Published September, 1966

Heterosis and Inbreeding Depression in Diploid and Tetraploid Cottons[1]

E. F. Young, Jr. and Jay C. Murray[2]

ABSTRACT

Heterosis was found in both the diploid and tetraploid species of cotton. Of the traits studied, heterosis was most pronounced in yield in both species. The degrees of heterosis shown by *G. arboreum* were similar to those reported for self-pollinated diploid species. The *G. hirsutum* hybrid combinations exhibited less heterosis than the *G. arboreum* hybrids and were less sensitive to inbreeding. These results indicate that the tetraploid species may carry an accumulation of favorable dominant growth genes in duplicate, a factor which results in a type of built-in heterosis.

HYBRID VIGOR and inbreeding depression often occur in the cultivated tetraploid cottons, *Gossypium hirsutum* and *G. barbadense.* However, such phenomena are less pronounced and less consistent in these cottons than in certain other species such as corn and tomatoes.

Kearney (6) obtained no inbreeding depression for yield during five successive generations of inbreeding Pima cotton. Jones and Loden (5), in a study of 9 F_1 hybrids, obtained yield increases from 0.8 to 47% over the better parent. In a study of 21 F_1 hybrids, Turner (16) found that 6 of the hybrids produced significantly higher yields than the check variety the first year. However, the following year only 2 of the 21 hybrids produced more seed cotton than the check. In studying the effects of inbreeding, Kime and Tilley (7) found the F_1, F_2, and F_3 hybrids produced 11%, 5.4%, and 0.5% respectively, more than the parental means, although greater increases were obtained in 2 previous years. These results show that heterotic effects in cotton are inconsistent.

Meyer and Justus (9) have presented data indicating that the cotton plant has considerable tolerance to inbreeding. They have found that doubled haploids, which are theoretically completely inbred, produce yields and fiber properties comparable to those of commercial varieties. If the cotton plant were rather sensitive to inbreeding, the performance of the doubled haploids would be inferior to that of the commercial varieties.

By comparison, Shull (15) in his early experiments with corn found that the average F_1 yields were 285% above those of the inbreds and the F_2 produced an average of 174% more than the inbred parents. In tomatoes, Powers (12) obtained an average yield increase of 59% in the F_1's as compared to the inbreds; the best hybrids produced 300% more than the recommended variety.

Two alternative hypotheses seem obvious to explain the somewhat lesser expression of heterosis and inbreeding depression in tetraploid cottons as compared to crops such as corn and tomato. First, the tetraploid cottons may have been sufficiently self-pollinated before domestication to develop genomes typical for self-pollinated plants. Plants which are predominately self-pollinated normally do not express the striking inbreeding depression and hybrid vigor typical of the cross-pollinated plants. Dobzhansky (1) has hypothesized that self-pollinated plants are expected to show little heterosis because the deleterious recessives and unfavorable recombinations are quickly eliminated from the population. Similarly, Mather (8) has suggested that inbreeding organisms achieve an internal chromosome balance and, as a result, are not upset by inbreeding.

The second hypothesis involves the polyploid condition of these cottons. Since the diploid parents each carry many genes with identical functions, new amphidiploids would be expected to carry duplicated genes at many loci. Since duplication has been found for several genes with qualitative effects in the tetraploid cottons (10, 14), duplication of many favorable dominant polygenes would also likely be present. If we accept the theory for heterosis proposed by Jones (3), inbreeding effects would be expected to be less pronounced in the tetraploids, because segregants lacking a dominant favorable allele at a particular duplicated locus would be less frequent than in the diploids. Hertzsch (3) has demonstrated that new polyploids are less sensitive to inbreeding than their diploid parents.

The present study was undertaken to determine whether polyploidy plays an important part in reducing the expression of heterosis and inbreeding depression. If polyploidy is important here, the diploid species would be expected to show considerably more heterosis and inbreeding depression than the tetraploid. On the other hand, if the chromosome structure is typical of inbreeding species and if diploidization of the tetraploid genomes is essentially complete, the diploid and tetraploid species would be expected to behave similarly and to typify inbreeding species. If the polyploid condition does reduce inbreeding depression, then duplication of favorable growth genes must be present. Certain hybrid combinations might then be found which would retain considerable heterosis for several generations. In the absence of a procedure for producing hybrid seed, this persistent heterosis could be utilized for several generations in synthetic varieties.

