

THE GENETICS OF COTTON.

PART XIV. THE INHERITANCE OF BROWN LINT IN NEW WORLD COTTONS.

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INTRODUCTION.

ALL cultivated species of *Gossypium* are characterised by the presence of unicellular, convoluted hairs springing from the seed coat. Two separate sets of hairs may be present: (a) dense short hairs forming the so-called "fuzz", (b) long hairs from 10 to 65 mm. in length forming the "lint".

According to the variety the lint hairs may range from white, through various shades of cream and brown to almost a mahogany red.

Previous work has been summarised by the writer (1932) and Ware (1932). The results of such investigations may be briefly summarised.

(1) Thadani (1923) and Brown (1927) reported yellow or yellowish brown and white to be allelomorphous in Upland varieties. The writer (1932) found a pale brown Upland type from Guatemala to segregate into brown, intermediate brown and white in a 1 : 2 : 1 ratio.

In the Upland cottons (*G. hirsutum* L.) Ware (1932) found each of the four lint colours, rust, dingy brown, yellowish brown, and green, to be allelomorphous to white. F_1 was always intermediate. To sum up: in Uplands, browns, of whatever shade, are allelomorphous to white, though no attempt has yet been made to elucidate the relationships of the various browns to each other.

(2) In the cross of the dark brown Egyptian variety "Enan's Brown" by pale cream Sea Island, the writer (*loc. cit.*) found inheritance in F_2 to be of the blending type. Later generations showed fairly good segregation into 3 brown : 1 white in some families, and it was considered that a factor pair **K-k** was involved, with several modifying factors.

AIM OF EXPERIMENTS.

The objects of the present experiments were as follows:

To study the inheritance of brown lint in *G. barbadense* L. (Egyptian), in *G. hirsutum* L. (Upland), and in crosses between these species.

METHODS.

The blending previously encountered in Egyptian-Sea Island crosses (1932) rendered it necessary to establish a series of grades by which the various grades of colour could be classified. The following grades were established:

Grade	Type	Species
1	T 57	<i>G. hirsutum</i> L.
2	—	—
3	—	—
4	—	—
5	T 244	<i>G. Darwinii</i> Watt.
6	—	—
7	T 34	<i>G. hirsutum</i> L.
8	T 3	<i>G. barbadense</i> L.
9	—	—
10	T 22	<i>G. tomentosum</i> Nutt.

In the above grades, pure white is grade 1, and grade 10 is the extremely dark brown characteristic of *G. tomentosum* Nutt., a species endemic to the Hawaiian Islands. Between these extremes are eight grades, of which Nos. 5, 7 and 8 are represented by homozygous types. Grades 2-4, 6 and 9 have been encountered in interspecific crosses.

THE EXPERIMENTS.

(1) *Inheritance of brown lint in G. barbadense L.*

Sea Island White T 4 (grade 1) × Enan's Brown Egyptian T 3 (grade 8).

F_1 : Fourteen plants were of grade 3, and two plants of grade 4.

First back-cross— F_1 × Enan's Brown.

Twenty plants were grown. These segregated into light brown and dark brown, though classification was difficult. Eight of each class were selfed, with the results given in Table I.

All plants recorded as full brown produced only browns, *i.e.* grade 6 and above. The different homozygous families varied considerably in grade, some plants being more strongly coloured than the brown parent.

The intermediate brown plants all segregated, sometimes erratically into brown and lighter brown. The parental Sea Island (grade 1) was only

TABLE I.

The first back-cross selfed.

Colour of parent	Family	Grades of brown										Remarks	
		1	2	3	4	5	6	7	8	9	10		
Full brown	G 515	3	2	1	4	.	Homozygous for brown	
	G 516	1	7	2	.		" "
	G 518	6	22	1		" "
	G 519	5	5	6	2	.		" "
	G 522	2	3	3	6	.		" "
	G 523	4	4	.		" "
	G 524	4	8	.		" "
Intermediate brown	G 529	8	10	.	" "	
	G 512	.	1	.	.	1	2	3	4	1	.		
	G 513	.	.	2	1	.	3	5	5	.	.		
	G 514	.	2	6	4	.	4	4	5	.	.		
	G 517	.	.	2	2	2	.	1	2	1	.		
	G 526	3	4	.	4	3	8	3	.	1	.		
	G 527	.	.	2	1	.	7	2	1	.	.		
	G 528	1	.	2	4	2	5	.	4	3	.		
	G 530	1	2	1	.	3	3	1	.	.	.		
	Total	5	9	15	16	11	32	19	21	6	.		

produced in five plants out of 136. Some families of G 513, G 526 and G 527 gave fairly clear segregation into dark brown and light brown, but seriation gives the impression of continuous blending.

