

Short-Branch and Cluster-Fruiting Habit Inheritance in Crosses of Eight Cotton Lines¹

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ABSTRACT

The potential value of fruiting branches (sympodia) of intermediate length in an ideotype for a high-yielding line of F₁ hybrid cotton grown for stripper harvest led us to research for modifier genes that affect the expression of alleles at the two known major gene loci (*cl*₁ and *cl*₂) that exert primary control over sympodial length. Six stocks of *Gossypium hirsutum* L., and two *G. barbadense* L. stocks representing three basic branching habits, normal (*Cl*₁ *Cl*₁ *Cl*₂ *Cl*₂), cluster (*cl*₁ *cl*₁ *Cl*₂ *Cl*₂), and short branch (*Cl*₁ *Cl*₁ *cl*₂ *cl*₂), were crossed in all possible one-way combinations to assess the expression of the mutant alleles in the F₁ generation in various genetic backgrounds. Lateral internode distance to the first fruiting form (square) was measured at the ninth vertical node in the parental and F₁ field-grown populations. Twenty of the 25 crosses showed full dominance of the normal allele over the mutant allele. However, five of the crosses were bimodal with a progeny class of intermediate length occurring in addition to a dominant normal length class. This was interpreted to mean that one or both of the parental lines involved harbored a gene that modified the dominance relationships between the normal and mutant genes conditioning sympodial length. Modified activity in cluster (*cl*₁) expression was observed in four crosses, and modified short-branch (*cl*₂) expression was detected in one cross.

Additional index words: *Gossypium hirsutum* L., *G. barbadense* L., Monogenic inheritance, Modifier genes.

THE increasing use of stripper-type cotton harvesting machinery in southwestern U.S. production areas has intensified the need for high-yielding cotton cultivars suitable for once-over harvesting.

Cultivars that possess excessive vegetative growth (limby phenotypes) result in more trash being harvested with the cotton, have higher ginning costs, and often cause lower-grade fiber as well.

Development of a suitable cotton hybrid with fruiting branches of intermediate length would allow growers to take advantage of a phenotype that is potentially higher yielding than determinate homozygous cluster types and still benefit from the lower costs of operating and maintaining stripper-harvesting machinery.

The most common commercial cotton cultivars possess sympodia that can be characterized as long and multinoded and bear one mature fruiting form (square) per node. The mean length between sympodial nodes can vary considerably among cultivars that are considered to have normal or long sympodia. Several researchers working with various species of cotton have reported the existence of deviant *Gossypium hirsutum* L. plant types having either sympodia bearing two to five squares per node (1, 2, 5, 7, 9, 10, 13, 14), deviant *G. barbadense* L. types with sympodia reduced to one internode (3, 6, 8, 12), or a combination of both characters (4).

In general, two classes of cluster expression have been noted (1). The first class exhibits sympodia (usually of only a single reduced node) that terminate in a group of two or more squares. This is sometimes

referred to as tip clustering and represents the short-branch type of cluster character controlled by the gene *cl*₂. The second class, termed semicluster or intermediate cluster, is demonstrated by plants possessing two to three (rarely four or five) nodes per fruiting branch. The average internode distances are extremely reduced; however, a composite of both normal and reduced length internodes is not uncommon on the same sympodium. This internode length reduction results in a pronounced shortening of the sympodia and tight grouping of the fruiting forms (squares) and is conditioned by the cluster gene *cl*₁.

Pathak and Singh (11) and Thadani (14) indicated that cluster (*cl*₁) is a monogenic recessive trait conditioning branching habit in allotetraploid *Gossypium* species.

The short-branch (*cl*₂) character is found primarily in *G. barbadense*, and its inheritance has been reported as a simple recessive (3, 6, 8, 12). Kearney (8) reported intermediate-branched F₁ progenies obtained from an intraspecific *G. barbadense* cross, indicating incomplete dominance of the gene *Cl*₂.

