsutum* background developed in the Mississippi Delta.

DPL was crossed with each of the six remaining entries to produce six intercross groups. Within each group six populations were studied. These were P_1, P_2, F_1, F_2, BC_1, and BC_2. A split-plot design with four replications was used with groups serving as whole plots and populations as subplots. Whole plots were randomized in a complete-block design. The 36 treatments were grown at four rather diverse locations in the Mississippi Delta in 1969. These were Sumner, Yazoo City, a sandy soil at Stoneville, and clay soil at Stoneville. One plant from each variety was used to make the initial crosses. Subsequent crosses and backcrosses were made using selfed seed from these individual plants. With the exception of Q, which was in the F_6 generation, all entries had a long history of selfing.

Indivdiual plots were single rows, 1.0 m wide and 8.2 m long, at Stoneville and 6.5 m long at the other two locations. Plots were harvested by hand with seed cotton weights recorded for each plot. The first harvests from the first two replications were bulked to form a composite, with the last two replications bulked to form another. The percentage of the total crop harvested in the first harvest ranged from approximately 20% on the sandy site at Stoneville to 100% at Yazoo City. Lint percent for each entry was determined from saw-ginned composite samples. The average lint percent for a given location was multiplied by its seed cotton yield per plot to obtain lint yield per plot. The number of harvestable bolls in the first harvest was counted. The average boll size in grams was determined by dividing the total seed cotton weight for each composite sample by the number of bolls harvested to form that composite. The weight of 100 seeds in grams from each composite was used to estimate seed index. Fiber length in inches was measured as 50% and 2.5% span length (SL) on a digital fibrograph. Strength (T_1) expressed as grams per tex, and elongation (E_1) were measured on the $\frac{1}{8}$-inch gauge stelometer. Fiber fineness was expressed in micronaire units. Fiber determinations were made by the US Cotton Fiber Laboratory of the Plant Science Research Division, ARS, USDA, at Knoxville, Tenn.

Each crossing group contained five degrees of freedom for populations and 15 for the interaction of populations with locations. The analyses were combined into two sets as indicated in Table 2. Statistical tests of significance for heterosis $(F_1 - MP)$ and "useful" heterosis $(F_1 - DPL)$ were made on the computed differences. The differences were expressed as a percentage of the midparent (MP) or DPL. However, these statistical tests were not made on percents *per se*. Tests of significance for heterosis and "useful" heterosis were made with a one degree-of-freedom 'F' test using error mean square as the denominator for those comparisons where no significant interaction with locations occurred. Where heterotic and "useful" heterotic interactions did occur, tests of significance using the interaction term with three degrees of freedom were used.

Genetic analysis of generation means to give unique estimates of additive (A) and dominance (D) effects were obtained by the methods suggested by Hayman (10, 12). These two parameters and an estimate of the additive by additive (AA) type of epistasis were estimated as follows:

$$A = (2P_1 - 2P_2 + BC_1 - BC_2)/5$$

$$D = (-10P_1 - 10P_2 + 14F_1 + 2F_2 + 2BC_1 + 2BC_2)/17$$

$$AA = (-4F_2 + 2BC_1 + 2BC_2)$$

Within each crossing group the five degrees of freedom for genetic populations were partitioned into a one degree-of-freedom test for the A, D, and AA parameters. The two remaining degrees of freedom involve the remaining combined epistatic effects (E). The estimates of A, D, and AA parameters are independent and uncorrelated only if E is not significant. The 'F' test was used to determine significance of all effects and their interactions with locations.

