

Interaction of Combining Ability Effects with Environments in Diallel Crosses of Upland Cotton (*Gossypium hirsutum* L.)¹

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ABSTRACT

Ten strains of Upland cotton, *Gossypium hirsutum* L., representing a broad array of germ plasm, were crossed in all possible combinations, and the parents and F₁ progenies were reared in replicated experiments at two locations in North Carolina for 2 years. Heterosis for lint yield, measured as departure from the average mid-parent value, was about 26% for the pooled experiments. Estimates of heterosis for boll size, lint percentage, and some fiber properties were small but significant. When summed over all environments, the estimate of general combining ability for lint yield was not significant. However, the interaction of general combining ability by locations for lint yield was significant. Significant estimates of general combining ability were obtained for boll size, lint percentage, and all fiber properties. None of the interactions of general combining ability by environments were significant for these characters. The estimate of specific combining ability for fiber yield, though fairly large, was not significant. Estimates of specific combining ability for lint percentage, boll size, and all fiber properties were not greater than zero. These results were interpreted to mean that no difficulties should be encountered in selecting for changes in fiber properties. Any gains realized should remain stable over the environments sampled. On the other hand, advances in fiber yield could be achieved only at individual locations and, even then, interactions with years and locations would reduce the effectiveness of selection. Some high-yielding combinations with desirable lint properties were detected.

Additional index words: environmental interaction, additive genetic variance, dominance genetic variance, heterosis, projected population.

THE diallel crossing scheme is a method which can be used to detect the kinds and relative magnitudes of genetic variability among the crosses of a given group of inbred lines. The estimates stemming

therefrom can be used to characterize, through projection, the population one would expect from randomly mating the lines⁴. This application is perhaps more realistic from the standpoint of plant improvement than assuming that the lines are random samples from some population, since plant breeding is based upon attempts to select parents which incorporate the features desired in the offspring.

Diallel crosses have been used frequently in the past in attempts to assess the genetic worth of groups of selected cotton lines. In most of these experiments prediction of potential breeding worth were largely based on estimates of general and specific combining ability after the methods of Sprague and Tatum (9), Griffing (3), and others. Miller and Marani (6) reviewed the literature on hybridization experiments in Upland cotton (*Gossypium hirsutum* L.). They found that the relative importance of general and specific combining ability effects, as they influence lint yield of F₁ hybrids and subsequent generations, differed among experiments. For example, Turner (10) concluded that specific combining ability effects were more important in determining fiber yields, whereas Miller and Marani (6) and White and Richmond (11) reported a preponderance of general combining ability for this character. Barnes and Staten (2) reported important specific combining ability effects for lint yield among hybrids of various Acala strains. Acala cottons are specifically adapted for growth under irrigated farming in arid regions, a fact which suggests that specific combining ability for lint yield might be a special trait of these cottons, in contrast to the preponderance of general combining effects found among commercial and near-commercial types of rain-grown cottons by Miller and Marani (6). Fiber traits in all experiments reviewed were generally found to be inherited in an additive fashion; that is to say, general combining ability effects predominated for these characters.

Two factors could account for the differences in the relative importance of the two types of combining ability in the various experiments reported: (1) inherent differences in the varieties used, (2) the discrepancy is related to the number of environments sampled in each study. In few of the experiments were the number of environments sampled such that allowance would be made for the possibility that combining ability effects might interact with environments.

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The problems of producing F_1 seed in cotton places a severe limitation on the number of experiments any one worker might attempt in a study of problems of heterosis and combining ability. Such information must come from many studies, in different environments, toward a useful synthesis of knowledge concerning these phenomena. The present study incorporates more environments than have been previously reported in such a study with cotton. Our specific objectives were as follows: (1) to estimate the amounts of heterosis, involving several agronomic characters, among a set of diallel crosses of 10 Upland cotton strains thought to be representative of germ plasm of modern, obsolete, and new materials, (2) to obtain estimates of general and specific combining ability effects and determine the extent to which these quantities interact with the environments sampled, (3) to make inquiries as to the genetical nature of the projected population obtainable from intercrossing the lines.