Since short-branch (*cl*₂) expression normally results in plants with sympodia reduced to one developed internode, plants of this genotype appear to have elongated pedicels attached directly to the main stem. A small leaflet located a few millimeters below the square may indicate that the square actually surmounts a minute pedicel borne on a uninodal fruiting branch. One or more squares may be borne at the tip of the reduced sympodium, additional squares being initiated from accessory buds located at the tip of the reduced sympodium. Two or more short sympodia may arise simultaneously from axillary and accessory buds located at a common main stem node (8, 13).

In crosses involving one long- and one short-branched *G. barbadense* cultivar, Bahavandoss et al. (3) reported the F₂ generation segregated into three types and represented a 15:1 phenotypic ratio. The authors assumed any intermediate branching length observed was caused by modifier activity and not by any heterozygosity present. They concluded that the long-branched parent chosen for study had not undergone full diploidization for the trait and thus allowed digenic control of the short-branched character.

The objective of this study was to determine the effect of heterozygous cluster (*cl*₁) and short-branch (*cl*₂) alleles in several background genotypes and to determine if other genes in the various lines tested were interacting with the *cl*₁ or *cl*₂ factors to modify F₁ phenotypes.

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MATERIALS AND METHODS

Six *G. hirsutum* and two *G. barbadense* partially inbred lines were selected for use as parents to represent the various forms of branching and flowering habits expressed over a wide variety of phenotypes (Table 1).

Single crosses without reciprocals were performed among the parent lines during the summer of 1980. The eight

Table 1. Species, genotypes, phenotypes, and pedigrees of the *Gossypium* parents tested in an analysis of short-branch and cluster-fruited habit inheritance.

Parents	Species	Genotype	Phenotype	Pedigree
'ST213'	<i>G. hirsutum</i>	$Cl_1Cl_1Cl_1Cl_1$	Normal-branch	<i>G. hirsutum</i> commercial variety
M	<i>G. hirsutum</i>	$cl_1cl_1Cl_1Cl_1$	Cluster	<i>G. hirsutum</i> race Marie Galante \times <i>G. barbadense</i>
1.V-7	<i>G. hirsutum</i>	$cl_1cl_1Cl_1Cl_1$	Cluster	'Ysleta Yugoslav' \times <i>G. barbadense</i> 5-10
5-1.8	<i>G. hirsutum</i>	$cl_1cl_1Cl_1Cl_1$	Cluster	['Acala 1517d' \times Oklahoma CR-4] \times Stahmann 876] \times Stoneville Accession 107 'Hearin Cluster'
8a	<i>G. hirsutum</i>	$cl_1cl_1Cl_1Cl_1$	Cluster	Stoneville Accession 29 'Texas Short Fruiting Branch' \times 'Acala 1517' outcross
47t	<i>G. hirsutum</i>	$cl_1cl_1Cl_1Cl_1$	Cluster	V. G. Meyer 324-11 ['DES 16ne' \times F ₂ ('Delcot 277' \times <i>G. tomentosum</i> Nutt. ex Seem.)]
KD.E.	<i>G. barbadense</i>	$Cl_1Cl_1cl_1cl_1$	Short-branch	Arizona selection 7117-505 (<i>G. barbadense</i>) \times Russian <i>G. barbadense</i> 5904
L	<i>G. barbadense</i>	$Cl_1Cl_1Cl_1Cl_1$	Normal-branch	Ysleta E1024 (<i>G. barbadense</i>)

parental types and 25 of 28 F₁ progeny groups were grown during the summer of 1981 at the New Mexico State University Plant Science Research Center (PSRC) at Las Cruces in a randomized complete block design with three replications. Soil type at the PSRC is a Typic Torrifluvent. Each plot was a single row 4.6 m long, subsequently thinned to 15 plants per row (approximating a 30-cm plant spacing).

Data were obtained from all mature plants in each entry beginning in late July 1981. Distance to the first lateral sympodial node was measured (in centimeters) from the main stem to the first fruit-bearing pedicel on the sympodium located at the ninth main stem node.

