

A GENETIC STUDY OF STORM RESISTANCE
IN UPLAND COTTON, GOSSYPIMUM
HIRSUTUM L.

By

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CHAPTER I

INTRODUCTION

The cotton (Gossypium hirsutum L.) breeding effort in Oklahoma has been concerned for many years with the improvement of fiber quality in the storm resistant and stormproof types of cultivars grown in the state. To accomplish this objective, numerous crosses between cottons grown in Oklahoma and those from other areas in the United States (primarily open-boll types) have been initiated and selections made in segregating generations. Hardly any of the plants in the F_2 's of some such crosses displayed any visually detectable degree of storm resistance. This observation was in marked contrast with previously published literature on the subject, suggesting that perhaps not everything of value is known to cotton breeders about the inheritance of this character.

The purpose of this research was to estimate the number of genes controlling differences between various degrees of storm resistance in upland cotton, the types of gene action involved, and their narrow-sense heritabilities. In this experiment seven American cultivars and one from Bulgaria were utilized in four sets of two apiece representing four degrees of storm resistance, i.e., the very open, open, storm resistant, and stormproof boll types.

CHAPTER II

REVIEW OF LITERATURE

Definitions

Brown (8) defined stormproofness as the resistance expressed by mature, healthy bolls to loss of their seedcotton during stormy, rainy and windy weather. The bolls do not fully open; the locks do not fluff as in "normal" open bolls, but they are firmly packed into the bur and sometimes appear glued to the bur as if by a secretion. Fibers often are entangled in the carpel walls which are rough and cracked, especially on the peripheral edge (25). Open boll types have fully open burs and fluffy locks; and if mature bolls are left in the field for extended periods of time before harvest, one or more locks per boll will fall from the plant and be unavailable to the usual harvesting equipment. The storm resistant boll is phenotypically intermediate between the open boll and stormproof types.

History

In an evolutionary sense, the advantage for Gossypium species has been for individual plants in the wild to drop their seed to the ground upon boll opening...as it aided in distribution of offspring and perpetuation of the species. It was only after domestication by man that an advantage was entailed by the retention of seed within

the boll until it could be harvested (30). Selection for such a characteristic was probably unintentional at first; but gradually over time, conscious efforts were made in the direction of increased storm resistance.

The most recent and dramatic development of this sequence of events occurred in 1926. After a severe sandstorm in the Lubbock area on the Texas High Plains, a farmer, Mr. H. A. Macha, discovered a single plant in his field of 'Half and Half' cotton which had lost no seedcotton and which had retained comparatively little sand in the mature bolls. He increased the seed obtained from that plant and nine years later distributed the first commercial stormproof upland cultivar named 'Macha' (9, 22). Since that time, cotton breeders in the High and Rolling Plains of Texas and Oklahoma have considered storm resistance and stormproofness as highly desirable, even necessary, characters especially when stripper harvesters are to be used (10). Numerous storm resistant or stormproof cultivars have been and are being grown commercially and many more are in various stages of development. Most cultivars in other parts of the United States and the world continue to be of the open-boll types.

Factors Affecting Storm Resistance

Cardozier (10) suggested that storm resistance is a combination of several characters. Friesen (15) has identified the following factors which affect storm resistance:

- a. Convolution formation in the inner carpel wall during dehiscence, which actually clamps the fibers to the carpel wall especially near the base region or stem of the carpel. These

convolutions vary considerably from cultivar to cultivar and are difficult to measure.

b. Fibers pinched in the very base of the bur because of a pit formation at the base of each lock in the early stages of boll development. This character also varies with cultivar.

c. Microorganism infection attacking both the cotton fiber and carpel wall. This occurs under wet environmental conditions such as rain, dew, or very high relative humidity (i.e., above 95%). Infection glues the fibers to the carpel wall as well as weakening and discoloring them.

d. Friction between the fiber and the carpel wall when the lock is removed. This parameter varies with several factors such as the degree of opening in the boll, the number of locks per boll, the area or volume that each lock occupies in the boll, the angle of pulling force with respect to the boll during lock removal, lock weight, number of seed per lock, and the characteristics of the fibers being removed.

e. Protrusions near the suture cell structure (where separation occurs as the boll opens) over which the fibers are pulled during removal.

f. A water soluble mucous-type substance remaining after fiber formation which acts as a gluing agent and adheres the fibers to the carpel wall.

Friesen (15) believes that there are additional factors affecting lock tenacity though they are probably not as important as those listed above. Walter and Coleman (34) studied the role of free sugars and soluble polysaccharides in stormproof vs. nonstormproof types. They found both types had identical qualitative compositions of free

sugars; the quantitative compositions of the free sugars in the inner carpel walls were found either "not to vary significantly" or "to vary significantly but not consistently" for different sources. Also, there was no evidence of soluble polysaccharides in the inner carpel walls or in the entire internal portion of developing bolls from both types. They concluded that these factors were not involved in the expression of the stormproof characteristic nor could they be used to differentiate between the two specific types under study.

Measurement of the Character

When storm resistance was a relatively new character for breeders to select for in cotton, the primary method for measurement and classification was visual subjective judgment. Plants with loose-flared or "strung out" locks would be classified as open boll types, and plants with firm, well clung, partially opened, cuplike locks would be considered stormproof types. Degrees of storm resistance would be located between the two extremes. As well as using two variations of the above technique, Lynn (25) classified the character into three categories by grasping the first seed in the lock between the thumb and forefinger and pulling it vertically out of the bur. He concluded that in stormproof types, the lock would pull apart before it could be removed from the bur; in intermediate types, considerable resistance would be encountered, but the lock would pull from the bur without splitting; and in open boll type, little or no resistance was encountered when the lock was removed.

Jones and Ray (23) measured the actual force required to remove a single lock from the boll. They attached the peduncle of the boll to a

500-gram weight which was placed on a 500-gram direct reading scale, pulled the lock from the boll, and noted the reading. Subtraction of each reading from 500 gave the actual amount of pull in grams required to remove the seedcotton from the bur. Choudhury (11) used a resistance strain gauge to measure the dynamic force required to pull locks from the bur. He found that different amounts of work were required to remove the lock in different cultivars. He also concluded that dynamic force was negatively correlated with the angle of carpel opening. In 1975 Young (37) coined the term "lock tenacity" and defined it as "the grams of force required to remove a lock of seedcotton from the bur of a fully open boll". He used a 500-gram force gauge with a maximum-hold attachment to measure the trait; and to clamp the gauge to the seedcotton, he used an alligator-nosed electric quick connection.

Genetic Aspects of the Character

Jones and Ray (23) classified bolls into three types on the basis of force required to remove one lock of seedcotton from the bur. "Normal" boll types required less than 130 grams of force for removal; intermediate types, between 130 and 300 grams; and stormproof types, 300 grams or more. They concluded that one pair of major genes and presumably some modifying factors controlled the character. They suggested that the character lacked dominance because the F_1 generation was intermediate between the two parents and because the bulk of the F_2 also fell between the parents. They also noted that nongenetic factors exert considerable influence on the character.

Lynn (25) used three methods to classify different degrees of

stormproofness. His first was "appearance" which referred to the stretched appearance, fluffiness of locks, and "stringing out" or dropping of lock (if any). Chi square tests for 3:1 and 1:2:1 hypotheses indicated that the F_2 progenies fit a 3:1 ratio much better than a 1:2:1, apparently because of the difficulty in differentiating between homozygous dominant and heterozygous individuals. His second method was "pull" which referred to the pull necessary to remove a lock of seedcotton from the bur (as described in the previous section). His third method was "weathering" which referred to loss or "stringing out" of locks by allowing plants to remain in the field for a long period. He concluded that stormproofness is controlled by a single incompletely dominant gene with factors other than the major gene for stormproofness affecting the final expression of the trait.

