

CROP SCIENCE

Volume 17

May-June 1977

Number 3

Inheritance of Plant Height in Cotton.

II. Diallel Analyses Among Six Semidwarf Strains¹

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ABSTRACT

Semidwarf cultivars of upland cotton (*Gossypium hirsutum* L.) have been developed to meet the requirements of narrow-row, high-population cotton production. Six semidwarf stocks, the diallel set of F_2 hybrids among those stocks, and a "normal-height" stock were used to compare plant height and crop maturity characters among the semidwarf stocks and the normal-height stock and to evaluate the inheritance of those characters among the semidwarf stocks. The characters studied were plant height, mainstem and fruiting-branch internode length, number of mainstem nodes, node of the first fruiting branch, and mean maturity date. Diallel analyses were used to estimate genetic and environmental components. Comparisons between the normal-height and the semidwarf stocks showed that the semidwarf stocks were generally shorter in plant height, had shorter mainstem and fruiting-branch internodes, initiated their fruiting branches at a lower mainstem node, and were earlier in crop maturity than the normal-height stock. Diallel analyses indicated that the genetic variation for the plant height and maturity traits among the semidwarf stocks was primarily additive, with a small, although significant, dominance component associated with all the traits except number of mainstem nodes. Heritability was relatively low for plant height and mainstem internode length, intermediate for number of mainstem nodes and node of the first fruiting branch, and high for fruiting-branch internode length and mean maturity date.

Additional index words: *Gossypium hirsutum* L., Internode length, Node number, Earliness of maturity, Cotton genetics.

TO more effectively exploit the potential benefits associated with the narrow-row, high-population concept of cotton (*Gossypium hirsutum* L.) production, breeders have developed a number of semidwarf cultivars specifically adapted to this cultural system. Ray (1965, 1970) described such a cultivar as a short, compact plant that produced few vegetative branches, initiated fruiting branches at a low node on the mainstem, and was early in maturity. Niles (1969, 1973) showed that on a per-plant basis narrow-row cultivars tended to yield less than more conventional, full-season cultivars. He (1974) further demonstrated that narrow-row culture of adapted narrow-row cultivars increased lint yields per unit of land area an

average of 21%, whereas yields of conventional cultivars were essentially unaffected.

Narrow-row cultivars have been selected from several germplasm sources. Usually they were plant types that would have been discarded in a breeding program designed to develop conventional cotton cultivars because of their short and generally less productive phenotypes.

Data in the first paper of this series (Quisenberry, 1975), showed the inheritance and interrelationships in plant-height traits between a highly inbred normal-height stock, 'TM-1', and a highly inbred semidwarf stock, 'Lubbock Dwarf'. It was determined that (i) plant height traits were associated with additive genetic effects without any indication of dominance effects and (ii) mainstem internode length represented a genetic system different from that for fruiting-branch internode length.

The purpose of this research was to evaluate the amount of genetic and environmental variation that exists for plant height and maturity characters among semidwarf stocks developed for narrow-row production and to determine if more than one semidwarf genotype exists in upland cotton.

MATERIAL AND METHODS

The material included in this study were six semidwarf stocks, the diallel set of 15 possible F_2 hybrids among these stocks (reciprocal crosses not included), and a normal-height stock for comparison purposes. The six semidwarf stocks, cotton breeders, and institutions responsible for their development were: (i) Ysleta Compact, P. J. Lyerly (deceased), Texas A&M Univ.; (ii) CA 491 and CA 814, L. L. Ray, Texas A&M Univ.; (iii) 'Paymaster Dwarf' and Paymaster 266, D. C. Hess, ACCO Seed Co.; and (iv) DSR 6-19, G. A. Niles, Texas A&M Univ. The normal-height stock was Texas Marker-1 (TM-1), which was derived by long-term inbreeding of 'Deltapine 14' and has been used as a genetic standard in many cotton studies (Kohel et al., 1970).