RESULTS AND DISCUSSION

Mean performance of the 36 populations is given in Table 1, with their appropriate mean squares in Table 2. Due to the size of Table 1, multicomparison range tests were not attempted. The four parental lines, Q, DC, FTA, and A, originating from breeding programs outside the Delta, all produced yields significantly lower than DPL. The two varieties Mo and Stv, developed in the Delta, produced yields com-

parable to DPL. Boll sizes tended to be lower than those usually reported in the literature. There was a tendency for the seed cotton of Q to fall out of the boll and, thus, not to be harvested, thereby, contributing to smaller boll size estimates. It is unusual for boll size data to show an Acala (such as A) having a smaller boll size than DPL. Boll rot resulted in considerable two- and three-lock bolls of A. This variety was developed for the more arid regions of the West and probably has undergone little selection pressure for resistance to this particular type of boll rot. The procedural difference of using all the first pick harvestable bolls to compute boll size probably accounts for the major differences between this study and others. Most studies use 50- or 100-boll samples rather than the entire plot. This provides data useful for comparing relative genetic differences among lines, but it also allows selectivity and probably biases upward from the estimates of boll size. More critical is that selectivity of bolls may introduce a genotype by sampling technique interaction. This in turn could lead to incorrect inferences as to the contribution of boll size to yield as compared to other yield components.

Three of the parental lines (FTA, DC, and Stv) had lower lint percentages than DPL. DC, Mo, and FTA each had a higher seed index than DPL, while Q was smaller. Longer fiber was evident on four of the parental lines, while five possessed stronger fiber. Only Stv tended to have fiber length and strength similar to DPL. DPL had coarser fiber than that of any of the six lines with which it was crossed.

Interactions with Locations

The four crossing groups that involved a non-Delta parent tended to have larger population-by-location mean squares than did the two groups involving Delta-developed parents. Combining the analyses of the

Table 1. Mean performance of parental lines, F_1, F_2, and backcross populations.

Pop.	Lint, kg/ha	Lint, %	Boll size	Seed index	50% SL	2.5% SL	T_1	E_1	Mic.
DPL	880	36.0	4.59	11.3	.51	1.14	19.5	8.1	4.25
Q	432	35.8	2.64	10.0	.49	1.10	21.7	6.4	3.93
F_1	964	36.0	4.38	11.0	.53	1.17	20.6	6.8	4.14
F_2	843	35.7	4.15	11.1	.51	1.13	20.8	7.1	4.11
BC DPL	889	35.8	4.64	11.2	.52	1.16	20.7	7.5	4.10
BC Q	628	36.1	3.52	10.8	.51	1.13	21.9	6.5	4.15
DPL	792	35.2	4.62	12.0	.51	1.14	19.3	8.5	4.30
DC	537	31.0	4.74	15.0	.55	1.26	27.4	6.8	3.62
F_1	795	33.7	5.29	13.9	.55	1.24	23.2	7.4	3.85
F_2	768	33.5	5.10	13.5	.55	1.23	22.9	6.8	4.00
BC DPL	868	35.1	5.04	12.3	.53	1.19	21.1	7.9	4.13
BC DC	684	32.1	5.24	14.5	.56	1.25	25.2	6.7	3.78
DPL	907	35.6	4.56	11.8	.52	1.16	19.5	8.0	4.26
FTA	541	30.6	4.45	13.9	.55	1.24	24.1	5.5	3.75
F_1	835	33.9	4.95	13.0	.55	1.23	22.2	6.3	3.95
F_2	782	32.9	4.74	13.1	.54	1.22	22.0	6.6	3.90
BC DPL	853	34.7	4.69	12.2	.52	1.18	20.7	7.2	4.01
BC FTA	741	32.3	4.65	13.6	.55	1.24	23.5	5.6	3.85
DPL	876	36.4	4.48	11.5	.51	1.14	19.6	8.7	4.28
A	398	34.3	3.92	12.2	.53	1.13	24.6	5.8	3.84
F_1	877	35.5	4.88	12.5	.54	1.18	22.6	6.9	4.04
F_2	791	35.2	4.77	12.6	.54	1.17	22.2	7.0	4.06
BC DPL	880	35.5	4.91	11.9	.52	1.15	19.8	7.5	4.10
BC A	715	35.6	4.56	12.3	.53	1.16	23.3	6.3	3.97
DPL	813	35.7	4.63	11.6	.52	1.14	19.4	8.1	4.22
Mo	783	34.4	4.88	13.2	.55	1.18	21.3	8.3	3.85
F_1	936	35.2	5.40	12.2	.55	1.18	20.6	8.2	4.07
F_2	870	34.6	5.28	12.5	.53	1.16	19.8	8.1	4.01
BC DPL	911	35.3	4.97	11.5	.53	1.15	19.4	8.4	4.11
BC Mo	844	34.4	5.15	13.0	.54	1.17	20.9	8.2	3.80
DPL	856	35.9	4.78	11.7	.52	1.15	19.5	8.7	4.19
Stv	862	32.8	4.34	12.2	.51	1.12	19.6	7.5	4.07
F_1	920	34.9	4.93	11.7	.51	1.15	18.8	7.9	4.24
F_2	940	34.6	4.70	11.4	.51	1.13	19.1	7.8	4.17
BC DPL	892	35.1	4.72	11.6	.51	1.14	18.9	8.3	4.28
BC Stv	946	34.2	4.66	11.9	.51	1.13	19.0	7.5	4.15