MATERIALS AND METHODS

We used a group of lines representing obsolete varietal material, selections from currently grown commercial cottons, and new lines possessing properties thought to be of potential interest to growers and processors of cotton. The lines were designated 1 through 10 as follows:

- (1) Acala 5675 — A high performance line formerly used as breeding material at the Tennessee Experiment Station in the production of the variety 'Pope'
- (2) 'Cambodia' — A cotton adapted to Southeastern Asia but never grown commercially in the United States
- (3) 'Dixie Triumph' — An obsolete variety once grown in the southeastern United States
- (4) Earlistaple 7 — A long stapled, high lint strength line obtained from D. C. Harrell of the Pee Dee Experiment Station, Florence, S. C.
- (5) Empire 10 — A selection from the currently used variety 'Empire'
- (6) King 82 — A very early, low performance line from obsolete varietal material
- (7) North Carolina Margin — A new, high lint percent line obtained from introgressing germ plasm from *Gossypium arboreum* L. into Upland cotton
- (8) Sealand I — An Upland line introgressed with *Gossypium barbadense* L. as a source of long, strong lint
- (9) Station C-42 — A short stapled, high yielding line once used as breeding material at the Georgia Experiment Station
- (10) Triple Hybrid 131-4 — A low-yielding, high strength, line stemming from the introgression of the variety Empire with germ plasm from *Gossypium thurberi* Tod. and *Gossypium arboreum* L.

The 10 parental lines and all of the possible F_1 progenies (without reciprocals) plus a commercial check variety 'Coker 100-A' were grown at two locations for 2 years. The two locations, the Piedmont Research Station, Salisbury, N. C., and the Upper Coastal Plains Research Station, Rocky Mount, N. C., were remarkably similar in their temperature regimes and rainfall patterns for the 2 years in which the experiments were grown. The soil types on the stations differ markedly. At the Piedmont Station the soil types are primarily Davidson and Lloyd clay loams, whereas at the Upper Coastal Plains Station the soils are largely Goldsboro and Marlboro silty loams. All of these soil types are considered good for cotton. The 1961 season was cooler than normal and, as a result, the crop was late and fiber yields relatively low. Temperature-wise the 1964 season could be characterized as normal for North Carolina. The crop began to flower in early July with the result that fiber yields for the 1964 season were good.

The experiments were planted in randomized complete blocks with three replications per individual experiment. Each plot consisted of 3.67 m of row, with the rows spaced 1.08 m apart.

The stands were considered good for all experiments. What skip distances encountered were corrected for by linear projection from the actual yield of the plot (7). A skip was reckoned as the distance between the ends of the limbs of adjacent hills. The stands averaged three plants per 31 cm of row.

Data were obtained on lint yield, lint percentage (percent of the unginced cotton which was lint), and boll weight from all plots in all replications. A random sample of 25 bolls was harvested from each plot to measure lint percentage and boll weight. Lint yield was calculated by multiplying the total seed cotton harvested from a plot by the lint percentage value obtained from the boll sample of that plot. Fiber samples were taken from two replications in each individual experiment. These samples were analyzed by the U. S. Department of Agriculture Fiber Laboratory at Knoxville, Tenn., to obtain information on fiber properties. Fiber property measurements were as follows:

Fiber length — Upper half mean, U.H.M.—Average length, in mm, of the longer half of the fibers being tested

Fiber Strength — T_1 units — Strength of a bundle of fibers of standard weight measured on the Stelometer with two jaws holding the fiber bundle separated by a 3.2 mm space. Strength is expressed in terms of grams of force necessary to break the bundle

Fiber elongation — E_1 units — Percentage elongation at break of the center 3.2 mm of the fiber bundle measured for T_1 strength on a Stelometer

Fiber Fineness — Micronaire — Fineness of the sample measured by the Micronaire (an air-flow instrument) and expressed in standard (curvilinear scale) Micronaire units

For a more detailed explanation of the terminology and description of the instruments used in determining fiber properties see The 1965 Book of A.S.T.M. Standards, part 25 (11).

