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Heterosis and Combining Ability for Plant Height and Developmental Data in a Diallel Cross of Two Species of Cotton[1]

A. Marani[2]

RESULTS for yield and components of yield in intraspecific and interspecific crosses of *Gossypium hirsutum* L. and *G. barbadense* L. have been reported in a previous paper (6). It was found that the main factor for heterosis in yield in both types of crosses was the increase in the number of bolls produced. This trait is a product of the number of flowers produced by the plant, and the percentage of these flowers that are retained as mature bolls. The number of bolls produced might also be influenced by the time of flowering, time of maturity, vegetative height of plants, and their tendency to lodge. These traits will be discussed in the present paper.

Loden and Richmond (5) reviewed some of the early papers dealing with these traits in cotton hybrids. Ware (7) studied the interspectific cross 'Pima' *(G. barbadense* L.) × 'Upright' *(G. hirsutum* L.) and found that it was much higher than the parent varieties. Heterosis for height was mainly caused by heterosis for node length, while the number of nodes was similar to that of the Pima parent.

Data for flowering and earliness in cotton hybrids have been reported by very few workers. Kime and Tilley (4) found that intraspecific *G. hirsutum* L. hybrids produced more flowers at the beginning of the flowering period, and matured their bolls somewhat earlier than the parents. Jones and Loden (2) also reported that intraspecific *G. hirsutum* L. crosses matured earlier than the parent varieties. Worley[3] found that the interspecific hybrid 'Pima 32' × 'Acala 44' flowered earlier than its parents and produced more flowers. White and Richmond (8) did not find heterosis for plant height, days to anthesis of first flower, or earliness in a diallel cross among five primitive and foreign *G. hirsutum* L. varieties. They reported that variance for general combining ability was significant for these traits, while variance for specific combining ability was not significant.

Kearney and Peebles (3) reported that F_1 progenies of an 'Acala' × Pima cross shed 24% of their bolls, as compared to 67–81% and 9–19% of the Acala and Pima parent varieties, respectively.

MATERIALS AND METHODS

Two diallel cross experiments, involving varieties of *G. hirsutum* L. and *G. barbadense* L. were carried out in 1959 and 1960. These experiments have been described and results for yield and its components were given in a previous paper (6).

The *G. hirsutum* L. varieties were: *(1)* 'Acala 4–42'; *(2)* 'Coker 100 W'; *(3)* 'Empire'. The *G. barbadense* L. varieties were: *(4)* 'Pima 32'; *(5)* 'Pima S-1'; *(6)* 'Ashmuni'. The 15 crosses and the 6 parents were planted in 1959 at Rehovot, Israel. There were 5 replications in a Youden-Square design. In 1960 a second experiment was planted from which Pima S-1 and its crosses were excluded. The F_1 single crosses were made reciprocally in the preceding year. The 20 reciprocal crosses and the 5 parents were planted at the same location in 6 replications of a 5 × 5 lattice square design.

Both experiments were on fertile sandy loam, under irrigation. Each plot consisted of a single row, 3 m. long, with 1.50 m. spacing between rows. Planting was in hills spaced 25 cm., and seedlings thinned to 2 plants per hill.

The date of flower initiation was recorded when at least two open flowers per plant had appeared. Seed cotton was harvested at frequent intervals (10 harvests in 1959, 8 in 1960). The mean date of maturity was calculated by the method of Christidis and Harrison (1) as the mean, weighted by the yields of seed cotton at each harvest, of the maturity date of all the harvests. Height of plants was measured for three random plants in each plot. One height measurement was taken in July, when the plants started to flower, and a second measurement at the end of the season.

Flowers were counted once a week, interpolated for the week, and their total number for all the season estimated on this basis. The data for the number of bolls produced (6) were used to calculate the percentage of bolls retained. Lodging was scored 5 times during Septemer, using the following "lodging index": 0—no lodging, 1—slight lodging, 2—medium lodging, 3—severe lodging, 4—complete lodging. Average results of all five observations are given. Data for flowering, percentage bolls retained, and lodging index were available only for 1959.

There were no significant differences between the reciprocals of any cross in 1960. Therefore only the averages of these reciprocal crosses will be presented in the results.

