THE GENETICS OF COTTON.

PART VI. THE INHERITANCE OF CHLOROPHYLL DEFICIENCY IN NEW WORLD COTTONS.

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(With Plate VII.)

INTRODUCTION.

THE occurrence of chlorophyll deficiency in the F_2 of crosses between Upland and Sea Island or Egyptian (*G. hirsutum* Linn. × *G. barbadense* Linn.) was first noticed by Stroman and Mahoney (1925). A summary of their investigations is as follows:

Seedlings with yellow leaves occurred in a cross of Sea Island by Upland, and the progeny of one F_1 plant segregated into green and yellow in a 15 : 1 ratio. In the yellow seedlings the condition is noted as soon as the cotyledons unfold, and such seedlings die as soon as the stored food in the seed is exhausted.[1]

Another type of chlorophyll deficiency is shown by certain areas devoid of green colour on the cotyledons, surrounded by normal green pigment. These areas are not of uniform shape, but extend usually from the extreme edge half-way across the leaf. A type designated "light pattern" is so termed because the young leaves contain areas of light greenish colour instead of yellow or white colour. These light patterns vary in area of expression, and the authors consider it probable that pattern types do not mature. One family segregated for two genes:

	Dark green	Light green	Light pattern	Pattern
	166	64	54	19
Expected	*170*	*57*	*57*	*19*

The factors responsible are designated as $\mathbf{C}_1$ and $\mathbf{C}_2$. There is a third recessive gene which when present with $\mathbf{C}_1$ and $\mathbf{C}_2$, produces a 27 : 37 ratio. There is a slight possibility that two of the genes are linked.

[1] Stroman and Mahoney used the symbols $\mathbf{Y}_1$ and $\mathbf{Y}_2$ for the allelomorphs of chlorophyll deficiency. Since Leake has already employed the symbol $\mathbf{Y}$ for corolla colour, it seems preferable to adopt a fresh designation.

Texas workers (*Ann. Rept.* 1928) have studied a chlorophyll-deficient form known as virescent yellow, which occurred among commercial Upland. This proved to be a simple recessive to the normal green.

The present paper deals with the distribution of chlorophyll-deficient factors in the Upland and Peruvian groups of cultivated New World cottons, and in the Polynesian wild species *G. tomentosum* Nutt.

Material and methods.

It is stated by Stroman and Mahoney (*loc. cit.*) that the chlorophyll-deficients obtained in the F_2 of Sea Island × Upland, and Egyptian × Upland, fail to survive the seedling stage. Nevertheless, in an Upland × Egyptian cross made by the writer, there was considerable variability in the amount of chlorophyll present in the cotyledons of chlorophyll-deficient segregates which appeared in a 15 : 1 ratio (green to deficient). A certain number proved capable of reaching maturity if given careful cultivation in pots. A number of chlorophyll deficients were grafted on to normal stocks while in the cotyledon stage. The leaf colour of the adult plants varied from light yellowish green to a green which was scarcely distinguishable from that of normal Upland or Sea Island. Two generations of selection for viability gave rise to a pure chlorophyll-deficient race in which most of the seedlings were capable of arriving at maturity without grafting or special horticultural treatment. A single plant of this race, of genetic constitution **y** (cream corolla), **p** (cream pollen), **s** (spotless petal), was selected as a standard chlorophyll-deficient and propagated by grafting on a large scale. This type has been designated type 5.

The range of variability in the expression of chlorophyll deficiency in the F_2 segregates of Upland-Egyptian crosses is illustrated in Plate VII, where grades 1 to 8 are chlorophyll deficients and grade 9 is the normal green. Type 5 originated from a plant which as a seedling was grade 8. The offspring of type 5 range from grades 4 to 8, the extreme forms 1 to 3 failing to appear. Moreover, they are practically all capable of reaching maturity with no special treatment, and are distinguishable from normal greens only with difficulty. Selection for viability has thus resulted in an increase of the chlorophyll area, and the fact that the extreme forms of deficiency reappear in the F_2 of direct crosses of type 5 with Upland or Egyptian indicate that the differences between the extreme deficients and grade 8 are due to modifying factors.

