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Heterosis and Combining Ability for Yield and Components of Yields in a Diallel Cross of Two Species of Cotton[1]

A. Marani[2]

EARLY work on the performance of hybrid cottons was reviewed by Loden and Richmond (7) and by Fryxell.[3] Some degree of heterosis for lint yield and other traits was found in most of the works reviewed, both in intraspecific and interspecific crosses. Fryxell et al. (2) have found that 17 of the 36 *Gossypium hirsutum* L. × *G. barbadense* L. crosses they evaluated yielded more than the better parent, but only a few of these crosses were better than the adapted check variety. Barnes and Staten (1) reported a very high degree of heterosis for yield in the cross 'Pima 32' × 'Acala 1517C'. The possibilities of practical utilization of hybrid cottons were discussed by Fryxell[3] and Stroman (9).

Diallel-crossing is useful for evaluation of the combining ability of cotton varieties and lines. White and Richmond (11) studied a diallel cross among five primitive and foreign strains of *G. hirsutum* L., and reported that variance for general combining ability was predominant. This was also found by Miller and Marani (8) in a diallel cross among eight inbred lines of Upland cotton. On the other hand, Barnes and Staten (1) found that variance for specific combining ability was more important than variance for general combining ability in a diallel cross of seven Acala strains.

The approach of Hayman (4, 5) and Jinks (6) to the interpretation of diallel cross data is becoming of interest to cotton workers. Hayman (5) analyzed the data of a diallel cross among seven inbred lines of Upland cotton reported by Turner (10) and found significant "epistasis" for yield.

The concept of "yield components" has been used to interpret heterosis for yield. White and Richmond (11) reported that in one of their crosses heterosis for yield was due only to an increased number of bolls per plant, while in another cross boll size was also a contributing factor. Their data indicate that the increased number of bolls per plant was due to an increased size of the plant in aerial vegetative mass. Turner (10) stated that the number of bolls was more important than boll size in accounting for heterosis in yield.

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[2] Lecturer, Department of Field Crops.

[3] Fryxell, P. A. Hybrid cotton—selection of suitable parents. Proc. Cotton Imp. Conf. 11:66–78. 1958.

The purpose of this study was to estimate heterosis for lint yield in intraspecific and interspecific crosses among a set of varieties of *Gossypium hirsutum* L. and *G. barbadense* L. An attempt was also made to interpret the heterotic effects on the basis of yield components.

MATERIALS AND METHODS

All possible F_1 single crosses were made among 6 varieties of cotton in 1958. Three of these varieties were of *Gossypium hirsutum* L. and the other 3 of *G. barbadense* L. These varieties were inbred by selfing for two generations before making the crosses. The varieties were:

Code number	Variety
1	'Acala 4–42' (*G. hirsutum* L., Upland type)
2	'Coker 100 W' (*G. hirsutum* L., Upland type)
3	'Empire' (*G. hirsutum* L., Upland type)
4	'Pima 32' (*G. barbadense* L., American–Egyptian type)
5	'Pima S-1' (*G. barbadense* L., American–Egyptian type)
6	'Ashmuni' (*G. barbadense* L., Egyptian type).

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 (code number 5) 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 a 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. Normal cultural practices were followed throughout the season.

Harvests were made by hand at frequent intervals. Random samples of approximately 300 g. of seed cotton were taken from early, medium, and late harvests of each plot, and ginned by an 8" miniature roller gin. Lint percent (weighted mean) and lint yield were calculated from this. Bolls were counted at each harvest, to obtain information on the mean weight per boll. Seed index was determined by weighing 4 lots of 100 seeds each from each sample. Lint index was calculated from seed index and lint percent data. The average number of seeds per boll was calculated from boll size, seed index, and lint index data.

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 the hybrids above the average of the parents, was significant for many traits (Table 1).

Results show that heterosis for lint yield was associated with production of a greater number of bolls. This was apparent both in the intraspecific and interspecific crosses, but was much more appreciable in the interspecific crosses.

The bolls were somewhat smaller than the average of parental lines in the interspecific crosses, but in the intraspecific crosses the bolls were larger than the mid-parent, and in some cases larger than those of the best parent. Thus, in the latter case boll size as well as boll number was an important factor in heterosis for yield.

In the intraspecific *G. hirsutum* L. hybrids, heterosis for boll size was associated with heterosis for lint index and seed index, while increase in the number of seeds per boll was slight and in most cases not significant. Heterosis for lint index and seed index was of approximately the same magnitude in these crosses, so that the lint percent of the intraspecific crosses did not differ appreciably from the average of the parents.

