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Diallel analysis of yield and other traits in cotton

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ABSTRACT

Six cotton cultivars (*Gossypium hirsutum* L. var. *latifolium* Hutch) and their hybrid combinations were analyzed in a complete diallel. Yield, boll weight and earliness showed greater dominance than additive variance components, although both were significant. The additive component was more important for number of bolls per plant, plant height and fiber maturity. Yield showed low heritability (estimated to be 0.19), controlled predominantly by dominant genes. The cultivar with the greater concentration of favorable alleles for this trait is CNPA 3H.

INTRODUCTION

The choice of selection procedures and breeding methods are influenced by the type and quantity of genetic variation in the population. Diallel analyses have been carried out in cotton to partition these variances (White and Kohel, 1964; Al-Rawi and Kohel, 1970; Baker and Verhalen, 1974, among others). Distinct populations were used in these studies and the conclusions, in most cases, apply only to those specific populations. This experiment was carried out to obtain information on the genetic control of yield and other traits from a set of diallel crosses between six cultivars of *Gossypium hirsutum* L. variety *latifolium* Hutch. These cultivars are different in earliness and resistance to cotton "ramulose" disease and are divergent in origin.

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MATERIAL AND METHODS

The parental cultivars used in this study were: 1 = HR 102. 2 = CNPA 6 H, 3 = C-23-3-78, 4 = IAC 20, 5 = C-78-28-80 and 6 = CNPA 3H. Cultivars 1, 3 and 5 are introductions from the USA and the others are Brazilian. all the possible crossings including reciprocals were made among these six cultivars. The F_1 and their reciprocals together with the parents, were assessed in Viçosa, MG, in 1990 in a randomized complete block experiment with two replications. The yield was obtained by harvesting the whole plot. The mean weight of the cotton bolls in each plot was determined as the average of twenty randomly collected bolls. The number of bolls per plant was calculated as the average value of the number of bolls in ten competitive plants per plot. Fiber traits were obtained from analyses on samples of 20 bolls, randomly collected in the plot.

A diallel analysis using the various traits data was carried out according to Hayman (1954a) to obtain the mean squares components. The following statistical model was used:

$$Y_{rm} = m + J_r + J_m + J_{rm} + K_r - K_m + K_{rm} + E_{rm}$$

where:

$J_{rm} = L + L_r + L_m + L_{rm}$

and,

m = general mean;

J_r, J_m = average deviation from the general mean due to the r-th and m-th parents, respectively;

J_{rm} = residual difference of the mean of the reciprocal crossings;

K_r, K_m = difference between the r-th (or m-th) parent effect used as male or female in the crossings;

K_{rm} = residual difference in the reciprocal difference in the mr-th order;

L = average dominance deviation;

L_r = dominance deviation due to the r-th parent;

L_{rm} = deviation of the residual difference from the mean of the reciprocal crossings rm;

E_{rm} = average experimental error.

Hayman (1954a) shows the expected mean squares and the genetic interpretation of these sources of variation. The following assumptions (restrictions) are imposed on the diallel analysis of Hayman (1954b).

Diploid segregation

G. hirsutum L. is an amphi-diploid and segregates in a diploid manner, satisfying this condition.

Homozygous parents

The materials used in this study are self-pollinating varieties which may undergo natural cross-pollination and, therefore, present an undefined heterozygous residue. Verhalen and Murray (1969) commented that there is no clear-cut test to assess the parental heterozygosis and this can make the elaboration of tests for the restriction difficult. Some authors, however, have used the diallel method with varieties. In the absence of non-allelic interactions and with an independent distribution of the genes among the parents, W_r (the covariance among parents and the r-th line of the diallel table) relates to V_r (the within line or column variance) by a straight line with b = 1. Dickinson and Jinks (1956) commented that the deviation from 1.0 due to parental heterozygosis will not be great although it may be significant. They also stated that epistasis can cause more severe deviations and, in these cases, it should not be confounded with deviations due to heterozygoses. The doubt remains, however, when epistasis is relatively small relative to the deviations caused by dominance. According to Hayman (1957), it is still possible to obtain the estimates of the genetic components for those characteristics which show partial failure of the assumptions, although they are less precise than when all the assumptions are met.

Absence of reciprocal differences in the hybrids

The parameters were not calculated for the characteristics in which reciprocal differences were observed. The data in the diallel table were compiled from the mean of the two F_1s for the other characteristics.

The assumptions of no epistasis, no multiple allelism and independent gene distribution were tested by variance analysis (W_r - V_r). It is expected that this value remains constant among the arrays (lines on the diallel table) when all assumptions are met.

