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Breeding Potentials of Noncultivated Cottons. II. Inheritance of Peduncle Length[1]

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ABSTRACT

Long peduncles, characteristic of some primitive race stocks of cotton, *Gossypium hirsutum* L., could be disadvantageous agronomically because they may possibly grow at the expense of early maturity and of fiber production. However, they may have value as a deterrent to larvae of pink bollworm, *Pectinophora gossypiella* (Saunders), if incorporated into a pubescent strain. We determined that Texas 711, a primitive race stock with long peduncles, differed from 'Stoneville 7A' by two major factor pairs that act additively. Another cultivated parent, 'Deltapine 16,' apparently differs from Stoneville 7A in a recessive epistatic modifier. Two other race stocks, Texas 40Y and Texas 203, apparently carry a partially dominant epistatic modifier rather than a recessive one. The latter race stock may also be monomeric for the major factor pairs. Results suggest that transfer of long peduncles into improved agronomic types of cotton should be relatively easy.

Additional index words: ***Gossypium hirsutum*** **L., *Pectinophora gossypiella* (Saunders), Pink bollworm, Host-plant resistance, Additive variance, Nonadditive variance.**

THE inheritance of metrical characters may be analyzed qualitatively as well as quantitatively, if the phenotype of at least one of the parents can be reconstituted and identified. In practice, the parental phenotype is likely to be identifiable only when the inheritance pattern is simple and individual gene effects are large. Specification of a quantitative character by the action of one or a few major genes provides a valuable cross reference in the study of genetic variability, since qualitative and quantitative genetic methods may be compared directly.

Peduncle length varies significantly among strains of cotton, *Gossypium hirsutum* L. Currently grown cultivars have short (about 20 mm) peduncles that do not elongate after flowering. However, some primitive race stocks may have accrescent peduncles; that is, they may continue to grow until bolls reach full size.

The adaptive significance of long peduncles in certain wild strains of cotton is not known. However, peduncles could possibly grow at the expense of early maturity and of fiber production, making them an undesirable character in a cultivar. On the other hand, cottons with long, densely pubescent peduncles might deter young larvae of pink bollworm, *Pectinophora gossypiella* (Saunders) from reaching the bolls. Many eggs are laid on vegetative plant parts and migration to the bolls becomes difficult for these larvae if they encounter dense pubescence (5).

In the first paper of this series, we presented agronomic and fiber-quality data and analyses from a complete diallel involving two cultivars, three primitive race stocks, and F_1 hybrids of *G. hirsutum*. In this paper, we present data and analyses of the inheritance of peduncle length in these five cottons and their F_1, F_2, and backcross hybrids.

MATERIALS AND METHODS

Parents were two cultivars of *G. hirsutum*, 'Deltapine 16' (DPL 16) and 'Stoneville 7A' (St 7A), and three primitive race stocks, Texas 40Y (T-40Y), Texas 203 (T-203), and Texas 711 (T-711). T-711 has long (about 45 mm) peduncles, while the other parents have shorter ones.

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In 1973, we grew a complete diallel set of crosses (5 parents and 20 F_1 hybrids) in three randomized blocks at the Cotton Research Center, Arizona Agric. Exp. Stn., Phoenix (6). The study in 1974 consisted of four generations and included one set of diallel crosses. The 45 entries were the 5 parents, 10 F_1 hybrids (reciprocals not included), 10 F_2 hybrids, and 20 backcross hybrids grown in four randomized blocks at the Arizona State University Farm Laboratory, Tempe.

In 1973, each single-row plot contained 20 transplants, spaced 45.7 cm apart, that had been started in expanded peat pellets in a greenhouse. Plots were spaced 1.02 m apart. Each block contained one row of each parent and each F_1. In 1974, each single-row plot contained 25 transplants, spaced 30.5 cm apart. Plots were spaced 1.02 m apart, as in 1973. Each block contained one row of each parent and F_1, four rows of each F_2, and two rows of each backcross combination. In this paper, hybrid combinations are presented with the pistillate parent first, e.g., DPL 16 × St 7A F_1.

Conventional cultural practices were followed at both locations. However, the plants at the Arizona State University Farm in 1974 received no insecticide because a major objective was to determine their response to pink bollworm attack.

Peduncles were measured on two 16 to 25-day-old bolls/plant in 1973 and on two green, mature-sized, bolls/plant in 1974. Parental and hybrid means were compared with the use of the FLSD test (1). Both 1973 and 1974 parental and F_1 data were analyzed by the half diallel method of Jones (2) to determine the relative contributions of additive and nonadditive sources of genetic variation. The 1974 data were used in a generation-mean analysis (4) applied to individual hybrid combinations to estimate additive, dominance, and epistatic effects. These genetic parameters were not estimated independently of each other because the data were drawn from a single diallel test.

