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Flat-Square in Cotton, Acala Type. I. Its Mode of Inheritance and Heritability[1]

H. Khalifa, W. T. Starmer, W. D. Fisher, and L. S. Stith[2]

ABSTRACT

Flat-square, an unidentified flower disorder in cotton (*Gossypium hirsutum* L.) which is manifested at bloom time, appeared on a large scale in Arizona during 1962. Part of this study was designed to verify the mode of inheritance and heritability of this disorder.

Three homozygous inbred lines of Acala-type cotton known to exhibit flat-square were intercrossed with a doubled haploid line free from flat-square. Seeds of the F_1, F_2, BC_{nf}, and BC_f generations were grown simultaneously with the parental populations to evaluate its mode of inheritance and heritability.

Flat-square was found to be quantitatively inherited, with low heritability. The estimates of the genetic parameters indicate that the inhertance is mostly additive in nature with no evidence of epistasis or maternal effect.

Additional index words: **Genetic parameters, Additive effects, Dominance effects, Epistatic effects.**

FLAT-SQUARE first appeared in an epiphytotic proportion in 1962 in some areas of the Arizona cotton (*Gossypium hirsutum* L.) growing regions (1, 4). The phenomenon was more frequently observed in the fields of cultivar 'Deltapine Smooth Leaf.' Shields and Gries (4) described flat-square as an abnormality in which two or three bracts were present at the flower node while the sepals, petals, pistil and stamens were lacking. This disorder was usually associated with other growth abnormalities, such as development of extra-lateral branches (i.e. two or three fruiting branches or leaves growing from each node resulting in a bushy appearance). Wene and Sheets (5), as part of a study on the possible effect of lygus bug (*Lygus hesperus* Knight) on cotton plants, stated that flat-square may result from feeding by lygus bugs on meristematic tissues or presquaring coton. Most research workers, however, tried to explain the phenomenon of flat-square on the basis of obvious plant damage, nutrient supply, weather conditions, insecticide or herbicide application, etc., and apparently overlooked the possibility that it might be genetically controlled.

The purpose of the experiments reported herein was to investigate whether flat-square is genetically controlled and to describe its inheritance and heritability.

MATERIALS AND METHODS

The plant materials used in this study were selfed seed from lines of Acala-type cottons which exhibited flat-square and selfed seed from a doubled haploid of the same variety which was apparently free from flat-square. In the summer of 1966, progeny rows were grown and single plants were selected from both flat- and non-flat-square lines to serve as parental lines. To exclude the possibility that insects were the causative agents for this disorder, the flat-square parental lines were protected by nylon net-cages. Reciprocal crosses were made and simultaneously each parent was selfed. Seed were collected from the three pairs of parental plants, each hereafter representing a separate family. The three lots of seed (designated as families A, B, and C) were sent to Iguala, Mexico, for further propagation and hybridization. Each of the three families consisted of 10 populations which were produced and served as a basis for study. These were: Pnf. (non-flat-square), Pf (flat-square), and eight other populations involving the reciprocal F_1's, their backcrosses to each parent, and the two F_2 progenies.

In the summer of 1967, the three families were planted in two evaluation trials, one at Phoenix (Cotton Research Center) and the other at Tucson (Campbell Avenue Farm). A split-split-plot design with three replications was used at each location. The families were assigned to the main plots, and each family was subdivided into two parental cytoplasms. Each parental cytoplasm included the material to be referred to as generations P_{nf}, P_f, F_1, F_2 and the two backcrosses; each generation consisted of 10 plants.

The number of flat-squares produced by each plant in each generation was recorded when flat-square expression was highly evident. The data were then analyzed to evaluate differences between family, cytoplasm, and generation means.

A statistical model to describe genetic variation within two inbred lines and their subsequent progeny was proposed by Mather (3) and Hayman (2). Hayman's model was utilized to separate epistatic effects from additive and dominance effects in generation means. These latter parameters are considered as summations over all genes by which the parental lines differ. Parameter d measures pooled additive effects, h measures pooled dominance effects, and m denotes the base population mean.

The generation means were tested with a chi-square analysis to ascertain if m, d, and h fit a nonepistatic model; the F_2 generation w as the base population.

