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A Diallel Study of Bract Surface Area/Lint Weight per Boll Ratio in Cotton[1]

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ABSTRACT

A seven parent diallel study was conducted to determine the inheritance of the ratio bract surface area per lint weight per boll in cotton (*Gossypium hirsutum* L.). Experiments were performed in the field at Alexandria and Baton Rouge, LA in 1978 and 1979, and included the seven parents, their 21 F_1's and their 21 F_2's. Inbreeding depression and F_2 deviations were insignificant, suggesting that epistasis and dominance were not as important as additive effects. Partial failure of the assumptions of no epistasis, no multiple allelism, and independent gene distribution was observed in the three general tests. Epistasis and multiple allelism were specifically tested and found to be negligible. Genotype-environment interaction assumptions were specifically tested, and the additive and dominance effects were found to deviate among environments. A significant year-array interaction indicated that dominance relationships among parents were not constant between years, suggesting that one needs to test over years. Partial dominance was expressed at most loci where dominant alleles effected the bract surface area per lint weight per boll ratio, and these dominant alleles were effecting smaller ratios. Narrow-sense heritability estimates ranged from 0.20 to 0.92 and averaged 0.47, indicating that nearly one-half of the heritability was additive in nature.

Additional index words: **Byssinosis, Cultivar, Diallel analysis, *Gossypium hirsutum* L., Heritability, Heterosis.**

BRACT tissue of cotton (*Gossypium hirsutum* L.) has been suggested as a contributor to brown lung disease or byssinosis (3). Investigations into the genetic variability and nature of inheritance of bract surface area of cotton have been reported previously in the literature (4, 12, 13). These studies revealed considerable variability among genotypes for this trait and additive gene effects primarily were indicated to be responsible for bract surface area. One of these reports (12), along with a later report by Bowman and Jones (4), showed a positive association between bract surface area and boll weight (seed cotton and/or lint per boll). It was concluded that a better measure of heritable changes in bract surface area relative to byssinosis potential may be the ratio of bract surface area per lint weight per boll.

Utilizing data collected from the diallel study of bract surface area in the 1982 report (4), a Jinks-Hayman analysis was followed in determining the genetic nature of the bract surface area per lint weight per boll ratio. This report seeks to explain the results of this investigation.

MATERIALS AND METHODS

The materials and methods used in the diallel study have been reported previously in the literature (4, 5) and only an abbreviated version will appear here. The diallel consisted of the following seven parents:

1. MoBw 51849
2. 'LSS' (Pak) M71-010
3. NCJ-9 (B-5) 23790-1796-1167-657
4. 4S-180 (Greece) -1766-1149-636
5. La. DSIS 12513-245-1667-1015
6. Coker NF 73-809-060
7. La. 16ne-24-1-845-103-63-57

Parents will be identified by number. The parents used in this study were chosen specifically for their bract surface area based on previous screening studies (12, 13); they do not constitute a random sample of all Upland cotton cultivars and breeding lines. Thus, inferences derived herein are applicable only to the parents, crosses, and populations studied.

The experiments were conducted at the Perkins Road Agronomy Farm in Baton Rouge and at the Dean Lee Agricultural Center in Alexandria, LA in 1978 and 1979 and included the seven parents, their 21 F_1's, and their 21 F_2's. The soil types at Alexandria and Baton Rouge are Norwood silt loam (fine-silty, mixed (calcareous), thermic Typic Udifluvent) and Olivier silt loam (fine-silty, mixed, thermic Aquic Fragiudalf), respectively. A randomized, complete block design with four replications was employed at each location with the exception of Baton Rouge in 1978 where data were obtained from three replications. Twenty-four bracts and a 24-boll sample were collected from each plot to determine the ratio of bract surface are/lint weight per boll. Bract surface area was measured on a Hayashi Denko Area Meter, Model AAm-5[3] in centimeter^2. Lint per boll was weighed in grams.