MATERIALS AND METHODS

Four highly inbred strains, each of the tetraploid species, *G. hirsutum,* and the diploid species, *G. arboreum,* were used in the study. The four strains of *G. hirsutum* were the doubled haploids designated M-11, Z-104, Z-106, and M-8 described by Meyer and Justus (9). The four strains of *G. arboreum,* designated 1043, 1044, 1046, and 1047, were selections from strains CB 2646, Sanguineum, Sinese, and from a genetic marker stock, respectively. The strains of *G. hirsutum* had been maintained by forced self-pollination since chromosome doubling. The

[1] Contribution from the Department of Agronomy, Oklahoma Agricultural Experiment Station, Stillwater, Oklahoma. Published with the approval of the director as Paper No. 1231 of the Journal Series and with the approval of the Crops Research Division, ARS, USDA. Part of the data from a thesis submitted in partial fulfillment of the requirements for the Ph.D. degree. Received Nov. 29, 1965.

[2] Formerly Graduate Assistant (now Research Agronomist, Crops Research Division, ARS, USDA) and Associate Professor of Agronomy, Oklahoma State University.

strains of *G. arboreum* had been grown from self-pollinated seeds for at least eight generations prior to the initiation of this study. All strains were obtained from James R. Meyer of the U. S. Department of Agriculture.

The hybrid generations were established by crossing the strains within each species in all combinations. The F_1-hybrid and parental populations were grown in a replicated test in 1961. The two hybrids within each species which exhibited the highest degree of heterosis, as measured by percent increases of the F_1 hybrids over the midparent means, were selected for studying rates of inbreeding depression. The variance components for general and specific combining ability were calculated by the method of Griffing (2). In order to study the effects of inbreeding, the parental, F_1, F_2, F_3, and F_4, generations of the hybrids selected were grown in replicated tests in 1962 and 1964. The 1963 test was lost as a result of weather conditions.

The designs of the experiments were randomized blocks with 6 replications, except in 1961 when only 4 replications were included. The plots were 30 ft long. The row spacings were 40 inches, and the individual plants were spaced 36 inches within the rows. Whenever a plant died or was accidentally destroyed, the hill was immediately planted to a red-leafed strain to minimize border effects. The plants were harvested individually. The lint of each plant was ginned individually and analyzed for length, strength, and micronaire. The least squares method of analysis was used to obtain an adjusted error term for comparing populations with unequal numbers.

The effects of inbreeding in the two species were indicated by the slopes of the regressions of heterosis on the inbreeding coefficients. Since yield and fiber length exhibited the greatest degree of heterosis, measurements of only these traits were used for the study of inbreeding effects.

The tests were conducted near Perkins, Oklahoma, on a Vanoss loam. Planting dates were normal for the area. Before planting, 125 lb. of 15-15-0 fertilizer were applied in bands beneath the rows. Irrigation water was applied as needed to keep the plants growing vigorously.

RESULTS AND DISCUSSION

The comparisons of the *G. hirsutum* and *G. arboreum* F_1 means with the midparent means are presented in Tables 1 and 2, respectively. The 1961 data indicated that heterosis is expressed more in yield than in any of the other traits, although several cases of significant heterosis were found in both species for each of the other traits. The components of variance for general and specific combining ability presented in Table 3 show that specific combining ability is much more important than general combining ability in both species. These results indicate that nonadditive gene action predominates for lint yield.

The 1961 data indicated that heterosis was of approximately the same magnitude in the two species. However, in the 2 subsequent years, heterosis was much more pronounced in the two *G. arboreum* crosses than in the two *G. hirsutum* crosses. This could be a result of the particular strains being investigated. However, the inconsistency in heterotic expression was also present in the data presented by Turner (16). *G. hirsutum* apparently expresses heterosis more in certain environments, while *G. arboreum* is more consistent in expressing heterosis. Perhaps *G. hirsutum* carries many of the same favorable dominant genes on both genomes. Strains already carrying the favorable dominant growth genes would not be expected to express much heterosis.

Since yield in 1961 showed more pronounced heterosis in both species, and since combining ability was rather specific, 2 hybrid combinations of each species which showed considerable heterosis for yield in 1961 were selected for studying inbreeding depression. Crosses 1043 × 1046 and 1044 × 1046 of *G. arboreum* were selected because they showed considerable heterosis for yield and fiber length. The *G. hirsutum* M-11 × Z-106 and Z-106 × M-8 crosses were selected because of their high yield and heterosis in 1961.

The comparative sensitivity of the two levels of ploidy to inbreeding is shown by the regressions of yield and fiber length on the inbreeding coefficients presented in Figures 1 and 2. The regression lines are based on approximately 50 observations at each level of inbreeding within each species.

The regression slopes for yield and fiber length of *G. arboreum* were much greater than those of *G. hirsutum*, indicating that *G. arboreum* is more sensitive to inbreeding than *G. hirsutum*.