RESULTS AND DISCUSSION

The *G. barbadense* parent "L" had the greatest internode length and expressed the greatest range of variability ($\bar{x} = 15.7 \pm 1.7$ cm) for lateral internode distance of any of the parents (Table 2). The cl_1 parents could be separated into three distinct groups with internode lengths ranging from 0.4 ± 0.2 cm for 47t in the first group, 1.5 ± 0.6 cm, 2.4 ± 0.5 cm, and 3.5 ± 0.5 cm for M, 8a, and 1.V-7, respectively, in the second group, to 4.1 ± 0.9 cm for 5-1.8 in the third group. This shows the value of measurement as an indicator of subtypes within the phenotypic classification generally referred to as "cluster."

With one exception, progeny of all of the intercrosses between 47t, M, 8a, 5-1.8, and 1.V-7 fell either within the parental range or approximated the mid-parent value, indicating that all were homozygous for a recessive allele at the cl_1 locus. The cross 5-1.8 \times 1.V-7 was an anomaly producing both mutant and

Table 2. Diallel table of population means and standard errors for the length of the first internode on the ninth node sympodial branch on eight lines of cotton and their F₁ progenies. Progenies having bimodal distribution are listed as subpopulations \bar{x}_1 and \bar{x}_2 .

Female parental lines	Male parental lines							
	<i>G. hirsutum</i>						<i>G. barbadense</i>	
	ST213	M	1.V-7	5-1.8	8a	47t	KD.E	L
cm								
<i>G. hirsutum</i>								
ST213 (normal branch)	$\bar{x} = 13.0$ ± 0.7	$\bar{x}_1 = 4.3$ ± 1.1 $\bar{x}_2 = 9.9$ ± 1.1	$\bar{x}_1 = 2.6$ ± 0.6 $\bar{x}_2 = 10.3$ ± 1.9	$\bar{x}_1 = 5.6$ ± 1.6 $\bar{x}_2 = 10.8$ ± 1.4	$\bar{x} = 5.4$ ± 2.4	$\bar{x} = 2.8$ ± 0.7	$\bar{x} = 18.4$ ± 1.4	$\bar{x} = 19.3$ ± 2.0
M (cluster)		$\bar{x} = 1.5$ ± 0.6	$\bar{x} = 3.7$ ± 0.7	$\bar{x} = 3.0$ ± 1.0	$\bar{x} = 1.8$ ± 0.5	$\bar{x} = 1.0$ ± 0.3	$\bar{x} = 15.4$ ± 2.5	$\bar{x} = 19.8$ ± 1.3
1.V-7 (cluster)			$\bar{x} = 3.5$ ± 0.5	$\bar{x}_1 = 4.3$ ± 0.8 $\bar{x}_2 = 17.5$ ± 1.0	$\bar{x} = 3.8$ ± 0.7	†	$\bar{x} = 18.3$ ± 1.6	$\bar{x} = 18.5$ ± 0.9
5-1.8 (cluster)				$\bar{x} = 4.1$ ± 0.9	$\bar{x} = 3.6$ ± 0.9	$\bar{x} = 3.2$ ± 1.0	$\bar{x}_1 = 9.0$ ± 1.2 $\bar{x}_2 = 16.0$ ± 2.6	$\bar{x} = 18.8$ ± 1.7
8a (cluster)					$\bar{x} = 2.4$ ± 0.5	†	†	$\bar{x} = 19.0$ ± 1.5
47t (cluster)						$\bar{x} = 0.4$ ± 0.2	$\bar{x} = 17.3$ ± 1.3	$\bar{x} = 16.9$ ± 1.3
<i>G. barbadense</i>								
KD.E (short branch)							$\bar{x} = 5.0$ ± 0.3	$\bar{x} = 12.1$ ± 0.3 †
L (normal branch)								$\bar{x} = 15.7$ ± 1.7

† No data available; crossed seed inviable.

‡ Progeny of only four plants.

normal progeny. This result cannot be explained with the available data.