Heterosis, inbreeding depression, and F_2 deviations were calculated as follows:

$$\text{Heterosis} = (F_1 - \text{Midparent})/\text{Midparent},$$

$$\text{Inbreeding depression} = (F_1 - F_2)/F_1, \text{ and}$$

$$F_2 \text{ deviations} = (F_2 - 1/2(F_1 + \text{Midparent}))/(1/2)(F_1 + \text{Midparent})$$

Heterosis is expressed as a percent increase or decrease of the F_1 from the mean of its parents. Inbreeding depression is expressed as a percent change of the F_2 from the

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[3] Mention of a trademark or a proprietary product does not constitute a guarantee or warranty of the product by the Louisiana Agric. Exp. Stn. and does not imply its approval to the exclusion of other products that may also be suitable.

F_1. F_2 deviations are calculated as the percentage decrease or increase of mean F_2 performance from the mean of the F_1 and midparent performance.

Diallel analyses followed the procedure as outlined by Hayman and Jinks (7, 8, 9, 10, 11) and were analyzed on a plot-mean basis. All effects were assumed fixed. Statistical significance from zero was determined by the Student's *t-test.*

Notations and their definitions as used in this study are those of Hayman (7). Estimates of the degree of dominance were defined by Crumpacker and Allard (6). Formulae for narrow-sense heritability estimates were defined for the F_1 by Crumpacker and Allard (6) and for the F_2 by Verhalen and Murray (14).

Table 1. Combined analysis of bract surface area per lint weight per boll for the parents.

Source	df	Mean square	F
Years	1	0.3109	0.94
Locations	1	1.2945	3.91
Years × Locations	1	4.2299	12.78**
Rep (Years × Locations)	11	0.3310	0.97
Parents	6	12.8022	37.53**
Years × Parents	6	1.2156	3.56**
Locations × Parents	6	0.6213	1.82
Years × Locations × Parents	6	0.4584	1.34
Error	66	0.3411	

** Significant at the 0.01 level of probability.

Table 2. Parental means and their progeny mean performance, and estimates of heterosis, inbreeding depression and F_2 deviations for bract surface area per lint weight per boll.

Parent	P_j†	MP†	C_j† F_1	C_j† F_2	Mean heterosis	Inbreeding depression	F_2 Deviations
1	2.70	3.46	3.15	3.23	−8.6	0.0	−2.3
2	4.77	4.32	3.50	3.55	−17.8	−2.5	−8.7
3	5.62	4.68	4.03	4.25	−13.2	−7.3	−1.5
4	3.87	3.95	3.48	3.55	−10.4	−1.9	−4.5
5	3.68	3.87	3.55	3.60	−7.9	−2.9	−2.2
6	3.23	3.68	3.35	3.43	−9.2	−2.9	−2.4
7	4.14	4.06	3.63	3.65	−9.7	−2.1	−4.2

† P_j = Parental mean; MP = Midparent; C_j = F_1 or F_2 mean over all crosses involving the *jth* parent.

RESULTS AND DISCUSSION

Highly significant differences among parents for the ratio of bract surface are per lint weight per boll were detected (Table 1). Thus, it is appropriate to conduct a detailed analysis of gene action controlling this trait.

A moderately close correlation (pooled within years) was calculated between parental performance and means of their F_1 and F_2 progeny ($r = 0.80$ and 0.81, respectively). Parents 1 and 3, the lowest and highest, produced F_1 and F_2 progeny that were also the lowest and highest in this study (Table 2). Parents 2, 3, 4, 5, and 7 had mean progeny values generally smaller than parental values while the two parents with smallest values (1 and 6) had greater mean progeny values. Heterosis, inbreeding depression, and F_2 deviation estimates were not significant for any particular parent (Table 2); although nearly all estimates were in a negative direction.

F_1 and F_2 means were consistently lower than the midparent (MP), (Table 3). The range of variability of parents (HP/LP) averaged over 2.0, an indication of high genetic variability for this trait. All estimates of heterosis were negative and nonsignificant. Insignificant and low levels of inbreeding depression and F_2 deviations (Table 3) indicate that epistasis and dominance were not as important as additive effects for bract surface area per lint weight per boll.