The object of the experiments was to trace the distribution of the allelomorphs of chlorophyll-deficiency in representative types of Upland

(*G. hirsutum* Linn.), Peruvian (*G. barbadense* Linn.), and in the wild Polynesian species *G. tomentosum* Nutt.

The following types were used in the experiments:

(1) Upland: Type 2 Superokra.
,, 7 Texas Green Lint.
,, 9 Meade.
,, 19 Punjab Golden.
,, 34 Guatemala Khaki.

(2) Peruvian: Type 1 Trinidad Red Kidney.
,, 4 Crinkled Dwarf.
,, 6 Sea Island Naked.

(3) Polynesian Wild: *G. tomentosum* Nutt.

(1) *Crosses between Upland types and chlorophyll deficient.*

(*a*) Type 2 (Superokra) × type 5 (chlorophyll-deficient).

F_1. Green and indistinguishable from the green parent.

F_2, F_3, and back-crosses. The results are presented in Table I.

Conclusion. Green and chlorophyll deficient form a simple pair of allelomorphic characters in this cross. The factor pair concerned may be represented as $\mathbf{C^{hb}}$–$\mathbf{c^{hb}}$.

(*b*) Type 34 (Guatemala Khaki) × type 5 (chlorophyll deficient).

F_1. Green.

F_2 and back-crosses. The results are given in Table II.

Conclusion. It may be concluded that Guatemala Khaki contains two independently inherited factors for green, since a 15 : 1-ratio occurs in F_2, and a 3 : 1 ratio in back-crosses with deficient. It may be assumed that one of these factors is identical with that demonstrated in type 2, since crosses between various types of Upland have never given rise to chlorophyll deficient. An F_2 of 2 × 34 gave greens only.

The genetic constitution of Guatemala Khaki may therefore be represented as $\mathbf{C^{hb}}$, $\mathbf{C^{hb}}$, $\mathbf{C^{hc}}$, $\mathbf{C^{hc}}$.

(*c*) Miscellaneous Upland types × type 5.

Having established that Upland types may contain either one or two factors for green, it became of interest to determine the constitution of other Upland types. The results are placed below in Table III.

Conclusion. The above results, although in some cases not sufficiently full to establish the genetic constitution of the type with certainty, nevertheless fall into line with those previously dealt with.

Type 7. In crosses with type 2, no deficients appeared in F_2, so that type 7 is homozygous for C^{hb}. Two kinds of F_1 appear to be present,

TABLE I.

Type 2 (*Upland Superokra*) × *type* 5 (*chlorophyll deficient*).

Family	Generation	Green	Deficient
2 × 5–1	F_2	32	8
–2	,,	77	25
–3	,,	26	5
–4	,,	61	24
Total		196	62
Expected (3 : 1 basis)		*193·5*	*64·5*
5 × (2 × 5–1)	Back-cross	47	26
5 × (2 × 5–3)	,,	31	28
Total		78	54
Expected (1 : 1 basis)		*66*	*66*
1– 7	F_3	6	2
1– 8	,,	10	3
1–15	,,	9	5
1–17	,,	5	3
1–24	,,	4	1
2– 8	,,	12	1
2–29	,,	10	2
2–35	,,	13	4
2–37	,,	8	5
3– 5	,,	15	2
3– 6	,,	6	2
3–12	,,	5	4
3–21	,,	11	1
4– 7	,,	16	10
4–14	,,	21	6
4–41	,,	10	8
4–42	,,	16	3
Total		177	62
Expected (3 : 1 basis)		*179·25*	*59·75*
1– 1	F_3	11	0
2–45	,,	9	0
2–54	,,	12	0
2–58	,,	19	0
3–19	,,	14	0
3–25	,,	20	0
4–15	,,	12	0
4–21	,,	12	0
Total		122	0

		Expected
F_3 heterozygous families	17	*17·2*
Homozygous families	9	*8·6*

one giving monofactorial inheritance, and the other bifactorial. It may be assumed provisionally that the second factor C^{hc} is present in type 7 in a heterozygous condition.

