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Heterosis and Combining Ability in Upland Cotton—Effect on Yield[1]

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IN RECENT years the subject of heterosis, or the manifestation of heterosis known as hybrid vigor, has received increased attention from cotton breeders. Heterosis was first utilized in obtaining increased production in asexually propagated plants. Through the use of male-sterility, gametocides, and imperfect-flowered plants, heterosis is now used to advantage in many species.

Considerable evidence exists (4) that heterosis is expressed in crosses between *Gossypium hirsutum* (Upland cotton) and *G. barbadense* (extra-long staple cotton). There are indications that heterosis may exist also in crosses among different varieties of Upland cotton and that varieties may vary considerably in combining ability. Data from crosses among three varieties of Upland cotton, in a study begun in 1954 at the Georgia Experiment Station, indicated that appreciable heterosis existed in intervarietal crosses. Becauses of these favorable results, a larger study designed to obtain further information on heterosis and combining ability of other varieties was begun in 1956. The purpose of this paper is to report the magnitude of the heterotic effect in crosses among four varieties of Upland cotton.

REVIEW OF LITERATURE

Loden and Richmond (4) presented a thorough review of work on heterosis in cotton. One of their conclusions was that the maximum heterotic effect was obtained in the F_1 generation and few significant increases in yield occurred in subsequent generations. Ware (8), working with crosses between *G. hirsutum* and *G. barbadense,* found that heterosis occurred in the F_1 generation of species crosses in cotton but was not expressed for all plant characters.

In discussing heterosis in intraspecific crosses, Kime and Tilley (3) reported that the general assumption had been made that heterosis did not occur in crosses within cotton species. However, Brown (1) reported that F_1 hybrids were frequently larger, more vigorous, and more productive than their parents. Loden and Richmond (4) were of the opinion that the list of intraspecific crosses in which an appreciable amount of heterosis had been exhibited would have been rather extensive if all the cases observed had been recorded and published.

Simpson (6) studied 7 varieties of cotton with seed obtained from 2 sources. Seed produced in isolated fields were called inbred, and seed produced in a variety test and subjected to natural crossing were called crossed. Data were recorded for various characters and no significant differences were found between inbred and crossed seed for most characters. However, the yield of the crossed seed exceeded that of the inbred in each of the 7 varieties, with the range in yield increases being 5.7 to 44.2%. Three of the individual differences were more and 4 were less than required for significance. In Simpson's study the 7 crossed seed sources produced an average of 15.4% more than the inbred seed sources.

Turner (7) reported yield increases of 18 to 44% over the best locally adapted commercial variety for 14 different hybrid selections grown in 1947.

Kime (2) conducted a number of tests involving 10 inbred lines and their 45 single crosses. General and specific combining ability were calculated for lint yield, bolls per plot, seed per boll, and lint index. The value of the hybrids on the basis of combining ability varied according to the yield component under consideration. No important discrepancies were noted between general and specific combining ability, that is, parents high in general combining ability also exhibited high specific combining ability.

EXPERIMENTAL PROCEDURE

The study was begun in 1956 using 4 varieties of Upland cotton ('Empire WR', 'Pope', 'Plains', and 'Stoneville 7') adapted to the Piedmont Area of Georgia as parents. The parent varieties were chosen because of farmer acceptance and popularity and because they represent a range of different genotypes within the American Upland group of cultivated cottons. They are representative also of the small genetic differences which exist between varieties grown commercially in this area. Although genetic diversity is limited among these four varieties, they differ in genetic origin. Adequate foundation seed of each variety were obtained and stored to provide planting stock for parent entries for the 3-year period of the study.

Diallel controlled crosses were made in the field in 1956 among the 4 varieties, making a total of 6 single crosses. Concurrently, several bolls of each variety were covered with brown kraft paper bags to produce seed of the first selfed generation (S_1). Sufficient bolls were selfed to produce S_1 seed for the 3-year study. Likewise, enough crosses were made to produce sufficient seed of each cross for the 3-year experiment. About 100 seed each of the first

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filial (F_1) and S_1 generations were sent to Iguala, Mexico, in November 1956, for the production of F_2 and S_2 seed. Thus, seed of all parents, F_1, S_1, F_2, and S_2 were available for planting in the spring of 1957. The experimental design was that of a randomized block replicated 4 times with 25 hills per plot. The field design was changed in 1958 and 1959; the number of replications was increased from 4 to 6 and row length was reduced from 25 to 20 hills.