Table I shows the estimated genetic parameters and their significance. The t test was used for testing the significance of these parameters, and an estimate was considered significant at the 5% probability level, when its division by the respective standard deviation was greater than 1.96 (Singh and Chaudary, 1979). The following genetic parameter estimators were used:

$(H_1/D)^{1/2}$ = average degree of dominance

$H_2/4H_1$ = frequency of positive or negative alleles in loci which showed dominance, with a maximum value of 0.25.

$$\frac{K_D}{K_R} = \frac{(4DH_1)^{1/2} + F}{(4DH_1)^{1/2} - F}$$ = ratio between dominant and recessive genes in the parents

$$\frac{h^2}{H_2}$$ = number of gene groups which control the traits and show some degree of dominance

$$h_R = \frac{D - F + H_1 + H_2}{D - F + H_1 - (1/2)H_2 + 2E}$$ = heritability in the strict sense

$$h_A = \frac{D - F + H_1 - (1/2)H_2}{D - F + H_1 - (1/2)H_2 + 2E}$$ = heritability in the broad sense

The statistics ($W_r + V_r$), which ranks the parents according to their number of dominant genes, based on the principle that the parents with a larger number of dominant genes show smaller values of V_r and W_r when crossed with the others, was calculated. The correlation (r) between (W_r + V_r) and Y_{rr} (mean values of the parents), which is an indicator of the relationship between the favorable alleles and dominance, was also calculated. The theoretical limits of selection, referring to the mean of the completely dominant or recessive parent for the segregant genes of the diallel, was

Table I - Genetic variance components of the diallel analysis of Hayman (1954b), and their meaning.

Components	Meaning
D	Variation caused by the additive genetic effects
F_r	Co-variance among additive and dominant effects in the hybrids with i-th parent
H_1	Variation caused by the dominance effects
F	F_r mean. Relative frequency of the recessive and dominant genes in the population. F will be positive if the dominant alleles are more frequent than the recessive ones, and negative when the recessive alleles are more frequent
H_2	Variation caused by the dominance effects, corrected for gene distribution
H_1-H_2	Theoretically H_1-H_2 > 0. If $H_1 = H_2$, the genes with positive and negative effects are present at equal frequencies
h^2	Total genetic dominance component relative to the heterozygous loci. Refers to the square of the difference between the mean of the p^2 elements in the diallel table and the mean of the parents.

obtained by the regression of Y_{rr} on $(W_r + V_r)$. The theoretical limits of selection were given by Y_D or Y_R.

RESULTS AND DISCUSSION

Table II shows that, except for fiber resistance, all the assessed traits showed sgnificant J_r or general combining ability values indicating the importance of the additive variation in the control. The number of bolls per plant, plant height, fiber percentage and resistance did not show specific combining ability (or J_{rm}). A significant L effect, indicating the presence of directional (positive or negative) dominance deviation and mean heterosis was observed only for yield. However, some significant L_r values were detected for traits not showing significance for L, indicating that the dominance deviations for some parents are significant. This happens when the genotypic frequency among the parents does not satisfy the symmetry condition. For yield, L and L_r were significant, probably because parents four and six had a greater number of dominant genes. For earliness, in spite of a non-significant L value, a significant L_r was observed, probably due to the asymmetry of the genes among the parents. For some characteristics, such as weight of a hundred

Table II - Analysis of variance of the assessed traits in six cotton cultivars and their respective diallel cross hybrids. Viçosa, MG, 1990.

Source	df	Mean Squares								
		BW	NBP	PH	PRE	YLD x 10^5	WCS	PF	RES	MAT
Block	1	0.48	42.62	1,946.3	5,246.3	2.3	0.58	0.05	0.027	118.29
Treatment	35	0.45*	4.72^{ns}	462.2**	402.2**	2.7**	1.38**	3.20**	0.414^{ns}	30.34**
J_r	5	1.05*	9.16*	1,898.6**	1,302.7**	4.7**	2.48**	8.19**	0.325^{ns}	73.39**
J_{rm}	(15)	0.52*	3.41^{ns}	317.3**	392.1**	3.5**	1.54**	1.80^{ns}	0.272^{ns}	33.53*
L	1	0.004^{ns}	3.17^{ns}	179.2^{ns}	84.3^{ns}	2.1**	0.22^{ns}	0.79^{ns}	0.009^{ns}	47.01^{ns}
L_r	5	1.31**	4.70^{ns}	772.0**	1,012.9**	3.2**	3.66*	2.12^{ns}	0.261^{ns}	52.94*
L_{rm}	9	0.15^{ns}	2.72^{ns}	80.1^{ns}	81.5^{ns}	1.8^{ns}	0.51^{ns}	1.79^{ns}	0.307^{ns}	21.22^{ns}
K_r	5	0.21^{ns}	2.50^{ns}	163.4^{ns}	85.4^{ns}	1.7^{ns}	1.07*	3.17*	0.306^{ns}	10.73^{ns}
K_{rm}	10	0.16^{ns}	5.58^{ns}	128.1^{ns}	124.9^{ns}	1.1^{ns}	0.73*	2.80*	0.752*	13.84^{ns}
Resídual	35	0.16	3.45	183.8	62.0	1.2	0.30	1.00	0.258	14.99