TABLE II.

Type 34 (Guatemala Khaki) × type 5 (chlorophyll deficient).

Family	Generation	Green	Deficient
5 × 34–1	F_2	29	1
–2	,,	56	2
–3	,,	102	8
–4	,,	21	1
Total		208	12
Expected (15 : 1 basis)		*206·2*	*13·8*
(5 × 34–1) × 5	Back-cross	6	1
(5 × 34–4) × 5	,,	18	2
Total		24	3
Expected (3 : 1 basis)		*20·25*	*6·75*

TABLE III.

Results of crosses between various Upland types and type 5 (chlorophyll deficient).

Type	Family	Generation	Green	Deficient	Ratio
7	5 × 7–1	F_2	48	5	?
	–2	,,	71	5	15 : 1
	5 × (5 × 7–1)	Back-cross	53	36	1 : 1
	(5 × 7–2) × 5	,,	25	8	3 : 1
9	5 × 9–1	F_2	20	0	15 : 1 ?
	–2	,,	17	14	?
	–3	,,	11	0	15 : 1 ?
	–4	,,	7	1	?
	(5 × 9–1) × 5	Back-cross	104	42	3 : 1
	(5 × 9–4) × 5	,,	58	84	1 : 1
19	5 × 19–378	F_2	54	18	3 : 1
	–373	,,	99	6	15 : 1
	–374	,,	90	21	3 : 1
	–375	,,	71	5	15 : 1
	–376	,,	62	8	15 : 1 ?
	–377	,,	34	2	15 : 1
23	5 × 23–1	F_2	104	25	3 : 1
	–2	,,	127	38	3 : 1
	–3	,,	58	25	3 : 1
	–4	,,	246	52	3 : 1
	–6	,,	26	9	3 : 1
	–7	,,	23	4	3 : 1
	(5 × 23–1) × 5	Back-cross	5	7	1 : 1
	(5 × 23–2) × 5	,,	64	76	1 : 1
	(5 × 23–4) × 5	,,	76	72	1 : 1
	(5 × 23–5) × 5	,,	8	19	1 : 1
	(5 × 23–6) × 5	,,	15	10	1 : 1
	(5 × 23–7) × 5	,,	20	10	1 : 1
25	5 × 25–378	F_2	38	9	3 : 1
	–379	,,	30	6	3 : 1
	–381	,,	26	7	3 : 1

Type 9. The same remarks apply as to type 7.

Type 19. Ditto.

Type 23. This type contains only one factor. Since greens only are produced in the F_2 of 2 × 23, this factor is identical with that of type 2.

Type 25. This type gives monofactorial inheritance only, and since a cross of 23 by 25 gave no deficients in F_2, the constitution of 25 is established to be the same as that of 2 and 23.

To sum up: Upland × chlorophyll deficient gives either monofactorial or bifactorial inheritance. The factor $\mathbf{C}^{\mathbf{hb}}$ appears to be common to all the types. The second factor, $\mathbf{C}^{\mathbf{hc}}$, is homozygous in type 34, but heterozygous in types 7, 9 and 19.

(2) *Crosses between Peruvian types and chlorophyll deficient.*

(*a*) Crinkled Dwarf Sea Island (type 4) × chlorophyll deficient (type 5).

F_1. Green.

F_2. The results are given in Table IV.

TABLE IV.

Type 4 (*Sea Island Crinkled Dwarf*) × *type* 5 (*chlorophyll deficient*).