Heritability in the broad sense was estimated using the formula H = (100 × genetic variance)/(genetic variance + environmental variance).

RESULTS AND DISCUSSION

The plant materials used in this study exhibited various abnormalities in the formation of the flower structures. Fig. 1 shows the morphological structures of the prevalent types of flat-squares. Flat-squares designated as 1, 2, 3 and 4 represent types with two bracts enclosing the rudimentary gynoecium, 5 consists of three bracts, 6 and 7 have the entire gynoecium missing, while 8 was a single bract. In almost all plants showing the disorder, flat-squares were found at the appropriate flower positions. Fig. 2 shows two sympodial branches; branch 1 was cut from a plant possessing flat squares. It is clear that the sympodial branch 2 carries four flat-squares at successive nodal positions and that these positions coincide with those occupied by the complete flowers on the normal sympodial branch. This observation indicates that flat-squares and complete flowers have the same nodal origin. Most of the plants showing flat-square in this study expressed this trait consistently, whether grown under open-field conditions or under

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[2] Presently Senior Cotton Breeder, Shambat, P. O. Box 30, Khartoum North, Sudan (former Graduate Student at the University of Arizona); Instructor, Department of Biological Sciences, and Professors in the Department of Agronomy and Plant Genetics, University of Arizona, respectively.

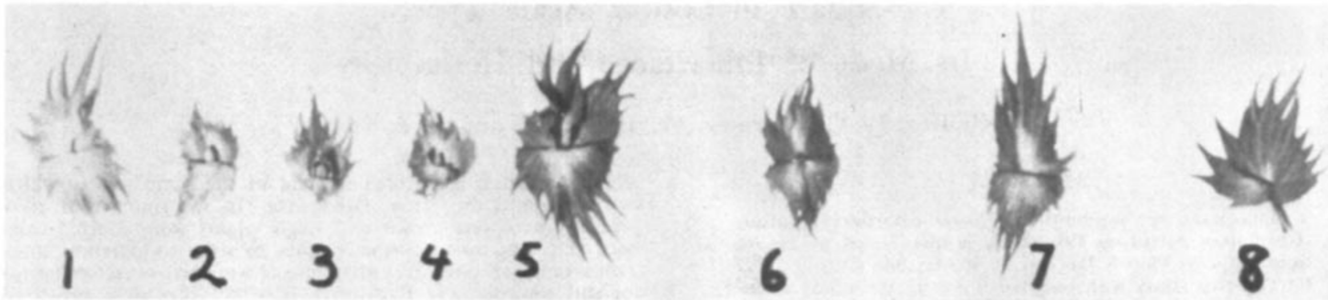

Fig. 1. Typical morphological structures of the prevalent types of flat-squares.

Fig. 2. Two sympodial branches displaying: normal development of complete flowers, and development of flat-squares.

nylon net-cages from which insects were excluded. The occurrence of flat-square under cages largely excludes the possibility that this disorder is a manifestation of insect damage by lygus as suggested by Wene and Sheets (5). The maximum frequency of flat-squares was found to coincide with the peak of the flowering period.

The summary of the statistical analysis of the generation means for flat-square (based on the average number of flat-squares per plant) for 1967 is given in an abbreviated table showing only relevant comparisons (Table 1). These results indicate that localities did not differ significantly and that there is no cytoplasmic effect involved in the expression of the disorder. The significant interaction of generations and families is mainly due to the differing magnitudes of differences between generations for the separate families. Also the significant difference exhibited by families indicates the families should be treated separately in any genetic analysis. The important result from this table is the highly significant difference that exists among the generations. Table 2 shows flat-square generation means within families and averaged over families and family means averaged over generations. In all three families, P_{nf} is significantly different from P_f. The BC_f also produced significantly more flat-squares than the BC_{nf} in families A and C.

The genetic parameters d and h were estimated using the method described by Hayman (2). These parameters are considered as summations over all genes by which the parental lines differ. The assumptions underlying the estimation of these parameters are that the parents are inbred lines and there is no linkage. The d and h parameters are defined against the F_2 base population. As seen in Table 3, the chi-square (χ^2) values for the three families were not significant (.03 probability level); thus, the data fit a nonepistatic model and a test for additive and dominance components can be constructed. Significant (.05 probability level) values for d and h were obtained in families A and B, whereas family C had only significant additive effects d. In families A and B, it is evident that the estimates of the additive effects

Table 1. Analysis of variance of flat-square occurring in *Gossypium hirsutum* L., Acala type.