Table 2. Mean squares for combined analyses for Delta- and non-Delta-derived parental groups.

Source of variability		df	Lint yield	Lint %	Line size	Boll index	Seed SL	50%† SL	2.5%† T_1	E_1	Mic.
Delta	Pop wn groups	10	39,001	5.592**	0.469**	2.328**	.068**	.160**	3.087**	0.880	.1276**
	Pop × L wn Gr	30	25,112**	0.451	0.043	0.110	.026	.035	0.644	0.436	.0349
Non-Delta	Pop wn groups	20	388,052**	12.830**	1.659**	4.969**	.149*	.787**	31.519**	5.653**	.2455**
	Pop × L wn Gr	60	31,808**	1.173**	0.193**	0.387**	.069**	.120**	1.283	0.466	.0685**
	Error	120‡	10,143	0.456	0.078	0.171	.026	.034	0.838	0.474	.0296

* and ** indicate statistical significance at the .05 and .01 levels respectively. † 50 and 2.5% span length (SL) × 100. ‡ Error df = 120 for all traits except yield which = 360.

non-Delta groups into one pooled analysis and the Delta groups into another (See Table 2) gives a relative comparison between the Delta and the non-Delta groups. For each trait the interaction mean square for non-Delta groups is larger than its corresponding Delta group. Seven of the nine traits exhibited highly significant interactions for the non-Delta group, whereas only yield was significant for the Delta-developed group.

A general summarization of the nature of various population-by-location interactions for yield is given in Table 3. Most of the interactions can be related to the performance of DPL, the only recurrent entry in all groups. DPL gave its best yield performance relative to the other populations at Sumner, the location with highest yield, and its poorest at Yazoo City, the location with lowest yield. For example, the average yield of the other parents is 327 kg/ha less at Sumner and only 54 kg/ha at Yazoo City. The measure of "useful" heterosis, F_1-DPL, also shows a progressive decrease from 85 kg/ha at Yazoo City to 4 kg/ha at Sumner. It is probably not a coincidence then that DPL has been used to a greater extent in areas that have a history of high yields and that it is used relatively infrequently in areas where the yield level is low. We were unable to show consistent trends for the other traits to explain the interaction variability encountered therein.

Heterosis

Percent heterosis and "useful" heterosis are given for each trait in Table 4. Heterosis for yield was significant in each cross, ranging from 7.1% to 47.0%. Hybrids with parents originating from outside the Delta tended to express the most heterosis. "Useful" heterosis for yield ranged from —8.0 to 15.0%. It was positive and significant in three cases. These results are somewhat lower than the maximum "useful" heterosis observed by others (7, 8, 13, 14, 20). However previous research in the Delta (19) has shown a response similar to ours. "Useful" heterosis, as has been pointed out, decreased as the yield environment was improved. It is evident that "useful" heterosis for yield still exists, even in an area that has a long history of applied breeding. Heterotic increases in boll size accounted for some of the heterotic yield responses observed. In particular, hybrids involving Q and A had less lint loss due to seed cotton falling out of the boll or boll rot, respectively, than their non-Delta parents. Previous research (1, 14, 15, 20, 21, 23) has also shown that both heterosis and "useful" heterosis for boll size contributed to favorable yield increases in hybrids. Other studies (1, 15, 16, 23, 29) have shown that an increased number of bolls is also an important contributor to yield. In these studies boll size and lint percent do not account for

Table 3. Mean lint yield, kg/ha, for DPL, parental lines and their various hybrid populations at each location.

