

THE INHERITANCE OF BROWN LINT IN NEW WORLD COTTONS

By J. B. HUTCHINSON

Empire Cotton Growing Corporation, Cotton Research Station, Trinidad, B.W.I.

I. INTRODUCTION

Harland (1935) summarized previous work on the inheritance of brown lint in New World cottons, and added an account of the genetics of the brown lint of Enan's brown Egyptian. He showed that the brown genes which he terms K^H (from Guatemala khaki) and K^B (from Enan's brown) are duplicates. They have been assigned the symbols Lc_1^K and Lc_2^K respectively by Hutchinson & Silow (1939). More recently, Silow (1944*a, b*) has made an extensive study of the inheritance of brown lint in Asiatic cottons, and has demonstrated a remarkable interrelation between selective forces and gene content in determining the genotypic pattern governing the expression of lint colour. The present investigation was undertaken with a view to comparing the lint-colour situation in the New World allopolyploid cottons with that in the Old World diploids, and though studies of main gene homology are not complete, the minor gene situation has been clarified, and much information worthy of record has been accumulated.

Lint colour has been graded against a series of standards first established by Harland (1935). Some modifications have become necessary since Harland's paper was published (see also Silow, 1944*a*). At the lower end of the scale finer distinctions are now recognized in order to facilitate the study of genes which impart a cream or very faint brown tinge to the lint. Harland's Triumph is now assigned to grade 0, and most white Sea Islands grade at 0-0.5, occasionally going as high as 1. 1.5 has been inserted to cover a common very faint brown type that does not reach the intensity of grade 2. The choice of standards to represent these fine distinctions has been a matter of considerable difficulty, and it should be emphasized that so far as possible only intensity of colour has been estimated, and not shade. Shade differs very considerably in different crosses but, so far, only general observations have been made on it. The greatest difference in shade is between *Gossypium barbadense* material, which gives a range of creams, and *G. hirsutum* vars. *punctatum* and *marie-galante*, which give faint grey-browns. Harland's *G. barbadense* var. *darwinii* strain T244 (W4-2) remains the standard grade 5. Evidence will be presented later for the conclusion that Harland's Guatemala khaki was heterozygous for a lint-colour intensifier, and the current representative of the type (strain UA3-7) only grades 5 or 6. Similarly, the current *G. tomentosum* (W9-1) grades 6, as against 10 recorded by Harland for the original T22. Seed cotton grading 10 is still in existence on herbarium sheets.

In taxonomy, the present author's classification (Hutchinson, 1946) has been used throughout. The strains used are listed in Table 1, and Harland's type numbers are given for all strains studied in his lint-colour papers.

II. DATA

(a) *Lint colour*

Crosses were made between brown and white, and between pairs of browns. F_1 's were backcrossed to white. Where necessary, 2nd and sometimes 3rd backcross generations were grown also. Early crosses were all intraspecific, as it was thought that interspecific hybridization would result in unclassifiable colour arrays. It soon became evident, however, that the nature of the minor genotype was the most important factor in

Table 1. *Name, origin and colour grade of strains used in lint-colour crosses*

Name	Harland's no.	Origin	Type no	Lint-colour grade
<i>G. hirsutum</i> (Upland)				
Triumph	T57	U.S.A.	UA2-1	0
Acala okra		U.S.A.	UA2-4	0
Virescent yellow		U.S.A.	UA2-7	0
U4		South Africa	{ UA8-1 UA8-22	{ 0 0
Guatemala khaki	T34	Guatemala	UA3-7	5-6
Oaxaca brown		Mexico	UA3-1	6
Mexican brown		Mexico	UA3-5	7
Cauca mahogany		Colombia	UA5-3	8
<i>G. hirsutum</i> var. <i>punctatum</i>				
Gambia brown		Gambia	RA8-1	3
Haiti wild		Haiti	RA1-1	5
Fiji wild		Fiji	W9-4	6
<i>G. hirsutum</i> var. <i>marie-galante</i>				
Conaree wild		St Kitts, B.W.I.	RP1-22	1-5
<i>G. mustelinum</i>		Colombia	RP5-4	5
<i>G. barbadense</i>				
Sea Island	T18	St Vincent, B.W.I.	BA1-1	0-5
Sea Island crinkled		St Vincent, B.W.I.	Gen. 19	0-5
Sea Island superokra		Hybrid origin	Gen. 27	0-5
Gen. 11		Hybrid origin	Gen. 11	0-5
Pardo 2		Piura, Peru	BP4-3	2
<i>G. barbadense</i> var. <i>darwinii</i> T244		Galapagos Islands	W4-2	5
Enan's brown	T3	Egypt	BA8-1	8
Pardo 1		Piura, Peru	BP4-2	9
Pardo 3		Piura, Peru	BP4-4	9
<i>G. tomentosum</i>				
Tomentosum		Hawaii	W9-1	6

determining the sharpness of the colour segregations. In inter-Upland crosses, and in many crosses between Uplands and other varieties of *G. hirsutum*, a white or 'off-white' class could be clearly distinguished from the brown classes. In *G. barbadense*, on the other hand, readily separable colour classes were only obtained in crosses involving very wide colour differences. *G. barbadense* browns were then crossed, and backcrossed, to Upland white, and a more satisfactory analysis was obtained. *G. tomentosum* was crossed by both *G. barbadense* and *G. hirsutum* white, but, as was expected, the *G. hirsutum* backcross gave the better data. Frequency arrays of lint-colour grade in segregating progenies are given in Tables 2-5.