Source of variation	df	Mean squares
Locations	1	13.505
Replications (R)/L	4	6.174
Families (F)	2	48.108*
R × F/L	8	5.642
Cytoplasms (C)	1	1.151
R × C/FL	12	0.560
Generations (G)	5	53.734**
G × F	10	5.767*
R × G/FCL	120	0.926

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

Table 2. Comparisons of generation means based on average number of flat-squares per plant observed in three families of *Gossypium hirsutum* L.

Generations	Observed means* Family A	Family B	Family C	Avg‡
P_{nf}	0.104	0.098	0.092	0.098
P_f	3.580	1.416	4.774	3.257
F_1	0.994	0.416	2.208	1.206
F_2	1.383	0.618	1.684	1.228
BC_{nf}	0.732	0.342	0.932	0.669
BC_f	2.561	1.346	4.351	2.753
Avg†	1.559	0.706	2.340	

* LSD .05 for generation means within families = 1.112; LSD .01 = 1.581. † LSD .05 for generation means averaged over families = 0.550; LSD .01 = .863.
‡ LSD .05 for family means averaged over generation means = 1.136; LSD .01 = 2.620.

Table 3. Testing of flat-square generation means for epistasis using the F_2 as the base population; Tucson and Phoenix, Ariz., 1967.

Parameters*	Model estimates ± standard errors Family A	Family B	Family C
m	1.462 ± 0.091	0.645 ± 0.073	2.265 ± 0.157
d	-1.777 ± 0.178	-0.720 ± 0.134	-2.405 ± 0.217
h	-0.852 ± 0.219	-0.396 ± 0.174	-0.456 ± 0.363
χ^2 (3df)	2.243	1.903	4.449

* m = F_2 mean, d = pooled additive effects, and h = pooled dominance effects.

Table 4. Genetic and environmental variances along with estimates of broad sense heritabilities for all families.

	Genetic variance*	Environmental variance†	Heritability‡
Family A	.0065	.0800	7.51%
Family B	.0025	.0773	3.13%
Family C	.0068	.0831	7.56%

* Estimated by the formula $V(F_2) - [V(P_{nf}) + V(P_f) + V(F_1)]/3$. † Estimated by the arithmetic average of the variance within the nonsegregating generations, P_{nf}, P_f and F_1. ‡ Estimated by the formula H = (100 × genetic variance)/(genetic variance + environmental variance).

were approximately twice those of the dominance effects. The genotypic differences among the generation means are therefore due mostly to pooled additive effects of genes and partly to pooled dominance effects with no epistasis indicated.

The estimates of broad sense heritabilities based on individually spaced plants are given in Table 4, along with the estimates of genetic and environmental variances for each family. Since genotypic differences within families are mainly due to pooled additive effects this estimate of broad sense heritability approximates the narrow sense heritability. The average heritability over families was low (6%) and the majority of variation was due to something other than genetic causes.

It can be hypothesized that the genetic factors controlling this phenomenon of flat-square were probably present in the germplasm of the parental lines of Acala. The phenotypic expression of the character, even if manifested, was undoubtedly unobserved during the early stages of seed propagation. During the increase of the breeder seed, the different genotypes will naturally intercross and increase the number of plants carrying the genes. The frequency of plants or genotypes showing flat-squares in the successive populations would be maintained and could even increase due to selection pressure which may have been inadvertently exerted in favor of plants showing flat-square.

The fact remains that flat-square appeared on an epiphytopic scale in 1962, and this may have been due to a threshold effect when environmental conditions, such as temperature or other microclimatic conditions, were prevailing for the expression of the phenomenon. When new seed stocks were used, flat-square only appeared sporadically.

This disorder has been greatly reduced or even eliminated in varieties currently being grown. Since it is genetically controlled with a low heritability, it may become disastrous through seed propagation. The breeder should therefore screen his breeding material to eliminate plants expressing this character.

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