Tests of Assumptions. The diallel analysis was based on the assumptions as follows:

1. Diploid segregation
2. No reciprocal effect
3. No epistasis
4. No multiple allelism
5. Homozygous parents
6. Independent gene distribution
7. No genotype-environment interaction

The third, fourth, and sixth assumptions were first subjected to three general tests as outlined by Allard (2), Hayman (9), and Jinks and Hayman (11); all other assumptions were presumed satisfied. Partial failure

Table 3. Average performance of parental, F_1, and F_2 generations and mean heterosis, inbreeding depression, and F_2 deviations for bract surface area per lint weight per boll.

Location	Year	Generation mean MP†	Generation mean F_1	Generation mean F_2	HP†/LP†	Mean heterosis	Inbreeding depression	F_2 Deviations
		cm²/g						
Alexandria	1978	4.14	3.38	3.58	2.18	−15.8	−4.7	−5.2
Alexandria	1979	4.01	3.61	3.59	1.71	−9.1	−2.6	−2.8
Baton Rouge	1978	3.60	3.13	3.38	2.38	−7.9	−6.4	1.1
Baton Rouge	1979	4.25	3.67	3.66	2.18	−11.0	0.9	−7.9

† MP = Midparent; HP = High parent; LP = Low parent.

Table 4. Analyses of variance of (Wr-Vr) values for the ratio of bract surface area per lint weight per boll.

Source	df	F_1 Mean squares Alexandria 1978	F_1 Alexandria 1979	F_1 Baton Rouge 1978	F_1 Baton Rouge 1979	F_2 Mean squares Alexandria 1978	F_2 Alexandria 1979	F_2 Baton Rouge 1978	F_2 Baton Rouge 1979
Rep	3	0.3886	0.3248	0.0027	0.0703	0.0581*	0.2724	10.4524*	0.0783*
Array	6	0.6563*	0.1987	0.0076	0.0271	0.0129	0.2800	1.5415	0.0130
Error	18	0.1975	0.1041	0.0110	0.0384	0.0130	0.2091	1.3605	0.0171

* Significant at the 0.05 level of probability.

of the assumptions were detected in the first test (Table 4) by a significant array source of variation in the F_1 population at Alexandria in 1978, in the second test (Table 5) by seven of eight (Wr, Wr') regression coefficients being significantly different from 0.5, and in the third test (Table 5) by four of eight (Vr, Wr) regression coefficients being significantly different from 1.0.

Based on the results of the general tests of the assumptions, specific tests were then performed to test the validity of the three assumptions. The first test was a chi-square analysis to detect epistasis (8). The heterogeneity chi-square was insignificant thus allowing the data to be pooled. The pooled chi-square (285.7 at 315 df) was also insignificant suggesting that there was not an appreciable amount of epistasis involved in bract surface area per lint weight per boll.

The second specific test was an analysis of $(Wr_1 - 2WR_2)$ values to detect multiple allelism (8). Only one of four array sources of variation was significant while all others did not approach significance. Though somewhat inconclusive, there was not a strong indication of multiple allelism being involved.

Since independent gene distribution was not specifically tested and since there was a partial failure of the three general tests, this assumption was not considered fulfilled.

The assumption of no genotype-environment interaction was subjected to tests outlined by Allard (1). The highly significant parent-year interaction (Table 1) suggests that the additive effects were not constant among environments.

Genotype-environment interactions were also tested for the dominance components of variation (Table 6). Significant dominance, years by dominance and locations by dominance sources of variance suggest, respectively, that the mean degree of dominance was either partial dominance or overdominance and that degree of dominance varied between years and locations. Significant arrays and years by arrays sources of variation suggest that there are differences in dominance among parents and that the relative dominance among parents was not constant between years; the former is seen in Table 2 in the heterosis and inbreeding depression estimates and the latter suggests that testing over years is needed. The dominance component of this assumption was therefore not fulfilled and will be reflected in order of dominance, estimates of mean degree of dominance, and in estimates of dominance gene effects. The insignificance of all interactions involving dominance with arrays provide additional evidence that epistasis did not contribute significantly to bract surface area/lint weight per boll inheritance.

