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Stormproof Boll in Upland Cotton. I. Development of Instrumentation and an Inheritance Study¹

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ABSTRACT

The stormproof boll is a desirable trait for cultivars of cotton (*Gossypium hirsutum* L.) grown for once-over stripper-type harvest. The purpose of this study was to develop instrumentation to measure stormproofness (lock tenacity) and to determine the inheritance of the stormproof boll in a particular cross using this instrumentation. Parental, F_1 , F_2 , and backcross populations from a cross between 'Acala 1517 Br-2' (non-stormproof) and Z-2557 (stormproof) were scored for visual appearance and by measurement of lock tenacity to study qualitative inheritance patterns. Analysis of variance and joint scaling tests were conducted on the lock tenacity data for quantitative determinations of inheritance.

The instrumentation developed was capable of detecting differences between stormproof and non-stormproof boll types. Differences between combinations (pulls per boll \times number of bolls per entry) were not significant, while differences between entries were significant. Visual classification of segregating populations indicated that a single dominant gene controlled the stormproof character. However, data from lock tenacity determinations made on these same populations indicated a more complex mode of inheritance. Estimates from the joint scaling test suggested that additive, dominant, and epistatic genetic effects controlled the expression of lock tenacity.

Additional index words: Lock tenacity, Storm loss, *Gossypium hirsutum* L., Mechanical harvest, Qualitative inheritance, Quantitative inheritance.

STORMPROOF cultivars of cotton (*Gossypium hirsutum* L.) have been accepted by producers in the high and rolling plains of Texas, New Mexico, and Oklahoma as a deterrent to losses caused by unfavorable weather conditions. In this region, where once-over stripper-type harvesters are used, cotton must remain in the field exposed to the weather until 90 to 95% of the crop is mature. The cotton crop is often subjected to violent weather in the form of high wind, rain, and, occasionally, ice and snow before the crop can be harvested. The term "stormproof" is applied to cotton cultivars in which the seedcotton remains in the boll (bur) during adverse weather that would scatter the seedcotton of conventional openboll cultivars over the ground.

The purposes of this study were (i) to develop equipment capable of detecting and measuring quantitative differences in stormproofness and (ii) to de-

termine the inheritance of the stormproof boll in a particular cross using this equipment.

LITERATURE REVIEW

Cook and Hubbard (1926) reported the discovery of a wild cotton in Mexico with stormproof boll characteristics. They described this stock as having

... numerous long fibers attached to the carpel walls sometimes over most of the surface In *Gossypium contextum* the inner surface of the mature carpels is very finely and closely wrinkled and the ends of some of the fibers apparently are caught and held in these wrinkles. In other cases, the fibers are held by what may prove to be hardened exudation . . .

However, stormproof cotton as it is known today began with the discovery of a plant with an unusual genetic boll type in a field of 'Half and Half' cotton. After several years of selection, the stormproof trait exhibited by this plant was fixed in a pure breeding strain and released as the cultivar 'Macha' (Brown and Ware, 1958).

Friesen (1968) developed equipment to measure the force needed to remove seedcotton from an open, dry boll. Young (1975) used a force meter with a maximum hold attachment to measure the maximum force required to remove a locule (lock) of seedcotton from the bur. He termed this force a measurement of "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."

Smith et al. (1946) studied characteristics of the cotton plant as they related to mechanical harvesting. They reported that the greatest field losses were associated with cultivars with flared carpels. Low (1962) reported that the degree of storm resistance of breeding material could be varied by changing the degree of boll opening, the twisting of the carpels, and the lint adherence to the carpel wall. Friesen (1968) considered the following characteristics important in determining relative stormproofness: (i) convolutions formed in the inner carpel wall during dehiscence; (ii) fibers pinched in the very base of the bur; (iii) microorganism infection attacking the cotton fiber and carpel wall; (iv) friction between the fiber and carpel wall as the lock is removed; (v) protrusions near the suture cell structure over which the fibers are pulled during removal; (vi) a mucous-type substance left on the fiber during its formation which causes the fibers to adhere to the carpel wall.