It is clear that accepting all grades below 5 as recessive, the allelomorph pair of characters concerned is not brown and white but *brown* and *less brown*.

The second back-cross to T 3 brown.

It was resolved to cross three demonstrated heterozygous plants to T 3 again. The results are as follows:

Family	Grade			
	5	6	7	8
G 513 × 3	.	4	4	2
G 530 × 3	.	4	3	2
G 528 × 3	1	2	5	1

The second back-cross selfed.

Six plants out of series G 530 × 3 were selected for selfing. The results are presented in Table II.

Here it will be seen that both grade 8 plants bred true to dark brown,

as did also a grade 7 plant. Two plants of grade 6 and one plant of grade 7 segregated clearly into dark and light brown.

TABLE II.
Results of selfing second back-cross plants.

Series	Family	Parent grade	Grades of brown								Brown	Light brown	
			1	2	3	4	5	6	7	8			
G 530 × 3	G 2223	8	3	7	10	0
	G 2226	8	5	7	12	0
	G 2232	7	1	3	8	0
	G 2225	6	1	1	2	.	2	4	2	.	.	8	4
	G 2227	6	.	1	2	1	.	2	4	1	.	7	4
	G 2229	7	.	1	3	1	.	4	1	1	.	6	5

The third back-cross to T 3 brown.

Plants known to be heterozygous and homozygous respectively were selected for the third back-cross with the following results:

Cross		Grades of brown		
		6	7	8
Heterozygous parents	G 2225 × 3	4	2	2
	G 2227 × 3	.	2	4
	G 2229 × 3	2	2	6
Homozygous parents	G 2226 × 3	.	1	4
	G 2232 × 3	.	3	3

Here it appears that the crosses of heterozygotes with T 3 give grades 6-8, while those of homozygotes by T 3 give only 7 and 8.

Grade 6 is probably nearly always heterozygous, 8 always homozygous and 7 sometimes homozygous and sometimes heterozygous.

The third back-cross selfed.

The results of selfing third back-cross plants are given in Table III.

The results of Table III will be briefly discussed.

The series G 2225 × 3, although giving five families clearly heterozygous, exhibits a range of 2-3 classes in the recessive group. The ratio of dominant to recessive in the five families is 45 : 26—a considerable excess of recessives not accountable for on the present data, and which should form the subject of further investigation.

The other two series exhibit clear monohybrid segregation into brown of grades 6 to 8, with an indication of two modes, one at 6 and the other at 8, and light brown of grade 3.

The sum total of families segregating in this manner is:

Grade of lint					
3	4	5	6	7	8
20	.	.	34	11	14
59					

This is an almost exact 3 : 1 ratio, and it is clear that the recessive of dark brown Egyptian is not white, but light brown of grade 3. The heterozygote approximates to grade 5, though distinction between homozygote and heterozygote is not clear.

TABLE III.

Results of selfing third back-cross plants.

Series	Family	Parent grade	Grade of brown								Brown	Light brown	
			1	2	3	4	5	6	7	8			
G 2225 × 3	G 3563	8	11		
	G 3566	8	9	17	
	G 3568	7	1	7	1		
„	G 3558	7	.	3	4	.	.	9	1	5	15	7	
	G 3560	6	.	2	1	.	.	6	.	.	6	3	
	G 3564	6	.	3	2	.	.	3	3	3	9	5	
	G 3567	6	1	.	1	1	.	1	1	2	4	3	
	G 3569	6	3	3	2	.	2	6	2	1	11	8	
G 2227 × 3	G 3586	8	2	22		
	G 3588	8	9		
	G 3589	8	5		
	G 3590	8	1	11			
	G 3593	7	10		
	G 3585	7	.	.	3	.	.	5	2	3	10	3	
G 2229 × 3	G 3594	8	2	9			
	G 3595	8	11			
	G 3597	8	13			
	G 3598	8	13			
	G 3603	8	1	11			
	G 3604	8	1	13			
	G 3599	6	.	.	4	.	.	3	4	2	9	4	
„	G 3600	6	.	.	5	.	.	10	3	3	16	5	
	G 3601	7	.	.	5	.	.	10	1	3	14	5	
	G 3602	7	.	.	3	.	.	6	1	3	10	3	

To sum up: dark brown and light brown constitute a simple pair of allelomorphs in *G. barbadense* L., with dark brown incompletely dominant. The factor pair responsible may be termed¹ K^B-k^B .