	Population								
Loc.	DPL	P	F_1	F_2	BC DPL	BC P	MP	F_1 - DPL	F_1 - MP
Y.C.	425	371	510	481	498	439	398	85	112
Stv.-S.	784	469	818	733	806	658	627	34	192
Stv.-C.	936	582	946	839	966	756	759	10	187
Summer	1,274	947	1,278	1,275	1,259	1,185	1,110	4	168
Mean	855	592	888	832	882	760	723	33	165

Table 4. Heterosis and "useful" heterosis expressed as percentages[1].

Population	Lint yield	Lint %	Boll size	Seed index	50% SL	2.5% SL	T_1	E_1	Mic.
DPL × Q	47.0*‡	0.2	21.1**	3.3	4.8**	3.8**	0.2	-5.9	1.2
	9.5**	-0.1	-4.7	-2.6	2.4	2.1*	5.9*	-15.8	-3.7
DPL × DC	19.6**	1.9*	13.1**	3.3**	4.3**	3.5**	-0.6	-3.8	-2.8
	.3	-4.3	14.5**	16.2**	7.8**	8.8**	20.3**	-13.6**	-10.4**
DPL × FTA	15.3**	2.5**	10.0**	1.1	3.3**	3.1**	1.8	-6.7	-1.5
	-8.0	-4.7*	8.7	10.3**	6.0**	6.7**	13.6**	-21.0**	-7.4**
DPL × A	37.7**	0.4	16.2	5.4**	3.7**	3.8	2.3	-4.8	-0.3
	0.1	-2.6	9.0	8.8**	5.6**	3.3**	15.3*	-21.8**	-5.3**
DPL × Mo	17.3**	0.5	13.6**	-1.5	2.3	1.7**	1.1	0.0	0.8
	15.0**	-1.3	16.7**	5.5**	5.3	3.4**	6.2**	1.3	-3.6
DPL × Stv	7.1*	1.6	8.4**	-2.2	0.0	0.9	-3.9	-1.8	2.6
	7.5*	-2.8	3.2	0.1	-0.7	-0.5	-3.6	-8.4	1.1
Average	22.7**	1.1**	13.4**	1.5**	3.1**	2.8*	0.2	-3.7*	0.0
All crosses	3.9*	-2.6**	8.0**	6.5**	4.4**	3.9**	9.6**	-13.0**	-4.8**

* and ** indicate significance at .05 and .01 levels, respectively. † Heterosis % = 100 × (F_1-MP)/MP and % DPL = 100 × (F_1-DPL)/DPL. ‡ Upper figure heterosis %, lower figure "useful" heterosis.

all of the yield increases observed for the hybrids. Since lint percent contributed very little, it is probable that an increase in boll number was a major contributing factor to heterosis and "useful" heterosis for yield in these populations as well.

Heterosis was detected for all traits except strength, elongation, and micronaire. However, the magnitude of heterosis for the remaining traits was usually smaller than that for boll size and lint yield. Heterosis and "useful" heterosis were usually consistent from location to location, but significant interactions did occur. Most of these interactions were small. Those for yield generally followed the pattern already discussed. The cross of DPL × A was the most variable from location to location.

The yield performance of the F_2 populations in the two crossed Delta parents indicated a potential for using F_2's. The heterotic response observed in the F_1 was reduced approximately 50% for most crosses. However, the F_2 for DPL × Stv produced yields 20 kg/ha greater than the F_1 and 84 kg/ha greater than DPL. Heterotic effects for yield were also evident for the backcross populations. As one might have anticipated, the backcross to DPL exhibited greater yield performance than its analogue in most cases. Several of the backcrosses (DC, A, Stv, and Mo) to DPL produced yields comparable to or in excess of DPL and the F_1. The backcross to Stv exceeded DPL, Stv, F_1, F_2, and the backcross to DPL.