The data combined over years and locations was analyzed as follows: the conventional diallel analysis of F_1 crosses only (method IV, model II of Griffing) (3) was used to give estimates of general and specific effects and variances. Then the parental and F_1 cross data were combined to provide estimates of additive and dominance variance, assuming no epistasis, for the projected population as described by Kuehl, Rawlings, and Cockerham⁴. The "projected population" is designated as a randomly mating population at linkage equilibrium and having gene frequencies identical to those in the parental material, i.e., presumably the synthetic population obtainable from the parents by several generations of random mating. The error variances for parents and crosses were significantly different, or bordering on significance in five of the seven characters reported. Consequently, all analyses were conducted assuming the error variances of parents and crosses were different.

RESULTS

Heterosis

Significant differences existed among parents for all traits measured. The parents ranged in lint yield from 274 to 387 g per plot, with an average yield of 327 g per plot. Only one strain, Acala 5675 (No. 1), exceeded the check variety, 'Coker 100-A', which had a mean yield of 373 g of lint per plot. Average parental and F_1 lint yields are given in Table 1. Average degree of heterosis, expressed as percent deviation of the mean of hybrids from the mean of parental values, was significant for all characters except fiber strength,

Table 1. Average performance of parental and F_1 generations and percent heterosis measured as deviation from mid-parent.

Character	Generation		Check variety	Percent heterosis
	Parent	F_1		
Lint yield, g/plot*	327	412	373	25.99**
Weight bolls, g	6.24	6.77	6.24	8.49**
Lint %	35.30	35.90	38.40	1.70*
Fiber length, UHM, mm	27.4	28.2	28.7	-1.03
Fiber strength, T_1 units	1.96	1.94	1.62	0.09
Fiber elongation	8.41	8.49	9.48	-0.05
Micronaire	3.90	3.88	3.87	-0.05

*, ** Significantly different from zero at the 0.05 and 0.01 levels, respectively.

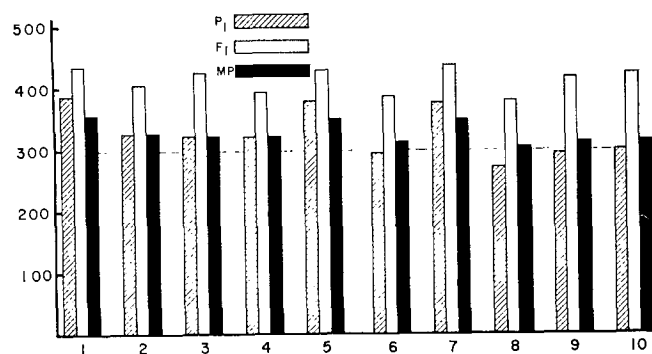


Fig. 1. Graphic presentation of mean yield of parents, F_1 arrays, and the average mid-parent in grams of lint per plot for the combined experiment.

fiber elongation, and Micronaire. These results agree with the findings of Miller and Marani (5) and others.

Fiber yields of parents, average mid-parent values, and means of F_1 arrays are presented graphically in Fig. 1. For a given parent the average F_1 yield was substantially higher than the mid-parent value and in all cases exceeded the parental value.

There was a high correlation between parental performance and the means of F_1 arrays. Miller and Marani (5) reported similar results in their experiments.

In traits other than lint yield the amounts of heterosis were usually small, though they were frequently significant. Fiber traits can be measured with a high degree of precision; therefore, very small differences are frequently detected.

Combining Ability

Variance components for estimates of general and specific combining ability and their interactions with years and locations are presented in Table 2. In most cases we determined significance levels by F-tests, comparing the appropriate mean square from the analysis of variance table with its proper error term. Approximate tests as outlined by Anderson and Bancroft (1) were used in those cases where appropriate error terms were not available.

Variance attributable to general combining ability as a main effect for lint yield was reckoned as zero. General combining ability by locations was the only estimate among the interaction terms for lint yield which was significant. Estimates of general combining ability for lint yield among individual parents in different environments (Table 3) shows that none

Table 2. Estimates of components of variance of general and specific combining ability and their interactions with locations and years.