In the Upland series (Table 2) Guatemala khaki was taken as the standard. According to Harland (1935) his type was graded 7. This appears inconsistent with his 1932 record, in which he stated that it was 'pale brown', and with the behaviour of current stocks, which grade at 5 or 6. Harland's field records show that in some F_2 progenies heterozygous browns as high as grade 5 were obtained, whereas in others the heterozygotes

graded 2 or occasionally 3. It is probable, therefore, that the original stock was heterozygous for an intensifier, which has now been lost. Pale brown Guatemala khaki gave a simple 1 : 2 : 1 ratio with white (Harland, 1932). In Table 2 is given a frequency array of an F_2 of Guatemala khaki \times Virescent yellow, in which there were

11 bright white : 15 grades 1-5-3 : 13 grades 5 and 6,

which is a fair approach to the expected 1 : 2 : 1. Fourteen of the fifteen intermediates were grades 1-5 and 2, and it will be shown below that this group matches a dilute heterozygous brown class obtained in other crosses involving Lc_1^K .

Table 2. *Frequency arrays of lint-colour grade in F_2 and backcrosses involving Upland brown*

Cross	Genera- tion	Lint-colour grade										Total		
		0	0.5	1	1.5	2	3	4	5	6	7		8	9
Brown \times white														
Guatemala khaki \times Virescent yellow	F_2	11	—	—	10	4	1	—	2	11	—	—	—	39
Oaxaca brown \times U4	F_2	5	—	—	3	—	1*	1	—	4	—	—	—	14
$F_1 \times U4$	B.C.	107	—	14	29	21	15	44	—	—	—	—	—	230
Mexican brown \times U4	F_2	3	—	2	2	—	—*	1	5	4	3	—	—	20
$F_1 \times U4$	B.C.	57	—	2	5	20	11	8	9	2	—	—	—	114
Cauca mahogany \times Acala okra	F_2	18	—	—	—	—	—	—	—	—	3*	31	7	59
$F_1 \times U4$	B.C.	51	—	—	—	—	—	—	—	—	54	—	—	105
Brown \times brown														
Oaxaca brown \times Guatemala khaki	F_2	—	—	—	—	—	—	—	9	39*	49	6	—	103
$F_1 \times U4$	B.C.	—	—	6	36	44	89	10	—	—	—	—	—	185
Mexican brown \times Guatemala khaki														
F_1 485	F_2	—	—	—	—	—	—	1	1	28*	17	—	—	47
F_1 485 \times U4	B.C.	—	—	—	25	49	14	24	23	—	—	—	—	135
F_1 486	F_2	—	—	—	—	—	—	—	—	36	76	16	5	133
Haiti wild \times Guatemala khaki														
$F_1 \times U4$	B.C.	3	—	3	4	1	3	3*	3	—	—	—	—	20

One grade 0 plant selfed gave 96 plants, all clear white

* Indicates grade of F_1 parent.

Two more browns from Central America, and Cauca mahogany from Colombia, gave single-factor segregation with white, the white class being sharply distinguished, and bright white. The segregating progenies may be summarized as follows:

Cross	Generation	Observed	Expected
Oaxaca brown \times U4	F_2	5 white : 9 grades 1-5-6	3.5 : 10.5
	B.C.	107 white : 123 grades 1-4	115 : 115
Mexican brown \times U4	F_2	3 white : 17 grades 1-7	5 : 15
	B.C.	57 white : 57 grades 1-6	57 : 57
Cauca mahogany \times Acala okra	F_2	18 white : 41 grades 7-9	14.75 : 44.25
	B.C.	51 white : 54 grade 7	52.5 : 52.5

The two Central American browns gave similar ranges in the brown class, but the coloured segregates in both F_2 and backcross of Cauca mahogany were very much darker than in the brown crosses, and the dominance of mahogany was very much higher than that of brown. All coloured segregates were definitely mahogany in colour, and distinct from all but the darkest segregates obtained in crosses of Upland browns. The belief that mahogany results from the action of a gene distinct from those governing brown is supported by its pleiotropic effects on the length and secondary thickening of the lint hairs (see below). Unfortunately, no data are available from crosses of mahogany with brown, and pending results from a direct test for allelomorphism, no symbol will be assigned to it.

The two other Central American browns were crossed by Guatemala khaki, and F_2 's and backcrosses to white were grown to test for homology. No whites were recovered from either of the crosses, so it is evident that all three strains carry brown genes at the Lc_1 locus. The other two browns are darker than Guatemala khaki, Mexican brown being almost mahogany. In the interbrown F_2 's, homogeneous frequency arrays were obtained, and it was evident that whatever minor differences existed between the parents, they were too small to give sharp segregation on selfing. In the backcrosses of the interbrown crosses to white, and in the direct crosses and backcrosses of the dark browns \times whites, most of the frequency arrays are bimodal with a minimum about grades 2-3, and even where they are not, when the material was set out for grading it could be separated on shade into light browns of grades 1, 1.5 and 2 similar to those obtained in the Guatemala khaki \times Virescent yellow cross, and rusty browns of grade 3 and upwards. Evidently, heterozygotes between brown and white are of two kinds,

Table 3. *Observed and expected frequencies of white, light brown, and rusty brown in crosses involving dark browns*