CHAPTER III

MATERIALS AND METHODS

Cultivars Investigated

This experiment included eight commercial cultivars of upland cotton described as follows:

a. '6111' (P.I. 362156, C.B. 3994) from Bulgaria (29) is an extremely early maturing cultivar which has displayed relatively good yield in Oklahoma; it is an open boll type; its fiber is medium to short with average uniformity index, fineness, and strength; and its plants are relatively short in height. It is susceptible to bacterial blight [Xanthomonas malvacearum (E. F. Sm.) Dows.], to the fusarium wilt [Fusarium oxysporum Schlecht. f. vasinfectum (Atk.) Snyder and Hansen] and root-knot nematode [Meloidogyne incognita (Kofoid and White) Chitwood (M. incognita acrita)] complex, and to verticillium wilt (Verticillium dahliae Kleb.).

b. 'Acala 1517-70' (6, 29) is an open boll type developed to replace 'Acala 1517 BR-2'; it has good resistance to bacterial blight and more tolerance to verticillium wilt than BR-2. It yielded more than BR-2 in New Mexico both on wilt-infested and wilt-free soils, but its fiber qualities were about the same, i.e., 1 1/8 inches (2.86 cm) staple length, strength of approximately 95,000 PSI, and micronaire readings of 4.0 to 4.2.

c. 'Stoneville 7A' (26, 29) has good tolerance to verticillium wilt, has a fair level of tolerance to bacterial blight, but is susceptible to the fusarium wilt and root-knot nematode complex. Its maturation is about average, and its plant height is average in the mid-South. Bolls and seed are small, but the seeds have good emerging quality. Bolls are classified as open under Oklahoma environmental conditions. Fiber is longer (1 1/16 to 1 1/8 inches - 2.70 to 2.86 cm) and a little coarser than the average with good strength.

d. 'Deltapine 16' (4, 5, 29) has similar characteristics and adaptability as had 'Deltapine 45' and 'Deltapine Smooth Leaf'. It has shown good tolerance to verticillium wilt and some tolerance to the fusarium wilt and root-knot nematode complex. Fibers are generally 1 3/32 to 1 5/32 inches (2.78 to 2.94 cm) long with a micronaire reading of about 4.5 and with excellent length uniformity and fiber elongation. Its bolls are of the open type.

e. 'Lankart LX 571' (4, 6, 29) is a relatively early cultivar with 1 1/16 inches (2.70 cm) fiber length, fineness of 4.2, and average strength of 90,000 PSI. Plants are short and susceptible to bacterial blight and verticillium wilt. Bolls are semi-storm resistant.

f. 'Lockett 4789-A' (4, 5, 6, 29) is an early cultivar yielding well under both dryland and irrigated conditions. Its plant is close fruiting (i.e., semicluster) with storm resistant and large bolls. Fibers are 1 1/32 inches (2.62 cm) and longer with strength of more than 85,000 PSI and fineness readings between 3.7 and 4.9 micronaire.

g. 'Westburn 70' (4, 29, 33) displays very good yield in Oklahoma, it is resistant to the fusarium wilt-nematode complex, but is susceptible to bacterial blight and verticillium wilt. Its fibers are 1 1/32 inches

(2.62 cm) or longer, fine, and strength is approximately 82,000 PSI.

Its bolls are stormproof.

h. 'Paymaster 202' (5, 29) is a stormproof stripper-type cultivar with medium fiber length, excellent fiber strength, and high yield. It is medium early and adapted to both dryland and irrigated conditions. The cultivar exhibits good field tolerance to bacterial blight and is moderately tolerant to verticillium. Its average staple length is 31/32 to 1 inch (2.46 to 2.54 cm), fiber strength is 80,000 to 85,000 PSI, and fineness is between 4.0 and 5.0 micronaire units.

Based on preliminary measurements of storm resistance among 40 foreign and domestic cultivars (29), the above eight cultivars were chosen and classified into four sets of two cultivars apiece as shown in Table I.

Experimental Procedures

This experiment was conducted on the Agronomy Research Station, Perkins, Oklahoma, on a Teller loam soil in 1975. In the previous year, the eight cultivars had been planted and all possible crosses (ignoring reciprocals) were made between the eight, except between parents within each set. Part of the F_1 seed from each combination as well as the parents were sent to Iguala, Mexico, during the 1974-1975 winter season to produce backcross seed of selected F_1 's to both parents, to produce F_2 seed of the 24 F_1 combinations, and to make the four F_1 crosses not previously made between entries within sets. The backcrosses were made to both parents for the 12 individual F_1 combinations between adjacent categories, i.e., between entries in I with those in II, II with III, and III with IV. All possible backcrosses could not be made because

TABLE I
CLASSIFICATION, CODE NUMBERS, AND MEAN LOCK TENACITY
OF CULTIVARS USED IN THIS STUDY

Sets	Degree of Storm Resistance	Cultivar Code Numbers	Cultivars	Lock Tenacity (gr.)	
				Preliminary Test	Overall Mean
I	very open	{ 1	6111	93.2	86.7
		{ 2	Acala 1517-70	90.2	54.0
II	open	{ 3	Stoneville 7A	132.0	89.8
		{ 4	Deltapine 16	129.6	93.1
III	storm resistant	{ 5	Lankart LX 571	200.0	128.5
		{ 6	Lockett 4789-A	203.1	168.5
IV	stormproof	{ 7	Westburn 70	219.7	181.0
		{ 8	Paymaster 202	237.0	200.5

of the expense.

In the 1975 season, the eight parents, 28 F_1 's, 24 F_2 's, and 24 Bc's were planted on June 5 in a randomized complete-block experimental design with four replications. Two independently assigned rows of each F_2 and a single row of all other entries were included in each replication. Plots were single rows 7.1 m long, 1.0 m apart, and plants in each row were thinned 20 to 30 cm apart (approximately 30 plants per plot) on July 3. Plants bordering alleys or skips in the row were not harvested because of possible border effects. Because of skips in some rows, the number of harvested plants per plot varied. Most rows had between 20 and 25 harvested plants; however, not more than 30 plants were harvested in any one plot. Harvesting was conducted from January 13-20, 1976. Three healthy, mature bolls were harvested from the middle portion of each plant using a hand clipper to cut the pedicel to avoid crushing the bur (as is common with hand pulling).

The harvested bolls were then taken to the Cotton Fiber Laboratory at Oklahoma State University, Stillwater; and lock tenacity was measured therein under the relatively constant temperature ($70^{\circ}\text{F} - 21^{\circ}\text{C}$) and relative humidity (65%) of the lab. The samples were kept in that environment for at least 24 hours before measurement. From the three harvested bolls per plant, the most healthy, mature one was tested. Two locks on opposite sides of that boll were measured, and readings recorded. A 500-gram force gauge was used to measure the force required to remove each of the two locks from the bur. The instrument is equipped with a dial indicator having 5-gram increments and a 500 gram capacity; a control button, which when in the "on" position, will hold the indicator dial on the maximum force reading; a reset tab, which when

pressed, releases the indicator dial from the control button, and the indicator hand returns to zero; and a tension head, to which an alligator-nosed, electric quick connection is attached and used to connect the gauge to the lock and to pull the seedcotton out of the bur. This is the same type and model of instrument that Young (37) utilized in his recent studies.

Analysis Procedures

When this experiment was originally planned, intentions were to concentrate on the genetics between the different degrees of storm resistance (i.e., between the very open, open, storm resistant, and stormproof boll categories). At the end of the first season, the decision was made to also conduct diallel analyses, which explains why the four within-set F_1 's were made later in Mexico. Only those four corresponding F_2 's were lacking for an F_2 diallel analysis as well.

For calculating narrow-sense heritabilities in the individual crosses, the formula suggested by Warner (35) was employed where possible:

$$\text{Heritability} = [2V_{F_2} - (V_{Bc_1} + V_{Bc_2})] / V_{F_2} = (1/2)D / [(1/2)D +$$

$$(1/4)H + E]$$

where V = variances for the indicated generations and D, H, and E represent the additive, dominance and environmental components of variance, respectively. This formula is credited with two advantages (a) estimation is entirely based on the F_2 and the backcrosses of the F_1 to each of its inbred parents and (b) there is no need to estimate non-heritable variance. Broad-sense heritabilities were estimated for all

crosses using the following formula:

$$\text{Heritability} = \left\{ V_{F_2} - [(V_{P_1} + V_{P_2} + V_{F_1})/3] \right\} / V_{F_2}$$

where V = variances for the indicated generations.

Many of the individual heritability estimates (both broad - and narrow sense) were negative especially for crosses including the first cultivar (6111 from Bulgaria). A Q-test as suggested by Foster (14) demonstrated that the parental variances are significantly different in each replication and that the variance for 6111 was significantly larger than for the other cultivars. It was concluded that 6111 retained a large amount of genetic variability for this trait, that it did not fit the genetic assumption of homozygous parents; and therefore, it and its crosses were eliminated from further analyses. The data for the remaining seven parents and their crosses were then transformed to a logarithmic basis so that the data would better fit the diallel assumptions. A 7 X 7 diallel table for each replication was constructed, and the necessary calculations were made using the Jinks-Hayman procedure (17, 20, 21) to estimate the related statistics and genetic components from those tables. The conformity of this trait with the overall assumptions of the diallel analysis was also examined. A test for epistasis was calculated. To obtain more genetic information about the heritability and gene action between the different categories of storm resistance, additional diallel analyses of the parental and F_1 data were conducted between all possible sets of categories taken two at a time.