Estimates of Genetic and Environment Parameters. Only one of four estimates of the environmental variance for the parents (E_o) was significant while three of four estimates for the F_1 (E_1) and F_2 (E_2) generations were significant (Table 7). The insignificance of some relatively high environmental variance estimates points to the high degree of variability among entries to environmental influence on bract surface area per lint weight per boll. The average environmental estimate of the parental, F_1, and F_2 populations were 0.32, 0.28, and 0.30, respectively. F_2 environmental estimates are generally found to be intermediate between parental and F_1 estimates, and these results conform to the general trend.

Estimates of additive gene effects (D) were highly

Table 5. (Wr, Wr') and (Vr, Wr) regression coefficients and their 95% confidence intervals.

Population	Location	Year	(Wr, Wr')	(Vr, Wr)
F_1	Alexandria	1978	0.334 ± 0.112	0.421 ± 0.149
	Alexandria	1979	0.390 ± 0.257	0.189 ± 0.174
	Baton Rouge	1978	0.299 ± 0.049	0.884 ± 0.214
	Baton Rouge	1979	0.283 ± 0.053	0.788 ± 0.216
F_2	Alexandria	1978	0.269 ± 0.060	0.927 ± 0.143
	Alexandria	1979	0.201 ± 0.135	0.016 ± 0.200
	Baton Rouge	1978	0.394 ± 0.072	0.038 ± 0.113
	Baton Rouge	1979	0.326 ± 0.056	0.853 ± 0.184

Table 6. Genotype by environment analysis of the dominance components of variation.

Source	df	Mean squares
Years	1	0.5010
Locations	1	1.3219*
Years × Locations	1	0.0454
Rep (Years × Locations)	11	0.1987*
Dominance	1	0.5099*
Years × Dominance	1	0.3928*
Locations × Dominance	1	0.9582**
Years × Locations × Dominance	1	0.1169
Arrays	6	0.6645**
Years × Arrays	6	0.6044**
Locations × Arrays	6	0.1932
Dominance × Arrays	6	0.0731
Years × Locations × Arrays	6	0.2081
Years × Dominance × Arrays	6	0.1506
Locations × Dominance × Arrays	6	0.0633
Years × Locations × Dominance × Arrays	6	0.1053
Residual	143	0.0983

*,** Significant at the 0.05 and 0.01 levels of probability, respectively.

Table 7. Mean environmental and genetic parameter estimates for F_1 and F_2 populations for the ratio bract surface area per lint weight per boll.

	F_1				F_2			
	Alexandria		Baton Rouge		Alexandria		Baton Rouge	
Parameter	1978	1979	1978	1979	1978	1979	1978	1979
E_o	0.31	0.27**	0.15	0.53	--	--	--	--
E_1	0.23	0.53**	0.10**	0.24*	--	--	--	--
E_2	--	--	--	--	0.13**	0.37**	0.57	0.12**
D	1.46**	0.48**	0.97**	0.94**	--	--	--	--
F	0.95**	0.17	0.75**	0.43**	1.77**	0.42**	0.94**	0.33*
H_1	0.58**	1.61**	0.30**	0.05	1.58**	0.66	7.65	0.32
H_2	0.54**	1.46**	0.16**	0.04	2.85**	4.50**	12.12**	2.41**

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

Table 8. Mean genetic estimator ratios for F_1 and F_2 populations and their 95% confidence intervals for bract surface area per lint weight per boll.

Estimator	Year	F_1		F_2	
		Alexandria	Baton Rouge	Alexandria	Baton Rouge
Dominance 1	1978	0.55 ± 0.22	0.28 ± 0.06	0.21 ± 0.11	1.27 ± 2.07
	1979	3.23 ± 1.28	−0.01 ± 0.11	−0.43 ± 0.85	−0.08 ± 0.24
Dominance 2	1978	0.74 ± 0.11	0.52 ± 0.06	0.53 ± 0.09	-
	1979	1.80 ± 1.28	-	-	-
Dominance 3	1978	0.59 ± 0.17	0.42 ± 0.03	0.50 ± 0.05	1.21 ± 1.60
	1979	−0.21 ± 0.47	0.45 ± 0.08	−0.01 ± 0.71	0.55 ± 0.06
Heritability	1978	0.74 ± 0.18	0.92 ± 0.04	0.66 ± 0.08	0.26 ± 0.66
	1979	0.27 ± 0.07	0.38 ± 0.07	0.20 ± 0.02	0.33 ± 0.05

significantly different from zero indicating that a major portion of the inheritance of bract surface area per lint weight per boll was additive in nature (Table 7); this agrees with the conclusion from examination of inbreeding depression and F_2 deviations.