Parents 47t, M, 5-1.8, and 1.V-7 produced long-branched progeny in crosses with the short-branched *G. barbadense* strain KD.E. This was expected since the respective recessive genes are located at unlinked loci (cl_1 vs. cl_2) in the two species.

The cross of 5-1.8 with KD.E gave 12 intermediate-length segregates in addition to 21 long-branched segregates. Since other crosses involving KD.E produced uniform F_1 progenies, 5-1.8 may carry a heterozygous modifier gene(s) that interacts with the $Cl_1 cl_1 Cl_2 cl_2$ genotype to produce an intermediate branch length phenotype in the interspecific hybrid.

The distributions of F_1 populations obtained from crosses using M as the maternal parent (except $M \times 1.V-7$) demonstrates simple additive action of modifiers because the F_1 progenies in these crosses centered around the midparent values.

The cross $1.V-7 \times 5-1.8$ produced unexpected results. The F_1 population exhibited transgressive segregates below the short parent and above the longer parent due to epistatic activity of minor genes on cl_1 . This demonstrates that 5-1.8 has a high level of modifier-gene action functioning to produce its particular cluster habit. Three of the six crosses involving 5-1.8 ($5-1.8 \times KD.E$, $1.V-7 \times 5-1.8$, and $ST213 \times 5-1.8$) had bimodal distributions. This also is attributed to modifier-gene activity on cl_1 .

Because the normal cluster allele, Cl_1 , has been reported as dominant, crosses of normal-branch ST213 with cluster parents should produce progeny with branches of normal length only. However, all crosses involving ST213 produced F_1 progenies with a class of short to intermediate branch length. Moreover, three of the five F_1 progeny groups obtained from intraspecific crosses of ST213 showed distinctly bimodal distributions (Table 2), indicating the existence, in a portion of the parent population, of a modifying gene that interacts with the cluster gene cl_1 .

The presence of modifiers was apparently the result of genotypic variation among the parent plants. Variation is to be expected in cotton cultivars or lines in which the process of selfing and single plant selection has not been carried to the point of virtual homozygosity. Most of these parent materials have been handled as bulk inbred lines after the F_4 or F_5 generation. The amount of heterozygosity remaining in the F_5 generation was still theoretically 6.25% (excluding selection-induced genetic drift). Unselected heterozygous loci may still be randomly dispersed within each population in low frequencies. On the other hand, conscious phenotypic selection in the cluster parents for short internode habit throughout all generations has caused artificial genetic drift resulting in genotypes homozygous at the cl_1 locus. This is indicated by the low variability exhibited for lateral internode length in the parental phenotypes. However, random accumulation of undetected genes modifying cl_1 may have resulted. No selection for modifier genes has been performed, and they are probably carried in the populations at varying levels of heterozygosity.

The absence of bimodal distributions among the F_1 progenies of $ST213 \times 8a$ and $ST213 \times 47t$ in-

dicates that these F_1 's may be free of heterozygous modifier genes for cluster expression. The 47t line is descended from *G. tomentosum* Nutt. ex Seem. and may carry a distinctive cl_1 allele.

The variability observed in interspecific crosses involving ST213 may be caused by residual heterozygosity in either the *G. hirsutum* or *G. barbadense* parent. Because cl_1 was not present in *G. barbadense*, any modifying genes present in these parents for cluster habit would not have been expressed in their phenotypes.

The intraspecific *G. barbadense* cross, $KD.E \times L$, produced an F_1 population of four viable plants that were uniform and slightly above the midparent value for lateral internode length. Accurate detection of possible cl_2 modifier activity was not possible, however, because the F_1 population contained only four plants. The lack of a larger F_1 population also precludes any statement as to whether or not Cl_2 is fully dominant in this cross over the alternate recessive condition.

We have found evidence for modifier gene(s) that significantly affect the phenotypic expression of the $Cl_1 cl_1$ genotype in certain populations. One line, designated 8a, has been uniform in response to all the other testers and may carry modifier(s) in a homozygous condition. More precise characterization of the modifier gene action involved awaits further purification of parental lines.

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