The results for individual traits in this study are comparable with those reported from many other areas. However, a breeder does not make decisions solely in terms of individual traits. When the combined results for yield and lint quality factors are observed, the superiority of hybrids is even more pronounced. Four of the six hybrids (Q, DC, A, and Mo) were equal to or superior in yield to DPL and in addition had longer and stronger fiber than DPL. For example, DPL × DC had a yield level approximately the same as DPL but had 2% longer lint and 20% stronger fiber. DPL × Mo had a yield advantage of 15% over DPL and had 3% longer and 6% stronger fibers. There can be little doubt that the small favorable increases in both yield and fiber properties can combine to produce hybrids with a much superior performance to that of an accepted variety like DPL.

Assumptions for Genetic Analysis

Hayman (12) described three situations under which nonadditive gene action would be operable in causing heterosis. In brief, epistasis is absent, is relatively small, or is of large magnitude relative to the additive and dominance effects. Problems in estimation of genetic parameters occur only when large amounts of additive-by-dominance and dominance-by-dominance epistasis are present. In those cases unique estimates of these and the other genetic effects are unattainable. The two degrees of freedom for E are used to test this assumption against the error mean square.

Other assumptions for the genetic analyses are that parental lines are highly inbred, that there are no reciprocal effects, and that the genes affecting the traits measured are not linked. With the exception of Q, which was an F_6 plant, all parental lines were highly inbred. Reciprocal effects have usually gone undetected in crosses of these types in cotton. However, it is unlikely that crosses involving parents as genetically diverse as these would be in linkage equilibrium. Only genetic estimates that depend entirely on the parental lines and the F_1 are free of linkage bias. It would also be assumed that intra-plot competition within segregating populations would not affect the estimation of generation means. To date, this phenomenon has not been adequately investigated in cotton.

Generation means for gene action estimates have been previously used in cotton (18, 19, 22) as well as in a large number of other crops. Means are usually estimated more accurately than variances, and the assumption of no epistasis often used in other genetic models can be tested with this approach. The method of estimating gene effects is primarily useful in detection if large amounts of epistasis are operable in the genetic population being investigated.

Gene Action Involved in Heterosis

Significant heterosis (F_1 — MP) indicates the presence of nonadditive gene effects caused either by dominance, or epistasis, or both. Heterosis in this study was detected for all traits except fiber strength, elongation, and fineness. Table 5 gives the mean squares for A, D, AA, and combined E effects for each trait in each group. Out of the 54 possible tests for epis-

tasis, only four cases of significant AA and five cases of significant E were detected. It is possible that Type I statistical error accounts for a portion of these results. In the instances of significant AA or E the magnitude of their mean squares relative to the additive and dominance effects was small. It is evident in this study that epistasis is either absent or of such small magnitude as to warrant little attention in a breeding program. The genetic situations in this study can then be ascribed to Hayman's (12) Group I, where epistasis is absent, or at most to Group II, where epistasis is small relative to additive and dominance effects.

This agrees with previous reports for lint yield (19, 21, 27, 28), in which epistasis was undetected or was of very small magnitude relative to additive and dominance effects. However, several other studies have indicated that epistasis may be as important as dominance for the heterotic effects observed (1, 9, 11, 18). From the data now available for cotton it should be evident that detection of epistasis is dependent on the particular genetic material involved, the traits being studied, and the particular genetic model used. For yield the tendency has been for heterosis to be largely attributed to dominance; however, exceptions are noted. Epistasis appears to be detected more in crosses of great genetic diversity than from those that are more closely related.

Crosses with DC and FTA indicate significance dominance for lint percentage, but additive effects

Table 5. Mean square estimates of genetic parameters for nine traits.