Except for one estimate in the F_1 population, estimates of relative frequency of dominant vs. recessive alleles in the parents (F) were positive and significantly different from zero. This suggests that there was a predominance of dominant alleles in the parents for this trait at those loci that exhibited dominance (Table 7).

Only one F_1 estimate of dominant gene effects (H_1) was greater than the estimate of additive gene effects (D) while only one F_2 estimate was significantly different from zero (Table 7). The three significant estimates suggest dominance is real but not necessarily of equal or greater magnitude than additive gene effects.

The estimates of dominance gene effects, corrected for gene distribution, (H_2) in the F_1 population were similar to the H_1 values, suggesting that there was little correlated gene distribution. The H_2 estimates in the F_2 population were all highly significantly different from zero and consistently greater than estimates of additive gene effects (D). These data again suggest that dominance gene effects are real. However, since only one set of dominance estimates was greater than estimates of additive gene effects then one may conclude that additive gene effects are more important than dominance.

Investigation of Genetic Systems. Estimates of mean degree of dominance (Dominance 1, 2, and 3) were highly variable among environments (Table 8) as would be expected from the previous analysis of the genotype-environment interaction of the dominance components of variation. Thirteen of 20 estimates were significantly different from zero; of these, two were in the overdominance range while the others were in the partial dominance range. Overall estimate of the mean degree of dominance was 0.61 while mean population estimates were 0.76 and 0.42 for the F_1 and F_2 populations respectively, suggesting partial dominance. This conclusion agrees with the interpretation of the analysis of the genotype environment interaction of the dominance components of variation.

Narrow-sense heritability estimates were, with one exception, significantly different from zero and highly variable. Values ranged from 0.20 to 0.92. Generally, heritability estimates in 1979 were considerably smaller than values obtained in 1978. The F_1 population had an average of 0.58 compared to an average of 0.36 for the F_2 population with an overall estimate of 0.47. If data sets not conforming to expectation were ignored, the narrow-sense heritability estimate would become 0.61. These estimates suggest that one-half or more of the heritability of bract surface area per lint weight per boll was additive in nature or that heritability was composed primarily of complete dominance. Since the overall estimate of mean degree of dominance was 0.61 and the significant dominance source of variation in the genotype-environment analysis of dominance components of variation suggested either partial or overdominance, the second interpretation does not seem feasible.

Hayman's (7) method of determining direction of dominance involving (Vr + Wr) correlations with parental means was utilized. Only half of the correlation coefficients were significantly different from zero; two other correlation coefficients approached significance, although all coefficients were positive. The six significant or near-significant correlation coefficients of eight estimates suggest most dominance alleles acted in one direction and the majority of recessive alleles acted in the opposite direction. The positive correlation coefficients would suggest the majority of dominant alleles were negative in direction, i.e., operating in the direction of smaller ratios of bract surface area per lint weight per boll; this is confirmed in Table 2 where estimates of heterosis were all negative and in Table 3 where F_1 means were smaller than midparent values.

Investigation of genetic systems involved in the ratio bract surface area per lint weight per boll revealed that nearly one-half of the inheritance was additive in nature. Thus, recurrent selection or any breeding procedure that seeks to concentrate favorable alleles would be advantageous in rapidly improving the trait in the direction of less bract surface area per lint weight per boll. A highly significant genotype-year interaction and a highly variable heritability estimate suggest that one needs to test selected lines over years between succeeding cycles of intercrossing. Breeders should be cautioned that reductions in this ratio are associated with a genotypic reduction in 50% span length and an increased fiber micronaire (5).

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