The breeding histories of the semidwarf stocks suggested that they represented several sources of germplasm. Ysleta Compact was developed from Acala 1517 germplasm. CA 491 was selected from a cross between a Yugoslavian strain (CB 3051) and 'storm-rider'. CA 814 originated from an interspecific cross between *Gossypium hirsutum* L. and *Gossypium barbadense* L.; phenotypically, it resembles *G. hirsutum* in plant type. Paymaster Dwarf resulted from a cross between a 'Paymaster 105' and an African upland that carried the b_4 gene for resistance to bacterial blight. Paymaster 266 resulted from a complex series of crosses involving 'Macha', 'Paymaster 101', 'Arizona 6024', 'Deltapine 5540', 'Paymaster 54', and an African upland with the b_4 gene. DSR 6-19 was selected as an early-maturing segregate from a cross between 'Lankart Sel. 57' and 'Acala 5675'.

¹Contribution from the ARS, USDA, in cooperation with the Texas Agric. Exp. Stn. Received 6 July 1976.

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Table 1. Comparisons of mean performance among the semi-dwarf strains and TM-1.

Stocks	Plant ht.	Internode length		No. of nodes	Node first fruiting branch	Mean maturity date
		Main stem	Fruiting branch			
		cm				days
TM-1	69.4 a*	3.47 a	5.50 a	20.0 a	7.4 a	169.3 a
Ysleta Compact	46.6 b	2.20 b	3.97 b	21.1 a	6.9 b	160.3 b
Paymaster Dwarf	35.8 c	2.04 bc	4.22 ab	17.6 b	6.3 c	145.3 c
Paymaster 266	35.3 c	1.78 de	4.40 ab	19.8 a	6.5 c	147.9 c
DSR 6-19	33.6 c	1.89 cd	2.41 c	17.7 b	7.2 ab	147.6 c
CA 491	28.6 d	1.62 ef	1.79 c	17.6 b	5.7 d	129.2 d
CA 814	25.5 d	1.56 f	1.70 c	16.3 b	5.2 e	126.7 d

* Means within columns followed by the same letter are not significantly different at the 0.05 level of probability according to Duncan's multiple range tests.

Table 2. Mean performance of parental and F_1 generations and mean heterosis.

Characters	Generation mean		Mean heterosis
	Parental	F_1	
			%
Plant ht. (cm)	34.2 b†	37.0 a	7.6*
Internode length (cm)			
main stem	1.85 b	1.98 a	6.6**
fruiting branch	3.08 b	3.24 a	4.9**
No. of nodes	18.38 a	18.63 a	1.1
Node first fruiting branch	6.31 a	6.09 b	-3.6**
Mean maturity date (days)	142.85 a	141.46 a	-1.4

*** Significant at the 0.05 and 0.01 probability levels, respectively, according to t-tests. † Means within rows followed by the same letter are not significantly different at the 0.05 level of probability according to Duncan's multiple range test.

Single-plant to progeny-row inbreeding, without intentional selection, was practiced on the semidwarf stocks for four generations prior to making F_1 hybrids. Phenotypically, the strains that resulted from the four generations of inbreeding appeared to be highly homogeneous for plant height and crop maturity. These inbred strains were assumed to be a fixed set of homozygous lines about which inferences could be drawn.

The six semidwarf strains, 15 F_1 hybrids, and TM-1 were planted in single-row plots in a randomized complete-block design with three replications on 15 May 1974, at Lubbock, Tex. The plots were 12 m long with 1 m between rows. Each plot was thinned to 35 plants/plot with about 30 cm between plants. Data were not taken from plants on the ends of the plots. The plots received 15 cm of irrigation water before planting and 10 cm during the summer. Fifty-six cm of rainfall occurred during the growing season.

The characters studied were plant height (cm), mainstem internode length (cm), fruiting-branch internode length (cm), number of mainstem nodes (no.), node of the first fruiting branch (no.), and mean maturity date (days). For further information on how these characters were measured, the reader is referred to Quisenberry (1975).

Analyses of variance procedures were used to compare the semidwarf strains to the normal-height stock. The diallel analysis developed by Jinks (1954) and Hayman (1954a, 1954b) was used to estimate the genetic and environmental parameters associated with the characters.