Lynn (1949) concluded that a single gene with complete dominance conditioned inheritance of the stormproof character. Jones and Ray (1953) adapted a direct reading scale to make pull determinations of the cotton boll. They estimated that a single gene controlled the expression of the stormproof boll but that the environment affected its expression. Hintz (1953) reported that several intermediate stormproof boll types occurred in the F_2 and F_3 generations of crosses between stormproof and non-stormproof cultivars and he concluded that either a large number of genes controlled the stormproof boll trait or environmental effects were great. Mamaghani (1976) reported that the storm resistance boll trait was inherited quantitatively. His narrow-sense heritability estimates ranged from 0.34 to 0.88 for different parental combinations, indicating the relative ease of selection for the trait.

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Table 1. Analysis of variance of selected combinations of pulls per boll and bolls per entry with 10 entries.

Source	df	Mean squares
Combinations (C)	19	1,103
Pulls per boll (P)	3	180
No. of bolls (N)	4	4,864
P × N	12	80
Reps (R)	2	43,646**
C × R	38	1,184**
P × R	6	215
N × R	8	5,193
P × N × R	24	90
Entries (E)	9	1,493,254**
C × E	171	481
P × E	27	415
N × E	36	1,642
P × E × N	108	110
R × E	18	33,870
C × R × E	342	702
P × R × E	54	402
N × R × E	72	2,680
P × N × R × E	216	118

** Significant at the 0.01 level of probability.

MATERIALS AND METHODS

To measure lock tenacity or the grams of force required to remove a lock of seedcotton from the bur of a fully open boll, an instrument was constructed that combined a force meter with a maximum hold attachment (Young, 1975) and a modified force measurement instrument (Friesen, 1968) (Fig. 1). The force meter was mounted on an adjustable platform to enable the operator to adjust the height of the meter to make a straight pull. This hybrid instrument is called a "Lock tenacity instrument." The boll peduncle was attached to the instrument by an alligator battery clip that was permanently attached to a double

Table 2. Lock tenacity means and standard errors averaged over 10 entries for selected combinations of pulls per boll and number of bolls per entry.

No. of bolls	Number of pulls per boll			
	1	2	3	4
	Mean	Mean	Mean	Mean
	g			
5	281.4 ± 43.8	281.0 ± 44.5	280.5 ± 42.4	278.5 ± 41.1
10	263.3 ± 31.7	268.6 ± 27.4	264.5 ± 25.1	268.2 ± 26.0
15	266.2 ± 26.2	269.6 ± 23.1	270.5 ± 21.4	267.6 ± 20.6
20	263.1 ± 22.2	266.5 ± 20.7	266.0 ± 18.3	265.3 ± 18.5
25	266.2 ± 19.0	267.4 ± 17.4	265.1 ± 18.9	264.2 ± 19.1

acting cylinder. Compressed air was regulated to 1.4 kg/cm² to prevent a sudden jerk of the cylinder ram and oil flow was restricted to control its rate of travel. The seedcotton was attached to the meter by a small battery clip and a 15-cm length of string. The battery clip was fastened to the seedcotton as deeply as possible without catching it on the carpal wall.

Ten entries that varied in stormproofness were used to evaluate this instrument. On 15 May 1972, these entries were planted in 1 × 10-m single-row plots in a randomized complete-block design with three replications. After frost, one boll per plant, with at least 2 cm of the peduncle attached, was harvested from 25 plants per entry per replication. These bolls were placed in the laboratory and allowed to dry. After all bolls were about common moisture, four lock tenacity readings were made from each harvested boll. Analysis of variance procedures were used to evaluate the data. Individual analysis of variance was conducted for several combinations of number of pull per boll and number of bolls per row. Means averaged over the 10 entries and standard errors estimated from the square root of error mean square divided by number of replications were