CHAPTER IV

RESULTS AND DISCUSSION

As previously mentioned, the estimation of heritability for specific parental combinations proved unsatisfactory because of the excessively large variances estimated for a number of entries, especially for the 6111 parent and its crosses. The Q-test for equality of variances was conducted in each replication by using the following formulas (14):

$$q = \bar{v} (v_1 s_1^4 + \dots + v_p s_p^4) / (v_1 s_1^2 + \dots + v_p s_p^2)^2$$
$$\chi_{p1} = [pv(pq-1)]/2.$$

The calculated chi-squares for four replications were 32.16, 39.18, 58.70, and 50.44, respectively. With seven degrees of freedom they all presented highly significant differences among parental variances. Because the calculated variances for 6111 were much larger than the others (considering the magnitude of their overall means) the conclusion was made that this cultivar was more genetically variable for this trait than were the other cultivars. Because one of the basic assumptions of the diallel analysis is that of homozygous parents, the data for this cultivar and its crosses were eliminated from further consideration in this study. A preliminary test of the data from the first replication for the remaining cultivars and their F_1 combinations showed that several crosses still provided unacceptable (i.e., negative) estimates for heritability. Because further elimination

of parents would have very severely reduced the quantity of data (which would also decrease the population of inference to which these analyses would apply), rescaling was chosen as an alternative. Two methods of rescaling were attempted, i.e., logarithms and square root. The transformation to logarithm was more successful because fewer of the heritability estimates were negative. Therefore, the original data were all transformed into logarithms. All subsequent calculations were made on the transformed data.

Analyses of variance were conducted for each generation (parents, F_1 's, and F_2 's) on a plot mean basis. Highly significant differences among entries were detected for all three generations (Table II). Because differences among entries were significant, a diallel analysis could be conducted. This analysis partitions phenotypic variation into genotypic and environmental components and the genotypic variance into its additive and dominance components (16, 21). The analysis can also detect the presence of epistasis. Therefore, it is a powerful method for investigating the relative genetic properties of the entries being compared.

With the diallel analysis as with all statistical analyses, a number of assumptions are made. These include diploid segregation, no reciprocal differences, no epistasis, no multiple alleles, homozygous parents, uncorrelated gene distributions, and no genotype-environmental interaction within locations and years (12) all of which can be tested by two kinds of tests, i.e., general and specific tests of the diallel assumptions.

TABLE II
ANALYSES OF VARIANCE FOR PARENTS, F_1 'S,
AND F_2 'S ON A PLOT-MEAN BASIS

Source	Parents		F_1 's		F_2 's	
	df	Mean Squares	df	Mean Squares	df	Mean Squares
Replication	3	.0262	3	.0071	3	.0027
Entry	6	.9726**	20	.3866**	17	.2782**
Residual	18	.0505	60	.0252	51	.0053

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

General Tests of the Diallel Assumptions

The first three broad, general tests in this subsection (31) as well as the last four (19) determine whether this trait fulfilled the assumptions of the analysis as a whole. The failure of one or more of the assumptions influences and likely reduces the reliability of the inferences derived from the analysis. The L_1 (parents and F_1 's) and L_2 (parents and F_2 's) diallel tables were constructed using plot mean data to permit the derivation of the necessary statistics as variances and covariances. The three missing F_2 values were estimated by the formula:

$$\bar{X}_{F_2} = (\bar{X}_{F_1} + \bar{X}_{MP})/2$$

Assuming p_r as the r^{th} parent, f_{rs} as the F_1 cross between r^{th} and s^{th} parents, and g_{rs} as the F_2 selfed progeny of f_{rs} , the statistics calculated are V_{OL0} , the variance of the parents; W_r , the covariance between the parents and their offspring in the r^{th} array; W_{OL01} , the mean of the W_r 's; W'_r , the covariance between the members of an array and the array means of their nonrecurrent parents; V_r , the variance of the r^{th} array; V_{1L1} , the mean of the V_r 's; and V_{OL1} , the variance of the array means (17).

a. Analysis of Variance of the Quantity $(W_r - V_r)$. The failure of this quantity to remain constant over arrays is an indicator of the failure of one or more of the assumptions (21). The results of the F_1 and F_2 analyses are summarized in Table III. The F_1 data did not display significant differences among arrays suggesting that the assumptions were fulfilled in that generation, but the F_2 data showed a highly significant difference among arrays implying the failure of one or more of the assumptions in that generation.

TABLE III
ANALYSES OF VARIANCE OF ($W_r - V_r$) VALUES

Source	df	Mean Squares ($\times 10^{-6}$)	
		$F_1(W_{r1} - V_{r1})$	$F_2(W_{r2} - V_{r2})$
Replications	3	1231	274
Arrays	6	339	838**
Residual	18	439	89

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

b. Analysis of the (W_r, W'_r) Regression. Hayman (19) noted that when the genes controlling a character were distributed symmetrically, the graph of W'_r against W_r should be a straight line with a slope of 0.5 which passes through the point (W_{OL01}, V_{OL1}). Asymmetry of distribution causes the points to scatter about the line of slope 0.5; the points above the line will be related to the most common genotypes, and those below to the more uncommon. Allard (1) stated that to fulfill the assumptions, the regression coefficient should not be significantly different from 0.5 but it should also be significantly different from zero. The regression of (W_r, W'_r) was calculated for both F_1 and F_2 data on a plot mean basis for each of four replications, and then the four estimates were averaged. The coefficient for the F_1 was 0.43 with 95 percent confidence limits of 0.35-0.51 while that for the F_2 was 0.46 with limits of 0.38-0.53. In both generations the regression coefficient was significantly different from zero but not from 0.5.

According to the results of this test, the hypotheses were fulfilled.

c. Analysis of the (V_r, W_r) Regression. This regression coefficient is expected to be significantly different from zero but not from unity if all assumptions are fulfilled (21). The regression was analyzed for F_1 and F_2 data on a plot mean basis for each replication, then the average of the four estimates was calculated. The result of this test for the F_1 was a coefficient of 0.81 with 95 percent confidence limits of 0.62-1.01. For the F_2 , a coefficient of 0.91 was calculated with confidence limits of 0.74-1.08. Neither confidence interval included zero, but both included 1.0. Therefore, this test also indicates that the assumptions of the analysis were fulfilled.

d. Analysis of Variance of the Quantity $(W_{r1} - 2W_{r2})$. Theoretically, $(W_{r1} - 2W_{r2})$ should be constant over arrays (17, 19) if the assumptions of the analysis are fulfilled. Significant variation of this quantity is an indication of at least partial failure of the assumptions. Because the arrays mean square for this test (Table IV) was highly significant, at least a partial failure of the assumptions was indicated.

e. Analysis of Variance of the Quantity $(V_{r1} - 2V_{r2})$. The quantity $(V_{r1} - 2V_{r2})$ should be constant over arrays if all assumptions of the analysis are fulfilled (17, 19). Arrays mean squares (Table IV) for the test were significantly different for this quantity implying at least a partial failure of the assumptions.

f-g. Analysis of the $(V_{r1}, 2V_{r2})$ and $(W_{r1}, 2W_{r2})$ Regressions. Because $(V_{r1} - 2V_{r2}) = -(1/4)D - (1/8)H_1 - [E_0 - (n-1)(E_1 - 2E_2)]/n$ and because $(W_{r1} - 2W_{r2}) = -(1/2)D - E_0/n$, the regression line for each equation should be a straight line of slope 0.5 if all assumptions of

TABLE IV
ANALYSES OF VARIANCE OF $(W_{r1} - 2W_{r2})$ AND
 $(V_{r1} - 2V_{r2})$ VALUES

Source	df	Mean Squares ($\times 10^{-6}$)	
		$(W_{r1} - 2W_{r2})$	$(V_{r1} - 2V_{r2})$
Replications	3	1780	2983
Arrays	6	9917**	13825**
Residual	18	1904	1890

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

the analysis hold true (19). These analyses resulted in estimates of 0.53 with a 95 percent confidence interval of 0.18-0.89 and of 0.64 with an interval of 0.34-0.93, respectively. In both tests, the confidence intervals did not include zero, but did include 0.5. Consequently, the assumptions according to this test can be considered fulfilled.