Cross	Genetic par.	Lint† yield	Lint %	Boll size	Seed index	50%‡ SL	2.5%‡ SL	T_1	E_1	Mic.
DPL	A	2,143**	.03	20.180**	7.50**	2.31	8.41	25.19	15.16**	.298
× Q	D	1,013*	.01	3.604**	1.05	3.14	9.88**	.31	1.06	.014
	AA	76**	-.30	.026	.08	.00	.47	1.04	.11	.002
	E	11	.35	.094	.33	.08	.10	1.66	.01	.070
	A×L	62**	1.29*	.045	.44	1.28**	.98*	3.21*	.28	.199**
	D×L	34**	.40	.019	.95**	.82*	.44	.32	.85	.147**
	AA×L	14	.05	.020	.04	.24	.33	.24	.38	.024
	E×L	35**	.58	.022	.23	.34	.73	.35	.21	.030
DPL	A	772**	106.03**	.151	52.98**	6.66	69.62*	332.62**	17.08*	2.295*
× DC	D	239*	2.54*	2.466**	.71	3.54**	10.24**	.30	1.06	.042
	AA	1	.08	.011	.09	.10	.21	.48	1.32	.008
	E	31*	1.23	.143	1.08**	.31	.05	.31	1.08	.025
	A×L	25	1.89**	.398**	.88*	1.67**	3.69**	4.90**	1.47*	.091*
	D×L	10	.95	.110	.36	.08	.31	.38	.29	.004
	AA×L	10	.46	.048	.12	.21	.36	1.58	.15	.007
	E×L	8	.42	.116	.31	.35	.23	.71	.10	.005
DPL	A	1,138*	120.30**	.052	26.57**	5.12**	37.41**	111.49**	32.90	1.123**
× FT	D	150**	3.11*	1.103	.13	1.46**	7.12**	.99	1.18	.037
	AA	2	1.73	.027	.15	.08	.17	.06	.26	.003
	E	18	.25	.006	.28	.82	.22	.37	.19	.036
	A×L	71**	1.14	.170	.76**	.30	.93*	.18	.64	.064
	D×L	2	.35	.223*	.12	.14	.24	.22	.55	.009
	AA×L	2	.20	.007	.16	.69	.27	.23	.23	.003
	E×L	11	.27	.063	.57**	1.03*	.54	.42	.31	.028
DPL	A	2,019	14.11	1.717	2.93	1.71	.15	143.59*	39.94**	.790
× A	D	731*	.09	3.226	2.57**	2.23**	9.88	.49	.87	.002
	AA	1	.65	.008	1.11	1.10*	2.00*	2.13	.02	.003
	E	35*	1.98	.260	.06	.01	.41	3.51*	.26	.014
	A×L	220**	9.66**	.324**	.62*	3.26**	9.83**	8.64**	1.14	.178**
	D×L	39*	1.35*	.885**	.08	.40	2.54**	.51	.10	.118**
	AA×L	20	.22	.124	.63*	.29	.10	.42	.89	.043
	E×L	10	1.40**	.216*	.19	.43	.45	.92	.56	.179**
DPL	A	27	9.66**	.380**	18.24**	4.21**	6.85**	22.93**	.02	.918*
× Mo	D	223**	.02	2.504**	.20	.50	1.40**	.03	.00	.000
	AA	1	.24	.272	.33	.30	.21	.67	.18	.019
	E	10	.82	.022	.68*	.44	.83	1.30	.22	.061
	A×L	93**	2.49**	.042	.11	.04	.07	.27	.31	.070
	D×L	6	.55	.097	.02	.91*	.56	.75	1.54*	.020
	AA×L	9	.43	.021	.05	.17	.09	1.42	.07	.057
	E×L	12	.33	.053	.19	.35	.34	.74	.14	.072*
DPL	A	7	41.18**	.639**	1.65**	.18	4.35**	.09	7.58**	.118**
× Stv	D	62	1.85	.758**	.58*	.03	.28	3.99**	.22	.074
	AA	5	.01	.001	.68*	.08	.35	.06	.01	.008
	E	24	.65	.046	.12	.30	.45	.24	.17	.009
	A×L	81**	.27	.017	.18	.24	.14	.34	.64	.013
	D×L	8	2.61**	.001	.14	.21	.54	1.27	.69	.048
	AA×L	2	.35	.095	.05	.24	.17	.32	.27	.011
	E×L	14	.18	.024	.06	.10	.68	.29	.28	.007
Error		10	.46	.076	.17	.27	.34	.84	.47	.030