A qualitative genetic analysis of T-711 progenies was carried out by determining the proportion of the total number of F_2 and testcross (i.e., crossed to the short-peduncled parent) plants that had peduncles no longer than those of the short-peduncled parent. The basic assumption of this analysis is that plants with peduncles in the same length range as those of the short-peduncled parent have the same genotype as that parent. This assumption will be realized if 1) the short-peduncled parents carry only minus factors for peduncle length in relation to those of T-711 and 2) heritability is complete, i.e., environment does not affect peduncle length. A breakdown of this assumption would result in an overestimate of plants in the short-peduncle class and, therefore, an underestimate of the number of factors conditioning peduncle length. The chi-square analysis was used to test goodness-of-fit to presumed segregation ratios.

RESULTS

Table 1 presents mean peduncle lengths for parents and F_1 hybrids in 1973 and for parents, F_1, F_2, and backcross hybrids in 1974. In both 1973 and 1974, T-711 and its combination had significantly longer peduncles than any of the other parents or hybrids. In 1973, peduncles of T-203 and its hybrids were longer, although not always significantly so, than those of the two cultivars (DPL 16 and St 7A), T-40Y, and their hybrid combinations. In 1974, however, peduncles of T-203 and its hybrids with the cultivars were significantly longer than those of T-40Y only. Means of the two cultivars, T-40Y, and their hybrids were not significantly different from each other. F_1 means were similar in 1973 and 1974 except for those involving T-711. In the latter combinations, 1973 means were consistently higher and 1974 means were consistently lower than the midparent value. The 1973 and 1974 F_1 means could not be compared directly, because their variances were not homogeneous. In only one instance, T-40Y × T-711 in 1974, was the F_2 mean significantly different from the F_1.

Table 2 presents mean squares from the half-diallel analysis of parents and F_1 hybrids, 1973 and 1974.

Table 1. Mean peduncle length in five parental lines of *G. hirsutum* and their hybrids; 1973 and 1974.

Parent or hybrid	Peduncle length			
	1973		1974	
	Parental mean		Parental mean	
	mm			
DPL 16	20.9 e-g*		21.7 n-r	
St 7A	19.7 fg		20.9 qr	
T-40Y	21.2 e-g		19.5 r	
T-203	26.1 cd		22.6 l-q	
T-711	44.3 a		45.3 a	
	1973	1974 mean		
	F_1 mean	F_1	F_2	BC†
DPL 16 × St 7A†	20.5 fg	21.5 o-r	20.8 qr	21.0 qr 20.9 qr
DPL 16 × T-40Y	21.9 d-g	22.3 m-q	22.0 m-r	20.9 qr 21.3 p-r
DPL 16 × T-203	25.4 c-e	23.3 k-q	22.5 l-q	24.5 i-m 24.1 i-o
DPL 16 × T-711	37.6 b	29.0 fg	29.7 ef	25.4 h-k 38.5 cd
St 7A × T-40Y	19.6 fg	22.3 m-q	21.2 qr	21.7 p-r 20.9 qr
St 7A × T-203	25.0 c-f	25.9 h-k	24.4 i-n	21.8 n-r 23.2 k-q
St 7A × T-711	36.6 b	30.7 ef	31.3 e	27.4 gh 37.3 d
T-40Y × T-203	26.9 c	24.0 j-p	23.3 k-q	21.0 qr 26.6 g-j
T-40Y × T-711	35.1 b	30.7 ef	26.9 g-i	24.6 h-m 40.7 bc
T-203 × T-711	36.4 b	30.6 ef	32.3 e	29.6 ef 42.7 ab

* Means with same letters in common, within year, are not significantly different, according to FLSD test ($L.S.D._{0.05}$ = 4.88 mm, 1973; 2.77 mm, 1974).
† Pistillate parent is listed first; in backcross column, the first mean within a hybrid combination specifies F_1 × original pistillate parent, the mean below it specifies F_1 × original staminate parent.

Table 2. Mean squares from half diallel analysis for mean peduncle length, five parents and F_1 hybrids; 1973 and 1974.

Source	1973 df	1973 MS	1974 df	1974 MS
Replicates	2	3.0	3	6.2*
Entries	14	195.3**	14	174.0**
a†	4	650.1**	4	564.7**
b_1	1	0.4	1	0.2
b_2	4	5.5	4	37.6**
b_3	5	22.3*	5	5.4*
Error	28	8.2	42	2.1

*,** P < 0.05, 0.01, respectively. † a = additive effects; b_1 = mean deviation from additivity; b_2 = consistency of nonadditive deviations from hybrid arrays; b_3 = deviation from additivity unique to each F_1.

Table 3. Segregation for peduncle length in hybrids from T-711.