Family	Generation	Green	Deficient
4 × 5–1	F_2	42	13
–2	,,	48	18
–3	,,	29	11
–4	,,	324	89
–5	,,	38	11
–6	,,	24	7
–7	,,	23	9
–8	,,	20	6
Total		548	164
Expected (3 : 1 basis)		*534*	*178*

These results indicate a monofactorial difference between the Sea Island type used and chlorophyll deficient, which may be represented by the factor pair $\mathbf{C}^{\mathbf{ha}}$–$\mathbf{c}^{\mathbf{ha}}$. From the fact that it is usual to get either 15 : 1 or 63 : 1 ratios of green to deficient in the F_2 of Upland-Peruvian crosses, it may be assumed that the allelomorphic pair green-deficient present in Peruvian is not the same as the two pairs which characterise Upland.

(*b*) Red Kidney (type 1) × chlorophyll deficient (type 5).

F_1. Normal (red).

F_2. Gave 85 normal: 19 deficient (expected 78 : 26).

Back-cross F_1 × deficient gave 118 normal : 101 deficient (expected 109·5 : 109·5).

Red Kidney × Crinkled Dwarf gave only greens in F_2 and subsequent generations, so that the genetic constitution of Red Kidney in respect of chlorophyll deficiency is identical with that of Crinkled Dwarf, *i.e.* $C^{ha}C^{ha}$.

(3) *Crosses between* G. tomentosum (*type* 22) *and chlorophyll deficient* (*type* 5).

F_1. Green.

Back-cross × recessive gave:

Family	Green	Deficient
5 × (5 × 22–1)	87	36
5 × (5 × 22–2)	52	21
5 × (5 × 22–3)	60	21
5 × (5 × 22–5)	90	51
Total	289	129
Expected (3 : 1 basis)	*313·5*	*104·5*

The back-cross ratio of 3 green to 1 deficient indicates that *G. tomentosum* carries two factor pairs for green deficient. A cross of *G. tomentosum* by Peruvian Crinkled Dwarf, which has been established to be $C^{ha}C^{ha}$, gave greens only in F_2, so that *G. tomentosum* carries C^{ha}. A cross of *G. tomentosum* by type 2 Upland Superokra also gave greens only in F_2. The genetic constitution of the wild *G. tomentosum* is therefore $C^{ha}C^{ha}$, $C^{hb}C^{hb}$. The fact that *G. tomentosum* has one Upland gene and one Peruvian gene is of considerable interest, since this species, in respect of its genetic behaviour in other characters, falls into an intermediate position between Upland and Peruvian.

(4) *Inter-specific crosses between Upland and Peruvian.*

(*a*) The cross Upland Superokra (type 2) × Sea Island Naked (type 6).

The back-cross of chlorophyll deficient by F_1 gave the following results:

Family	Green	Deficient	Ungerminated
5 × (2 × 6–1)	197	86	67
5 × (2 × 6–2)	158	68	33
Total	355	154	
Expected (3 : 1 basis)	*371·75*	*127·25*	

The cross is presumably $c^{ha}c^{hb} \times (C^{ha}c^{ha}c^{hb}C^{hb})$, and is expected to give 3 green to 1 deficient. There is, however, a noticeable excess of deficients. Some evidence is available that pollen tubes carrying chlorophyll deficiency may grow slightly faster than normal tubes in the styles of type 5.

(*b*) Upland (type 25) × Sea Island Naked (type 6).

The back-cross chlorophyll deficient × F_1 gave:

Family	Normal	Deficient
5 × (6 × 25–1)	105	39
Expected (3 : 1 basis)	*108*	*36*

The factors involved here are identical with those of the previous cross.

(*c*) Upland × Sea Island White Flower.

The genetic constitution with respect to chlorophyll deficiency of the parents was not known.

F_1. Green.

F_2 gave:

	Green	Deficient
	1360	28
Expected (63 : 1 basis)	*1366·3*	*21·7*

This result would be obtained if the cross were Upland ($c^{ha}c^{ha}$, $C^{hb}C^{hb}$, $C^{hc}C^{hc}$) × Peruvian ($C^{ha}C^{ha}$, $c^{hb}c^{hb}$, $c^{hc}c^{hc}$). There is a strong probability that C^{hc}, established to be homozygous in type 34, and heterozygous in types 7, 9 and 19, is homozygous in the Upland plant used in the above experiment.