Tests were planted between April 29 and May 5 each year. Seed were acid-delinted, treated with a fungicide, and hand-dropped at 15-inch intervals in 40-inch rows. Seedlings were thinned to one plant per hill. In 1957 a perfect stand for the entire test was 100 plants per entry; in 1958 and 1959, 120 plants. All missing hills were replanted with seedlings started in the greenhouse.

Field and laboratory data collected were pounds seed cotton per acre, pounds lint per acre, lint percentage, and percentage 5-lock bolls (bolls having 5 locules). Lint yield values were obtained by multiplying the total weight of seed cotton per plot by the lint percentage for that plot. Flowers per plant were recorded during a 5-week period in 1957 and 1958 and during a 6-week period in 1959. Flowers were counted daily on half the replications. Just before the first harvest, 3-, 4-, and 5-lock bolls were counted from 100 randomly chosen bolls per plot on half the replications.

Data from S_1 and S_2 generations of each variety are included as indicators of the homogeneity of the non-inbred parent varieties.

RESULTS AND DISCUSSION

Lint percentage and lint yield. Results of three year's data for lint percentage and lint yield are summarized in Table 1. No significant differences existed between the parents and respective S_1 and S_2 generations for either lint percentage or lint yield. Lack of such differences is an indication of the purity of the varieties used as parents. The 3-year average lint percentage of the F_1 and F_2 generations was, likewise, not different from that of the parent varieties.

F_1 lint yield was higher than the lint yield of the higher yielding parent variety in all cases. However, the lint yield of only 4 of the 6 F_1's was significantly ($P=.05$) higher than the lint yield of the corresponding better parent. The increase in lint yield of the F_1 over the better parent ranged from 11.7 to 24.2%, indicating the importance of parent variety combination in producing the best hybrid.

Although the lint yield of only 4 of the 6 F_1's was significantly higher than that of the corresponding F_2, the lint yield of the F_1 was higher than the lint yield of the corresponding F_2 without exception. When individual years were considered the lint yield of F_1's was higher, but not significantly so in all cases, than the lint yield of corresponding F_2's in all years with one exception. This exception occurred in 1959 when the F_2 of Empire WR $\times$ Stoneville 7 exceeded the F_1 yield. In view of the magnitude of the experimental error, relatively large random variations were expected; however, it is noteworthy that an F_2 of two cotton varieties should exceed the yield of the corresponding F_1. In general, the F_2 yield is expected to be considerably less than that of the F_1; therefore, an F_2 yield approaching or exceeding the F_1 yield is worthy of consideration. True F_1 cotton hybrids are not feasible on a commercial scale but F_2 hybrids could be a commercial reality.

As further evidence of the importance of parent variety combination, the lint yield of 1 of the 6 F_2's Empire WR $\times$ Pope, was significantly less than that of the higher yielding parent, Pope.

Flowers per plant and percentage 5-lock bolls. All varieties and crosses reached a bloom peak approximately 13 weeks after the planting date each year. The 3-year average number of flowers per plant for varieties and crosses is presented in Table 2. The selfed generations of Empire WR and Plains showed a significant increase in the number of flowers per plant when compared with the parents, whereas the selfed generations of Pope and Stoneville 7 were essentially the same as the parents. The flower production of the F_1 hybrids was about the same as that of the parent producing the most flowers.

Although not statistically significant, one F_2 (Empire WR $\times$ Plains) produced 5.9% more flowers per plant than its corresponding F_1. This is noteworthy since the F_2 was otherwise inferior to the F_1. The production of fewer

Table 1. Average lint yield and lint percentage of cotton varieties, selfed generations, diallel crosses, and F_2 generations comprising an intervarietal study, 1957–1959.

Entry	Lint		Lint percentage
	Per acre	Change from parent*	
	lb	%	
Empire WR	683	--	40.0
Empire WR S_1	767	12.3	40.0
Empire WR S_2	660	-3.4	39.3
Pope	777	--	41.2
Pope S_1	781	0.5	40.9
Pope S_2	776	-0.1	41.3
Plains	695	--	39.2
Plains S_1	701	0.9	38.8
Plains S_2	807	16.1	38.9
Stoneville 7	652	--	40.5
Stoneville 7 S_1	751	15.2	40.4
Stoneville 7 S_2	657	0.8	40.3
Empire WR × Pope F_1	946	21.8	41.2
Empire WR × Pope F_2	635	-18.3	40.6
Empire WR × Plains F_1	835	20.1	39.8
Empire WR × Plains F_2	720	3.6	39.3
Empire WR × Stoneville 7 F_1	848	24.2	40.3
Empire WR × Stoneville 7 F_2	758	11.0	39.5
Pope × Plains F_1	920	18.4	40.7
Pope × Plains F_2	780	0.4	40.2
Pope × Stoneville 7 F_1	868	11.7	41.0
Pope × Stoneville 7 F_2	703	-9.5	41.4
Plains × Stoneville 7 F_1	817	17.6	39.8
Plains × Stoneville 7 F_2	626	-9.9	40.0
LSD 5% level	128		NS
LSD 1% level	171		NS

* In F_1 and F_2 change is from the better parent involved in the respective hybrid.