Analysis of variance was computed for each year separately. The crosses were subdivided into 3 groups: *G. hirsutum* L. × *G. hirsutum* L., *G. barbadense* L. × *G. barbadense* L., and *G. hirsutum* L. × *G. barbadense* L. Variances among the groups and within each group were calculated. The variance within the *G. hirsutum* L. × *G. barbadense* L. group was subdivided to general and specific combining ability effects, as in a factorial design. In estimating the components of variance, varieties were assumed to be fixed effects.

RESULTS

The Expression of Heterosis

Heterosis, expressed as percent increase of hybrid performance above the average of the parents is given in Table 1.

Most of the hybrids started to flower earlier than the average of their parents. The interspecific crosses flowered earlier than the earliest parents in 1959, and almost as early as them in 1960.

There were no significant heterotic effects for mean date of maturity in 1959, but in 1960 the interspecific crosses matured later than the average of the parents, though not as late as the *G. barbadense* L. parents.

Significant heterosis for plant height was found in 1959 for the *G. hirsutum* L. intraspecific crosses, and in both years for the interspecific crosses. Environmental conditions in 1960 were not as suitable for vegetative development of *G. hirsutum* L. varieties as in 1959. This was probably the reason that no heterosis for the intraspecific crosses of these varieties was evident in 1960.

Heterosis for the number of flowers produced was significant for the *G. barbadense* L. intraspecific crosses and for the interspecific crosses. A smaller and non-significant heterosis for this trait was observed in the *G. hirsutum* L. intraspecific crosses.

The cumulative number of flowers for 1959 is presented in Figure 1. Flowering of *G. hirsutum* L. varieties and their

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[2] Lecturer, Department of Field Crops.

[3] Worley, S., Jr. Evaluation of an interspecific cotton hybrid *(G. barbadense* × *G. hirsutum).* Unpublished M.S. thesis, University of Arizona, 1953.

Table 1. Mean performance of varieties and crosses and the degree of heterosis.

	Variety or cross†	Date of flower initiation‡	Mean date of maturity§	Height, cm. At start of flowering	Height, cm. Final	No. of flowers/ m.²	% boll retention	Lodging index
				1959				
Mean performance	h	15.0	21.0	68	120	85	53	1.79
of parent varieties	b	19.2	35.2	77	150	132	49	0.66
	Average	17.1	28.1	73	135	108	51	1.23
Mean performance	h × h	11.4	18.9	80	130	89	56	2.72
of crosses	b × b	18.1	33.0	80	154	159	51	0.80
	h × b	12.6	27.9	97	170	152	70	1.07
Percentage increase	h × h	-24.0**	-10.0	17.6**	8.3*	4.7	5.7	52**
of cross performance	b × b	- 5.7	- 6.3	3.9	2.7	20.5**	4.1	21
over midparents	h × b	-26.3**	- 0.7	31.5**	25.9**	40.7**	37.3**	-13
				1960				
Mean performance	h	4.1	7.5	69	99			
of parent varieties	b	11.2	22.5	77	153			
	Average	7.7	15.0	73	126			
Mean performance	h × h	4.3	7.6	68	97			
of crosses	b × b	9.5	20.3	70	139			
	h × b	5.1	18.4	89	157			
Percentage increase	h × h	4.9	1.3	- 1.4	- 2.0			
of cross performance	b × b	-15.2	- 9.8	- 9.1	- 9.2			
over midparents	h × b	-33.8**	23.3**	22.0**	24.6**			

* Significant, 5% level; ** Significant, 1% level.
† h = G. hirsutum L. varieties; b = G. barbadense L. varieties. ‡ Days after June 30; § Days after August 31.

intraspecific crosses practically stopped in the middle of August, while the *G. barbadense* L. varieties, their intraspecific crosses and also the interspecific crosses continued to flower for an additional two or three weeks, producing many more flowers during the whole period. The interspecific crosses produced slightly fewer flowers than the *G. barbadense* L. intraspecific crosses, but a higher proportion of their flowers was produced during the earlier part of the season.