Cross	Generation	Lint colour			Total	
		White lc_1	Light brown $Lc_1^K lc_1 lru$	Rusty brown $Lc_1^K Lru$		
Intense brown \times white						
Oaxaca brown \times U4	Obs.	F_2	5	3	6	14
Expected (4 : 2 : 10)			3.5	1.75	8.75	14
$F_1 \times$ white	Obs.	B.C.	107	64	59	230
Expected (2 : 1 : 1)			115	57.5	57.5	230
Mexican brown \times U4	Obs.	F_2	3	4	13	20
Expected (4 : 2 : 10)			5	2.5	12.5	20
$F_1 \times$ white	Obs.	B.C.	57	27	30	114
Expected (2 : 1 : 1)			57	28.5	28.5	114
Intense brown \times brown						
Oaxaca brown \times Guatemala khaki						
$F_1 \times$ white		B.C.	—	85	99	185
Expected (1 : 1)			—	92.5	92.5	185
Mexican brown \times Guatemala khaki						
$F_1 \times$ white		B.C.	—	74	61	135
Expected (1 : 1)			—	67.5	67.5	135

and the difference between the grade 5-6 brown of Guatemala khaki and the intense brown of the other Central American types may be ascribed to an intensifier, Lru , which has its greatest effect in the range occupied by the heterozygous class. The observed proportions of white, light brown and rusty brown in crosses involving dark browns are compared with expectation in Table 3. Agreement with expectation was satisfactory, considering the small size of the F_2 families. The intensifier Lru acts very largely as a dominance modifier, but since there is a distinct difference between Guatemala khaki and the Mexican browns carrying the intensifier, it is evident that its effect is not confined to the heterozygote, and the smaller effect in the higher grades is as would be expected if colour is determined in such a way that saturation is approached asymptotically.

Two sister F_1 's of Mexican brown \times Guatemala khaki gave F_2 's differing somewhat in colour intensity, and it is possible that other minor colour intensifiers besides Lru are to be found among Upland browns. It will be seen that a cross between intense brown and a white carrying Lru would give a progeny closely similar to that obtained from Acala okra \times Cauca mahogany. Harland's field records show that in Acala okra \times

Guatemala khaki F_2 , a simple 1:2:1 distribution is obtained, similar to that in Guatemala khaki \times Virescent yellow F_2 . Hence, Acala okra lacks intensifiers, so it is clear that the mahogany colour of Cauca mahogany is not due to a K gene plus intensifiers, but to an intrinsically darker gene.

At the foot of Table 2 are given data from a cross of Haiti wild \times Guatemala khaki. In a backcross to white there were three clear white segregates in a progeny of twenty, which is close to expectation on a duplicate factor hypothesis. One of the whites was selfed and gave a progeny consisting of clear whites only, so there can be no doubt that the brown genes of Guatemala khaki and Haiti wild are distinct. The progeny was too

Table 4. Frequency arrays of lint-colour grade in F_2 's and backcrosses involving punctatum and marie-galante browns

Cross	Generation	Lint-colour grade								Total	
		0	0.5	1	1.5	2	3	4	5		6
Brown \times white											
Gambia brown \times Acala okra	F_2	23	—	11	10*	19	10	6	—	—	79
$F_1 \times U4$	B.C.	51	—	—	28	24	—	—	—	—	103
Haiti wild \times Acala okra	F_2	6	14	8	4	21	36*	36	11	1	137
$F_1 \times U4$	B.C.	24	4	21	12	24	5	—	—	—	90
Four grade 3 selections from the 1st backcross were backcrossed again.											
GC198 $\times U4$	2nd B.C.	11	20	7	6	11	12*	—	—	—	67
GC199 $\times U4$	2nd B.C.	6	2	1	1	3	1*	—	—	—	14
GC200 $\times U4$	2nd B.C.	21	10	4	5	19	15*	7	—	—	81
GC201 $\times U4$	2nd B.C.	28	—	18	9	17	15*	—	—	—	87
Fiji wild \times Acala okra	F_2	—	12	—	3	7*	29*	13	—	—	64
$F_1 \times U4$	B.C.	82	1	1	11	24	17	1	—	—	137
Fiji wild $\times U4$	F_2	26	11	5	8	11	45*	46	—	—	152
Conarec wild \times Acala okra	F_2	9	129	22	83*	49	9	—	—	—	301
$F_1 \times U4$	B.C.	175	36	48	67	—	—	—	—	—	327
<i>G. mustelinum</i> \times Acala okra	F_2	14	31	31	19	52*	23	—	—	—	170
$F_1 \times U4$	B.C.	61	25	7	22	37	19	—	—	—	169
Selections from 1st B.C. backcrossed a second time.											
One grade 1 plant gave whites and very light coloured up to grade 1.											
Grade 2 : 476 $\times U4$	2nd B.C.	35	—	17	17	6*	—	—	—	—	75
Grade 3 : 475 $\times U4$	2nd B.C.	36	6	14	13	7	—*	—	—	—	76
Brown \times brown											
Haiti wild \times Gambia brown	F_2	—	—	—	—	—	—	4*	32	8	44
$F_1 \times U4$	B.C.	Gave nearly all grade 2, with a few at 1.5 and 3									
Fiji wild \times Gambia brown	F_2	—	—	—	—	—	—	—*	19	—	19
$F_1 \times U4$	B.C.	—	—	5	26	8	9	—	—	—	48
<i>G. mustelinum</i> \times Gambia brown	F_2	—	—	—	—	—	—*	—	10	—	10
$F_1 \times U4$	B.C.	—	—	—	3	—	—	—	—	—	3

* Indicates grade of F_1 , or brown parent of 2nd backcross.

small to determine with confidence whether the browns fell into distinct classes. Haiti wild is a *G. hirsutum* var. *punctatum* type. This and other brown *punctatum*s, and two brown var. *marie-galante* types, were crossed to white Uplands, and all were intercrossed to test the identity of the brown genes concerned. Frequency arrays are given in Table 4.

