Heritability of Leaf Characteristics in Upland Cotton¹

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ABSTRACT

Plants of early maturing cottons (Gossypium hirsutum L.) developed for short growing seasons generally are smaller than those plants of cultivars developed for longer growing seasons. Reduced plant size may be accompanied by altered leaf size and/ or number. Information on leaf characteristics that can be genetically altered may indicate ways to enhance cotton productivity in short season environments. Two experiments were used to study leaf characteristics in cotton grown on the southern Great Plains. In a greenhouse experiment, three pairs of ancestral and descendant cultivars were compared for leaf traits. The descendant cultivars from two of the three pairs had significantly (P < 0.01) smaller and fewer leaves per plant. In a second experiment conducted in the field, random inbred lines from a composite cross population were used to study the heritability of leaf size, leaves per plant, and leaf area per plant. Of the three traits studied, only leaf size displayed a significant level of genetic variability. Heritability estimates on a family mean basis for leaf size, calculated from variance components, progeny-parent regression, and standard units were 67, 48, and 57%, respectively.

Additional index words: Gossypium hirsutum L., Morphological traits, Leaf area, Leaf number, Leaf size, Heritability, Variance components.

SHORT-SEASON environments, typified by the southern Great Plains, provide a challenge to the plant breeder to develop better adapted, high yielding cotton (Gossypium hirsutum L.) cultivars. Early crop maturity is a prerequisite for cultivars grown in such environments because it enables a marketable crop to be produced prior to frost. Early maturing cultivars usually result in smaller plants compared with late maturing cultivars. Niles (5, 6) observed that "short-season" strains flowered earlier, had more rapid flowering rates, and exhibited earlier boll maturity when compared with standard cultivars. Even though "short-season" strains possessed fewer fruiting sites and produced less lint yield per plant, lint yield per unit land area was maintained by increased plant populations (6, 9).

In the development of the cultivars currently grown on the southern Great Plains, breeders selected plants that produced and matured cotton lint in a relatively short growing season. Besides the obvious adaptation of earlier crop maturity, it is not known whether the long-term selection process also modified other traits. Knowing how other traits are changed indirectly through plant breeding may be useful in the development of cotton germplasm better adapted to specific environments. Our objectives were to compare ancestral and descendant cultivars for leaf characteristics and to determine the heritability of these leaf

characteristics.

¹Cooperative investigation among Texas Tech Univ., The Texas Agric. Exp. Stn., and USDA-ARS. Published as Paper no. T-4-182. Received 18 Apr. 1984.

MATERIALS AND METHODS

Two experiments were conducted at Lubbock, TX. Experiment 1 included the ancestral cotton cultivars, 'Lone Star', 'Half and Half', and 'Kekchi', and their respective descendant cultivars, 'Lockett 4789', 'Gregg 35', and 'Paymaster 54B' (8). Lockett 4789, a 1962 release, descended from both Lone Star and Half and Half. Gregg 35, a 1956 release, was derived from a series of selections tracing to 'Macha', which in turn, resulted as a selection from Half and Half which expressed the stormproof boll trait. Paymaster 54B, a 1953 release, was the last of a series of selections from Kekchi. Characteristics measured on each plant at 70 days after planting (DAP) were: (i) leaf area per plant (dm²); (ii) number of leaves per plant; and (iii) average leaf size (cm²). Plants of ancestral and descendant cultivars were grown in 19-L pots in a greenhouse during December to February. Each cultivar was represented by six plants, with one plant per pot, giving a total of 36 pots. Pots were arranged in a completely randomized design.

Experiment 2 included germplasm from six experimental stocks. The six stocks were: Ysleta Compact; DSR 6-19; CA 491; CA 814; 'Paymaster 266'; and 'Paymaster Dwarf' (7). Ysleta Compact is a derivative from 'Acala 1517'. DSR 6-19 represents a selection from a hybrid population between 'Acala 5675' and 'Lankart Sel. 57'. CA 491 was derived as a selection from a hybrid population between CB 3051 (a Yugoslavian source) and 'Stormrider'. CA 814 is a selection displaying G. hirsutum morphology but resulted from an interspecific hybridization between G. hirsutum and G. barbadense L. Paymaster 266 is the result of a complex series of hybridizations among Macha, 'Paymaster 54', and an African upland possessing the b_4 allele for bacterial blight resistance. Paymaster Dwarf represents a selection from a hybrid population between 'Paymaster 105' and the Afri-

can upland possessing the b_4 allele.

These six stocks were crossed in a diallel set of crosses, including reciprocals. F₁ plants from all 30 crosses were self-pollinated, bulk harvested, and equal numbers of F2 seed from each cross were composited. The population was handled in bulk during subsequent segregating generations. Lines were generated by harvesting random F₆ plants in 1979. Seed from each F₆ plant were used to plant an F₇ progeny row in 1980. Plants in these F₇ progeny rows were self-pollinated to provide adequate F₈ seed for a replicated test in 1981. F₈ progeny rows, tracing to individual F₆ plants, were self-pollinated in 1981 to provide adequate seed for a replicated test in 1982.