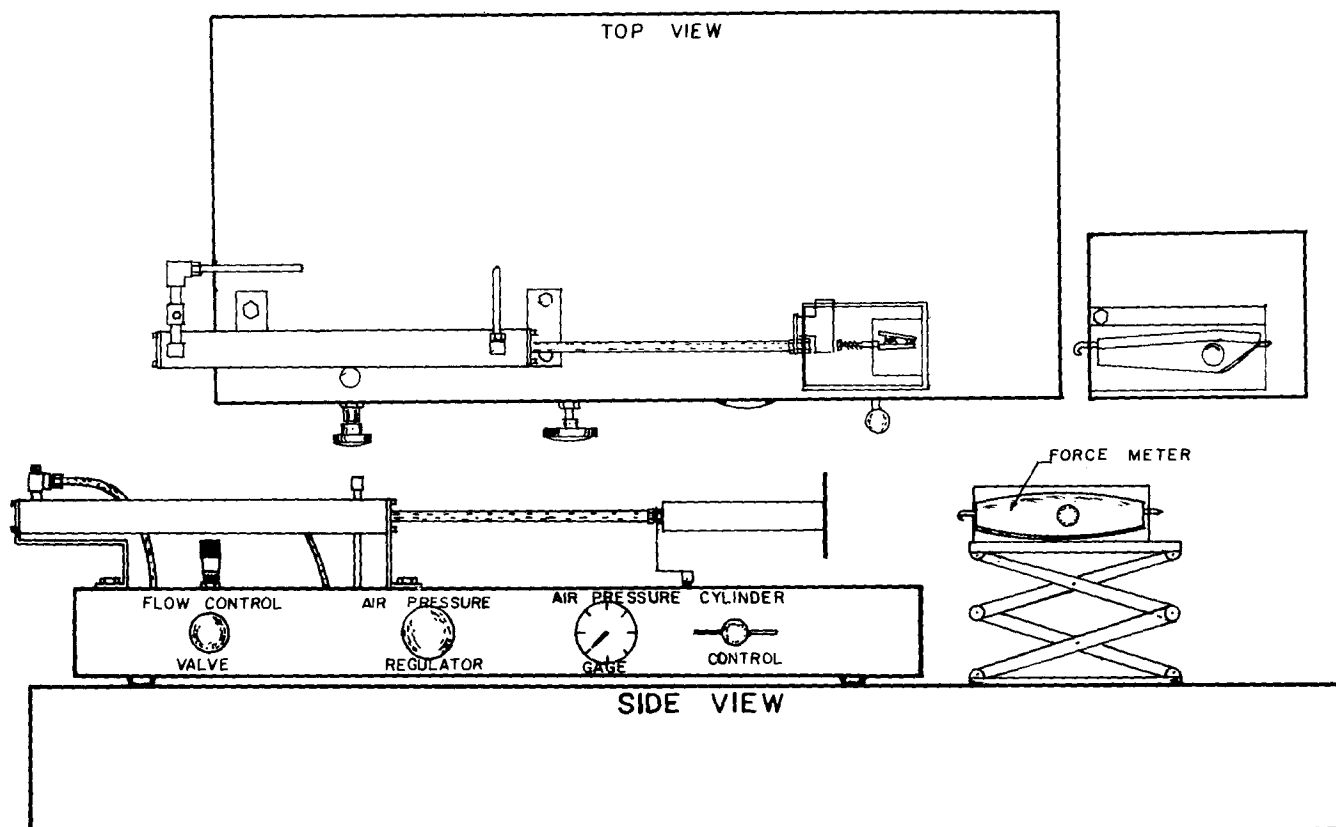
**Fig. 1. Instrument used to measure lock tenacity.**

Table 3. Chi-square tests for a single gene segregation of the stormproof boll.

Population	Appearance					Lock tenacity									
	1974					1974					1975				
	SP†	INT‡	NSP§	χ^2	P	SP	INT	NSP	χ^2	P	SP	INT	NSP	χ^2	P
Acala 1517															
Br-2 (A)	0	0	46	-		0	0	46	-		0	0	25	-	
X-2557 (Z)	33	0	0	-		33	0	0	-		25	0	0	-	
(A × Z) F ₁	3	40	0	-		25	18	0	-		17	8	0	-	
(A × Z) F ₂	100	-	27	0.95	0.3-0.5	83	-	44	6.31	<0.01	251	-	49	12.01	<0.01
(A × Z) F ₃	59	41	27	32.08	<0.01	45	38	44	20.50	<0.01	121	130	49	39.89	<0.01
[(A × Z) × Z] B ₁	1	12	15	0.14	0.7-0.8	1	5	22	9.14	<0.01	6	41	53	0.36	0.5-0.7
[(Z × A) × Z] B ₂	32	0	0	32.00	<0.01	31	1	0	29.12	<0.01	97	3	0	88.36	<0.01

† Stormproof category.

‡ Intermediate.

§ Non-stormproof category.