Gambia brown, which is representative of the commensal or cultivated races of var. *punctatum* (see Hutchinson & Silow, 1946), gave clear single-factor segregation with white, the white class being distinct, and bright white (grade 0). The distribution of the brown class was lower than in the Guatemala khaki \times Virescent yellow cross, as would be expected from the lower grade of the Gambia brown parent. Moreover, the homozygous and heterozygous browns do not fall into distinct classes. The *punctatum* brown

gene, therefore, is of lower intensity than Lc_1^K , and from the Haiti wild \times Guatemala khaki cross it is evident that it occupies a duplicate locus.

Haiti wild and Fiji wild represent the secondarily wild xerophytic form of var. *punctatum* formerly known as *G. taitense* (see Hutchinson & Silow, 1946). In crosses and backcrosses to white, bimodal frequency arrays were obtained with minima at 1-1.5. The lower class consisted of whites and 'off-whites', and although in two backcross progenies a minimum at 0.5 was also recorded, it was not possible to distinguish clear whites from 'off-whites' with certainty. Between browns and white plus 'off-white', however, single-factor segregation occurred. Inspection of the seed cotton led to the conclusion that plants graded 1.5 belonged in the brown class, and with this assumption the F_2 and backcross data may be summarized as follows:

Haiti wild \times Acala okra			
F_2	28 white and 'off-white' :	109 brown	137
	34	102	
$F_1 \times$ white	49 white and 'off-white' :	41 brown	90
	45	45	
1st b.c. browns \times white	128 white and 'off-white' :	121 brown	249
	125	125	
Fiji wild \times Acala okra			
F_2	12 'off-white' :	52 brown	64
	16	48	
$F_1 \times$ white	83 white and 'off-white' :	52 brown	135
	67	67	
Fiji wild \times U4			
F_2	42 white and 'off-white' :	110 brown	152
	38	114	

Agreement with expectation on a single major factor difference was satisfactory.

The type of var. *marie-galante* from Colombia classified by Watt (1907) as *G. mustelinum* was also crossed by white and gave a minimum at grade 1.5 in F_2 and at grade 1 in the backcross. A first backcross grade 1 plant backcrossed a second time gave whites and 'off-whites' only, so at least a part of the grade 1 class should be included in the non-browns. Dividing between grades 1 and 1.5 there were:

In F_2	76 white and 'off-white' :	94 brown
In the b.c.	91 white and 'off-white' :	78 brown

The fit to expectation on a single-factor basis was very poor in F_2 , but the distinction between the brown and white classes was poor, and with such an ill-defined minimum in the array, considerable misclassification is to be expected. One grade 2 and one grade 3 plant from the first backcross were backcrossed again to white and gave clear segregation to white and brown as follows:

Grade 2 parent	35 clear white	: 40 brown
Grade 3 parent	42 white and 'off-white' :	34 brown

Evidently one major factor difference accounts for the greater part of the variation.

Haiti wild, Fiji wild, and *G. mustelinum* were all crossed with Gambia brown, and F_2 's and backcrosses to white were grown to test for identity of the brown genes. F_2 's gave browns about grade 5, and backcrosses gave browns of grades 1.5-2 only. The data fit expectation on the theory that the same major brown-lint factor is concerned in each cross. The range of brown grades covered is similar in all cases, and a comparison of F_2 and backcross browns in the intercrosses shows that dominance is absent.

The grade 3 brown (Gambia brown) gave clear segregation into browns and bright whites. The grades 5 and 6 browns gave less clear segregation, generally some higher

grades in the brown class, and a proportion of 'off-whites' (grades 0.5 and 1) in the white class, indicating the presence of minor genes for brown that change white to 'off-white', and act as intensifiers in the presence of a major brown gene. It will be noted that the intensifier effect in these crosses is quite different from that observed in Upland crosses segregating for *Lru*. The major effect of the *punctatum* minor genes is the production of 'off-whites' in the non-brown class. In the brown class the range of the heterozygotes

Table 5. Frequency arrays of lint-colour grade in F_2 's and backcrosses involving *G. barbadense* brown