* - Significant at 5% probability by F test.

** - Significant at 1% probability by F test.

df = degrees of freedom; BW = boll weight; NBP = number of bolls/plant; PH = plant height; PRE = precociousness; YLD = yield; WCS = weight of a hundred seeds; PF = percent fiber; RES = resistance; MAT = maturity.

seeds, fiber percentage and fiber resistance, significant reciprocal effects were detected and, therefore, the genetic parameters were not estimated.

Table III shows the least square estimates of the components of the genetic variation. Except for h^2 and H_2, almost all parameters were significantly different from zero. The dominance (H_1) variation for yield, boll weight and earliness, was greater than the additive component (D), although both were significant. Similar results were found by Baker and Verhalen (1974) and Singh and Chahal (1974). These three characteristics showed overdominance, with $(H_1/D)^{1/2}$ greater than one. The component due to additive effects (D) was greater than that due to dominance effects (H_1) for the boll number per plant, plant height and maturity. The observed results for the first two characteristics agreed with those of Al-Rawi (1969). The three characteristics show partial dominance (Table IV). The estimates of F were positive and significantly different from zero for all traits, indicating that the parents have a high concentration of dominant genes. The estimate of the mean frequency of positive and negative alleles in the loci with dominance, for all traits (Table IV), showed that they are not equally distributed among the parents. The ratio among the dominant and recessive genes K_D/K_R showed, with the exception of the number of bolls per plant, a predominance of dominant alleles in the parents (Table IV). Some estimates of the number of genes that control the trait and show dominance h^2/H_2 were low or nil. However, it is known that they can be underestimated when the genes do not have the same effects. There are at least three genes or gene blocks controlling yield and number of bolls per plant. White and Kohel (1964) found the value of 3.32 for yield while other authors found alues between 11 and 13 genes. There are at least two genes controlling number of bolls per plant; White and Kohel (1964) found a value of 3.76.

Among the estimates of heritability in the strict sense, only plant height and earliness showed values above 0.40 (Table IV). Al-Rawi and Kohel (1969) quoted the value of 0.37 for plant height. The heritability of yield found in this study was 0.19. The majority of the diallel estimates of the yield heritability found in the literature are smaller than this value. An exception was the value

Table III - Variance component estimates of the traits obtained from a diallel among six cotton cultivars. Viçosa, MG, 1990.

Characteristics	Genetic parameter[1]					
	D	H_1	H_2	h^2	F	E
Yield	255, 273.8*	303,663.3*	235,350.6*	550,567.5*	264,349.3*	61,848.3
Boll weight	0.44*	0.75*	0.36*	-0.04^{ns}	0.67*	0.08
Number of bolls/plant	3.49*	0.38^{ns}	-1.03^{ns}	-0.07^{ns}	2.96*	1.72
Plant height	823.93*	329.64*	133.54^{ns}	-1.28^{ns}	734.20*	91.91
Precociousness	294.62*	647.08*	330.12*	6.20^{ns}	404.79*	31.01
Maturity	34.98*	31.29*	18.54*	8.89*	37.91*	7.49*

[1]Table I shows a description of these parameters.
*Significant at 5% probability.

Table IV - Genetic parameter estimates of the traits assessed in a diallel among six cotton cultivars. Viçosa, MG, 1990.