In the intraspecific hybrids of *G. barbadense* L. heterosis for lint yield and yield of seed cotton was significant in 1959 only, and it was mainly associated with an increase in the number of bolls produced. In this case, heterosis for boll weight and number of seeds per boll was not statistically significant, but there was a significant heterosis for lint index and seed index. No heterotic effects were significant for these hybrids in 1960.

In the interspecific crosses, the number of seeds per boll was smaller than the average of the parents, and much nearer to that of the *G. barbadense* L. parents. There was a significant heterosis for lint index and seed index. The extent of heterosis for seed index was much larger than the extent of heterosis for lint index. This resulted in a very low lint percent of these crosses, which was even lower than that of the *G. barbadense* L. parents.

Performance of Parental Varieties and Their Intraspecific Crosses

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

The *G. hirsutum* L. varieties which were included in this study did not differ significantly in their yields and in the number of bolls they produced. There were also no significant differences between their intraspecific hybrids for these traits. There were significant differences among these varieties and among their intraspecific crosses for boll weight, lint index, seed index, and lint percent. For these traits, the performance of the intraspecific crosses was related to the performance of the parental varieties. For example, Coker 100 W had a smaller boll than the other two varieties, and the crosses involving this variety had smaller bolls than the Acala 4–42 × Empire cross.

There were no significant differences between the *G. barbadense* L. varieties in yield or number of bolls. However, in 1959 Pima S-1 had appreciably lower yields of seed cotton and lint and a lower number of bolls than the other 2 varieties. The intraspecific crosses involving Pima S-1 had significantly lower yields and boll numbers than did the Pima 32 × Ashmuni cross. A similar trend is evident for seed index and lint percent. There were no significant differences for boll weight, number of seeds per boll, or lint index.

Combining Ability in the Interspecific Crosses

Estimates of variances for general and specific combining ability in the interspecific crosses are given in Table 3. The general effects of parental varieties, expressed as the mean performance of the crosses of each variety with all the varieties of the other species, are given in Table 2.

There were significant general combining ability effects of *G. hirsutum* L. varieties, in the interspecific crosses, for all the traits in 1959, and for all traits except boll weight in 1960. This effect was, however, different from year to year for yield of seed cotton, yield of lint, and number of bolls produced. These differences were related to differences in the performance of the parental varieties in these years. The general combining ability effects for the other traits were more consistent from year to year. For example, Coker 100 W had significant general effects for more seeds per boll, a lower lint index, a lower seed index, and a lower lint percent.

General combining ability effects of *G. barbadense* L. varieties, in the interspecific crosses, were significant in 1959 for all traits except yield of seed cotton and yield of lint. Pima S-1 had significant general effects for a small number of bolls, large boll weight, more seeds per boll

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

		Yield of seed cotton, g./m.^{2}	Yield of lint, g./m.^{2}	Number of bolls per m.^{2}	Boll weight, g.	Number of seeds per boll	Lint index, g.	Seed index, g.	Lint percent
				1959					
Mean performance of parent varieties	h†	318	116	44	7.14	34.5	7.7	13.0	37.1
	b†	192	66	65	2.99	17.3	5.9	11.4	34.2
	Average	255	91	55	5.07	25.9	6.8	12.2	35.7
Mean performance of crosses	h × h	390	143	50	7.63	35.0	8.1	13.6	37.4
	b × b	269	93	82	3.21	17.7	6.3	11.8	34.7
	h × b	526	176	106	4.89	21.9	7.5	14.9	33.6
Percentage increase of cross performance over mid-parents	h × h	22.6*	23.3**	13.6	6.9**	1.4	5.2**	4.6**	0.8
	b × b	40.1**	40.9**	41.5**	7.4	2.3	6.8**	3.5*	1.5
	h × b	106.3**	93.4**	92.7**	-3.5*	-15.4**	10.3**	22.1**	-5.9**
				1960					
Mean performance of parent varieties	h	291	108	42	6.84	34.9	7.3	12.4	37.0
	b	261	92	84	3.08	16.7	6.5	12.1	35.1
	Average	276	100	63	4.96	25.8	6.9	12.3	36.1
Mean performance of crosses	h × h	328	127	45	7.37	36.0	7.6	12.8	37.2
	b × b	302	103	90	3.18	17.8	6.2	11.8	34.3
	h × b	518	170	108	4.82	21.9	7.3	14.7	33.2
Percentage increase of cross performance over mid-parents	h × h	12.7	17.6	7.1	7.7**	3.2*	4.1*	3.2*	0.6
	b × b	15.7	12.0	7.1	3.2	6.6	-4.6	-2.5	-2.3
	h × b	87.7**	70.0**	71.4**	-2.8**	-15.1**	5.8**	19.5**	-8.0**

* Significant, 5% level. ** Significant, 1% level. † h = G. hirsutum varieties. b = G. barbadense varieties.