(2) *Relationship of brown lint factor pair K^B-k^B to lint length.*

Throughout the experiments it was noticed that the plants with brown lint tended to be shorter in staple than the lighter coloured types.

The clearness of segregation in some of the third back-cross selfed families rendered it possible to establish a quantitative basis for the correlation between lint length and lint colour. The correlation for lint

¹ The symbol K^B is used to indicate that the K factor is found in the species *G. barbadense* L., as it is possible that other allelomorphs at this locus may occur in some of the other species in the New World group.

length and lint colour for heterozygous third back-cross selfed families is given in Table IV.

TABLE IV.

The correlation between lint length and grade of lint colour in heterozygous third back-cross selfed families.

Families G 3585, G 3599, G 3600, G 3601, G 3602.

Mean max. lint length mm.	Grade of brown								Total
	1	2	3	4	5	6	7	8	
27.0	1	1
27.5	—
28.0	3	3
28.5	1	.	1	2
29.0	2	2
29.5	3	3
30.0	4	4	2	10
30.5	1	1
31.0	3	4	.	7
31.5	5	1	1	7
32.0	10	.	.	10
32.5	.	.	1	.	.	4	1	.	6
33.0	.	.	3	.	.	4	1	.	8
33.5	.	.	7	.	.	1	.	.	8
34.0	2	.	.	2
34.5	.	.	2	2
35.0	.	.	4	4
35.5	.	.	1	1
36.0	—
36.5	—
37.0	.	.	2	2

From this table it is evident that a strong correlation exists between colour and lint length, as follows:

Mean of k^Bk^B (grade 3)	34.2 mm.
Mean of K^Bk^B (heterozygote, grade 6)		31.5 mm.
Mean of K^BK^B (homozygote, grade 8)		29.1 mm.

The mean of the heterozygote is almost exactly at the arithmetic mean of the two homozygotes.

The explanation is that either a lint length factor pair conditioning a difference of 5.1 mm. in mean maximum lint length, *i.e.* the difference between 29.1 and 34.2 mm., is so closely linked with K^B , the main gene for brown lint, as to show no crossing-over in the present experiments or that one of the manifestations of K^B is a reduction in lint length.

Correlation between lint length and lint colour in homozygous k^Bk^B and K^BK^B families.

The third back-cross selfed families of series G 2225 \times 3 showed a variation in lint colour grade in the k^Bk^B section of heterozygous families from grades 1-3. It is therefore possible to see whether correlation exists between lint length and lint colour grade within the limits of the k^Bk^B

group. A similar correlation may be studied in third back-cross families homozygous for $K^B K^B$ but showing variation in lint colour from grade 6 to 8. The results of such correlations are given in Tables V and VI.

TABLE V.

Correlation of lint grade and lint length in $k^B k^B$ section of heterozygous families of series G 2225 \times 3.

Mean max. lint length mm.	Grade of brown		
	1	2	3
32.0	.	2	.
32.5	.	.	1
33.0	.	.	1
33.5	.	1	1
34.0	1	2	1
34.5	.	1	.
35.0	.	.	2
35.5	1	.	1
36.0	.	1	1
36.5	.	1	.
37.0	1	.	.
37.5	.	.	.
38.0	.	.	.
38.5	.	.	.
39.0	1	.	.
Mean of grade 1		36.4 mm.	
” ” 2		34.1 mm.	
” ” 3		34.3 mm.	

TABLE VI.

Correlation of lint length and lint colour grade in third back-cross selfed families homozygous for $K^B K^B$.