The percentage of bolls retained on the plant was much higher in the interspecific crosses than in the parental varieties or the intraspecific crosses. A significant heterotic effect for this trait was evident only in the interspecific crosses.

The average lodging index of the intraspecific *G. hirsutum* L. crosses was greater than the mean of their parents, but the intraspecific *G. barbadense* L. crosses and the interspecific crosses did not differ appreciably in this respect from the mean of their parents.

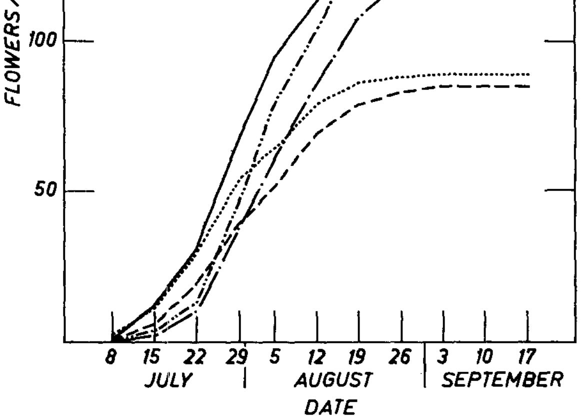

Figure 1. Cumulative number of flowers per m.²

Performance of Parental Varieties and Their Intraspecific Crosses

Performance of parental varieties, their intraspecific crosses, and the means of the interspecific crosses of each parent, are given in Tables 2 and 3.

There were some differences among *G. hirsutum* L. varieties in their date of flowering initiation, mean date of maturity, and height, but these differences were not consistent from year to year. The *G. hirsutum L.* varieties did not differ significantly in the number of flowers produced, but Coker 100W retained a significantly higher percentage of its bolls.

There were no significant differences among *G. hirsutum* L. intraspecific crosses for all these traits.

Ashmuni started to flower earlier than the other *G. barbadense* L. varieties, though this was significant only in 1959. There were no significant differences for the mean date of maturity among the *G. barbadense* L. varieties or among their intraspecific crosses.

Combining Ability in the Interspecific Crosses

Estimates of variances for general and specific combining ability in the interspecific crosses are given in Table 4. The limited number of varieties included in this experiment cannot be considered as an adequate sample representing populations of the two species. Therefore, in estimating the components of variance, the 'fixed effects' model was used, making the results pertinent only for this particular set of varieties. The general effects of the parental varieties, expressed as the mean performance of the crosses of each variety with all the varieties of the other species, are given in Tables 2 and 3.

Variances for specific combining ability were usually smaller than those for general combining ability, and were not significant for any trait.

There was a significant general combining ability effect of the *G. hirsutum* L. varieties, in the interspecific crosses, for plant height and percentage of boll retention in 1959, and for mean date of maturity in 1960.

A significant general combining ability effect of the *G. barbadense* L. varieties was found for mean date of maturity, height, number of flowers, percentage of boll retention and lodging in 1959, and for final height in 1960.

Table 2. Performance of *G. hirsutum* L. varieties and their crosses.*

	Variety or cross†	Date of flower initiation‡	Mean date of maturity§	Height, cm. At start of flowering	Height, cm. Final	No. of flowers/ m.²	% boll retention	Lodging index
				1959				
Performance of parent varieties	1	12.2 a	17.6 a	79 a	126 a	88	51 b	0.8 a
	2	14.8 b	24.0b	75 a	127 a	76	68 a	2.6 b
	3	17.6 c	21.4 ab	51 b	107 b	90	40 b	2.0 b
Performance of intraspecific crosses	1 × 2	11.2	17.8	79	133	88	62	2.4 a
	1 × 3	12.6	18.4	82	133	86	58	2.0 a
	2 × 3	10.8	20.6	80	125	92	49	3.7 b
Mean performance of interspecific crosses with all G. barbadense L. varieties	1 × b	12.7	27.5	102 a	179 a	145	76 a	1.0
	2 × b	12.3	27.8	97 ab	171 ab	155	75 a	1.1
	3 × b	12.7	28.3	92 b	161 b	155	60 b	1.1
				1960				
Performance of parent varieties	1	6.3 b	8.2	67	108			
	2	3.3 a	7.0	72	94			
	3	2.7 a	7.5	68	95			
Performance of intraspecific crosses	1 × 2	5.0	8.5	72	99			
	1 × 3	4.2	6.7	64	94			
	2 × 3	3.7	7.5	68	97			
Mean performance of interspecific crosses with all G. barbadense L. varieties	1 × b	5.3	19.5 b	88	161			
	2 × b	6.0	19.3 b	89	160			
	3 × b	3.8	16.5 a	90	151			