Cross	Genera- tion	Lint-colour grade										Total			
		0	0.5	1	1.5	2	3	4	5	6	7		8	9	
Pardo 2 × Acala okra															
$F_1 \times U4$	B.C.	41	37*	8	12	—	—	—	—	—	—	—	—	—	98
<i>darwinii</i> × Sea Island superokra															
-49	F_2	—	1	2	16*	13	11	2	—	—	—	—	—	—	45
-50	F_2	—	—	1	6	7*	16	3	—	—	—	—	—	—	33
		B.C. to Sea Island ranged from 1.5 to 0. Too much stain for accurate grading, and no sign of segregation into distinct classes.													
<i>darwinii</i> × Acala okra															
Three 1st B.C. browns × Triumph	2nd B.C.	1	2	3	6	3	3	—	—	—	—	—	—	—	18
		1	1	1	2	1	—	—	—	—	—	—	—	—	6
		5	18	3	7	2	—	—	—	—	—	—	—	—	35
Five 2nd B.C. browns (grades 1.5 and 2) × U4	3rd B.C.	33	6	—	27*	11	—	—	—	—	—	—	—	—	77
		11	5	4	5*	10	—	—	—	—	—	—	—	—	35
		7	13	6	6	16*	6	—	—	—	—	—	—	—	54
		72	—	—	46	13*	2	—	—	—	—	—	—	—	133
		17	4	4	7	8*	6	—	—	—	—	—	—	—	46
Euan's brown × U4	F_2	5	—	—	6	5	8*	1	5	5	1	—	—	—	36
$F_1 \times U4$	B.C.	85	10	43	9	19	85	16	—	—	—	—	—	—	267
Pardo 1 × Sea Island superokra	F_2	—	1	1	4	—	—	—	—	—	—*	—	—	—	38
$F_1 \times$ Gen. 11	B.C.	22	4	15	—	—	—	—	—	—	—	—	—	—	42
Pardo 1 × U4	F_2	—	4	—	3	—	—	—	—	—*	4	5	2	—	18
$F_1 \times U4$	B.C.	10	—	1	3	1	—	—	—	3	4	9	—	—	31
Pardo 1 × Acala okra	F_2	1	6	—	—	1	—	—	—	4	2	11	4	—	29
$F_1 \times U4$	B.C.	22	—	2	—	—	—	—	—	3	14	1	—	—	42
Pardo 3 × Sea Island superokra	F_2	47			—	—	—	—	—	—	9*	33	105	—	194
$F_1 \times$ Gen. 11	B.C.	35			—	—	—	—	—	—	—	16	23	—	74
Guatemala khaki × Sea Island crinkled	$F_1 \times$ Sea Island selfed three times gave G1046 (grade 3 brown)														
G1046 × Sea Island	F_2	—	5	5	18	40*	14	—	—	—	—	—	—	—	82
$F_1 \times$ Sea Island	3rd B.C.	—	21	35	46	12*	—	—	—	—	—	—	—	—	114
B.C. brown × Sea Island	4th B.C.	4	5	10	10*	—	—	—	—	—	—	—	—	—	29

* Indicates grade of F_1 or brown parent in a backcross.

is extended upward somewhat, but only by simple intensification and not by the formation of a distinct class, as is the case with the development of rusty brown by *Lru*.

One other var. *marie-galante* brown was tested. Conaree wild is a very light brown grading 1.5. The F_1 of Conaree wild × Acala okra was also grade 1.5. In F_2 an array extending from grade 0 to grade 3 was obtained, with a minimum at grade 1. Separating at that point, however, did not give any approach to a single-factor ratio. In the backcross to U4 a bimodal array was obtained with a minimum at 0.5, but again the distribution could not be accepted as representing simple mono-factorial segregation. Conaree wild was also crossed by Gambia brown, and the F_1 was grade 3. A rather small

F_2 gave an unclassifiable series which included some clear whites. It may be concluded, therefore, that Conaree wild carries one or more minor genes, but not a major brown gene.

Three types of brown were studied in *G. barbadense*, a very light brown (grade 2), two dark browns (grades 5 and 8), and two mahoganies (grades 7 and 9). In the first instance, crosses were made with *G. barbadense* white-lint types, but it soon became evident that, with the exception of the mahogany crosses, clear segregation was not to be expected. For the dual purpose of establishing *G. barbadense* browns on a genotypic background known to give clear segregation with Upland browns, and to provide material for testing homology with Upland browns, the *G. barbadense* coloured types were crossed to Upland whites, and the F_1 's backcrossed to Upland whites. F_2 's, 1st backcrosses, and some 2nd and 3rd backcrosses are available. In addition, a grade 3 brown-lint type (G1046) extracted from a 1st backcross selfed of (Sea Island crinkled \times Guatemala khaki) \times Sea Island was backcrossed three times more to Sea Island (selecting brown segregates each time) to study the effect on Lc_1^K of transference to the Sea Island genotype. Frequency arrays of lint colour in segregating progenies are given in Table 5.

The grade 2 brown Pardo 2 gave with Upland Acala okra an F_1 that was no more than 'off-white' (grade 0.5), and as was to be expected with such a dilute F_1 , it was not possible in F_2 to separate the browns into distinct classes. This brown probably carries one or more minor genes similar to those of Conaree wild (see above).

G. barbadense var. *darwinii*, which is grade 5, gave grade 1.5 and 2 heterozygotes with Sea Island superokra. No clear whites were obtained in F_2 ; and an F_2 from a grade 2 heterozygote gave a rather higher grade frequency array than that from the grade 1.5 F_1 . No clear segregation occurred, and in the backcross a continuous array between 0 and 1.5 was obtained. In a cross to Acala okra, the F_1 was backcrossed to Triumph, and three brown backcross plants backcrossed again. Even in the 2nd backcross no clear segregation was obtained, but two grade 1.5 and three grade 2 plants were backcrossed a third time, and gave clear bimodal frequency arrays with minima at grade 1. In all there were:

Grade	Frequencies					Total
0, 0.5 and 1	39	20	26	72	25	182
1.5, 2 and 3	38	15	28	61	21	163
Total	77	35	54	133	46	345

Evidently one major gene was segregating, and there were also minor genes which resulted in the appearance of forty-two 'off-whites' (grades 0.5 and 1) among the 182 plants in the non-brown class. Harland (MS. data) crossed Guatemala khaki \times *darwinii* and backcrossed the F_1 to U4. In a backcross progeny of twenty-five plants he obtained the following:

Grade	1	1.5	2	3	4	5	6	7
Frequency	2	1	8	7	—	4	2	1

On Harland's system white was grade 1, so there were three whites and 'off-whites' in twenty-five plants. It may be concluded that brown from *darwinii* is independent of Lc_1^K .