Because the presence of epistasis was demonstrated by a chi-square test (discussed later in this thesis), the analysis of variance of deviations (19), which is a general test of all hypotheses (as well as of four specific assumptions in a stepwise process), could not give additional information other than in a general sense. When epistasis is present, the other three individual assumptions cannot be tested. Therefore, that additional test was not conducted herein.

The results of the above general tests cannot be used as a whole to state that the assumptions of the analysis were fulfilled because

there were some cases of failure. The F_2 analysis in the first test as well as the fourth and fifth tests did not conform to expectations had the assumptions been entirely correct. Being broad and general, these tests were not capable of detecting the specific assumptions which failed. To pinpoint those assumptions, several specific tests were available and are discussed in the next section.

Specific Tests of the Diallel Assumptions

a. Diploid Segregation. Endrizzi (13) studied the pairing behavior of upland cotton and suggested that although it is a tetraploid species, its behavior in pairing is diploid-like. Kimber (24) also believes that cotton has been diploidized by some unknown genetical process. Considerable cytological and genetic evidence exists that cotton essentially satisfies this assumption of the diallel analysis.

b. No Reciprocal Differences. It is generally assumed that significant differences between reciprocal crosses are not present for most traits in upland cotton. White and Richmond (36) found no significant differences between reciprocal crosses for characters such as yield, earliness, lint percent, and several fiber properties. Al-Rawi and Kohel (2, 3) did detect a significant reciprocal difference for lint percent in their diallel cross analyses among nine upland cultivars. However, they also observed no significant differences for yield, earliness, or any fiber property. This author is aware of no study conducted to test different degrees of storm resistance for reciprocal differences. Such a test was not possible in this study because reciprocals were not included.

c. No Epistasis. The presence of epistasis was tested using the

chi-square test devised by Hayman (18). His formula is as follows:

$$\chi^2 = k_2 [(n-1)(V_{1LX} - V_{OLX}) + n(\bar{p} - \bar{x})^2 / (1 + k) + (n-1)(V_{OLO} - 4W_{OLOX} + 4V_{OLX}) / (2 + k)]$$

with $n(n-1)/2$ degrees of freedom where:

$$k = nE_0 / (8E_2 + 2E_1 - E_0); k_2 = n / (8E_2 + 2E_1);$$

E_0 , E_1 , and E_2 = Mean environmental variances of the parents F_1 's and F_2 's, respectively;

n = Number of parents; \bar{p} = Mean of the parents; and

\bar{x} = Overall mean of the entries in the experiment.

Designating the diallel table of parents and F_1 's as the L_1 and that of the parents and F_2 's as the L_2 a $2L_2 - L_1$ table was constructed to calculate the statistical terms in the formula. This table is constructed by subtracting each term of the L_1 table from twice the term in the same position of the L_2 table. The diagonal terms do not change because they are identical for both tables. The following quantities can then be computed:

$$p_r = \text{Mean of the } r^{\text{th}} \text{ parent,}$$

$$\bar{x} = \text{Mean of the } r^{\text{th}} \text{ array,}$$

$$V_{OLO} = \text{Var}(p_r),$$

$$W_{OLOX} = \text{Cov}(p_r, \bar{x}_r),$$

$$V_{OLX} = \text{Var}(\bar{x}_r), \text{ and}$$

$$nV_{1LX} = \sum_s \text{Var}(x_{rs}).$$

The calculations were made in each replication using the above formula; and values of 47.45, 62.21, 93.26, and 128.30 were obtained in replications one through four, respectively. With 21 degrees of freedom, they were all significant at the 0.01 level of probability.

Therefore, the presence of epistasis is a factor which probably decreases to some extent the reliability of the results reported herein.

To obtain more detailed information about the types of epistasis involved, the procedure suggested by Hayman (18) was followed. The quantities for epistatic deviations from the expected simple dominance model (y_{rs}) and values of apparent dominance (\hat{h}_{rs}) were calculated in each replication using the following formulas and were then averaged over replications:

$$(1+k)(2+k)y_{rs} = (1+k)(2+k) X_{rs} - k(1+k)(\bar{X}_r + \bar{X}_s) + k^2 \bar{X} \\ - (1+k)(p_r + p_s) + k \bar{p} \text{ and} \\ \hat{h}_{rs} = 2f_{rs} - 2g_{rs} + 2k_1 y_{rs}$$

where:

$$k = nE_0/(8E_2 + 2E_1 - E_0), \text{ and } k_1 = (2E_2 + E_1)/(4E_2 + E_1).$$

Graphing y_{rs} against \hat{h}_{rs} provides a pattern for comparing epistatic deviations with apparent dominance. In the idealized form, when epistasis is absent, all points are located on the \hat{h}_{rs} axis; but when epistasis is present, points representing different parental combinations will be scattered above and below the line. A confidence limit can be used to determine upper and lower limits beyond which significant epistasis is present. Hayman (18) suggested that the crosses outside those limits in quadrants I and III exhibit the duplicate form of epistasis (because y_{rs} and \hat{h}_{rs} have the same sign) while those in quadrants II and IV have the complementary form (because of different signs). Table V lists the mean numerical values calculated for \hat{h}_{rs} and y_{rs} , and Figure 1 shows those values graphed with 95 percent confidence limits. Four individual combinations exhibited significant epistasis. Three of the four had parent eight

TABLE V
 \hat{h}_{rs} AND y_{rs} VALUES AVERAGED OVER REPLICATIONS

\hat{h}_{rs} (Lower Left-Hand Corner	y_{rs} (Upper Right-Hand Corner)						
	2 †	3	4	5	6	7	8
2†	(-.0856)*	.0972	.1736	-.1374	.0011	.1384	.3908*
3	.0180	(.1022)*	.0862	-.2897	.1061	-.4244	-.3170*
4	.2351	.0363	(.0702)	-.1962	-.0035	-.2204	-.3498*
5	-.0527	-.0913	-.1733	(.0753)	-.0713	.2950	-.1920
6	.0074	-.1303	-.2307	.0407	(.0320)	-.1548	-.0789
7	.2667	-.1999	-.2142	.1088	-.1385	(.0416)	.0543
8	.4363	-.2725	.0259	-.0083	.0104	.2741	(.0669)

* Epistatic deviations significant at the 0.05 level of probability.

† Cultivar code number (See Table I).