* Results followed by the same letter within each group are not significantly different, 5% level, by Duncan's multiple range test. There were no significant differences within any group where no letters follow the results.
† 1 = Acala 4-42; 2 = Coker 100W; 3 = Empire; b = G. barbadense L. varieties. ‡ Days after June 30. § Days after August 31.

Table 3. Performance of *G. barbadense* L. varieties and their crosses.

	Variety or cross†	Date of flower initiation‡	Mean date of maturity§	Height, cm. At start of flowering	Height, cm. Final	No. of flowers/ m.²	% boll retention	Lodging index
				1959				
Performance of parent varieties	4	20.6 b	35.0	80	150	131	54	0.2 a
	5	20.4 b	37.0	76	147	122	41	0.4 a
	6	16.2 a	34.4	75	153	143	52	1.4 b
Performance of intraspecific crosses	4 × 5	18.4 b	32.2	81 a	143 b	144 b	54	0.5 a
	4 × 6	16.4 a	32.0	90 a	175 a	190 a	55	0.5 a
	5 × 6	19.6 b	34.8	69 b	142 b	142 b	45	1.4 b
Mean performance of the interspecific crosses with all G. hirsutum L. varieties	4 × h	13.1	29.9 b	102 a	181 a	139 b	83 a	0.9 a
	5 × h	12.5	27.7 ab	92 b	160 b	147 b	62 b	0.9 a
	6 × h	12.2	25.9 a	98 ab	170 ab	169 a	66 b	1.4 b
				1960				
Performance of parent varieties	4	12.5	23.7	82	153			
	6	10.0	21.3	72	154			
Performance of intraspecific cross	4 × 6	9.5	20.3	70	139			
Mean performance of the interspecific crosses with all G. hirsutum L. varieties	4 × h	5.5	18.9	92	164 a			
	6 × h	4.6	17.9	86	151 b			

* Results followed by the same letter within each group are not significantly different, 5% level, by Duncan's multiple range test. There were no significant differences within any group where no letters follow the results.
† 4 = Pima 32; 5 = Pima S-1; 6 = Ashmuni; h = G. hirsutum L. varieties. ‡ Days after June 30. § Days after August 31.

Table 4. Components of variance in the interspecific crosses.

	Date of flower initiation†	Mean date of maturity‡	Height, cm. At start of flowering	Height, cm. Final	No. of flowers/ m.²	% boll retention	Lodging index
			1959				
σ^2 g.c.a.§ G. hirsutum L.	-0.1	-0.7	25**	78**	3	64**	-0.02
σ^2 g.c.a. G. barbadense L.	0.0	3.3**	22**	89**	213**	81**	0.05*
σ^2 s.c.a.	0.0	0.6	- 2	50	- 4	40	0.07
			1960				
σ^2 g.c.a. G. hirsutum L.	0.5	1.4*	- 4	24			
σ^2 g.c.a. G. barbadense L.	-0.1	0.2	14	120*			
σ^2 s.c.a.	-0.3	-1.2	- 9	- 36			

* Significant, 5% level. ** Significant, 1% level.
† Days after June 30. ‡ Days after August 31. § σ^2 g.c.a. = general combining ability variance. σ^2 s.c.a. = specific combining ability variance.

The ranking of the varieties for their general combining ability in the interspecific crosses tended in many cases to be the same as that for the performance of the varieties themselves, but in some cases this was not evident because there were no significant differences between the varieties.