Enan's brown (carrying Lc_2^K) crossed by Upland white and backcrossed to Upland white gave similar arrays but with rather higher grades in the brown class. In the backcross it was noted that there was a sharp break at grade 1.5, but that the minimum at 0.5 did not appear to represent a real discontinuity. The absence of 'off-whites' in

the F_2 may be ascribed to the small size of the white class: F_2 and backcross gave satisfactory fits to single-factor expectation, giving in all

F_2 5 whites : 31 browns
 B.C. 138 whites and 'off-whites' : 129 browns

The two Pardo mahoganies (Pardo 1 and Pardo 3), gave single-factor segregation between mahogany and white plus 'off-white', the latter grading up to 1.5. From the distribution in the white plus 'off-white' class in the Pardo 1 crosses it may be concluded that the minor gene content responsible for 'off-white' was similar to that in Enan's brown.

The effect of transferring Lc_1^K from Guatemala khaki to *G. barbadense* is illustrated by the frequency arrays of successive backcrosses of (*G.* 1046 × Sea Island) to Sea Island. From the Upland brown crosses it was concluded that in the absence of intensifiers the Lc_1^K heterozygote grades 1, 1.5 and 2. On a *G. barbadense* background it appears to be of about the same intensity, but, presumably on account of the presence of minor genes, the white class is not distinct from it.

Table 6. Frequency arrays of lint-colour grade in backcrosses involving *G. tomentosum*

Cross	Hair grade	Lint-colour grade						Total	
		0	0.5	1	1.5	2	3		4
Tomentosum × Sea Island superokra F_1 × Gen. 11	T	—	—	1	3	6	5	4*	19
	O	—	3	2	3	—	2	—	10
	Total	—	3	3	6	6	7	4	29
Tomentosum × Acala okra F_1 × U4	T	—	—	—	1	3	12	—*	16
	O	—	10	1	1	1	4	1	18
	Not classed	—	2	1	1	—	1	—	5
	Total	—	12	2	3	4	17	1	39

* F_1 grade.

G. tomentosum was crossed to *G. barbadense* (Sea Island superokra), and Upland (Acala okra). In interspecific F_2 's involving *G. tomentosum* a great range of weak and unbalanced types is obtained, and seedling mortality was so heavy in the field that no data were obtained. In the backcrosses to white, losses were considerable, and the proportions observed must be interpreted with caution on account of the possibility of selective elimination. Frequency arrays of lint colour are given in Table 6. Both F_1 's were grade 4. In the backcross of the *barbadense* hybrid a unimodal array was obtained that could not be further analysed. In the Upland cross, however, the backcross gave a bimodal array with a minimum at grade 1. Dividing between grades 1 and 1.5 there were

14 'off-white' : 25 brown,

which is intermediate between a 1 : 1 and a 1 : 3 ratio. The occurrence of a linkage between brown lint and the characteristic fine tomentum of *G. tomentosum* made it possible to distinguish between single-factor and duplicate-factor segregation. In both backcrosses there were no plants with tomentum in the lowest lint-colour classes, whereas there were tomentose plants in the darkest brown classes. In the Upland backcross, in which the lint-colour segregation was clear, there were

11 'off-white' not tomentose
 7 brown not tomentose
 16 brown tomentose

If there were a single major gene for brown lint, loosely linked with tomentum, 'off-white' tomentose should be as frequent as brown not tomentose, whereas, if there are duplicate brown-lint genes, with tomentose closely linked to one of them, 'off-white' tomentose should be much less frequent than brown not tomentose, as was actually the case. It may be concluded, therefore, that *G. tomentosum* carries duplicate brown-lint genes, one being closely linked to *G. tomentosum* tomentum.

Minor colour genes of the type encountered in *G. barbadense* and in *punctatum* and *marie-galante* are also present in *G. tomentosum*, all the 'white' class being 'off-white'

(b) *Lint-colour and lint-hair characters*

Harland (1935) concluded that in *G. barbadense* both the main gene Lc_2^K (Harland's K^B) and minor genes responsible for the development of light brown in the absence of Lc_2^K have a considerable effect on lint length. In the experiments here reported halo length measurements were made on some crosses, and the available data are summarized in Tables 7-9. The only data available from a cross involving Lc_1^K are from a backcross of (Acala okra \times Guatemala khaki) \times Triumph. The cross was made to discover whether Lc_1^K and leaf shape are linked. Lint colour was classified only as brown or white, and hence the cross is not included in Table 2. The mean lint length of the brown class was slightly greater than that of the white class, but the difference does not appear to be of any significance. Data from crosses involving three types carrying the *punctatum* brown gene are given in Table 8. Differences in length between brown and not-brown classes were very small and without significance. In Table 9 are given data from three crosses involving mahogany, and in these the mahogany class was from 5 to 11 mm. shorter than the white and 'off-white' class.

Lint from selected plants of three crosses, the F_2 of Acala okra \times Gambia brown and two backcrosses of (mahogany \times white) \times white, were submitted to the Shirley Institute for hair tests. Data were provided on effective length, hair weight per cm., hair maturity, and standard hair weight (i.e. hair weight corrected for immaturity count) and are summarized in Table 10. It will be seen that there was no difference in length between white and brown classes in the Gambia brown cross, but brown lint was more immature and coarser (higher standard hair weight) than white cotton. Grade 2 was intermediate between grade 4 and grade 0. In the two mahogany crosses, mahogany lint was very much shorter, more immature, and coarser than white lint. There was little difference between grade 8 and grade 9 mahogany.