The greater sensitivity of *G. arboreum* to inbreeding and outcrossing strongly suggests that these two

Table 1. Percent increases in means observed for five agronomic traits in *G. hirsutum* F_1 hybrids compared to the means of their respective parents in tests conducted in 1961, 1962, and 1964.

Population	Fiber length	Micronaire	Fiber strength	Plant height	Wt. of lint
(M-11 × Z-106)F_1†	2.87%	3.69%	4.91%	2.17%	53.19%**
(M-11 × M-8)F_1†	.59	2.33	0.00	3.22	4.24
(M-11 × Z-104) F_1†	-1.35	11.78**	− 3.20	0.14	46.43**
(Z-106 × M-8) F_1	2.73	4.75	-11.32*	2.85	43.60**
(Z-106 × Z-104) F_1	4.44**	2.33	1.19	4.36	44.01**
(M-8 × Z-104) F_1	1.85	1.05	− 0.90	10.32	13.34
			1962		
(M-11 × Z-106) F_1	3.38**	3.04%**	− 1.87%	4.89%	14.00%
Z-106 × M-8) F_1	2.19*	4.50	− 1.64	2.02	12.79
			1964		
(M-11 × Z-106) F_1	1.65%	3.65%	0.00		− 7.49%
(Z-106 × M-8) F_1	2.00	5.99	1.12%		25.63

*, ** Significantly different from Mid-parent value at .05 and .01 levels of probability, respectively. † The M-11 parent was not available in 1961, hence the mean of the other parent was used to evaluate hybrid vigor.

Table 2. Percent increases in means observed for five agronomic traits in *G. arboreum* F_1 hybrids compared to the means of their respective parents in tests conducted in 1961, 1962, and 1964.

Population	Fiber length	Micronaire	Fiber strength	Plant height	Wt. of lint
			1961		
(1043 × 1044) F_1	2.37%	-3.24%	3.96%*	28.51**	11.46%
(1043 × 1046) F_1	6.14**	-2.05	2.93	16.00	40.05**
(1043 × 1047) F_1	4.84**	1.02	3.38	24.17*	50.80**
(1044 × 1046) F_1	7.00**	-7.68	7.82**	17.19*	35.29**
(1044 × 1047) F_1	5.67**	-3.85	8.72**	4.24	34.67*
(1046 × 1047) F_1	0.14	2.23	2.84	3.80	48.98**
			1962		
(1043 × 1046) F_1 †					
(1044 × 1046) F_1	8.58**	-2.61	11.66**	24.16**	54.02**
			1964		
(1043 × 1046) F_1	7.85%	-2.77	5.16%		48.07%**
(1044 × 1046) F_1	5.99	-4.06	13.80		43.27**

† The 1043 × 1046 hybrid seeds were destroyed in delinting in 1962.

Table 3. Mean squares from combining ability analysis of seed cotton yield and fiber length in *G. arboreum* and *G. hirsutum*.

Source	d. f.	Mean squares			
		Yield		Length	
		Arboreum	hirsutum	Arboreum	hirsutum
General combining ability	3	−1,317.0**	−5,478**	− 5.969**	−34.000**
Specific combining ability	2	2,004.0**	8,380**	11.394**	21.089**

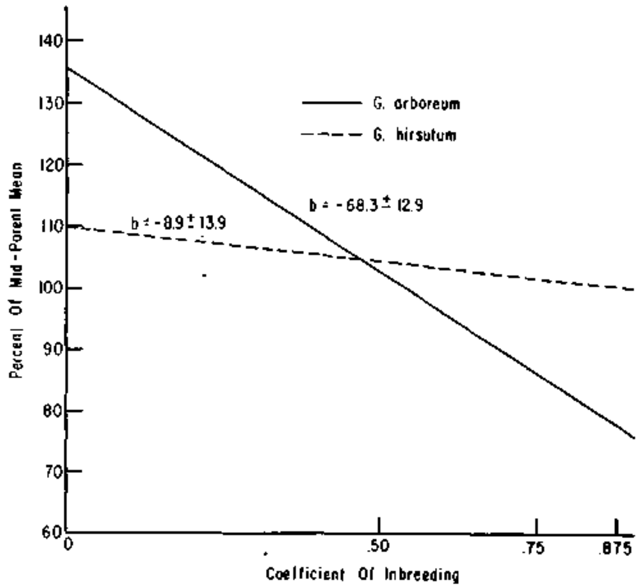

Figure 1. Comparative effects of inbreeding on the weight of seed cotton produced by two *G. hirsutum* hybrids and by two *G. arboreum* hybrids.