Population	No. plants			Expected ratio	Chi square	P
	Total	Low parent range: Above	Low parent range: In			
DPL 16 × T-711 F_2	332	262	70	49:15	1.02	0.30-0.40
testcross to DPL 16	124	53	71	3:5	1.45	0.20-0.30
St 7A × T-711 F_2	295	277	18	15:1	0.01	0.90-0.95
testcross to Stv 7A	185	143	42	3:1	0.52	0.40-0.50
T-40Y × T-711 F_2	323	142	181	33:31	7.47	0.005-0.01
testcross to T-40Y	161	74	87	1:1	1.04	0.30-0.40
T-203 × T-711 F_2	238	192	46	13:3	0.05	0.80-0.90
testcross to T-203	138	100	38	3:1	0.48	0.40-0.50

Table 4. Estimates of genetic effects from analysis of peduncle-length generation means; 1974.

Combination	Genetic effects ± S.E.				
			Epistasis		
	Additive [d]	Dominance [h]	Homozygous X homozygous [i]	Homozygous X heterozygous [j]	Heterozygous X heterozygous [l]
DPL 16 X T-711	11.8 ± 0.5*	12.3 ± 4.0*	7.6 ± 1.5*	2.5 ± 1.5	9.4 ± 2.6*
St 7A X T-711	12.3 ± 0.5*	−1.5 ± 4.9	0.7 ± 1.7	−7.3 ± 1.7*	−0.1 ± 3.2
T-40Y X T-203	1.6 ± 0.2*	2.4 ± 2.3	−1.7 ± 1.9	5.5 ± 0.7*	−1.7 ± 1.5
T-40Y X T-711	13.0 ± 0.5*	46.6 ± 4.8*	22.0 ± 1.9*	6.7 ± 1.6*	−26.4 ± 3.1*
T-203 X T-711	11.4 ± 0.5*	43.4 ± 4.1*	16.2 ± 1.5*	2.6 ± 1.5	−30.5 ± 2.6*

* Significantly different from 0, according to t-test.

Additive effects (a) were highly significant and of similar magnitude both years. Of the nonadditive effects, the mean deviation from additivity (b_1) was very small and not significant either year, the deviation from additivity unique to each F_1 (b_3) was significant both years, and the consistency of the nonadditive deviations from hybrid arrays (b_2) was not significant in 1973 but was highly significant in 1974.

Table 3 presents the results of the qualitative analysis of segregating progenies from T-711 in 1974. Both testcross and F_2 ratios varied among combinations. All of the observed ratios fit the expected ratios well, except T-40Y × T-711 F_2.

Table 4 presents estimates of genetic effects from the generation-mean analysis for the five combinations in which the parents differed significantly. The only consistent result was the significant additive effect [d] in each combination. Dominance [h], homozygous × homozygous [i], and heterozygous × heterozygous [l] interaction effects were significant for the same three combinations. Homozygous × heterozygous effects [j] were also significant for three combinations, but not the same three.

DISCUSSION

Results of the half-diallel analysis of parents and F_1 hybrids in 1973 and 1974 (Table 2) emphasize the similarity of all the genetic effects except the b_2 component, which measures the consistency of the nonadditive deviations among hybrid arrays. Mean deviation from midparent/array ranged only from 1.42 to 3.29 mm in 1973 but from −3.02 to 1.54 mm in 1974. The major difference in 1974 occurred in the T-711 hybrid array, with F_1 means consistently below the midparent value, whereas, F_1 means were close to that of the midparent in the other arrays. We do not know why F_1 means in the T-711 array differed in 1973 and 1974, but they may reflect the two different methods of data collection. We measured peduncles of known age the first year and merely estimated age the second year.

The qualitative genetic analysis of F_2 and testcross populations (Table 3) yielded only one unequivocal result, a two-factor pair difference in St 7A and T-711, with negligible effects from modifiers. This result is not surprising, because duplicate-factor inheritance is common in the allotetraploid *G. hirsutum* (3). Nonetheless, the result is remarkable because the two parents are presumably not closely related and modifying complexes could be expected. For discussion in this paper, we designated these two peduncle-length factors as *A* and *B* (genotype of T-711 is thus *AABB*; genotype of St 7A is *aabb*).

The generation mean analysis (Table 4) of St 7A × T-711 showed that gene action was largely additive, but we could not determine the relative contributions of the two alleles. Dominance was negligible, but a significant homozygous × heterozygous negative interaction resulted from means of backcrosses to St 7A and to T-711 that were higher and lower, respectively, than expected on the basis of additivity.