* and ** indicate statistical significance at the .05 and .01 level, respectively. † Lint yield mean square has been divided by 1,000. ‡ 50% and 2.5% span length (SL) × 1,000.

tended to be of much greater magnitude. Heterosis for boll size was caused by dominance. Significant dominance for boll size has been reported by several authors (1, 27, 28). Dominance gene action for increased boll size is probably partially responsible for the expression of dominance for lint yield. Additive effects tended to be more important than dominance effects for seed index. Significant dominance for fiber length was evident in all crosses except DPL × Stv. The remaining fiber properties tended to be inherited in a predominantly additive manner. One case of negative dominance for fiber strength was detected in the cross of DPL × Stv.

Interactions with Locations

The interactions of genetic effects with locations are also given in Table 5. The interaction of additive effects and locations, due to the method of calculation, is a reflection largely of the differences among parental lines not remaining constant over locations. For lint yield significant additive-by-location interactions were evident for five of the six crosses. From populations derived from the crosses involving the two Delta-developed parental lines, the additive-by-location interaction mean squares were larger than the additive mean squares. This indicates that even for testing segregating material from adapted varieties, there is a need for using several environments to adequately estimate yield performance. Dominance-by-location interactions were usually small; however, two cases of significance were detected.

Over all traits there were 28 and 13 instances in which the additive-by-location and dominance-by-location interactions, respectively, were significant. There was one case of significant additive-by-additive epistasis, and there were seven cases of combined epistasis (E) interacting with locations. The interactions involving additive effects by locations were usually of much greater magnitude than were those for the other interaction effects.

The interaction mean squares for yield components and for fiber properties, while frequently significant, are usually small relative to the overall additive and dominance effects. Significant interactions for gene effflfects were particularly evident in the cross of DPL × A. Aattempts in the past to find adapted Acala varieties for the Mississippi Delta have not been successful. Crosses involving Acala have also not usually been successful. Favorable responses for Acala types have often been measured in one environment, but after repeated testing are generally eliminated from the breeding programs. This inability to adapt to Delta conditions is reflected in the numerous interactions with gene effects for DPL × A.

Breeding Implications

The presence of large amounts of additive effects suggests the potential for obtaining further yield and fiber property improvements without resorting to the use of hybrids. El-Adl and Miller (6) reported obtaining transgressive segregates that were better than the original F_1. Those segregates were selected from advanced generations of the F_1. These positive results imply that other populations may have the same po-

tential of equaling the performance of their F_1's. However, in this study the presence of significant dominance in most crosses indicate that at this point in a breeding program, hybrids would be an improvement over existing commercial varieties. The primary limiting factor to producing hybrids or synthetics is the lack of sufficient insect vectors to insure cross-pollination. The dominance effects tended to interact less with environments than additive effects. This gives some evidence that F_1's should be at least as adapted as good commercial varieties.

The relatively small interactions of additive gene effects with locations for yield components and fiber properties indicate that selection for these traits should be effective in a single environment. For lint yield more environments would be required.