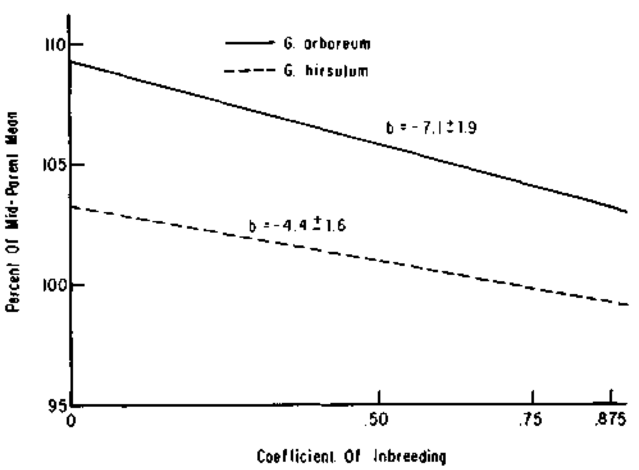

Figure 2. Comparative effects of inbreeding on the upper 2.5% span length of lint produced by two *G. hirsutum* hybrids and by two *G. arboreum* hybrids.

G. hirsutum strains carry many of the favorable dominant genes in duplicate. This would suggest that the smallness of the heterotic effects normally found in *G. hirsutum* can be at least partially attributed to genetic duplication. On the other hand, the magnitude of the heterotic effects in *G. arboreum* crosses are less than those typical for cross-pollinated species such as corn. The heterotic effects of the combinations reported here for *G. arboreum* approach those reported by Pawlisch and Van Dijk (11) for barley, which is a self-pollinated species, and are somewhat less than Powers (12) reported for tomato, which is approximately 50% cross-pollinated in its natural habitat (13). These observations suggest that the genomes of the diploid Gossypium species carry genomes somewhat characteristic of self-pollinated species. Consequently, hybrids in cotton probably will not have the potential that they have had in such species as corn. Since *G. hirsutum* appears to exhibit less heterosis than *G. arboreum,* rather small amounts of heterosis appear likely in *G. hirsutum* from the standpoint of commercial production. On the other hand, since inbreeding depression is also reduced in *G. hirsutum,* any heterosis found in particularly good hybrid combinations will probably persist for several generations and will be of importance in synthetic variety production.

LITERATURE CITED

1. Dobzhansky, Th. Genetics of natural population. XIII. Recombination and variability in populations of *Drosophila pseudoobscura.* Genetics 31:269-290. 1946.
2. Griffing, B. Concept of general and specific combining ability in relation to diallel crossing systems. Australian J. Biol. Sci. 9:463-493. 1956.
3. Hertzsch, W. Beobachtungen an kunztlich hergestellten polyploiden futterpflanzen. Pflanzenzuchtung 41:271-293. 1959.
4. Jones, D. F. Dominance of linked factors as a means of accounting for heterosis. Proc. Nat. Acad. Sci. 3:310-312. 1917.
5. Jones, J. E., and H. D. Loden. Heterosis and combining ability in upland cotton. Agron. J. 43:514-516. 1951.
6. Kearney, T. H. Self-fertilization and cross-fertilization in pima cotton. U. S. Dept. Agr. Bul. 1134, 68 p. 1923.
7. Kime, P. H., and R. H. Tilley. Hybrid vigor in upland cotton. J. Am. Soc. Agron. 39:308-317. 1947.
8. Mather, K. Polygenic inheritance and natural selection. Bio. Rev. 18:32-64. 1943.
9. Meyer, J. R., and N. Justus. Properties of doubled haploids of cotton. Crop Sci. 1:462-464. 1961.
10. Murray, J. C. A new locus for glanded stem in tetraploid cotton. J. Hered. 56:42-44. 1965.
11. Pawlish, P. E., and A. H. Van Dijk. Forage and grain production of four F_1 barley hybrids and their parents. Crop Sci. 5:135-136. 1965.
12. Powers, L. Relative yields of inbred lines and F_1 hybrids of tomato Bot. Gaz. 106:247-268. 1945.
13. Rick, C. M. Pollination relations of *Lycoperscion esculentum* in native and foreign regions. Evolution 4:110-122. 1950.
14. Rhyne, C. L. Duplicated linkage groups in cotton. J. Hered. 48:59-62. 1957.
15. Shull, G. H. Beginnings of the heterosis concept. p 14-48. *In* J. W. Cowen, Heterosis. Iowa State Press, Ames, Iowa. 552 p.
16. Turner, J. H. A study of heterosis in upland cotton. I. Yield of Hybrids compared with varieties. Agron. J. 45:485-486. 1953.