Mean max. lint length mm.	Grade of brown		
	6	7	8
27.0	.	.	1
27.5	.	.	1
28.0	.	1	5
28.5	.	.	2
29.0	.	2	1
29.5	.	5	1
30.0	1	7	2
30.5	.	7	.
31.0	2	3	.
31.5	5	2	.
32.0	3	2	.
33.0	4	.	.
33.5	1	.	.
Mean lint length grade 6		32.0 mm.	
” ” ” 7		30.3 mm.	
” ” ” 8		28.4 mm.	

It is evident that a correlation exists between length and colour even within the limits of grades 1-3. *Minor modifiers of K^B thus also modify*

lint length, and are responsible for a total effect of about 2.3 mm. in the $\mathbf{k^Bk^B}$ section of heterozygous families.

These results indicate that differences in lint length are also correlated with variations in lint colour in families homozygous for $\mathbf{K^BK^B}$. Assuming that some part of the variation in lint colour is genetic, it may be concluded that minor factors are responsible for a total effect of 3.6 mm. in the $\mathbf{K^BK^B}$ class.

(3) *Inheritance of brown lint in the interspecific cross*

G. barbadense L. × G. hirsutum L.

Having established that brown and white (or pale brown) form an allelomorphous pair of characters in both Egyptian (*barbadense*) and Upland (*hirsutum*) cotton, it became of interest to investigate the mode of inheritance of brown lint in the cross between brown linted forms of the two species. The experimental results follow.

The parents.

Egyptian Enan's Brown (grade 8) × Upland Guatemala Khaki (grade 7).

The F₁.

As the distinction between the parents was only slight it was difficult to assign the F_1 plants definitely to either of the parental classes. The six plants grown varied from grade 7 to 8.

The first back-cross of heterozygote to hirsutum white.

Previous experience had led us to conclude that the simplest way of elucidating the genetic relationship of brown lint in the two species was to back-cross heterozygotes to *hirsutum* white as many times as should prove necessary. The results of the first back-cross are placed below:

Family	Grades of brown								
	1	2	3	4	5	6	7	8	9
5 × G 320	19	13	(7)	20	16	17	17	17	2

Here it will be seen that whites appear in the back-cross. Neglecting the seven plants of grade 3, the class of minimum frequency, we have:

Expected on a 3 : 1 basis	Brown	Light brown -white
		89
	90.75	30.25

It was concluded that brown lint in *barbadense* and *hirsutum* was not determined by the same gene, but by a pair of duplicate genes which could be termed $\mathbf{K^B}$ (*barbadense* brown) and $\mathbf{K^H}$ (*hirsutum* brown).

The second back-cross to hirsutum white.

In order to confirm the hypothesis that duplicate genes are concerned in this cross, a representative number of plants with grades ranging from 1 to 7 were back-crossed again to *hirsutum* white. The results are presented in Table VII.

TABLE VII.
Second back-cross to hirsutum white of various colour grades of first back-cross.

Family	Parent grade	Grade of brown							Brown	Light brown -white	Ratio
		1	2	3	4	5	6	7			
5 × 18078	1	37	0	37	
18145	1	3	5	1	0	9	
18189	1	10	5	0	15	
18054	2	3	2	0	5	
18070	2	19	5	1	0	25	
18107	2	15	2	1	0	18	
18061	3	9	3	1	0	13	
18154	5	1	1	.	.	1	.	.	1	2	?
18108	6	4	8	(1)	6	1	3	.	10	12	1:1
18162	6	8	(1)	2	3	.	1	.	6	8	1:1
18185	6	16	4	(3)	10	8	3	1	22	20	1:1
18122	7	8	5	(3)	4	5	10	.	19	13	1:1
18072	7	10	.	8	6	3	2	2	21	10	3:1?

The above results indicate that the division of the first back-cross plants into brown (grades 4 and above) and light brown to white (grades 1 and 2) was justified, since all offspring of plants of grades 1 and 2 gave only recessives when crossed again with white. The crosses of white with grades 5-7 gave definite monohybrid ratios in four families, with minimum frequency at 3 (three cases) and 2 (one case). One family (5 × 18072) was probably of dihybrid type, giving 21 brown to 10 white. Equal numbers of dihybrid and monohybrid families are expected, though to get this result a more representative selection of grades should have been employed for the second back-cross. To sum up: the brown colour of the lint of Egyptian (*G. barbadense*) and Upland (*G. hirsutum*) is conditioned by duplicate genes:

K^B-k^B Brown-light brown *G. barbadense* L.
 K^H-k^H Brown-white *G. hirsutum* L.