DISCUSSION

Nature of Genetic Variance

For the traits studied in the present paper, as for the yield and components of yield discussed previously (6), variances of general combining ability were larger than variances of specific combining ability. Actually, no significant variance of specific combining ability was found for any of these traits. In cases where there were significant effects of general combining ability, the ranking of the performance of the crosses tended to be similar to the ranking of parent varieties. Therefore it may be assumed, with all the limitations discussed in the previous paper (6), that the most important component of genetic variance for these traits is of the additive type.

The high degree of heterosis for plant height, number of flowers, and percentage of boll retention indicates that some of the genetic variance for these traits is non-additive (dominance or epistasis). Non-additive genetic variance seems to be of less importance for date of flowering initiation, mean date of maturity and lodging index, because of a smaller degree of heterosis for these traits.

Implications on Breeding Methodology

Previous results (6) indicated the importance of the number of bolls as a factor for increased yields of cotton hybrids. The number of bolls is a function of the total number of flowers and the percentage of these flowers retained as mature bolls.

Increase in the total number of flowers was significant and quite substantial in the interspecific crosses and the intraspecific crosses of *G. barbadense* L. The significant general combining ability effects for this trait (e.g., Ashmuni had an especially high general combining ability) and the apparent dominance of *G. barbadense* L. suggest that the selection of the *G. barbadense* L. parents for a high total number of flowers would be advantageous.

The percentage of boll retention was one of the main factors for the good performance of the interspecific hybrids. These hybrids actually produced somewhat fewer flowers than the intraspecific *G. barbadense* L. hybrids, but retained more mature bolls. Acala 4–42, Coker 100W, and Pima 32 had significantly higher general combining ability for this trait. It may therefore be suggested that both parents of the interspecific hybrids should be selected on the basis of general combining ability for percentage of boll retention.

Early initiation of flowering may be one of the causes for the better performance of the interspecific hybrids, but neither general nor specific combining ability effects were significant for this trait. It is therefore doubtful whether it would be of any advantage to select parents on the basis of this character.

The absence of appreciable heterosis for mean date of maturity in the interspecific crosses may be attributed to the fact that although these crosses started to flower and to produce bolls earlier than the parental varieties, they also produced more bolls than the parental varieties during the later part of the season. Some cases of significant general combining ability for this trait may suggest selection for earlier maturity for environments where this might be important.

The large heterosis for plant height in the interspecific hybrids is undesirable from the agronomic point of view—because of difficulties in harvesting, cultivation, irrigation and other cultural practices. The large effects of general combining ability for this trait indicate that it would be advantageous to select parents on the basis of general combining ability for lower plants.

In spite of their height and vigorous vegetative growth, the interspecific hybrids did not lodge more severely than the parental varieties. There was, though, some general combining ability effect for lodging of the *G. barbadense* L. varieties, caused by the somewhat higher lodging index of the Ashmuni crosses. The *G. hirsutum* L. varieties did not show any general combining ability effect for this trait. Acala 4–42 was more resistant to lodging than the other two *G. hirsutum* L. varieties, but it was apparently recessive for this trait.

SUMMARY

Two diallel cross experiments involving varieties of *Gossypium hirsutum* L. and *G. barbadense* L. are evaluated for date of flowering initiation, mean date of maturity, height of plants, number of flowers, percentage boll retention, and lodging.

The interspecific crosses started to flower earlier than the mean of their parents, but were not earlier in their mean date of maturity. These crosses exhibited a large heterotic effect for plant height, number of flowers and percentage of boll retention. They did not lodge more severely than the parental varieties.

The intraspecific crosses of *G. hirsutum* L. exhibited heterosis for earlier flowering and taller plants in 1959 only; they also lodged more severely. In the intraspecific *G. barbadense* L. crosses there was a significant heterosis for the number of flowers.

The performance of the intraspecific crosses was in many cases related to the performance of the parental varieties. General combining ability effects were significant in the interspecific crosses in many cases, while specific combining ability effects were not significant for any of the traits examined.

It was indicated that the most important component of genetic variance for the traits examined was of the additive type. However, some of the genetic variance, for some of these traits, was non-additive (dominance and epistasis) in nature.

It was suggested that it would be advantageous, in breeding hybrid cotton varieties, to select the parents on the basis of their general combining ability for lower plants, production of more flowers and a high percentage of boll retention.

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