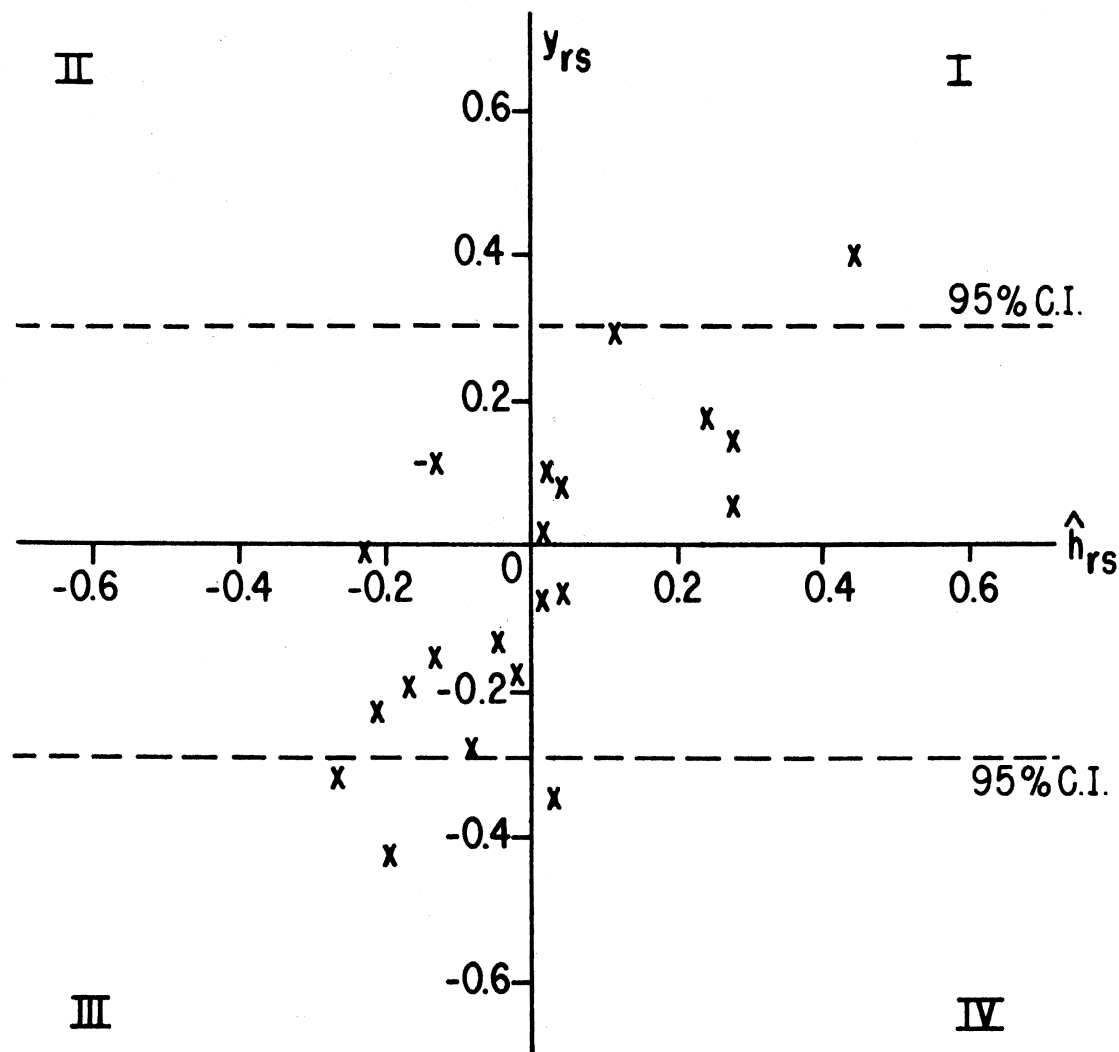


Figure 1. \hat{h}_{rs} Graphed Against y_{rs} for Individual Crosses Averaged Over Replications.

in common even though that parent did not itself show epistasis. Parents one and two exhibited epistasis as did their crosses with parent eight. From Figure 1, it is apparent that three of the four epistatic crosses were of the duplicate form while the other was of the complementary type.

d. No Multiple Alleles. Hayman (19) suggested the analysis of variance of $W_{r1} - 2W_{r2}$ (Table IV) as a simple and quick, but not extremely sensitive, test for multiple alleles. When this test is significant but the chi-square test for epistasis is not, multiple allelism is suspected. Since both tests were significant, conclusions about multiple allelism are not possible based on the $W_{r1} - 2W_{r2}$ analysis.

e-f. Homozygous Parents and Uncorrelated Gene Distributions. According to Hayman (19), when the second-degree statistics do not fit the simple system, any one or a combination of the last five assumptions (i.e., no epistasis, no multiple alleles, homozygosity of parents, uncorrelated gene distributions, and no genotype-environment interactions within locations and years) may have failed. If the chi-square test for epistasis is not significant and the second-degree statistics still fail to fit the simple model, the genes in the parents are probably correlated or the parents are only partly inbred (i.e., there is residual heterozygosity) or both. There is no satisfactory method currently available to separate those two components. However, Hayman has suggested that visual inspection of the scatter of points in the $(V_{r1} - 2V_{r2})$ graph can give one a general idea of the homozygosity of parents. Heterozygosity causes the points to scatter about the regression line of slope 0.5. When a simple correlation

between parents exists, the straight line will assume a curvilinear form. However, in mixed correlations a combination of curves will be present making the graph indistinguishable from one depicting heterozygosity. In a practical sense, this confusion is rare because only a small amount of heterozygosity can remain undetected in the parents. In fact, a large part of the parental heterozygosity originally present in this material was eliminated when parent 6111 was omitted. When epistasis and multiple allelism are both absent, gene correlations can be examined. In the present study, because significant epistasis was found, homozygosity of parents and parental correlation as well as multiple allelism could not be tested.

g. No Genotype-Environment Interactions Within Locations and Years. Because this experiment was conducted in only one year at a single location, this assumption could not be tested. Location and year effects (if any) were confounded in the results of this experiment.

Estimates of Environmental and Genetic Parameters

Hayman (17) stated that even in cases of partial failure of the assumptions (which merely indicate that more complex genetic systems are involved), estimates of population parameters and genetic components can still be made. However, it should be recognized that such estimators are not as reliable as they would have been had all the assumptions been fulfilled. Parameters in this experiment were estimated in each replication separately; then, standard errors of the mean were calculated from the variance of the individual estimates around the overall mean (28).

The parameters estimated can be classified into two categories.

The first group is environmental and includes E_0 , E_1 , and E_2 - the environmental variances for the parental, F_1 , and F_2 generations, respectively. These estimates were obtained within each block from between plot-within plot analyses of variance for the parental, F_1 , and F_2 generations. The within plot (i.e., residual) mean square was divided by the mean number of plants per plot for that generation within that block to place the estimates on an equal basis with the other parameters (i.e., on a plot mean basis). The second group of parameters is genetic and includes D , F , H_1 , and H_2 . D is the component of variance due to additive effects of genes as well as a portion of the additive by additive epistatic variance; F is an indicator of the relative frequency of dominant vs. recessive alleles in the parents; H_1 is the component of variation due to non-additive effects; and H_2 is the component of variation due to non-additive effects corrected for gene distribution. H_1 and H_2 may also be defined as dominance genetic variance parameters which may include the dominance genetic variance proper, dominance by dominance epistatic variance, and additive by dominance as well as the portion of the additive by additive variance not included within D (17). Each parameter was estimated separately for the F_1 and F_2 generations. As Baker and Verhalen (7) have pointed out, the F_1 and F_2 data could have been pooled to obtain combined parameter estimates; but because the F_1 is a non-segregating and the F_2 is a segregating generation, the estimates would probably exhibit considerable differences in each situation. The combined analysis would probably result in biased estimates of genetic variance components which would, in turn, provide biased genetic ratios and consequently contribute to inaccurate decisions by breeders.

As variances, D , H_1 , and H_2 are expected to be positive whereas F may take sign. When dominant alleles are in excess, F is positive; when recessive alleles are in the majority, F is negative. F is not significantly different from zero when no genes show dominance effects or if the dominant and recessive alleles of each gene are distributed equally among the parents. The four genetic parameters were estimated in the F_1 by solving the following equations (17):

$$\begin{aligned} V_{OL0} &= (\text{var } p_r) = \text{Variance of the parents} = D + E_0, \\ W_{OL01} &= (\text{cov } p_s, \bar{f}_s) = \text{Mean of the } W_r \text{'s} = (1/2)D - (1/4)F + E_0/n, \\ V_{1L1} &= (\sum_s \text{var } f_{rs}) = \text{Mean of the } V_r \text{'s} = (1/4)D + (1/4)H_1 - (1/4)F \\ &\quad + [E_0 + (n-1)E_1]/n, \text{ and } V_{OL1} = (\text{var } \bar{f}_s) \\ &= \text{Variance of array means} = (1/4)D + (1/4)H_1 - (1/4)H_2 - (1/4)F \\ &\quad + [E_0 + (n-2)E_1]/n^2. \end{aligned}$$

In the F_2 , the same parameters were estimated by these equations (19):

$$\begin{aligned} V_{OL0} &= (\text{var } p_r) = \text{Variance of the parents} = D + E_0, \\ W_{OL02} &= (\text{cov } p_s, \bar{g}_s) = \text{Mean of the } W_r \text{'s} = (1/2)D - (1/8)F + E_0/n, \\ V_{2L2} &= (\sum_s \text{var } g_{rs}) = \text{Mean of the } V_r \text{'s} = (1/4)D + (1/16)H_1 - (1/8)F \\ &\quad + [E_0 + (n-1)E_2]/n, \text{ and} \\ V_{OL2} &= (\text{var } \bar{g}_s) = \text{Variance of array means} = (1/4)D + (1/16)H_1 \\ &\quad - (1/16)H_2 - (1/8)F + [E_0 + (n-2)E_2]/n^2. \end{aligned}$$

Parental variance (V_{OL0}) and its components (D and E_0) are identical in both generations since they are calculated by the same formula using the same estimates irrespective of the generation of the progeny.

Table VI presents the environmental and genetic variance components for the F_1 and F_2 , and the significance levels on those estimates.