RESULTS AND DISCUSSION

The normal-height stock, TM-1, was greater in plant height, had longer mainstem internodes, and was later in crop maturity than the semidwarf strains (Table 1). The length of the fruiting-branch internodes was statistically the same for TM-1 and the Paymaster entries. The number of mainstem nodes was the same for TM-1, Ysleta compact, and Paymaster 266.

Table 3. Mean squares from analyses of variance of diallel tables for each character.

Source	df	Plant ht.	Internode length		No. of nodes	Node first fruiting branch	Mean maturity date
			Main stem	Fruiting branch			
			cm				days
a	5	389.13**	0.445**	9.62**	20.43**	5.39**	1,480.38**
b	15	48.01	0.099*	0.64*	1.74	0.30*	60.56*
b_1	1	111.52	0.243	0.37*	0.90	0.76*	28.98
b_2	5	88.37**	0.201**	1.46**	0.82	0.25**	103.99**
b_3	9	18.54	0.027	0.21	2.34	0.25	39.94
rx a	10	37.24	0.067	0.50	1.12	0.08	33.52
rx b	30	29.38	0.039	0.29	1.49	0.15	24.19
rx b_1	2	43.57	0.056	0.01	0.92	0.04	39.11
rx b_2	10	14.41	0.027	0.15	0.65	0.04	8.25
rx b_3	18	36.12	0.043	0.41	2.01	0.22	31.38

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

Table 4. Analyses of variance of W_r-V_r regression of W_r on V_r to test the adequacy of the model.

	Plant ht.	Internode length		No. of nodes	Node of fruiting branch	Mean maturity date	
		Main stem	Fruiting branch				
Analyses of W_R-V_R :							
Source	df	Mean squares					
Replications	2	155.55	0.0004	0.07	1.33	0.02	182.19
Arrays	5	182.07	0.0004	0.02	0.41	0.01	221.13
Error	10	246.77	0.0005	0.03	0.19	0.01	334.51
Regressions of W_R-V_R :							
Regression coefficient (b_1)	0.64	0.77	0.70	0.56	0.78	0.95	
$b_1 - \bar{x}, t =$	2.18	0.87	1.99	4.70**	2.19	0.90	
$b_1 = 0, t =$	3.84*	2.91*	4.64**	5.98**	7.78**	18.74**	

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

TM-1 and DSR 6-19 had the same node of the first fruiting branch. The two CA strains were short, compact plants, with a low node of the first fruiting branch, and extremely early in crop maturity. Significant variation existed among the semidwarf strains for each of the characters measured. Significant differences for at least one character (and usually more than one) differentiated each possible pair of semidwarf strains.

The F_1 hybrids were taller in plant height, had longer mainstem and fruiting-branch internodes, initiated fruiting branches at a lower node on the mainstem, and were earlier in crop maturity than the parental strains (Table 2). Overall heterosis, expressed as the percent deviation of the F_1 hybrids from mid-parent values, was small but significant for plant height, mainstem and fruiting-branch internode length, and node of the first fruiting branch.

Mean square values from diallel analyses of variance for each character are shown in Table 3. The a item, which measures only additive genetic variance in the absence of a significant b_2 item, was highly significant for every character measured. The b_1 item was significant for fruiting branch internode length and node of the first fruiting branch. This item evaluated the mean deviations of the F_1 's from their mid-parental values and was significant when the domi-

Table 5. Mean estimates and standard errors of genetic and environmental parameters and mean ratios to estimate genetic characteristics of the population.