REFERENCES

1. Al-Rawi, K. M., and R. J. Kohel. 1969. Diallel analyses of yield and other agronomic characters in Gossypium hirsutum L. Crop Sci. 9:779-783.
2. ————, and ————. 1970. Gene action in the inheritance of fiber properties in intervarietal diallel crosses of upland cotton, Gossypium hirsutum L. Crop Sci. 10:82-85.
3. Anon. 1968. Notice to growers relative to the naming and release of a commercial variety of upland cotton, Acala 3080. New Mexico Agr. Exp. Sta. and US Dep. Agr. Memo. 6 p.
4. ————. 1970. Cotton varieties planted 1966-70. US Dep. Agr. Consumers and Marketing Service Report, Cotton Division, Memphis, Tenn. 30 p.
5. ————. 1970. Notice of release of a variety of upland cotton, Delcot 277. Missouri Agr. Exp. Sta. and US Dep. Agr. Memo. 8 p.
6. El-Adl, A. M., and P. A. Miller. 1971. Transgressive segregation and the nature of gene action for yield in an intervarietal cross of upland cotton. Crop Sci. 11:381-384.
7. Fryxell, P. A., G. Staten, and J. H. Porter. 1958. Performance of some wide crosses in Gossypium. New Mexico Agr. Exp. Sta. Bull. 419. 15 p.
8. Hawkins, B. S., H. A. Peacock, and W. W. Ballard. 1965. Heterosis and combining ability in upland cotton—Effect on yield. Crop Sci. 5:543-546.
9. Hayman, B. I. 1957. Interaction, heterosis and diallel crosses. Genetics 42:336-355.
10. ————. 1958. The separation of epistatic from additive and dominance variation in generation means. Heredity 12:371-390.
11. ————. 1958b. The theory and analysis of diallel crosses. II. Genetics 43:63-85.
12. ————. 1960. The separation of epistatic from additive and dominance variation in generation means II. Genetica 31:133-146.
13. Jones, J. E., and H. D. Loden. 1951. Heterosis and combining ability in upland cotton. Agron. J. 43:514-516.
14. Lee, J. A., P. A. Miller, and J. O. Rawlings. 1967. Interaction of combining ability effects with environments in diallel crosses of upland cotton (Gossypium hirsutum L.). Crop Sci. 7:477-481.
15. Marani, A. 1963. Heterosis and combining ability for yield and components of yields in a diallel cross of two species of cotton. Crop Sci. 3:552-555.
16. ————. 1967. Heterosis and combining ability in intraspecific and interspecific crosses of cotton. Crop Sci. 7:519-522.
17. ————. 1968. Inheritance of lint quality characteristics in intraspecific crosses among varieties of Gossypium hirsutum L. and of G. barbadense L. Crop Sci. 8:36-38.
18. ————. 1968b. Heterosis and inheritance of quantitative characters in interspecific crosses of cotton. Crop Sci. 8:299-303.
19. Meredith, W. R., Jr., R. R. Bridge, and J. F. Chism. 1970. Relative performance of F_1 and F_2 hybrids from doubled haploids and their parent varieties in upland cotton, Gossypium hirsutum L. Crop Sci. 10:295-298.
20. Miller, P. A., and J. A. Lee. 1964. Heterosis and combining abiilty in varietal top crosses of upland cotton, Gossypium hirsutum L. Crop Sci. 4:646-649.

21. ————, and A. Marani. 1963. Heterosis and combining ability in diallel crosses of upland cotton, *Gossypium hirsutum* L. Crop Sci. 3:441-444.
22. Ramey, H. H. 1963. Gene action in the inheritance of lint index in upland cotton. Crop Sci. 3:32-33.
23. Turner, J. H., Jr. 1953. A study of heterosis in upland cotton. I. Yield of hybrids compared with varieties. Agron. J. 45:484-486.
24. ————. 1953b. A study of heterosis in upland cotton. II. Combining ability and inbreeding effects. Agron. J. 45: 487-490.
25. Verhalen, L. M., and J. C. Murray. 1969. A diallel analysis of several fiber property traits in upland cotton (*Gossypium hirsutum* L.) II. Crop Sci. 9:311-315.
26. ————, W. C. Morrison, B. A. Al-Rawi, K. C. Fun, and J. C. Murray. 1971. A diallel analysis of several agronomic traits in upland cotton (*Gossypium hirsutum* L.). Crop Sci. 11:92-96.
27. White, T. G. 1966. Diallel analyses of quantitatively inherited characters in *Gossypium hirsutum* L. Crop Sci. 6: 253-255.
28. ————, and R. J. Kohel. 1964. A diallel analysis of agronomic characters in selected lines of cotton, *Gossypium hirsutum* L. Crop Sci. 4:254-257.
29. ————, and T. R. Richmond. 1963. Heterosis and combining ability in top and diallel crosses among primitive, foreign, and cultivated American upland cottons. Crop Sci. 3:58-63.