All estimates of environmental variance were significantly different from zero at the 0.01 level of probability. E_1 was larger than E_0 which

TABLE VI
MEAN ESTIMATES OF ENVIRONMENTAL AND GENETIC VARIANCE
COMPONENTS FROM THE PARENTAL F_1 , AND F_2 DATA

Parameter	F_1		F_2	
	Mean	95% Confidence Limits	Mean	95% Confidence Limits
E_0	.0062**	.0056 , .0067	.0062**	.0056 , .0067
E_1	.0084**	.0066 , .0102	--	-- , --
E_2	--	-- , --	.0036**	.0036 , .0036†
D	.2297**	.1839 , .2755	.2297**	.1839 , .2755
F	.0355	(-.0408) , .1117	.1164*	.0430 , .1898
H_1	.1167**	.0761 , .1574	.3703**	.2802 , .4604
H_2	.0828	(-.3751) , .5408	.2804**	.2301 , .3308

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

†The true mean value for E_2 and its confidence limits were .003625, .003622, and .003628, respectively.

was larger than E_2 . D was also significantly different from zero at the 0.01 level of probability. The F was significantly different from zero in the F_2 at the 0.05 level, but not in the F_1 . However, the estimates were positive in both generations. When F is positive, dominant alleles are presumed to have greater frequency in the parents than do recessives for that specific trait. Therefore, it is likely that dominant genes are more frequent in this material than are recessives.

H_1 was significantly different from zero in both generations at the 0.01 level of probability while H_2 showed significant differences only in the F_2 . As expected (17), H_2 was smaller than H_1 in both generations. Among the four genetic parameters in the F_1 , the higher quantity was represented by D indicating that additive variance was relatively more important for storm resistance than was dominance variance in that generation. The storm resistance character is significantly influenced by environmental, additive, and dominance variance components as well as the epistatic component detected earlier in this paper.

Genetic Ratios

To provide additional information about the genetic systems operating for storm resistance calculations of genetic ratios were made using the parameters described in the previous section. The ratios were estimated in each replication separately; and as with the parameters, the mean ratio over replications was then estimated as was its standard error to set confidence limits on each mean. Table VII summarizes the results obtained.

TABLE VII
MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS
OF THE POPULATION

Ratio	F_1		F_2	
	Mean	95% Confidence Limits	Mean	95% Confidence Limits
Dominance	.72**	.53 , .90	.63**	.56 , .71
$(\bar{F} - \bar{P})$	-.01	(-.03) , .02	-.09	(-.22) , .05
$H_2/4H_1$.18**	.16 , .20	.19**	.16 , .22
K_D/K_R	1.30**	.74 , 1.85	1.50**	1.18 , 1.82
K	.01	(-.02) , .05	.47	(-.20) , 1.13
h^2	.69**	.45 , .93	.81**	.70 , .92

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

Dominance. $(H_1/D)^{1/2}$ and $[(1/4 H_1)/D]^{1/2}$ were the ratios used herein to estimate degree of dominance in the F_1 and F_2 , respectively (17). With no dominance, the ratios should equal zero; with partial dominance values should range between zero and one; with complete dominance, the estimates should equal one; and with overdominance the ratios should be greater than one. The ratios estimated in this study were between zero and one for both generations, and both were also significantly different from both zero and one. Therefore, the presence of partial dominance is clearly indicated for gene(s) controlling different degrees of storm resistance.

Another method used to inspect the dominance situation in a set of diallel crosses was accomplished by constructing the (V_r, W_r) graph as suggested by Hayman (17). Parents which contain a greater number of dominant genes controlling the character tested produce offspring with less variation among themselves (i.e., V_r) and with less co-variation (i.e., W_r) than with the more recessive parents for that character. The ratio of $(H_1/D)^{1/2}$ can also be derived from the graph of W_r against V_r . Considering that array points can only lie on that part of the regression inside the parabola $W_r^2 = V_r V_{OL0}$, then $AB/OB = H_1/D$ where A is the Y intercept on the OW axis, and B is the intercept of the OW axis and a tangent to the limiting parabola which is also parallel to the regression line. The graphs are shown for the F_1 (Figure 2) and F_2 (Figure 3) generations showing the limiting parabola and regression line for each with the array points in each of the four replications. In both cases because A is above the origin, i.e., $AB < OB$, the ratio of $AB/OB = H_1/D$ would be positive and less than one. Therefore, the genes are partially dominant which is in agreement

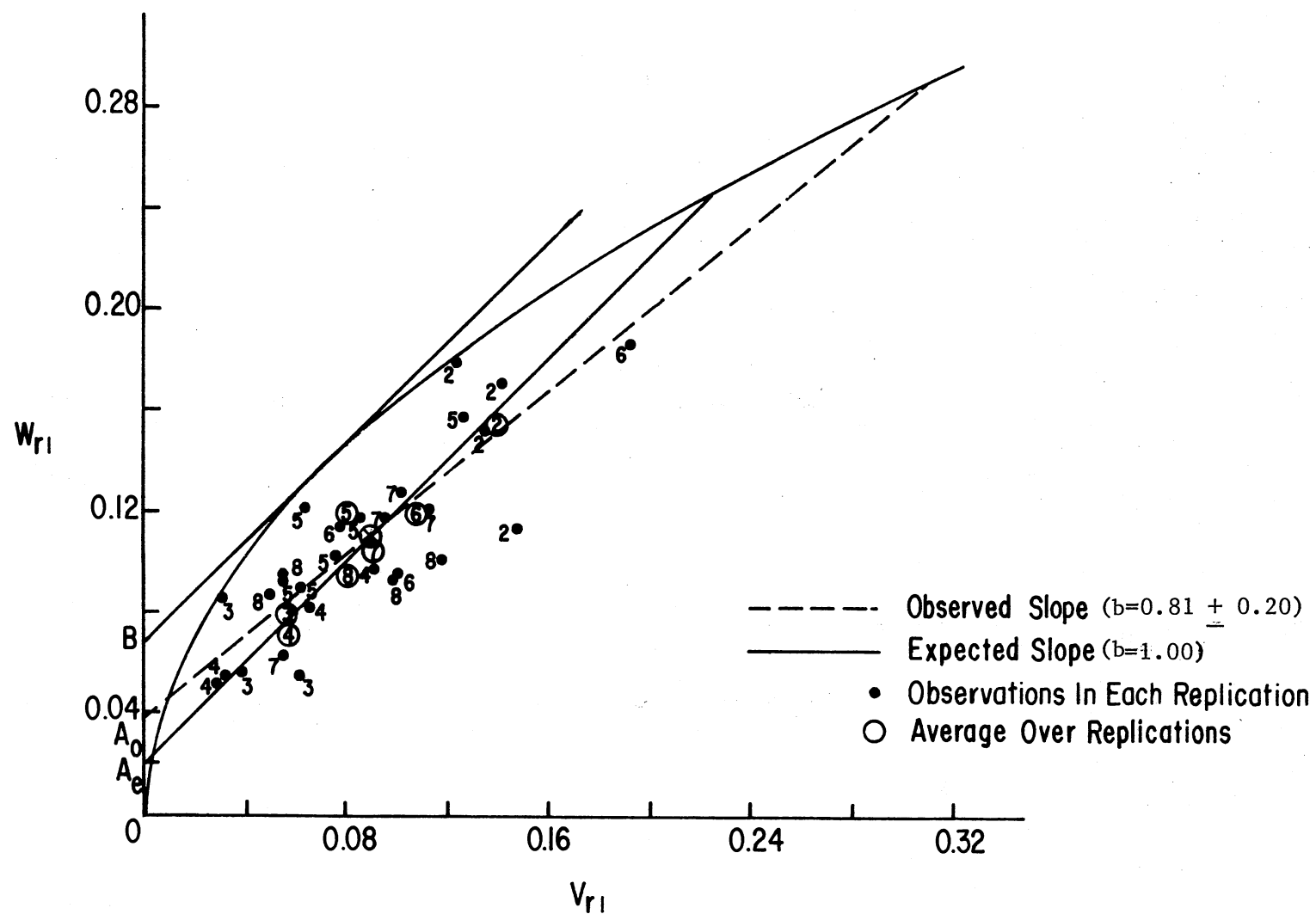


Figure 2. Dominance Relationships Among the Parents in Terms of V_{r1} and W_{r1} .