Parameters	Plant ht.	Internode length		No. of nodes	Node of fruiting branch	Mean maturity date
		Main stem	Fruiting branch			
D [†]	40.07 ± 6.38	0.042 ± 0.009	1.53 ± 0.12	2.68 ± 0.28	0.52 ± 0.04	151.67 ± 7.31
H ₁	51.07 ± 16.20	0.108 ± 0.024	0.66 ± 0.30	1.52 ± 0.71	0.28 ± 0.08	62.08 ± 18.56
H ₂	36.56 ± 14.47	0.068 ± 0.022	0.40 ± 0.27	1.54 ± 0.64	0.25 ± 0.08	43.59 ± 16.58
F	8.83 ± 15.59	0.026 ± 0.023	0.66 ± 0.29	0.04 ± 0.13	-0.04 ± 0.09	3.00 ± 17.86
h ₂	27.17 ± 9.74	0.051 ± 0.015	0.14 ± 0.18	0.07 ± 0.43	0.32 ± 0.06	11.79 ± 11.16
E	17.31 ± 2.41	0.025 ± 0.004	0.21 ± 0.05	0.78 ± 0.11	0.07 ± 0.01	14.50 ± 2.76
Ratios						
Dominance	1.13 ± 0.17	1.60 ± 0.45	0.66 ± 0.05	0.75 ± 0.22	0.74 ± 0.16	0.64 ± 0.03
$\bar{u}\bar{v}$ ‡	0.18 ± 0.01	0.16 ± 0.02	0.15 ± 0.02	0.25 ± 0.03	0.22 ± 0.03	0.18 ± 0.02
K _D /K _R §	1.22 ± 0.06	1.47 ± 0.53	2.00 ± 0.30	1.20 ± 0.34	0.88 ± 0.15	1.03 ± 0.18
Heritability	0.33 ± 0.12	0.23 ± 0.11	0.76 ± 0.07	0.47 ± 0.08	0.51 ± 0.09	0.62 ± 0.04

† D is the additive genetic variance, H₁ and H₂ are dominance genetic variances, F is the covariance of additive and non-additive effects, h₂ is the overall dominance of all heterozygous loci, and E is the environmental variance.

‡ $\bar{u}\bar{v}$ is H₂/4H₁ and estimates the average frequency of negative vs. positive alleles.

§ K_D/K_R is the ratio of dominance to recessive alleles.

nance deviations of the genes were predominately in one direction. The b_2 item was significant for all characters except for the number of mainstem nodes. Significance of this source indicated that the mean dominance deviations of the F₁'s from their mid-parental values differed over the F₁ arrays. These arrays differed if some parents contained more dominant alleles than others did. The test of the b_3 item was non-significant for all characters. This indicated that specific combining ability was not associated with any of the hybrid combinations. Analyses of the environmental variances of the parents ($r \times a$) and of the F₁ hybrids ($r \times b$) indicated that they were not significantly different. In relative size, the parents had the larger environmental variance for four characters; the F₁ hybrids for two.

Analyses of variance of $W_r - V_r$ and the regression between the array variances (V_r) and the parent-offspring covariances (W_r) were conducted to test the assumption of an additive-dominance model with additive environmental effects and independence of the genes in action and in distribution (Mather and Jinks, 1971). The difference in the magnitude of $W_r - V_r$ over arrays was not significant for any character (Table 4). Since $W_r - V_r$ is expected to be constant for an additive-dominance model with independent gene distribution, there is little reason to doubt the adequacy of the model for the six characters. The linear regression of V_r on W_r showed that the regression coefficients (b_1) were significantly greater than zero for each character but significantly less than one for only the number of mainstem nodes. The value of one is expected if nonadditive genetic variation is present as dominance variation only. Thus, the two analyses agreed in showing that the additive-dominance model was satisfactory to explain the variation present.

The use of second-degree statistics allowed estimates of genetic and environmental components to be made for each character (Table 5). Although no precise estimate of the errors of these components are available, the consistency of their relative magnitude over replicates provides some indication of their statistical significance. The additive component (D) was significant for all characters. Generally, levels of significance for the dominance components H₁ and H₂ varied,

depending upon the character. The environmental component (E) was significant for all characters.

The estimated genetic and environmental components were combined into ratios to estimate additional genetic characteristics of this fixed population (Table 5). All characters, except plant height and mainstem internode length, fell within the range of partial dominance as measured by the ratio (H₁/D)^{1/2}. The ratio for plant height and mainstem internode length was in the overdominance range (> 1); however, when confidence limits were placed on the ratios, the lower limit of the interval fell within the region of partial dominance as was suggested by the parental and F₁ means.