Planting dates were 20 May 1981 and 2 June 1982. Plots consisted of single rows for each line, 6.7 m long with 102 cm between rows. Plots were purposely overseeded and later thinned to 10 cm between plants within a row. Soil type was a Pullman clay loam (fine, mixed, thermic Torrertic Paleustoll). Treflan (a, a, a-Trifluoro-2, 6-dinitro-N, N-dipropyl- p-toluidine), a trifluralin herbicide, was applied preplant at 0.5 kg/ha in both years. In 1981, fertilizer (8-16-0) was applied at the rate of 336 kg/ha. No fertilizer was applied in 1982 based on recommendations from standard soil tests.

Two water regimes, irrigated and nonirrigated, were provided each year. In 1981, all plots received 15 cm of water applied by furrow irrigation prior to planting and 30.5 cm of rainfall during the cropping season. Irrigated

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Pair	Cultivar†	Trait		
		Leaves per plant	Leaf size	
		no.	cm²	
1	Lockett 4789	75 a**	29.1 a	
	Lone Star	89 a	29.7 a	
2	Gregg 35	76 b	18.3 b	
	Half and Half	131 a	25.1 a	
3	Paymaster 54B	77 b	18.8 b	
	Kekchi	103 a	25.3 a	
Mean	Descendant	76 b	22.1 b	
	Ancestral	108 a	26.7 a	

^{**} Means for a cultivar pair followed by different letters are significantly different at the 0.01 probability level based on orthogonal comparisons.

† For a pair, upper cultivar is descendant.

plots also received 15 cm of water at 42 days after planting (DAP). In 1982, preplant irrigation water was not applied prior to planting due to high rainfall. All plots received 37.4 cm of rainfall during the growing season and irrigated plots received 1.3 cm, 7.6 cm, and 5.1 cm, at 50, 64, and 85 DAP, respectively, by sprinkler irrigation.

Data were collected at 88 DAP. Characteristics measured as the per plant mean of five random plants per plot were: (i) leaf area per plant (dm²); (ii) leaves per plant; and (iii) average leaf size per leaf (cm²).

The experimental design for Exp. 2 was randomized complete block with two replications of each line in each of two water regimes in each of the two years. Data were analyzed by analyses of variance techniques. Heritability estimates were made on a family mean basis using variance components from an analysis of variance (4), progeny-parent regression (3), and correlation (standard unit method) (2). Standard errors were calculated for variance components as described by Crump (1), and for heritability estimates as described by Hallauer and Miranda (3).

RESULTS AND DISCUSSION

Experiment 1. In the comparison of ancestral and descendant cultivars, significant differences in leaf characteristics occurred between cultivars of two pairs (Gregg 35 and Half and Half, Paymaster 54B and Kekchi) (Table 1). For these pairs, the ancestral cultivars exceeded their respective descendant cultivars for the number of leaves produced. Of the third pair, Lockett 4789 produced 16% fewer leaves than did Lone Star, but this difference was not significant. Since Lockett 4789 also descends from Half and Half, comparison of these two cultivars shows that Lockett 4789 produced 43% fewer leaves than did Half and Half. The comparison is consistent with other pairs shown. Overall, descendant cultivars produced 30% fewer leaves than did the ancestral cultivars.

In two of the three pairs (Gregg 35 and Half and Half, Paymaster 54B and Kekchi), the descendant cultivar had significantly smaller leaves than did the ancestral cultivars. As with leaf number, Lockett 4789 and Lone Star were not significantly different for leaf size. Overall, leaf size of the descendant cultivars was 17% smaller than those of the ancestral cultivars. These data suggest that as new cultivars were developed for improved lint yield and climatic adaptation in the southern Great Plains, plant breeders selected indirectly for reduced leafiness and smaller leaves.

Table 2. Analyses of variance for leaf traits for random lines grown in 1981 and 1982 at Lubbock, TX.

	Mean squares			
Source	df	Plant leaf area (× 104)	Leaves per plant	Leaf size
Years (Y)	1	10 663	27 128	3 034
Water Regimes (W)/Y	2	1 570**	6 696**	355
Replications (R)/W/Y	4	30	121	92
Lines (L)	39	169	485	288**
$\mathbf{L} \times \mathbf{Y}$	39	122	502*	93
$L \times W/Y$	78	81	280	77
$L \times R/W/Y$	156†	76	270	76

^{*,**} Significant at the 0.05 and 0.01 probability levels, respectively.
† Due to missing plots, df values for traits are shown in parentheses: leaf number (131), leaf size (131).

Table 3. Trait means of 40 random cotton lines grown at Lubbock, TX for water regimes within each of 2 years.