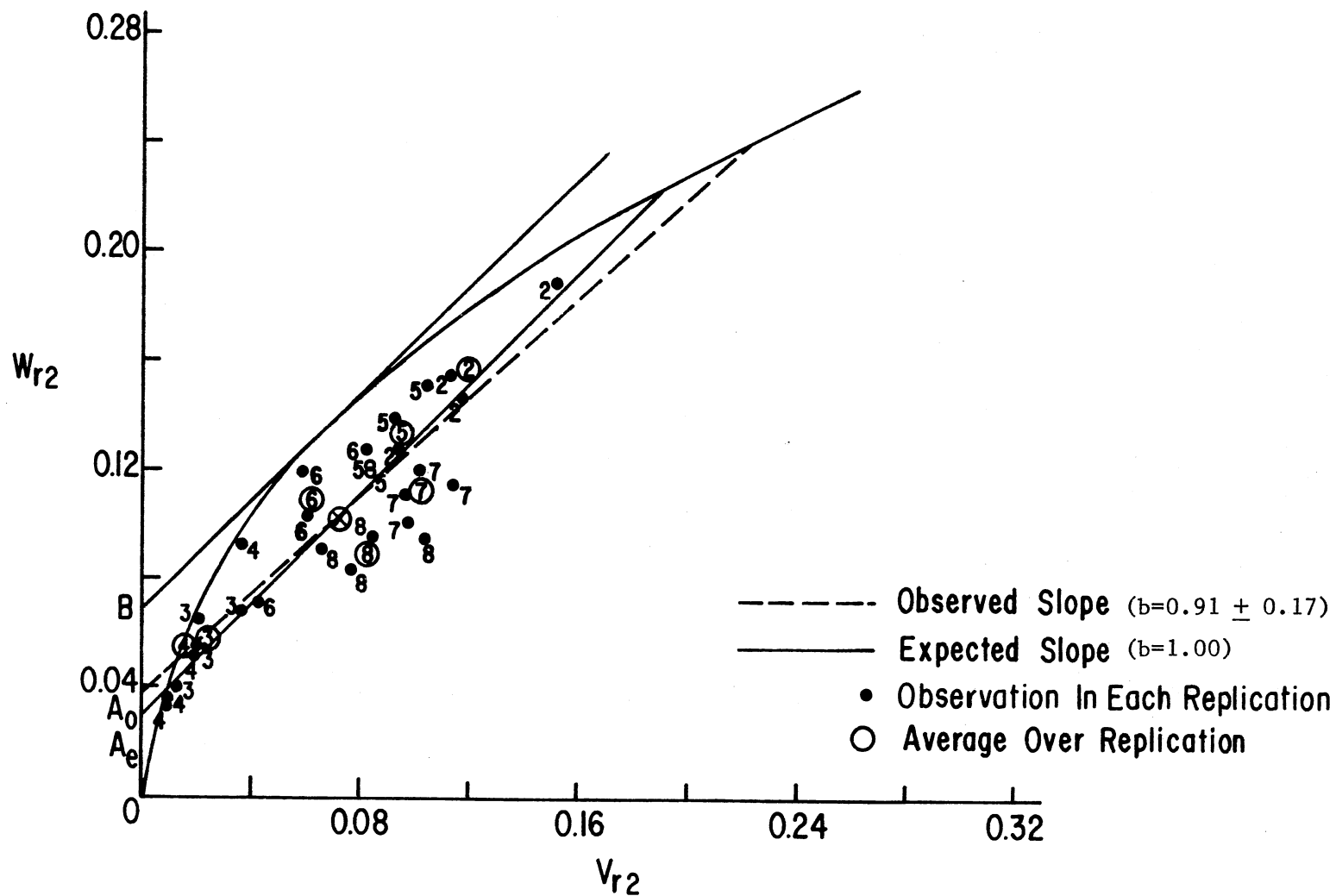


Figure 3. Dominance Relationships Among the Parents in Terms of V_{r2} and W_{r2} .

with the estimates discussed above. Both Figures 2 and 3 indicate that Stoneville 7A and Deltapine 16 contained the greatest number of dominant and least number of recessive genes, while Acala 1517-70 had the least number of dominant and greatest number of recessive genes among cultivars tested. In all parents except Acala 1517-70 the dominant genes were in excess of recessive genes.

Direction of Dominance. The quantities $(\bar{F}_1 - \bar{P})$ and $(\bar{F}_2 - \bar{P})$ can be used to estimate the direction of dominance. This quantity was consistently negative, though not significantly different from zero in either generation providing tentative evidence that the overall dominance for this character was in the negative direction, i.e., toward less storm resistance. However, because the estimates were not significantly different from zero, it may well be that the direction of dominance varies from one type of cross to another.

Distribution of Alleles. Hayman (17) has used $H_2/4H_1 = \bar{u}\bar{v}$ as an estimator of the frequency of positive versus negative alleles in the parents at loci which exhibit dominance. When $u_i = v_i = 0.5$, this quantity will have its maximum value of 0.25; when $u_i \neq v_i$, the quantity will be less than 0.25. Values in both generations were significantly less than 0.25 indicating that $u_i \neq v_i$. Consequently, the parents in this study did not have an equal distribution of positive versus negative alleles for this trait.

Ratio of Dominant to Recessive Genes. The ratio of dominant to recessive alleles in the parents can be estimated by the following formula (17):

$$K_D/K_R = [(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F].$$

The estimated ratio was higher than one for both generations in this

study indicating an excess of dominant genes in the parents. However, only one of the two was significantly higher than one at the 0.05 level. This result is similar to that derived from testing the distribution of alleles above in that a skewed distribution is indicated.

Number of Effective Factors. Mather (27) defined K as the smallest unit of hereditary material recognizable using biometrical genetic methodology and which at its lower limits can be a single gene or a group of closely linked genes exhibiting some degree of dominance. Jinks (20) and Mather (27) have stressed that K will be underestimated unless dominance effects are equal in sign and magnitude and unless the gene distribution is uncorrelated. The following formulas were used to estimate K in the F_1 and F_2 , respectively:

$$K_{F_1} = (\bar{F}_1 - \bar{P})^2 / (1/4 H_2) \text{ and}$$

$$K_{F_2} = (\bar{F}_2 - \bar{P})^2 / (1/16 H_2).$$

In the present study K was not significantly different from zero at the 0.05 probability level in either generation. The parents are phenotypically different for this trait, and breeding experience has demonstrated that selections in segregating populations can be effective. Therefore, at least part of those phenotypic differences are genetic. The unrealistically low estimates of K (i.e., below 1.0) obtained are therefore due either to a faulty formula or to a lack of fulfillment of the assumptions of estimating that quantity.

Heritability. Narrow-sense heritabilities were calculated on a plot mean basis. The formulas used for the F_1 (12) and F_2 (32) data, respectively, were as follows:

$$h^2(F_1) = (1/4 D)/(1/4 D + 1/4 H_1 - 1/4 F + E) \text{ and}$$

$$h^2(F_2) = (1/4 D)/(1/4 D + 1/16 H_1 - 1/8 F + E).$$

The relatively high level of heritability obtained in both generations indicates that about three-fourths of the total phenotypic variance for storm resistance among these parents was due to additive genetic variance. The high level of heritability for this character would lead the breeder to choose those methods which result in the accumulation of desirable genes into one genotype (if, as would seem likely, more than one gene is involved). Therefore, simple mass selection or recurrent selection for general combining ability would both be effective methods.

Between-Set Diallel Analyses

To obtain more information about the genetic relationships among the four sets of cultivars under study (Table I), diallel cross combinations between all possible sets taken two at a time were studied. The six combinations of sets were set I with set II, I with III, I with IV, II with III, II with IV and III with IV. The first three sets included only three cultivars (6111 was eliminated earlier from set I for its excessive heterozygosity) while the last three sets had four cultivars apiece. General and specific tests of the assumptions were not conducted for these smaller diallels. Because one-third of the F_2 data in each small diallel table would have to have been estimated rather than being actual observations, only F_1 data were analyzed in this subsection.

E_0 , E_1 , D , F , H_1 , and H_2 were estimated in each combination by replications and then averaged as was done earlier. Table VIII

TABLE VIII

MEAN ESTIMATES OF ENVIRONMENTAL AND GENETIC VARIANCE COMPONENTS FROM
THE PARENTAL- F_1 DATA AMONG DIFFERENT CLASSES FOR STORM RESISTANCE

Parameter	Between-Set Combinations					
	I X II	I X III	I X IV	II X III	II X IV	III X IV
E_0	.0063**	.0068**	.0063**	.0061**	.0058**	.0061**
E_1	.0080**	.0078**	.0073**	.0082**	.0059**	.0104*
D	.1044*	.3721**	.5535**	.0877*	.1794**	.0381*
F	.0402	-.0048	.0369	-.0067	-.0641	.0103
H_1	.1034	.1200	.0827*	.0967*	.1306**	.0494*
H_2	.0829	.1047	.0822*	.0801*	.1113**	.0468*

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

summarizes the results for those parameters. The estimates of E_0 and E_1 were significantly different from zero at the 0.05 or 0.01 levels of probability in all cases. Also, E_1 was greater than E_0 in every instance. D was larger in these diallels when the parents belonged to sets farther apart in their storm resistance, e.g., the combination of I X IV showed a higher value than did I X III which itself was higher than I X II. D was significantly different from zero in all cases. F was inconsistent; it was positive in three cases and negative in three. However, it was not significantly different from zero in any instance. H_1 and H_2 were not significantly different from zero in the I X II or I X III combinations, but they were significantly different at the 0.05 and higher levels of probability in the other four combinations.