	$(H_1/D)^{1/2}$	$\frac{H_2}{4H_1}$	$\frac{K_D}{K_R}$	$\frac{h^2}{H_2}$	h_R	h_A	r	Y_D	Y_R	Value of the largest mean	Order of dominance**
Yield	1.09	0.19	2.80	2.33	0.19	0.58	-0.78	2,582.95	-	29.86 (6)	6,4,1,2,5,3
Boll weight	1.30	0.12	3.85	0.00	0.30	0.67	0.77	-	8.62	7.50 (4)	1,3,2,6,5,4
Number of bolls/plant	0.33	-0.02	-8.14	2.15	0.21	0.21	0.20	-	12.14	14.19 (6)	1,3,2,4,6,5
Plant height	0.63	0.10	5.76	0.00	0.53	0.65	0.62	-	179.43	171.10 (6)	4,5,2,1,3,6
Precociousness	1.45	0.12	2.63	0.03	0.42	0.75	0.17	-	71.31	60.25 (1)	2,1,6,3,5,4
Maturity	0.94	0.14	3.69	0.47	0.28	0.55	-0.92	62.25	-	64.19 (3)	2,6,3,4,1,5

*The number in brackets refers to the parent which shows the greatest mean.
**Parents with greater concentration of dominant genes in decreasing order.

of 0.46 cited by Al-Rawi and Kohel (1969). The heritability for the number of bolls per plant was also low (Table IV).

The positive correlation between ($W_r + V_r$) and Y_{rr} (mean value of parents), r = 0.77 for boll weight, revealed that the recessive alleles are responsible for the increase of the mean of this trait, which can reach 8.62 g by selection. The progenitor r (IAC 20) presents a higher mean and also a greater concentration of recessive genes, being preferred when an increase in this characteristic is desired. A high negative correlation (r = -0.78), showed that generally dominant alleles are responsible for the increase of yield. Ordering of the parents with regard to the concentration of dominant genes shows that parent six (CNPA 3H) has a greater concentration and a higher mean. There is no possibility of increasing yield through selection since Y_D is smaller than the yield of some parents. The correlation for bolls per plant is low (0.20) and no inference about gene action or selection can be made. The correlation for plant height is relatively high and so the recessive alleles are responsible for increasing this trait. Cultivar six had a higher mean and a greater number of recessive genes. The correlation of r = -0.92 showed that the dominant genes lengthen fiber maturity. Cultivars two (CNPA 6H) and six (CNPA 3H) showed higher means and greater number of dominant genes.

RESUMO

Analisaram-se seis cultivares de algodão (*Gossypium hirsutum* L. var. *latifolium* Hutch) e suas combinações híbridas em um dialelo completo. O rendimento, peso de capulhos e precocidade apresentaram o componente de variação atribuído à dominância maior que o componente aditivo, porém ambos significativos. Para o número de capulhos por planta, altura de plantas e maturidade da fibra o componente aditivo foi mais importante.

Análise do rendimento permitiu concluir que se trata de um caráter de baixa herdabilidade (estimada em 0,19), determinado por genes predominantemente dominantes e que o cultivar de maior concentração de alelos favoráveis para este caráter é o CNPA 3H.

REFERENCES

Al-Rawi, K.W. and **Kohel, R.J.** (1969). Diallel analysis of yield and other agronomic characteres in *Gossypium hirsutum* L. *Crop. Sci. 9*: 779-783.

Al-Rawi, K.W. and **Kohel, R.J.** (1970). Gene action in the inheritance of fiber properties in intervarietal diallel crosses of upland cottons. *Gossypium hirsutum* L. *Crop. Sci.* 82-85.

Baker, J.R. and **Verhalen, L.V.** (1974). The inheritance of several agronomic and fiber properties among selected lines of upland cotton. *Gossypium hirsutum. Crop. Sci. 13*: 444-450.

Dickinson, A.G. and **Jinks, J.L.** (1956). A generalized analysis of diallel crosses. *Genetics 41*: 65-77.

Hayman, B.I. (1954a). The analysis of variance of diallel tables. *Biometrics 10*: 235-244.

Hayman, B.I. (1954b). The theory and analysis of diallel crosses. *Genetics 39*: 789-790.

Hayman, B.I. (1957). Interaction, heterosis and diallel crosses. *Genetics 42*: 336-355.

Singh, T.H. and **Chahal, G.S.** (1974). Diallel, analysis of yield and its components in desi cotton. *Ind. J. Genet. Plant. Breed. 34*: 323-327.

Singh, T.K. and **Chaudary, B.D.** (1979). *Biometrical Methods in Quantitative Genetic Analysis*. Kalyani Publishers, Ludhiana, pp. 304.

Verhalen, L.N. and **Murray, J.C.** (1969). A diallel analysis of several fiber property traits in upland cotton *Gossypium hirsutum*. II. *Crop. Sci. 9*: 311-315.

White, T.G. and **Kohel, R.J.** (1964). A diallel analysis of agronomic characters in selected lines of cotton, *Gossypium hirsutum* L. *Crop. Sci. 4*: 254-257.

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