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

Performance of		Yield of seed cotton, g./m.^{2}	Yield of lint, g./m.^{2}	Number of bolls per m.^{2}	Boll weight, g.	Number of seeds per boll	Lint index, g.	Seed index, g.	Lint percent
			G. hirsutum, 1959						
Parent varieties	Acala 4-42	356	123	45	7.82 a	37.0 a	7.5 b	13.7 a	35.4 c
	Coker 100 W	338	125	52	6.44 c	34.8 b	6.9 c	11.6 b	37.1 b
	Empire	260	100	36	7.16 b	31.8 c	8.7 a	13.8 a	38.8 a
Intraspecific crosses	Acala 4-42 × Coker 100 W	416	150	55	7.32 b	34.8 b	7.8 b	13.2 b	37.1
	Acala 4-42 × Empire	424	154	50	8.36 a	36.6 a	8.7 a	14.2 a	37.9
	Coker 100 W × Empire	330	124	45	7.20 b	33.6 b	7.9 b	13.4 b	37.2
Interspecific crosses with all G. barbadense varieties	Acala 4-42 × G. barbadense†	557 a	187 a	109 a	4.90 ab	21.3 b	7.8 b	15.3 a	33.9 a
	Coker 100 W × G. barbadense†	541 a	177 ab	116 a	4.67 b	22.9 a	6.7 c	13.7 b	33.0 b
	Empire × G. barbadense†	481 b	162 b	93 b	5.12 a	21.7 b	8.1 a	15.6 a	34.1 a
			G. hirsutum, 1960						
Parent varieties	Acala 4-42	280	101	36	7.43 a	35.0	7.8 a	13.5 a	36.5 b
	Coker 100 W	281	103	45	6.18 c	34.8	6.5 b	11.3 c	36.6 b
	Empire	313	119	45	6.90 b	35.0	7.7 a	12.5 b	37.9 a
Intraspecific crosses	Acala 4-42 × Coker 100 W	350	126	48	7.30 ab	36.1	7.2 b	12.9	35.8 b
	Acala 4-42 × Empire	288	110	38	7.77 a	36.6	8.1 a	13.0	38.3 a
	Coker 100 W × Empire	347	145	50	7.03 b	35.2	7.5 b	12.4	37.4 ab
Interspecific crosses with all G. barbadense varieties	Acala 4-42 × G. barbadense†	454 b	141 b	99 b	4.78	20.6 b	7.7 a	15.7 a	32.9 b
	Coker 100 W × G. barbadense†	571 a	188 a	121 a	4.69	23.0 a	6.8 b	13.8 c	32.9 b
	Empire × G. barbadense†	530 a	180 a	106 b	4.99	22.3 a	7.6 a	14.7 b	33.9 a
			G. barbadense, 1959						
Parent varieties	Pima 32	208	69	70	2.96	16.6	5.9	11.9 a	33.0 c
	Pima S-1	156	54	50	3.10	17.6	6.0	11.7 a	34.2 b
	Ashmuni	212	75	75	2.92	17.6	5.9	10.6 b	35.6 a
Intraspecific crosses	Pima 32 × Pima S-1	250 ab	85 ab	77 b	3.10	17.0	6.2	12.0 a	34.1 b
	Pima 32 × Ashmuni	352 a	114 a	104 a	3.36	18.0	6.4	12.1 a	34.7 ab
	Pima S-1 × Ashmuni	206 b	70 b	65 b	3.18	18.2	6.2	11.3 b	35.4 a
Interspecific crosses with all G. hirsutum varieties	Pima 32 × G. hirsutum†	540	176	114 a	4.72 b	21.5 b	7.2 b	14.8 ab	32.7 c
	Pima S-1 × G. hirsutum†	508	169	91 b	5.27 a	23.3 a	7.6 a	15.1 a	33.5 b
	Ashmuni × G. hirsutum†	530	181	112 a	4.71 b	21.1 b	7.8 a	14.7 b	34.7 a
			G. barbadense, 1960						
Parent varieties	Pima 32	263	88	86	3.08	15.8 b	6.5	13.1 a	33.0 b
	Ashmuni	259	96	83	3.08	17.6 a	6.6	11.1 b	37.2 a
Intraspecific cross	Pima 32 × Ashmuni	302	103	90	3.18	17.8	6.2	11.8	34.3
Interspecific crosses with all G. hirsutum varieties	Pima 32 × G. hirsutum†	527	172	112	4.76	21.8	7.1 b	14.8	32.5 b
	Ashmuni × G. hirsutum†	510	168	104	4.87	22.1	7.6 a	14.7	33.9 a

* 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. † Varieties.