Table 2. Average number of flowers per plant and percentage 5-lock bolls of cotton varieties, selfed generations, diallel crosses, and F_2 generations comprising an intervarietal study, 1957–1959.

Entry	Flowers		Bolls	
	Per plant	Change from parent*	5-lock	Change from parent*
	no.	%	%	%
Empire WR	27.7	--	52.6	--
Empire WR S_1	27.2	-1.8	53.7	2.1
Empire WR S_2	30.8	11.2	59.7	13.5
Pope	32.0	--	14.3	--
Pope S_1	31.9	-0.3	21.0	46.8
Pope S_2	29.9	-6.6	18.6	30.1
Plains	27.3	--	49.0	--
Plains S_1	29.6	8.4	57.6	17.6
Plains S_2	31.6	15.8	52.4	6.9
Stoneville 7	29.4	--	40.0	--
Stoneville 7 S_1	29.9	1.7	42.6	6.5
Stoneville 7 S_2	28.4	-3.4	44.4	11.0
Empire WR × Pope F_1	32.9	2.8	40.8	-22.4
Empire WR × Pope F_2	30.8	-3.8	40.3	-23.4
Empire WR × Plains F_1	28.8	4.0	57.2	8.7
Empire WR × Plains F_2	30.5	10.1	60.0	14.1
Empire WR × Stoneville 7 F_1	29.6	0.7	55.4	5.3
Empire WR × Stoneville 7 F_2	28.0	-4.8	47.5	-9.7
Pope × Plains F_1	31.6	-1.2	33.0	-32.6
Pope × Plains F_2	29.6	-7.5	33.2	-32.2
Pope × Stoneville 7 F_1	31.4	-1.9	27.3	-31.8
Pope × Stoneville 7 F_2	28.5	-10.9	33.0	-17.5
Plains × Stoneville 7 F_1	29.9	1.7	46.2	-5.7
Plains × Stoneville 7 F_2	28.6	-2.7	52.0	6.1
LSD 5% level	2.7		7.5	
LSD 1% level	3.7		10.2	

* In F_1 and F_2 change is from the better parent involved in the respective hybrid.

flowers per plant by the other F_2 populations was reflected in yield.

Considerable variation in percentage 5-lock bolls was evident within varieties, selfed generations, diallel crosses, and the F_2 generations from year to year. However, when the yearly values were combined into a 3-year average much of the variation disappeared. Data presented in Table 2 show a nonsignificant increase in percentage 5-lock bolls in selfed generations of all parent varieties. A similar increase was evident in 4 of the 6 F_2 hybrids when compared with the F_1's. However, the Empire WR × Stoneville 7 cross showed a significant decrease in percentage 5-lock bolls from F_1 to F_2.

Heterosis and combining ability. Shull (5) defined heterosis as "the interpretation of increased vigor, size, fruitfulness, speed of development, resistance to disease and to insect pests, or to climatic rigors of any kind, manifested by crossbred organisms as compared with corresponding inbreds, as the specific results of unlikeness in the constitution of the uniting parental gametes." Heterosis is thus recognized as "the result of the interaction of unlike gametes" (5), and the manifestations expressed are measured in terms of hybrid vigor. Combining ability, the average performance of a variety or line in hybrid combinations, has been shown to be an inherited character by many workers in various fields. Combining ability is associated with heterosis in that combining ability also is measured in terms of hybrid vigor.

An estimate of general combining ability for a character may be obtained from the average of the character of the single crosses involving a given variety.

Table 3 shows the 3-year average lint yields, flowers per plant, and percentage 5-lock bolls of diallel crosses and parent varieties, and their significance. The general combining ability effects of the F_1's are significant only for percentage 5-lock bolls. Empire WR was significantly superior in general combining ability for percentage 5-lock bolls to Pope. In 2 of the 3 years, the relative rank of varieties in general combining ability for percentage 5-lock bolls remained the same. Parental performance is a good indicator of general combining ability for percentage 5-lock bolls since the ranking of the parent varieties for their general combining ability in the crosses tended to be the same as that for the performance of the varieties themselves.