The ratio (H₂/4H₁) provides an estimate of the average frequency of negative (u) vs. positive (v) alleles (at loci exhibiting dominance) in the parents with a maximum value of 0.25. Estimates of uv showed that for plant height, mainstem and fruiting-branch internode lengths and mean maturity date the parents probably had an unequal distribution of alleles at those loci that exhibited dominance. These results agreed with the previously discussed significant b_2 items (Table 3).

The ratio of $[4(DH_1)^{1/2} + F]/[(DH_1)^{1/2} - F]$ estimates the total number of dominant (K_D) to recessive (K_R) alleles in the parents. This ratio (K_D/K_R) indicated that more dominant than recessive alleles were present for plant height and mainstem and fruiting-branch internode length (K_D/K_R > 1) and that the dominants and recessives were fairly evenly divided for node of the first fruiting branch, and mean maturity date (K_D/K_R ≤ 1).

Heritability was measured as the ratio of the additive, or additive × additive variance, or both, to the total phenotypic variance (Crumpacker and Allard, 1962). Heritability was relatively low for plant height and mainstem internode length, intermediate for number of mainstem nodes and node of the first fruiting branch, and high for fruiting-branch internode length and mean maturity date (Table 5).

Several assumptions are made when diallel analyses are used to evaluate the genetic and environmental components associated with quantitatively inherited characters (Hayman, 1954b). These assumptions are: (i) diploid segregation, (ii) homozygous parents, (iii)

no reciprocal differences, (iv) no genotype-environmental interaction within locations and years, (v) no epistatic gene action, (vi) no multiple alleles, and (vii) uncorrelated gene distributions (Crumpacker and Allard, 1962). Generally, those assumptions were met. Upland cotton is an amphidiploid and segregates in a diploid-like manner (Endrizzi, 1962). The parental semidwarf strains were self-pollinated for four generations and appeared to be phenotypically uniform within strains; however, some heterozygosity probably remained. This residual heterozygosity in the parents probably caused the degree of dominance to be underestimated, asymmetry of the gene distribution to be exaggerated, and the proportion of dominants to be overestimated (Hayman, 1954b). Studies by White and Kohel (1964) and Al-Rawi and Kohel (1969) indicated that reciprocal differences did not occur for plant height, number of mainstem nodes, node of the first fruiting branch, and earliness of crop maturity in the stocks they studied. A Barlett's test for homogeneity of variances showed no significant chi-square deviations for any of the characters, indicating that genotype-environment interactions within the location were not present. The assumptions of (v) no epistatic gene action, (vi) no multiple alleles, and (vii) uncorrelated gene distributions were tested with the other assumptions as a whole by the analyses of variance of $W_r - V_r$ and the regressions of W_r on V_r (Table 4); those results showed that these assumptions were valid.

In summary, the genetic variation for all plant height and crop maturity traits was primarily additive with an indication of a small dominance component for all traits except number of mainstem nodes. Relatively large environmental components (E) were associated with plant height and mainstem internode length. The inheritance of plant height and mainstem and fruiting-branch internode length were somewhat similar, i.e., the F_1 hybrids were larger in these traits than the parental lines, and the environmental variances of the parents were larger than the F_1 's. However, fruiting-branch internode length appeared to differ somewhat from plant height and mainstem internode length in the relative magnitude of the environmental components, as exhibited in heritability. The number of mainstem nodes appeared to be associated with additive genetic variance. The inheritance of node

of the first fruiting branch and mean maturity date were similar, i.e., the F_1 hybrids were smaller than the parents in mean performance, and the size of the dominance ratio and heritability estimates were similar.

The data suggest that several types of semidwarfism have been developed in upland cotton. Since these different types of semidwarfism are primarily associated with additive genetic variance, they should respond to selection for plant height and maturity traits in the development of new cultivars. If these sources vary in agronomic traits, besides those that control plant height and crop maturity, it should be possible to generate new semidwarf populations from which selection and cultivar improvement for various traits would be feasible.

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