Variance component estimated	Lint yield	Boll size ($\times 10^3$)	Lint percent ($\times 10^3$)	Fiber length ($\times 10^3$)	Fiber strength ($\times 10^4$)	Fiber elongation ($\times 10^4$)	Micronaire ($\times 10^4$)
σ^2_g	-22	288**	1637**	379**	360**	583**	378**
σ^2_{gy}	374	-8	42	1	0	15	7
σ^2_{gl}	503*	-11	91	18	4	1	47
σ^2_{gyl}	237	20**	13	0	-2	-6	48
σ^2_s	272	2	71	20	-9	-25	37
σ^2_{sy}	-208	8	60	1	18	2	38
σ^2_{sl}	-85	-5	-24	53	8	63	-24
σ^2_{syl}	325	3	364*	0	8	-19	-10

*, ** Component of variance significantly greater than zero at the 0.05 and 0.01 levels, respectively, as determined by F-tests of mean squares.

of the parents whose array mean tended to deviate from the grand mean in a particular environment did so consistently over all environments. One line, TH-131-4 (No. 10), showed high general combining ability in only one environment. Another line, N. C. Margin (No. 7), showed a marked locations effect. These results indicate that some strains do combine well in a general way in some environments, but the overall estimates for the four environments show that these effects average out to zero.

Estimates of general combining ability as a main effect were highly significant for all characters other than lint yield. One of the interaction terms was also significant but, in general, these variance components were relatively small when compared with the variance components for main effects.

None of the estimates of specific combining ability for lint yield were significant. The only interaction term for specific combining ability which was significant was the second order interaction for lint percentage. This result has been interpreted to mean that some combinations for lint percentage were occasionally outstanding, but these did not behave in a consistent manner over years and locations.

Genetic Variances

For all traits except lint yield, the estimates of additive genetic variance were highly significant and varied from approximately equal to error, for lint percentage and Micronaire, to 20 times error for fiber length. The additive genetic by environment interaction variances were relatively small, although significant in some cases (Table 4).

For lint yield, the additive genetic by environment interaction variances were two to four times as large as the nonsignificant estimate of additive variance, but considerably smaller than the experimental error variances.

Table 3. Estimates of relative combining ability (g_i) for lint yield in grams per plot for parental lines in the F_1 generation by individual experiment.

Line No.	Salisbury						Rocky Mount					
	1961			1964			1961			1964		
	g_i	Array mean	Grand mean	g_i	Array mean	Grand mean	g_i	Array mean	Grand mean	g_i	Array mean	Grand mean
1	18.00	407	391	16.88	525	510	15.75	335	321	23.62	458	437
2	9.00	399		-24.75	488		4.50	325		-34.88	406	
3	-19.12	374		56.25	560		-7.88	314		28.12	462	
4	-21.38	372		-4.50	506		-15.75	307		-14.62	424	
5	60.75	445		0	510		4.5	325		4.50	441	
6	-3.38	388		-13.50	498		-55.12	272		-49.50	393	
7	40.50	427		74.25	576		28.12	346		-2.25	435	
8	-55.12	342		-60.75	456		9.00	329		-54.00	389	
9	6.75	397		-27.00	486		24.75	343		12.38	448	
10	-33.75	361		-16.88	495		11.25	311		85.5	513	

Table 4. Estimates of components of additive and dominance variance in the projected population* and their interactions with locations and years.

Variance component estimated	Lint† yield	Boll size (× 10 ³)	Lint percent (× 10 ³)	Fiber length (× 10 ³)	Fiber strength (× 10 ⁴)	Fiber elongation (× 10 ³)	Micronaire (× 10 ⁴)
σ ² _a	170	484**	2929**	671**	680**	949**	670**
σ ² _{ay}	476	-7	103	10*	6	23	11
σ ² _{al}	705*	-14	186**	3*	7*	15	64
σ ² _{ayl}	383*	28**	56	0	-4	9	100**
σ ² _d	183	7	78	10	-4	2	26
σ ² _{dy}	-136	3	64	32**	8	-15	39
σ ² _{dl}	-34	-9	-3	-1	2	35	-20
σ ² _{dyl}	372	9	270*	-1	17	7	-20
σ ² _{E₁} †	3145	135	2297	26	148	512	630
σ ² _{E₂}	4929	184	1642	35	116	603	360