DISCUSSION.

The mode of inheritance of brown lint in the inter-*barbadense* cross Egyptian × Sea Island is of the blending type characteristic of inter-specific hybrids rather than the relatively clear-cut type usually found in Egyptian-Sea Island crosses.

The factor $\mathbf{K}^{\mathbf{B}}$ (brown lint) is accompanied in Egyptian by a constellation of plus modifiers, and as a secondary effect $\mathbf{K}^{\mathbf{B}}$, and some at least of the minor colour factors shorten the lint. An association between short staple and brown lint was noticed by Kottur (1923) in Asiatic cottons. Now length of staple has been an important factor throughout the history of cotton cultivation, and it may be imagined that selection for this character has been continuously practised by cultivators since this species was domesticated in pre-Columbian times. Selection for long-linted types would thus have the effect first of eliminating the main $\mathbf{K}^{\mathbf{B}}$ factor and subsequently also many of the minor colour factors from Sea Island and other white-linted types of *barbadense*.

The presence of white or nearly white-linted types in *barbadense* thus seems to be due to the disintegration by human agency of a primitive brown-lint character complex. It is important to note, however, that the breaking up of the complex has not apparently affected modifier complexes accompanying other factors, *e.g.* \mathbf{Y} (yellow corolla), \mathbf{P} (yellow pollen) and \mathbf{S} (petal spot), etc. The modifier complexes accompanying these genes seem to be essentially similar throughout the *barbadense* group even in types so different as the wild or semi-wild kidney tree cottons and the cultivated Egyptian or Sea Island. This means that it is possible to substitute most of the genes of a character complex by their allelomorphs without any noticeable effects on the manifestation of other characters, though doubtless many modifiers are held in common by one or more character complexes.

Duplicate genes for brown lint constitute the third case of duplication found in the New World *Gossypium*s. In this case, as in two previous examples, red *v.* green plant body, \mathbf{R}^1 and \mathbf{R}^2 , and green *v.* chlorophyll deficiency, $\mathbf{C}^{\mathbf{ha}}$ and $\mathbf{C}^{\mathbf{hb}}$, it has been the rule that one member of the pair is confined to *hirsutum* and the other to *barbadense*. In the case of the chlorophyll deficiency pair, $\mathbf{C}^{\mathbf{hb}}$ is never found in *barbadense* but only $\mathbf{C}^{\mathbf{ha}}$, and though both members are found in some *hirsutum* types, $\mathbf{C}^{\mathbf{hb}}$ is always found in those which are monomeric.

The existence of pairs of duplicate genes is to be expected on Skovsted's (1934) hypothesis of the amphidiploid nature of New World cottons. The method of distribution whereby one member of a pair is characteristic of *hirsutum* and the other of *barbadense* leads to the tentative suggestion that the present New World $n = 26$ species are descended from amphidiploids arising from more than one original cross, in which different varieties of two original species may have taken part, or even possibly more than two species.

SUMMARY.

1. The inter-*barbadense* cross Egyptian brown \times Sea Island white gave F_1 intermediate and complicated segregation of the blending type in F_2 . This was demonstrated to be due to the fact that the factor K^B of the brown parent was accompanied by a number of plus modifiers absent in the white parent.

2. Repeated back-crossing of heterozygotes to the brown parent had the effect of equalising the plus modifiers of both the dominant and recessive phases of the factor K^B . Selfing after three back-crosses gave simple segregation into 3 brown : 1 light brown.

3. A negative correlation was shown to exist between lint colour and lint length, the factor K^B or a factor closely linked to it conditioning a shortening in the lint length of approximately 5.1 mm. in the homozygous phase and 2.7 mm. in the heterozygous phase.

4. Minor colour factors were also correlated with variations in lint length.

5. The blending type of inheritance of brown lint in Egyptian \times Sea Island is considered to be due to the disintegration by human agency of an original brown-lint factor complex.

6. The cross of brown *barbadense* \times brown *hirsutum* was found to involve duplicate genes for lint colour. The distribution of the known pairs of duplicate genes in *G. barbadense* and *G. hirsutum* is discussed.

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