Table 4. Analysis of lock tenacity over the 2 years and six populations (observed and log-transformed data).

Source	df	Mean squares	
		Observed	Log-transformed
Year (Y)	1	17,330**	0.414*
Rep/year (R/Y)	2	7	0.007
Populations (P)	5	42,724**	1.406**
P × Y	5	1,174*	0.004
Residual	10	241	0.007

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

used to determine which combination of the number of pulls per boll and number of bolls per row was used in future tests.

The relationship between storm loss (the amount of seed-cotton that falls on the ground prior to harvest) and lock tenacity measurements was tested on 80 random progeny rows from a composite cross population that had both stormproof and non-stormproof parents (Quisenberry, 1975). These rows were grown in 1 × 10-m plots with two replications. Prior to harvest, the seedcotton from a strip 1 m wide (50 cm on each side of the drill row) × 3 m long was picked up from the ground, air-dried, and run through a bur extractor to remove excess dirt and trash. The percentage of storm loss based on total seed-cotton yield was calculated for comparison with lock tenacity values taken from the same plots. Means from the 80 entries were used in regression analysis to evaluate the relationship.

'Acala 1517 Br-2' and Z-2557 were used to study the inheritance of the stormproof boll. Acala 1517 Br-2 has a large non-stormproof boll and had been inbred for three generations. Z-2557 is a doubled haploid strain with a stormproof boll discovered in a segregating population involving Macha germplasm (Kohel et al., 1974). Crosses between these two lines were made to generate F₁, F₂, and both backcross populations.

In 1974 and 1975, Acala 1517 Br-2, Z-2557, and their F₁, F₂, and backcrosses were planted in 1 × 10-m plots with 40 to 60 plants/plot. A preplant and one summer irrigation were applied, and normal tillage and cultural practices were followed. In 1974, each plant from each population was scored by visual observation as being either stormproof, intermediate, or non-stormproof. Following these phenotypic evaluations, three bolls per plant were harvested for lock tenacity determinations. Parental minima and maxima were used to establish the class frequencies for the lock tenacity determinations. These data were tested by chi-square for goodness-of-fit to 1:2:1, 3:1, and 1:1 ratios.

Analyses of variance were conducted on the 1974 and 1975 lock tenacity values and a joint scaling test was used to determine if an additive-dominance model adequately evaluated the variation present (Mather and Jinks, 1971). The joint scaling test consisted of estimating the parameters m , (d) , and (h) from generation means. The parameter m was the estimated mid-point between the parental means, (d) was the fixable or additive portion of the genetic variation, and (h) reflected the dominance properties of the genes and represented the contribution to the nonfixable heritable variation. The observed generation means were compared with expected values derived from estimates of the three parameters. The parameters were estimated by weighted least squares and the comparisons between

observed and expected generation means were made by assuming that the sums of squares minimized in the fitting process had a chi-square distribution.

RESULTS AND DISCUSSION

The differences among the tested combinations of pulls per boll and bolls per entry were nonsignificant (Table 1). Number of pulls per boll and the number of bolls per entry and their interactions were also nonsignificant, but entries were significant. The analysis of variance indicated that any of the tested combinations of pulls per boll and bolls per entry gave reliable estimates of stormproofness. Means and standard errors for each combination of pulls per boll and bolls per entry are shown in Table 2. One pull from each of 25 bolls was chosen because the combination had a standard error among the lowest, and required fewer pulls than the other combinations with low standard errors. This choice was arbitrary and several other combinations could have been chosen.

Bolls from 80 randomly selected progeny rows from a composite population were used to test the relationship between the percentage storm loss (Y) and lock tenacity (X) measurements. The following cubic equation was shown to best fit this relationship:

$$\hat{Y} = 63.95 - 0.93 \times X + 4.61 \times 10^{-3} X^2 - 7.24 \times 10^{-6} X^3.$$

The standard errors for the regression coefficient were 6.33, 0.14, 8.77×10^{-4} , 1.66×10^{-6} . The R² was 0.7033 and was highly significant for 78 degrees of freedom. The relationship showed that as the lock tenacity values increased the amount of storm loss decreased until a threshold in lock tenacity was reached. After this threshold value, additional lock tenacity did not reduce the amount of storm loss.