Another character which could be a contributing factor to increase in lint yield of F_1's over parents is number of flowers per plant. Although not significant, Pope ranked first and Stoneville 7 second (Table 3) in number of flowers per plant. Even though Empire WR and crosses involving Empire WR are relatively low in number of flowers per plant, the crosses involving Empire WR are second in lint yield. Possible factors contributing to the good yield of Empire WR crosses are the large percentage of 5-lock bolls in combination with the large boll size of the variety.

Although not significantly different, Pope was best and Empire WR second best in general combining ability for lint yield. When the 3-year average lint yields are broken down into yearly means, the relative rank in yield is different each year demonstrating the need for testing hybrids for more than one year.

The means for each single cross for each F_1 character and their significance relationships are presented in Table

Table 3. Average lint yield, flowers per plant, and percentage 5-lock bolls of diallel crosses and parent cotton varieties in an intervarietal study, 1957–1959.

Entry	Lint per acre		Flowers per plant		5-lock bolls	
	Crosses*	Parents	Crosses*	Parents	Crosses*	Parents
	lb	lb	no.	no.	%	%
Empire WR	876	683	30.4	27.7	51.1	52.6
Pope	911	777	32.0	32.0	33.7	14.3
Plains	857	695	30.1	27.3	45.5	49.0
Stoneville 7	844	652	30.3	29.4	43.0	40.0
LSD 5% level	NS	NS	NS	3.7	8.6	8.6
LSD 1% level	NS	NS	NS	NS	12.3	12.3

* Mean of three crosses involving the given parent variety.

Table 4. Average lint yield, flowers per plant, and percentage 5-lock bolls of single crosses of cotton in an intervarietal study, 1957–1959.

Entry	Lint per acre	Flowers per plant	5-lock bolls
	lb	no.	%
Empire WR × Pope	946	32.9	40.8
Empire WR × Plains	835	28.8	57.2
Empire WR × Stoneville 7	848	29.6	55.4
Pope × Plains	920	31.6	33.0
Pope × Stoneville 7	868	31.4	27.3
Plains × Stoneville 7	817	29.9	46.2
LSD 5% level	NS	3.7	8.6
LSD 1% level	NS	NS	12.3

4. The specific combining ability effects are significant for both flowers per plant and percentage 5-lock bolls.

Empire WR × Pope was best in specific combining ability for flowers per plant and lint per acre indicating that number of flowers per plant was partially responsible for the lint-yield heterosis exhibited.

In percentage 5-lock bolls the F_1 of Empire WR × Plains was best and was significantly higher in specific combining ability for this character than the F_1 of Empire WR × Pope. This was as expected from general combining ability performance since the varieties Empire WR and Plains ranked first and second in general combining ability for percentage 5-lock bolls. However, the data in Tables 3 and 4 indicate that some factor or combination of factors other than 5-lock bolls is responsible for the lint-yield heterosis exhibited in the F_1 of Empire WR × Pope, since Empire WR expressed high general combining ability for 5-lock bolls and Pope did not. There is little evidence in these data to indicate that percentage 5-lock bolls either increases or decreases yield.

Pope and Empire WR ranked first and second in general combining ability for lint yield. The F_1 of Empire WR × Pope was highest (not significantly) in lint yield of the 6 F_1's. It seems more than coincidence that the two varieties ranking first and second in general combining ability for yield, when crossed together, produced the best specific combination for that character. Although the 6 F_1's were not significantly different in lint yield, when each was compared with its respective better parent, heterotic effects were significantly evident. Therefore, those specific crosses which were numerically superior in lint yield appeared to have the best specific combining ability. Other single crosses which appeared to show specific combining ability, that is, superiority over the average single-cross performance were Pope × Plains and possibly Pope × Stoneville 7.

The percentage increase in lint yield of F_1 hybrids over the higher yielding parent variety is presented in Table 5. The percentage increase over the better parent ranged from a high of 50.5 in 1957 to a low of 4.2 in 1959. The data show in general a considerably larger increase in yield

Table 5. Lint yield of four cotton varieties and F_1 crosses with percentage increase in lint of F_1's over better parent in an intervarietal study, 1957–1959.