Genetic ratios were also calculated in each replication for the six combinations on a plot mean basis and then averaged. Table IX presents the results of those calculations. The degree of dominance, $(H_1/D)^{1/2}$, was significantly different from zero in all combinations. In general, this quantity decreased with increasing mean distance between sets within a combination. Two combinations i.e., II X III and III X IV, exhibited overdominance while all others were in the partial dominance range. However, confidence limits included unity in all cases except for the combination of I X IV indicating that it is the only combination clearly defined within the partial dominance range. The direction of dominance $(\bar{F}_1 - \bar{P})$ for the first three combinations (which had set I in common) was positive, but negative for the last three. However, the estimated values for this quantity did not differ from zero except for the combination I X IV. The quantity $\bar{u}\bar{v}$ estimated

TABLE IX
MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS AMONG
DIFFERENT CLASSES FOR STORM RESISTANCE

Ratio	Between-Set Combinations					
	I X II		I X III		I X IV	
	Mean	95% C.L.	Mean	95% C.L.	Mean	95% C.L.
Dominance	.93	.22 , 1.64	.55	.01 , 1.08	.38	.16 , .59
$(\bar{F} - \bar{P})$.02	-.11 , .15	.01	-.35 , .37	.25	.15 , .35
$H_2/4H_1$.21	.16 , .26	.23	.20 , .26	.25	.24 , .26
K_D/K_R	1.75	-.04 , 3.55	1.37	.03 , 2.71	1.19	.71 , 1.67
K	1.29	-2.48 , 5.06	2.12	-.04 , 4.28	3.36	2.49 , 4.22
h^2	.57	.17 , .97	.78	.25 , 1.31	.88	.74 , 1.02
Ratio	II X III		II X IV		III X IV	
	Mean	95% C.L.	Mean	95% C.L.	Mean	95% C.L.
	Mean	95% C.L.	Mean	95% C.L.	Mean	95% C.L.
Dominance	1.15	.10 , 2.20	.86	.55 , 1.18	1.34	.71 , 1.96
$(\bar{F} - \bar{P})$	-.14	-.36 , .08	-.06	-.17 , .06	.00	-.26 , .26
$H_2/4H_1$.21	.19 , .22	.21	.20 , .23	.20	.15 , .24
K_D/K_R	1.02	.17 , 1.86	.67	.34 , 1.00	1.22	-.06 , 2.49
K	4.38	-7.77 , 16.52	.23	-.26 , .72	2.17	-2.85 , 7.19
h^2	.44	.02 , .86	.46	.26 , .65	.34	.05 , .62

by $H_2/4H_1$ and used to evaluate the distribution of positive versus negative alleles exhibiting dominance was not significantly different from 0.25 for the three combinations having set I in common indicating that genes were equally distributed in those parents while it was significantly less than 0.25 for the other three combinations indicating that $u_i \neq v_i$ in these parents. The ratio of dominant to recessive genes (K_D/K_R) was greater than one in all cases except for combination II X IV. However, a 95 percent confidence interval included the unity in all cases suggesting that dominant genes were in excess of recessives. K , the number of effective factors, varied considerably for different combinations among sets. Only the combination of I X IV was significantly different from zero at the 0.05 level. As previously stated, factors such as lack of directional dominance, dominance effects differing in magnitude, and correlated gene distributions may have been at least partially responsible for these rather inconclusive results.

Narrow-sense heritability (h^2) was greater for combinations of sets with greater mean differences between sets. This was not an entirely unexpected conclusion because if all other factors remain constant, heritability is positively correlated with additive variance. The relationship between additive variance and mean differences between sets was discussed previously in this subsection. All of the heritability estimates were significantly different from zero at the 0.05 or higher level. The estimates were medium (III X IV) to high (II X III, II X IV, and I X II) to very high (I X III and I X IV) which implies relative ease of selection for storm resistance between progeny derived from each of those types of crosses.

CHAPTER V

SUMMARY AND CONCLUSIONS

Based on preliminary measurements of storm resistance, eight upland cotton (Gossypium hirsutum L.) cultivars were classified into four sets of two apiece as: very open, open, storm resistant, and stormproof boll types and were used to estimate the number of genes controlling differences between various degrees of storm resistance, the types of gene action involved, and their narrow-sense heritabilities. In 1975 the eight parents, 28 F_1 's, 24 F_2 's and 24 Bc's were grown in a replicated randomized complete-block experiment. Two independent rows of each F_2 and a single row of the other entries were planted per replication. A maximum of 30 plants per row were harvested using a hand clipper. Bolls were measured under conditions of relatively constant temperature and humidity. A 500-gram force gauge was used to measure the force required to remove one lock from the bur. One boll per plant was measured, and one reading from each of two opposite locks in that boll were taken and recorded.

Unusually large variation within the cultivar 6111 was attributed to lack of homogeneity and homozygosity for storm resistance; therefore, 6111 and its crosses were eliminated. The remaining data were transformed to a logarithmic basis to obtain a better fit of the data to the diallel assumptions. Analyses of variance were highly significant among parents, F_1 's and F_2 's indicating significant

differences among the entries. A 7 X 7 diallel table was analyzed for each replication; then, the results were averaged over replications.

Six general tests were used to test the diallel assumptions as a whole for both the F_1 and F_2 generations. One test failed in the F_2 , but not the F_1 . Two others also failed. In specific tests of the assumptions, significant epistasis was detected; and because epistasis was present, tests for multiple allelism, homozygosity of parents, and uncorrelated gene distributions could not be conducted. Because this experiment was conducted in one year at a single location, the assumption of no genotype-environment interaction could not be tested either. The assumptions of diploid segregation and no reciprocal differences were assumed fulfilled based on previous studies.

All environmental variances (i.e., E_0 , E_1 , and E_2) exhibited highly significant differences from zero; E_1 was the largest of the three; E_2 , the smallest; and E_0 intermediate. D displayed a highly significant difference from zero. F was significantly different from zero in the F_2 , but not in the F_1 . H_1 was larger than H_2 and significantly different from zero in both the F_1 and F_2 while H_2 was significant only in the F_2 .

Degree of dominance was between zero and one and was significantly different from both zero and one in the F_1 and F_2 indicating partial dominance. The direction of dominance was toward less storm resistance although the estimated value was not significantly different from zero. The average frequency of negative versus positive alleles in parents was unequal and apparently skewed toward dominant alleles. The number

of effective factors estimated for this character was less than one and not significantly different from zero in either F_1 or F_2 . Heritability was relatively high showing that about three-fourths of the total phenotypic variation for storm resistance is due to additive genetic variance. This observation suggests that mass selection and possibly recurrent selection for general combining ability are efficient breeding methods for producing more storm resistant and stormproof types of cultivars.

Diallel analyses were conducted for between-set combinations taken two at a time to obtain more information about the genetic relationship among the sets. E_1 was larger than E_0 in all cases and both were significantly different from zero. Investigation of D showed that it was generally larger when the cultivars combined belonged to sets with means farther apart, and it was significantly different from zero in every case. F showed neither consistent results, nor significant differences from zero.

Degree of dominance was significantly different from zero in every combination; and except for II X III and III X IV which exhibited overdominance, the combinations were within the partial dominance range. The direction of dominance was positive for the three combinations which included set I while it was negative for the others. However, except for I X IV, those estimates were not significantly different from zero. The $\bar{u}\bar{v}$ values for the first three combinations indicated that positive and negative alleles were equally distributed among the parents while the other three did not. Dominant genes were in excess of recessive ones in all combinations except II X IV. Effective factor number varied inconsistently; and only

in one case did it differ significantly from zero. Narrow-sense heritability estimates were higher for combinations of sets with means farther apart, and all were significantly different from zero. The estimates were from 0.34 to 0.88 implying the relative ease of selection for storm resistance between progeny derived from each of these types of crosses.

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VITA 2

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