(c) *Linkage relations*

Data on the association of brown lint with other genes were collected where possible. The use of crosses to Upland white, though simplifying the classification of lint colour, obscured the segregation of some other characters that can be scored with ease on inter-*barbadense* material. Corolla colour and pollen colour are so dilute on *G. hirsutum* that separation of heterozygotes from the yy and pp homozygotes could not be carried out with confidence. Petal spot (R_2^{AS}) is very unstable on the Upland background, and a large excess of spotless plants was recorded in all progenies, no doubt due to mutation. For these reasons no data are given for the relation between lint-colour genes and Y, P, and R_2^{AS} . No associations suggestive of linkage were observed.

Since lint colour and leaf shape are linked in Old World cottons (Silow, 1944a),

it was of particular interest to see whether a parallel linkage could be found among the New World species. In Table 11 data are given showing the relation of leaf shape to Upland brown (Lc_1^K), *punctatum* brown, Enan's brown (Lc_2^K), *G. tomentosum* brown, and mahogany. It will be seen that free assortment occurred in all crosses.

Table 10. *Hair characters of mahogany, brown, and white classes in crosses involving Gambia brown and Cauca mahogany*

Lint colour	No. of plants	Effective length (1/32 in.)	Hair weight per cm. (10^{-6} mg.)	Immaturity count		Standard hair weight
				Normal	Dead	
Gambia brown \times Acala okra						
4	5	35	168	40	37	320
2	4	35	184	63	11	191
0	5	35	174	70	10	174
(Cauca mahogany \times Acala okra) \times U4						
7	10	30	100	5	70	367
0	10	37	208	58	16	229
(Pardo 3 \times Sea Island superokra) \times Gen. 11						
9	4	36	132	14	40	332
8	6	36	118	14	47	221
White	10	49	122	44	25	153

Table 11. *The relation of leaf shape to lint colour*

Cross	Genera- tion	Brown		White or 'off-white'		Total
		Narrow	Broad	Narrow	Broad	
Upland brown (Lc_1^K)						
(Guatemala khaki \times Acala okra) \times Triumph T57	B.C.	76	83	93	76	328
<i>punctatum</i> brown						
Gambia brown \times Acala okra	F_2	44	12	17	6	79
$F_1 \times U4$	B.C.	29	23	26	25	103
Enan's brown (Lc_2^K)						
(Enan's brown \times Sea Island superokra) \times Sea Island B.C.		26	31	19	26	102
<i>G. tomentosum</i> brown						
(Tomentosum \times Acala okra) \times U4	B.C.	11	11	6	5	33
Mahogany						
Cauca mahogany \times Acala okra	F_2	28	13	12	6	59
$F_1 \times U4$	B.C.	24	30	29	22	105

It has been shown above that the characteristic leaf tomentum of *G. tomentosum* is linked with lint colour. *G. mustelinum* has a dense coating of hair on the leaves, but the hairs are considerably longer than those of *G. tomentosum*. In a backcross of *G. mustelinum* \times Acala okra to the hairy U4, three grades of hairiness could be distinguished with some confidence if grading was done when the plants were growing vigorously. Fifty-one plants were classified for hairiness and lint colour, and gave:

	Very hairy	Hairy	Slightly hairy	Total
Brown	15	12	5	32
'Off-white'	9	7	3	19

There was no suggestion of association between the two characters.

Guatemala khaki Lc_1^K and mahogany were tested for linkage with Virescent yellow (V-v). In F_2 there were obtained:

	Brown grades 5 and 6		Brown grades 1-5-3		White		Total
	Green	Yellow	Green	Yellow	Green	Yellow	
Guatemala khaki × Virescent yellow	9	4	13	2	9	2	39
	Mahogany				White		Total
	Green	Yellow	Green	Yellow	Green	Yellow	
Cauca mahogany × Virescent yellow	176	60	53	31			310

Free assortment occurred in both crosses.

III. DISCUSSION

Since identity tests are not complete, no estimate can yet be made of the number of genes involved in the production of brown lint in New World cottons. Harland has shown that Lc_1^K of Guatemala khaki and Lc_2^K of Enan's brown are independent, and it has been shown above that the major brown gene in *punctatum* is distinct from Lc_1^K . Harland's unpublished data are quoted to show that the major brown gene in *G. barbadense* var. *darwinii* is also independent of Lc_1^K . Beyond this, no data are at present available on major gene homologies. It may be suggested, however, that the mahogany of the Pardos in *G. barbadense* and of Cauca mahogany in *G. hirsutum* are due to the same gene. Cauca mahogany, the only mahogany known in Upland, was collected by Harland in the Cauca Valley in Colombia, an area which is right outside the natural range of *G. hirsutum* and near the centre of variability of *G. barbadense*, and on morphological grounds it is believed to be a dilute hybrid with *G. barbadense*. It is not unlikely, therefore, that the mahogany gene in Cauca mahogany may have been acquired by transference from the latter species.