* The equilibrium random mating population having the same gene frequencies as the set of parents in the diallel. † †, ††, †††. Component of variance is significantly greater than zero at the 0.05 and 0.01 levels, respectively, as determined by appropriate F-tests of mean squares. In some cases approximate tests were necessary. † σ²_{E₁} and σ²_{E₂} are the error variances for parents and crosses respectively, and were estimated with 72 and 352 degrees of freedom, respectively, for lint yield, boll size, and lint percent, and with 36 and 176 degrees of freedom for the fiber quality traits.

In no case was the estimate of dominance variance significant, and only two of the 21 dominance by environment components were significant. In one case σ²_{dy} was of the same order of magnitude as the error variance.

DISCUSSION

Gene Action

Matzinger and Kempthorne (4) have shown that the components of variance for general σ²_g and specific σ²_s combining ability are related to genetic variance in some parental population, if the diallel set is a random sample from that population. The relationships were given as:

$$\sigma_g^2 = 1/2 \sigma_a^2 + 1/4 \sigma_{AA}^2 + 1/8 \sigma_{AAA}^2 + \dots$$

$$\text{and } \sigma_s^2 = \sigma_D^2 + 1/2 \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 +$$

$$3/4 \sigma_{AAA}^2 + \sigma_{AAD}^2 + \dots$$

where σ²_A = additive genetic variance, σ²_D = dominance variance, σ²_{AA} = additive by additive genetic variance, etc.

In an analogous manner, Kuehl et al.⁴ showed that the quadratic statistics from the diallel set are relatable to the components of genetic variance in the projected population, and that, in the absence of epistasis, unbiased estimates of additive and dominance variance can be obtained if parental information is also available. Explicit in these derivations is the assumption that the alleles in the parental set are distributed at random among the parents or that the covariances between effects of different loci are zero on the average over repeated applications of the method.

Departures from this assumption such as may result, for example, when lines representing only the extremes of a trait are chosen as parental material in the diallel, lead to unknown biases. Such biases might be present in this study, since the genes introgressed into *G. hirsutum* from *G. arboreum*, *G. thurberi*, and *G. barbadense* were restricted to a few parents. Moreover, some of the parents were chosen because of their extreme type with respect to various characters.

There is no method for detecting and quantifying such biases if they are present. Except for the interaction of additive effects with environment for lint yield, the results of these experiments agree in general

with results of similar experiments performed by other workers (5, 10). However, it is possible that the results of all of these experiments were biased in the same direction.

The estimates of σ²_a and σ²_d for lint yield being nearly equal in magnitude, although not significant, suggests that a goodly portion of the small amount of genetic variance present is other than additive in nature. Yet the estimates of σ²_g from single environments give the impression that additive factors account for most of the genetic variance. This discrepancy reflects the bias attributable to σ²_{gy}, σ²_{gl}, and σ²_{gyl} in the single environment estimates of σ²_g. The propensity for a given parent to combine well at a given location in a single year would not appear indicate potential progress in selecting for lint yield if general adaptation is the goal.

Triple Hybrid 131-4 (No. 10) is an example of a strain which combines well only occasionally. In one environment (Rocky Mount, 1964) it proved to be a good general combiner for lint yield, whereas in the other three environments it proved to be mediocre. This line is noted for lateness. As a rule, late cottons do poorly in North Carolina, because this region is on the northern border of cotton's adaptive range and seasons are usually short. The 1964 season at Rocky Mount was longer than usual, chiefly because of favorable moisture and temperature conditions late in the season coupled with good insect control. The longer season apparently provided this line and its offspring with ample opportunity to mature a maximum crop, whereas some of the more "determinate" lines such as Empire 10 (No. 5) and N. C. Margin (No. 7) were not capable of taking full advantage of the unusual situation. Thus, the biological properties of a given strain may interact through its offspring favorably in some environments but not in others. North Carolina Margin (No. 7) showed a marked locations effect with regard to general combining ability for lint yield.