Entry	1957		1958		1959		3-year average	
	Lint per acre	Change from better parent	Lint per acre	Change from better parent	Lint per acre	Change from better parent	Lint per acre	Change from better parent
	lb	%	lb	%	lb	%	lb	%
Empire WR	590		617		841		683	
Pope	579		743		1,010		777	
Plains	547		830		907		695	
Stoneville 7	578		652		829		652	
Empire WR × Pope	888	50.5	897	20.7	1,053	4.2	946	21.8
Empire WR × Plains	782	32.5	735	16.7	987	8.8	835	20.1
Empire WR × Stoneville 7	787	33.4	789	27.8	868	15.3	848	24.2
Pope × Plains	828	43.0	871	17.2	1,062	5.1	920	18.4
Pope × Stoneville 7	693	19.7	814	9.6	1,096	8.5	868	11.7
Plains × Stoneville 7	752	30.6	676	7.3	1,026	13.0	817	17.6
LSD 5% level	49		162		258		128	
LSD 1% level	66		201		NS		171	

of the F_1 over the better parent in 1957 than in 1959. The year 1957 was a relatively poor year for variety yields while 1959 was a good one. The average lint yields of the parent varieties were 573, 636, and 897 pounds per acre for 1957, 1958, and 1959, respectively. The average increase of the hybrids over the better parent varieties for the same years was 35.0, 16.6, and 9.2%. These findings indicate that hybrids were relatively much more productive than parent varieties in a poor year than in a good year. The 3-year average lint yield increase for the 6 crosses over the better parent variety involved was 19.0%. The largest increase was from the Empire WR × Stoneville 7 cross with an increase of 24.2%, whereas the smallest increase was from Pope × Stoneville 7, which showed a gain of 11.7%. On the basis of total yield and largest increase in pounds lint over the better parent variety, the Empire WR × Pope cross was best.

SUMMARY AND CONCLUSIONS

A 3-year intervarietal study involving varieties of Upland cotton and their diallel crosses was begun in 1956. To provide genetically different varieties for testing, four varieties of different genetic origin (Empire WR, Pope, Plains, and Stoneville 7) adapted to the Piedmont of Georgia were chosen as parents. Emphasis was placed on testing 4 agronomic characters (lint yield, lint percent, flowers per plant, and percentage 5-lock bolls) for the expression of heterosis [significant ($P = .05$) superiority of the F_1 over the better performing parent that entered into the cross] and for general and specific combining ability. Data on the first (S_1) and second (S_2) selfed generations of each parent variety are included as an indication of the homogeneity of the non-inbred varieties used as parents. Data on the F_2 generation are included also for comparison with F_1, S_1, S_2, and parent varieties.

S_1 and S_2 yields were equal to the yields of the respective parent varieties. Flowers per plant and percentage 5-lock bolls of S_1 and S_2 generations were equal to or better than those of the parent variety.

Flowers per plant of F_2's were less, on the average, than those of F_1, S_1, S_2, or parents. However, the F_2 progenies were equal to or higher in percentage 5-lock bolls than the F_1. F_2 lint yields, on the average, were less than those of F_1, S_1, or parent varieties.

F_1 yields were significantly higher than the better parent variety in 4 of the 6 crosses. The 3-year average lint yield increase for the 6 crosses over the better parent was 19.0%. The lint yield of 4 of the 6 F_1's was significantly higher than the corresponding F_2.

In general combining ability the best and second best varieties were as follows: for lint yield, Pope and Empire WR; for number of flowers per plant, Pope and Empire WR; and for percentage of 5-lock bolls, Empire WR and Plains.

In specific combining ability the best cross for yield and number of flowers per plant was Empire WR × Pope; and for percentage of 5-lock bolls, Empire WR × Plains.

Throughout the entire experiment, only four individual cases of heterosis were found, all in lint yield. These four F_1's exceeded their better parent in lint yield by 18.4 to 24.2%.

For each character studied there appeared to be a relatively close relationship between the performance of the parent varieties and the average performance of their crosses. Since the ranking of the varieties for their general combining ability in the crosses tended to be the same as that for the performance of the varieties themselves, the characters of the parent varieties were as good an indication of the specific combining ability of a parent variety as that obtained from a study of general combining ability in the six crosses. It should be kept in mind, however that the varieties tested thus far have been adapted to the testing area. This relationship may not exist when crosses are made between adapted and nonadapted varieties. However, as has been found in crops such as flax and tomatoes, the only means of selecting the most desirable F_1 cross may be by actual trial.

Apparently the first step in the utilization of heterosis in cotton is the selection of good parents. The parents selected should be varieties which have the best combination of characters from genetically diverse backgrounds. In breeding for heterosis, genetic diversity of parent varieties appears to be as important as combining ability. Heterosis is probably not due to any single genetic cause; however, at least a rough relationship exists between the amount of heterosis in a hybrid and the extent of the genetic differences between the parents since the two most genetically diverse varieties in this study produced the most desirable F_1 cross from the viewpoint of lint yield.

From data presented, useful heterosis in intervarietal cotton hybrids can be utilized for an advance in productivity over the relatively homozygous variety. However, an economically feasible increase in lint yield from hybrids depends upon the development of some production technique other than hand-crossing.

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