A rational explanation of the qualitative results in the testcross (DPL 16 × T-711) × DPL 16 is the assumption of the action of a recessive epistatic modifier (c) plus the action of the two major factor pairs (thus the genotype of DPL 16 would be *aabbcc*; that of T-711 would be *AABBCC*). This assumption could explain the 5 "short":3 "long" peduncle testcross ratio, because all of the testcross progeny carrying the recessive modifier, plus one-fourth of the progeny carrying its dominant allele, would have peduncles in the same range as DPL 16. The observed F_2 results do not fit the expected complementary epistatic ratio of 19 "short":45 "long" implied by the testcross ratio. However, the expected F_2 ratio could be as low as 15:49 if the homozygous major-factor alleles could override the recessive modifier and thus produce peduncles longer than those in the DPL 16 range.

The generation mean analysis of DPL 16 × T-711 is consistent with these assumptions. The additive effect is significant and of the same magnitude as that of the St 7A × T-711 combination, thus implicating the two major factor pairs. The dominance effect is also significant, suggesting the action of at least one dominant factor not present in St 7A × T-711. Finally, the dominance and the heterozygous × heterozygous interaction effects are of the same sign, suggesting a complementary type of epistasis (4).

Thus, the differences in breeding behavior for peduncle length exhibited by DPL 16 and St 7A, when crossed with the common parent T-711, can be explained as the action of a recessive modifier in DPL 16 that is absent in St 7A.

Qualitative results in T-40Y × T-711 suggest the presence of a dominant epistatic modifier (D), since both the F_2 and testcross populations had more plants in the T-40Y range than above it. The actual expected ratios in these populations would depend on the specific action of the modifier and its epistatic effects on the major factors. The F_1 mean is intermediate to the parents, showing that the modifier is not completely dominant. Assuming the action of a partially domi-

nant modifier, epistasis of the major factors would produce a 1:1 testcross ratio and a 31 "short":33 "long" F_2 ratio. The actual ratios in both populations are closer to 9 "short":7 "long".

Generation mean analysis of T-40Y × T-711 shows that the additive effect is of the same magnitude as in the other combinations involving T-711. Thus, T-40Y probably carries the same two additive factors that condition short peduncle in DPL 16 and St 7A. The presence of at least one dominant factor that influences peduncle length is indicated by the significant dominance effect (thus, the genotype of T-40Y could be *aabbDD*; that of T-711, *AABBdd*). The difference in sign of the dominance and the heterozygous × heterozygous interaction effects shows that most of the epistasis is of a duplicate type, rather than a complementary type as in DPL 16 × T-711. Finally, both the homozygous × homozygous and homozygous × heterozygous interaction effects are significant in T-40Y × T-711, further emphasizing the genetic uniqueness of T-40Y.

T-203 strongly resembles T-40Y in its breeding behavior, but the genetic analyses suggest that it is distinct. The qualitative analysis of T-40Y × T-203 was uninformative. However, the generation mean analysis revealed small but significant additive and homozygous × heterozygous interaction effects, indicating that these two cottons differ in at least two factor pairs.

The generation mean analyses of T-40Y × T-711 and T-203 × T-711 are strikingly similar, except that the homozygous × heterozygons interaction effect was not significant in the latter combination. Because of this similarity, it seems likely that T-203 carries the same partially dominant epistatic modifier as T-40Y. However, we do not know how these two race stocks differ genetically. The significant additive effect shown in T-40Y × T-203 might mean that T-203 is monomeric for the major factor pairs. If so, then the two major alleles are not equal in their expression. Also, T-203 may carry one or more modifiers that behave additively.

Mean peduncle lengths of T-203 and its hybrids in 1973 suggest that this race stock does carry plus factors for peduncle length. In fact, in 1973, peduncles of T-203 were significantly longer than those of DPL 16, St 7A, and T-40Y, and length was inherited as a complete dominant in F_1 (6). The 1974 mean peduncle length of T-203 seems to be too low, based on its previous performance and that of its hybrids. The possibility of contamination in the 1974 T-203 plots was rejected because T-203 has such a distinctive growth habit. The possibility of residual heterozygosity for peduncle length in this line cannot be ruled out.

If we assume, for purposes of discussion, that T-203 carries the same modifier as T-40Y and is monomeric for the major factor pairs, then we can explain the results of the qualitative genetic analysis. Under these assumptions, the only class of segregates with peduncle length in the T-203 range would be that with the reconstituted T-203 genotype. In the F_2, the expected proportion of this genotype wonld be 3/16, and in testcross population it would be 1/4; the data fit these ratios (Table 3). This explanation, however, accounts for only one of two or more gene differences between T-40Y and T-203, as indicated by the significant epistasis indicated in this latter combination.

Even though some of the details of the genetic analysis presented here may not be correct, a single theme emerges from our data: each of the parents is unique genetically for peduncle length. Some genetic differences are subtle, such as those between DPL 16, St 7A, and T-40Y; others are conspicuous, such as those between T-711 and the other parents.

An encouraging result is that St 7A and T-711 differ only in two major factor pairs that act additively. Therefore, we should be able to transfer the long peduncles easily into more productive cottons to test their effects on insect populations and agronomic properties.

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