Year		Trait			
	Water regime	Leaf area per plant	Leaves per plant	Leaf size	
		dm²	no.	cm²	
1981	Optimal Suboptimal	28.4 a* 20.9 b	68.7 a 56.1 a	40.4 a 36.9 a	
1982	Optimal Suboptimal	15.4 a 10.8 b	50.7 a 35.2 b	33.7 a 30.7 a	

^{*} Means for a trait within a year followed by different letters are different at the 0.05 probability level.

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Experiment 2. From analyses of variance of leaf traits, only leaf size was significantly different among lines (Table 2). There were no significant interactions between lines and years or water regimes for leaf size. Neither years nor water regimes influenced leaf size, but the number of leaves per plant and the leaf area per plant differed between water regimes within years, and the interaction between lines and years for leaves per plant was significant. These results indicate that water stress had a greater influence on leaf area and leaves per plant than on leaf size.

Since the number of leaves per plant had a significant line by years interaction, means are presented by water regimes within years (Table 3). Leaf area per plant in the suboptimal water regime was 26.6% less than the optimal water regime in 1981 and 29.6% less in 1982. The number of leaves per plant was reduced by water stress in both years. These reductions were 18.3% in 1981 and 30.6% in 1982, but only the difference in 1982 was significant statistically. Reductions in leaf size for the suboptimal water regime, compared to the optimal water regime for both 1981 and 1982, were not significantly different either year.

Heritability estimates were calculated from variance components based on the occurrence of significant differences among lines from analyses of variance. Therefore, heritability could only be estimated for leaf size (Table 4). For leaf area per plant, the estimated variance component for lines and its standard error were nearly equal. The estimated variance component for lines for the number of leaves per plant was negative, indicating that little, if any, genetic variability exists for this trait within the germplasm sampled. Estimated heritability for leaf size was

Table 4. Variance components, heritability, and associated standard errors from analyses of variance of random lines for leaf traits.

		Trait	-
Variance component or heritability	Leaf area per plant	Leaves per plant	Leaf size
$L \times R/W/Y$	75.5 ± 8.5	270 ± 33	75.90 ± 9.31
$L \times W/Y$	2.8 ± 7.7	5 ± 28	0.50 ± 7.66
$L \times Y$	10.2 ± 7.5	56 ± 30	3.92 ± 5.95
L	5.9 ± 5.8	-2 ± 20	24.40 ± 8.35
Phenotypic variance			36.10
Heritability			0.67 ± 0.48

Table 5. Heritability estimates for cotton leaf characteristics in \mathbf{F}_{ϑ} and \mathbf{F}_{ϑ} generations grown in 1981 and 1982, respectively, at Lubbock, TX using progeny-parent regression and standard unit methods.

		Trait	
Method of estimation	Leaf area per plant	Leaves per plant	Leaf size
Regression	0.10	0.04	0.48**
Standard unit	0.23	0.06	0.57**

^{**} Significant at the 0.01 probability level.

relatively high, but the standard error was 72% of the estimate itself. The relatively high standard error of the heritability estimate for leaf size indicates the need to adequately sample a population and to determine the degree to which year, water regime, and replication effects contribute to the standard errors obtained from the analyses of variance.

The estimated variance components indicate the relative importance of each source of variation (Table 4). Those of major importance according to the estimates are lines by replications within water regimes and years for all three leaf traits, and lines by years for the number of leaves per plant. The variance component of lines by replications in water regimes and years represents the residual variance and the associated standard errors averages 12% of the estimates. Heritability estimated on a progeny mean basis will vary, depending on the number of years, water regimes, and replications.

Heritability estimates calculated by progeny-parent regression and standard unit methods (Table 5) were in agreement with results using the variance component method. Leaf size was the only trait to show heritability estimates that were significantly different from zero. Comparing heritabilities estimated by the two methods presented in Table 5 provides a means of determining the degree to which environment influences phenotypic variability (2). The use of progeny-parent regression can result in heritability estimates greater than 100% because environmental influences can increase or decrease progeny variance when compared to the parental variance. If environmental influences do not inflate or deflate phenotypic variances, then heritability estimates from these two methods should be similar. Environmental influences do not appear to have affected phenotypic variability for leaf size of either the progeny or parents as evidenced by the rather close agreement of the two values of estimated heritability (Table 5).

Results of experiments presented in this paper provide evidence that ancestral cultivars produced larger leaves and more leaves per plant than cultivars currently grown on the southern Great Plains. Results from a composite population indicate that selection for leaf size should be possible, but that the number of leaves and leaf area per plant display little genetic variability. Consequently, effective selection for these traits would be difficult. Additional research will be needed to demonstrate that selecting materials with smaller leaves results in higher yields and earlier crop maturity. If we assume that selection was for both yield and earlier crop maturity and not for reduced leaf size as new cultivars were developed for the southern Great Plains, additional studies are needed to determine why leaves became smaller while cotton productivity was increased. These studies will require an understanding of the development of leaf size and the relationship among leaf size, metabolism, and water relations.

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