All characters other than lint yield showed high estimates of additive variance. With all of these characters, errors were relatively small and estimates were believed to be precise. Other workers have obtained similar results. Thus, there seems to be little doubt that fiber properties, boll size, and lint percentage are inherited in an additive fashion.

The apparent lack of agreement between the highly significant estimate of heterosis for lint yield (ca. 26%) and the lack of a significant estimate of either σ²_s or σ²_d can be reconciled to some extent. In the first place, heterosis is based on mean comparisons which are generally estimated with more precision than variance components from the same amount of data. Secondly, assuming no epistasis, the expectation of the mean square deriving from the heterosis contrast contains, in addition to additive and dominance variance, product terms which are predominantly positive if dominance effects are mostly unidirectional. That is, σ²_d = 4Σ_i p_i² (1 - p_i)² a_i² u_i², whereas the genetic portion of the heterosis mean square is: [Σ_i p_i (1 - p_i) a_i u_i]² = σ²_d + 2Σ_{i<j} p_i (1 - p_i) p_j (1 - p_j) a_i u_i a_j u_j, where p_i is the frequency of the favorable alleles, u_i is half the difference in effect between the two homozygous genotypes, and a_i u_i is the deviation of the effect of the heterozygous genotype from the mean effect of the homozygous genotype. The summation

is over all segregating loci. It is clear that if there is no dominance, i.e., all $a_i = 0$, both σ_d^2 and heterosis should be zero. However, the product terms in the heterosis mean square will contribute to heterosis if most of the a_i are of the same sign. A third possibility for the discrepancy may, of course, be because of epistasis entering into the two quantities to different degrees.

Implications in Plant Improvements

The relatively high level of heterosis detected suggests that some potentially useful combinations might be obtained from these lines, provided that ways are found to produce hybrid seed in quantity. The Empire 10 (No. 5) \times N. C. Margin (No. 7) cross was particularly outstanding, especially in the Piedmont area where this hybrid produced 49.7% more lint than the commercial variety 'Coker 100-A'. Both Empire and Margin have fiber properties comparable to commercial cottons, although neither is competitive in lint yield.

Since fiber properties are inherited in an additive fashion, hybridization can only partially obscure the deficiencies of a poor parent. This fact alone tends to exclude much obsolete varietal material from consideration as possible parents for hybrids. If hybrid seed in quantity becomes possible, breeders will need to prepare lines with the proper fiber attributes and disease and insect resistance, and which, in addition, combine well. Miller and Lee (6), in a series of topcrosses of adapted varietal material to the variety 'Coker 100-A,' found that intercrossing currently used varietal material might be as good a way as any to produce desirable hybrids.

One of the objectives of these experiments was to determine the feasibility of selecting in a population whose genetical structure could be inferred from parental and F_1 data. The results suggest that little progress could be expected if the breeder wished to select for stable fiber yields over a variety of environments. If adaptation to a single location is desired, some of the combinations show promise, particularly the N. C. Margin and Empire 10 families. However, the effectiveness of selection, even for a single location or area, will be reduced by the significant general combining ability by year within location interaction. Also, narrow adaptation is a trait which, historically, has not been tolerable in southeastern cottons, because growing, processing, and distributing the seed involve special problems which can only be met through handling of large volumes.

There seems to be a real potential here for selecting more desirable fiber properties, particularly fiber strength and length. However, with advances in yield not readily predictable, other than through the hybrid route, it is doubtful if simultaneous response to selection for both yield advance and better lint quality could be obtained. More information in this particular area is needed.

The general properties desired in modern cottons are found in a few closely related strains. It would perhaps be better to use these strains as the nucleus for any further breeding efforts than to attempt to reselect the entire spectrum of characters needed from a new base which consisted mostly of obsolete or other unimproved material. It would be better to add characters to such cottons rather than to start anew. Radical changes in thinking about how cottons are to be grown and utilized could, however, drastically alter this line of thought.

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