Qualitative inheritance was evaluated by both visual appearance and lock tenacity values. The appearance classification was made only in 1974. Segregation of the F₂ population did not fit a 1:2:1 ratio, but did fit a 3:1 ratio of stormproof to non-stormproof boll types when the stormproof and intermediate classes were combined (Table 3). The backcross [(Acala × Z-2557) × Acala] fit a 1:1 ratio. Data from the visual classification suggested that the stormproof boll trait was inherited as a single gene with partial dominance of the stormproof character.

Lock tenacity measurements of the F₂ populations did not fit a 1:2:1 or a 3:1 ratio in either 1974 or

Table 5. Lock tenacity generation means with their standard errors and results of the joint scaling test for the adequacy of the additive-dominance model.

Generation	1974		1975	
	Observed mean	Log mean	Observed mean	Log mean
	g	log g	g	log g
(A)	83.8 ± 4.6	4.36 ± 0.06	59.2 ± 4.2	4.02 ± 0.08
[(A × Z) A] B ₁	125.9 ± 10.1	4.76 ± 0.07	105.2 ± 3.4	4.60 ± 0.03
(A × Z) F ₁	240.0 ± 7.6	5.46 ± 0.03	185.7 ± 5.8	5.20 ± 0.03
(A × Z) F ₂	201.9 ± 8.2	5.19 ± 0.05	159.6 ± 3.3	5.01 ± 0.02
[(Z × A) Z] B ₁	331.3 ± 13.7	5.78 ± 0.04	263.6 ± 7.3	5.54 ± 0.03
(Z)	397.0 ± 15.2	5.96 ± 0.01	283.3 ± 17.9	5.61 ± 0.06
m	261.3 ± 7.5	5.12 ± 0.03	171.9 ± 5.4	4.84 ± 0.03
(d)	178.7 ± 7.6	0.84 ± 0.03	121.3 ± 5.2	0.87 ± 0.03
(h)	-59.7 ± 11.9	0.30 ± 0.05	-1.8 ± 8.7	0.42 ± 0.05
χ ² (3 df)	49.97	12.61	44.89	15.20
P	<0.001	0.01-0.001	<0.001	<0.001

1975 (Table 3). The backcross of [(Acala × Z-2557) × Acala] fit a 1:1 ratio in 1975, but not in 1974. The lock tenacity data suggested that inheritance was not accounted for by segregation of a single gene pair. The number of plants in the non-stormproof (Acala) class, however, suggests that very few genes are involved. The lock tenacity values approximated a normal distribution in the F₂ generation; however, a log conversion of the observed data improved the normality of that distribution. This lack of fit to the expected single gene ratios plus the normal distributions in the F₂ suggested that stormproofness probably was inherited in a quantitative manner.

Analyses of variance of lock tenacity over the 2 years for the observed data and log transformations are shown in Table 4. For the observed data, the years source of variation was significant, indicating that strains differed in their level of stormproofness from year to year. An interaction effect of population × years was significant also. However, analysis of the log transformation of lock tenacity revealed that population × years was not statistically significant.

The chi-square values from the joint scaling test showed that the data did not fit an additive-dominance model whether or not the data were transformed (Table 5). Estimates of *m*, (*d*), and (*h*) were biased by effects other than additive or dominance genetic effects. The estimates of *m*, (*d*), and (*h*) were significantly different from zero for all estimates except the observed (*h*) in 1975. Therefore, with our instrumentation epistatic genetic effects were shown to be a factor in the inheritance of lock tenacity. Additional transformations did not provide an adequate fit to the additive-dominance model.

Two theories have been advanced on the inheritance of the stormproof boll. Lynn (1949) and Jones and Ray (1953) presented data based on visual scoring that suggest the stormproof boll trait was inherited through a single dominant or partially dominant gene. Conversely, Hintz (1953), Mamaghani (1976), and Dilbeck (1977) reported data indicating that the inheritance of the stormproof boll was controlled by

many genes acting primarily additively. In the present study we attempted to reconcile the two theories. We obtained data consistent with those expected for a simply inherited trait when we examined bolls visually as Lynn (1949) suggested. On the other hand, lock tenacity data seemed to fit a quantitative model. Presence of a single major gene is clearly indicated, but other possible components of the genetic system governing stormproofness have not been identified.

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