Silow (1944 a, b) distinguished two classes of genes affecting the lint-colour situation in Old World cottons; colour genes, which change clear white to some shade of brown, and modifiers, which affect the intensity of brown when a colour gene is present. He was able to isolate and study all the colour genes which occurred in his material. Moreover, he showed that most so-called white strains of *G. herbaceum* are very slightly coloured, and with the aid of the Ha- Lc_2 linkage, he demonstrated that this colour is due to the presence of the light brown Lc_2^B colour gene acting with a diluting modifier complex. The situation in the New World cottons has not been so completely analysed. No genotype has been found on which all colour genes give clear segregation and accordingly the group has been subdivided, genes which give brown and mahogany, and which usually segregate clearly from white and 'off-white', being called for convenience major genes, and genes which give light browns, greys and 'off-whites' that are not usually clearly separable from true whites being termed minor genes. It is possible that the synthesis of a strongly intensifying genotype, or the discovery of a linkage with a minor colour gene, might reveal a situation as simple as that in the Old World cottons. On the other hand, it is not unlikely that there are in the New World cottons, which are allopolyploids, considerably more colour genes of small individual effect than there are in the diploids, and their isolation and individual study may be impracticable.

Modifier relationships, on the other hand, seem to be comparatively simple in the New World cottons. Judging by the effect on Lc_1^K of transference from *G. hirsutum* (Guatemala khaki) to *G. barbadense* (Sea Island), there is little difference in modifier

level between the two species. The only well-established modifier effect is that of *Lru* on Lc_1^K in *G. hirsutum* (Upland), where the modifier gene difference is of sufficient magnitude to allow of straightforward Mendelian analysis.

The demonstration that mahogany and Lc_2^K affect lint length and that mahogany and *punctatum* brown affect both hair maturity and fineness adds to the evidence produced by Neely (1943), working with green lint, that colour genes have a profound effect on lint hair development. Harland has suggested that the predominance of white-linted cottons is the result of the disintegration of a primitive brown-lint character complex by human selection for lint length. This does not seem to be supported by the evidence here presented. The colour of most wild species is rather dilute grey-brown, nearer to Conaree wild, than to such types as the Mexican browns or the mahoganies. These dilute browns have little, if any, effect on length in most cases.

Silow (1944 *a, b*) has recently drawn attention to the influence of human selection on the genetics of lint colour. Wherever cotton has been spun by non-industrial communities, naturally coloured lint has been used as a contrast to white or cream in pattern weaving. Silow (1944 *a, b*) pointed out that for such purposes intermediate colours are useless, and the textile craftsman would demand only highly coloured or white lint and not pale browns and greys. Hence a human selection for widely contrasted types arose and Silow was able to detect its effects in the lint colour genotype of the diploid cottons.

The situation in the New World cottons is complicated by their allopolyploid constitution (Hutchinson & Stephens, 1946). Since all American wild species have light brown or greenish brown seed hairs, there can be little doubt that the American wild parent contributed genes for light brown lint to the allopolyploid. In the absence of strong human selection against them, these light brown genes would persist, and may be taken to account for the occurrence of light brown types in areas of high variability, as, for example, Pardo 2 from Peru, and among secondarily wild types such as Conaree wild. Similarly, the minor colour genes giving rise to 'off-whites' in crosses of *punctatum*, *marie-galante* and *barbadense* browns with white may be accepted as relics of the early allopolyploid constitution.

Among the cultivated types of South and Central America, on the other hand, human selection would be practised for colour contrasts, in the same way as it was in the Asiatic cottons. In *G. barbadense*, as in *G. herbaceum* (Silow, 1944*a*), true whites are rare and the commercial whites are, with a few exceptions such as Tanguis, very light creams. Browns are of two kinds. Enan's brown resembles the dark browns of *G. herbaceum* in carrying more than one colour gene and giving complex segregation in crosses with creams of the same species. Mahogany, on the other hand, gives sharp segregation even with the creams of *G. barbadense*. The advantages to a textile craftsman of a genetic mechanism giving a switch from one extreme of colour to the other are manifest, and from illustrations given by Crawford (1942) and from an examination of specimens in the American Museum of Natural History, it is evident that it was the mahogany-cream contrast that was used in pattern weaving by the craftsmen of the ancient Peruvian civilizations.

In *G. hirsutum* true whites are common, and in this respect the species resembles *G. arboreum*, though it does not carry the intensifying modifier complex demonstrated by Silow in the latter species. Mahogany, which corresponds to Silow's khaki in Asiatic cottons, has only been recorded once (in Cauca mahogany) in *G. hirsutum*, and reasons have been given above for believing that in this case it may have been recently intro-

duced from *G. barbadense*. An efficient switch from full colour to white is provided, however, by the use of Lc_1^K with the rusty modifier Lru , and it may be suggested that this combination was probably used for pattern weaving in Central America.

IV. SUMMARY

An account is given of genes causing brown coloration in the lint of New World cottons and of their modifiers. Of the four genes, the independence of Lc_1^K in Upland and Lc_2^K in Egyptian has been demonstrated by Harland (1935). It is here shown that *punctatum* brown and brown from *darwinii* are also independent of Lc_1^K . Mahogany is distinct from these in the intensity of the colour induced, and in being highly dominant. It also has large effects on hair length, maturity and fineness. Two brown genes are present in *G. tomentosum*, but no evidence is available on their homologies.

Emphasis is laid on the distinction between genes which cause the development of colour, and those which only affect intensity when colour is already present. In Upland a gene occurs which intensifies brown but has no effect on white. In its vars. *punctatum* and *marie-galante*, and in *G. barbadense* and *G. tomentosum*, minor colour genes change white to 'off-white', or even pale brown, as well as intensifying brown.

It is shown that the genotypic situation with regard to lint colour can be explained as the consequence of the comparatively recent origin of allopolyploidy from a cross between an Old World cotton and an American wild species with light brown seed hairs, followed by human selection for widely contrasted lint colours (white and deep brown or mahogany) for use in the weaving of patterned textiles.

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