Table 3—Components of variance in the interspecific crosses.

	Seed cotton yield, g./m.^{2}	Lint yield, g./m.^{2}	No. bolls per m.^{2}	Boll wt., g.	No. seeds per boll	Lint index, g.	Seed index, g.	Lint percent
				1959				
σ^2 g.c.a.†								
G. hir.	1200*	107*	124**	0.04**	0.6**	0.49**	0.95**	0.33**
G. bar.	-140	-4	143**	0.09**	1.3**	0.09**	0.04*	0.94**
σ^2 s.c.a.†	1760	252*	120*	-0.02	-0.3	-0.01	-0.02	-0.01
				1960				
σ^2 g.c.a.								
G. hir.	1970**	380**	67*	0.01	0.9**	0.16**	0.63**	0.20**
G. bar.	-240	-40	120	0.00	-0.1	0.08**	-0.01	0.96**
σ^2 s.c.a.	-700	-8	-38	0.00	0.0	0.04	0.10*	0.03

* Significant, 5% level. ** Significant, 1% level. † σ^2 g.c.a. = general combining ability variance. σ^2 s.c.a. = specific combining ability variance.

and high seed index. For lint index and lint percent there was a significant general combining ability effect in both years, mainly caused by differences in the general combining abilities of Pima 32 and Ashmuni.

Variances for specific combining ability in the interspecific crosses were significant only in a few cases, and not consistent from year to year.

DISCUSSION

Nature of Genetic Variance

Miller and Marani (8) and White and Richmond (11) reported that variances of general combining ability were larger than those for specific combining ability in a diallel cross among inbred lines of *G. hirsutum* L. and concluded that the major portion of the genetic variance in the base population was additive in nature.

The data in the present study also indicate that in the case of interspecific crosses variances of general combining ability are larger than variances of specific combining ability. The findings that the average performance of the crosses of any parent is related to the performance of that parent *per se,* and that there is a preponderance of general combining ability effects, may indicate that the main component of genetic variance is of the additive type. This may be especially true for boll weight, number of seeds per boll, lint index, and lint percent, where specific combining ability was not significant in either year of the experiment. For yield of seed cotton, yield of lint, number of bolls, and seed index, significant specific combining ability variances were found in 1 of the 2 years. This and the high degree of heterosis for these traits suggest that some of the genetic variance for these traits is non-additive (dominance and epistasis).

Implications on Breeding Methodology

If hybrid cotton varieties are to be of practical importance, the results of this study show that attempts should be made to utilize the large heterosis for lint yield obtained from the interspecific crosses. Some practical aspects concerning the actual use of this type of hybrids were discussed by Fryxell[3] and Stroman (9).

The preponderance of additive genetic variance suggests that the parents of these crosses should be selected on the basis of their own performance and their general combining ability. Relationships between the performance of parent varieties for some yield components and the mean performance of their interspecific crosses indicate that the *G. hirsutum* L. parent should be selected mainly for high lint index, and the *G. barbadense* L. parent mainly for high number of bolls and high lint percent.

Differences in general and specific combining ability effects between the years indicate that these crosses should be evaluated in a number of environments. General combining ability probably has a greater effect on the lint yield of these crosses than does specific combining ability, but the possibility that some crosses may exhibit persistent specific combining ability effects should not be overlooked.

SUMMARY

A diallel cross of 3 varieties of *G. hirsutum* L. and 3 of *G. barbadense* L. was evaluated in 1959 in a replicated trial. The trial was repeated in 1960, with the exclusion of 1 *G. barbadense* L. variety.

The extent of heterosis for yield was higher in the interspecific crosses than in the intraspecific crosses. In the interspecific crosses heterosis was due to a large increase in the number of bolls produced, while boll size was less than the midparental value. In the intraspecific crosses heterosis was due both to increase in boll size and the number of bolls produced. In most cases there was also a significant heterosis for lint index and seed index. In the interspecific crosses heterosis for seed index was much larger than for lint index, and these crosses therefore had a very low lint percent.

Performance of intraspecific crosses was usually related to the performance of the parental varieties. In the interspecific crosses, effects of general combining ability were most important, while effects of specific combining ability were significant only in a few cases and were not consistent from year to year.

It was suggested that the main component of genetic variance was of the additive type. For some traits, however, the presence of some non-additive genetic variance was also indicated.

Implications on the breeding methodology of hybrid cotton varieties are discussed.

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