To sum up: The evidence presented above indicates that three pairs of factors are responsible for the normal green colour of the leaf in New World cottons. The distribution of the three factor pairs may be provisionally set forth as follows:

Peruvian group—$C^{ha}C^{ha}$.
Upland group—$C^{hb}C^{hb}C^{hc}C^{hc}$, or $C^{hb}C^{hb}$.
G. tomentosum—$C^{ha}C^{ha}C^{hb}C^{hb}$.

In crosses of Upland × type 5, two cases have been encountered where the F_1 apparently consisted of two genotypes, one giving the 3 : 1 type of ratio in F_2 and the other the 15 : 1.

These have not yet been fully investigated, but a plant which was homozygous for one green factor and heterozygous for the other would give such a result.

Discussion.

The type of chlorophyll deficiency here investigated differs from most of those previously described in other plants in two respects. First, it occurs only in interspecific crosses, and second, it is affected profoundly by modifiers which enable a viable race to be selected from a population which consisted almost wholly of lethal types. The only other case of variability in chlorophyll-deficient segregates known to the writer is that described by Kristofferson (1924). He found yellow and white seedlings in the F_2 of crosses between cabbage and kale (varieties of *Brassica oleracea*). He presents no numerical data, but states that in the green class the colour of the leaves varied from dark green to a very light green shade. Presumably variation was continuous from green to chlorophyll deficient. He states that there may be different factors for normal distribution of the chlorophyll in the parent lines, the absence of some of these factors resulting in the appearance of chlorophyll variations.

In previous papers (1929 *a*, *b*, *c*) it has been shown that where two members of an allelomorphic pair occur in different species of *Gossypium* (*G. hirsutum* and *G. barbadense*), blending of the character occurs in F_2 due to segregation of modifiers. The present case of variability in the expression of chlorophyll deficiency may be ascribed to the segregation of modifying factors which have little or no effect in the green class. The leaf colour of Uplands is as a rule lighter than that of Peruvians, and it is clear that the green colour of the leaf is built up by a different combination of genes in the two species.

It has been shown by *Drosophila* workers (cf. Fisher, 1928) that many mutants become more viable by the selection of modifiers, approaching the wild type as they do so. By crossing the modified mutant with unrelated normals the original unmodified mutant can be made to appear. This is the case also in the present experiments, since the F_2 segregates of Upland or Peruvian by modified deficient give rise to the original extreme non-viable forms (see Plate VII for range of chlorophyll-deficient types in F_2). The bearing of these experiments on Fisher's theory of dominance (*loc. cit.*) will be deferred until chlorophyll deficient has been transferred by repeated back-crossing on to both the Peruvian and Upland genotypes.

SUMMARY.

1. The occurrence of relative chlorophyll deficiency in crosses between *G. barbadense* and *G. hirsutum* is shown to be dependent upon three pairs of factors, probably independently inherited, which are designated as follows:

C^{ha}–c^{ha}—Green deficient.
C^{hb}–c^{hb} ,,
C^{hc}–c^{hc} ,,

2. Modifying factors considerably affect the distribution of chlorophyll deficiency in the chlorophyll-deficient class, and within it was found a range from completely lethal to fully viable.

3. The distribution of the chlorophyll-deficient factors was investigated in *G. barbadense*, *G. hirsutum* and *G. tomentosum*. *G. barbadense* carried only C^{ha}. *G. hirsutum* always carried C^{hb}, but C^{hc} was found in all three phases of the gene—$C^{hc}C^{hc}$, $C^{hc}c^{hc}$ and $c^{hc}c^{hc}$. *G. tomentosum* carried the combination C^{ha} with C^{hb}.

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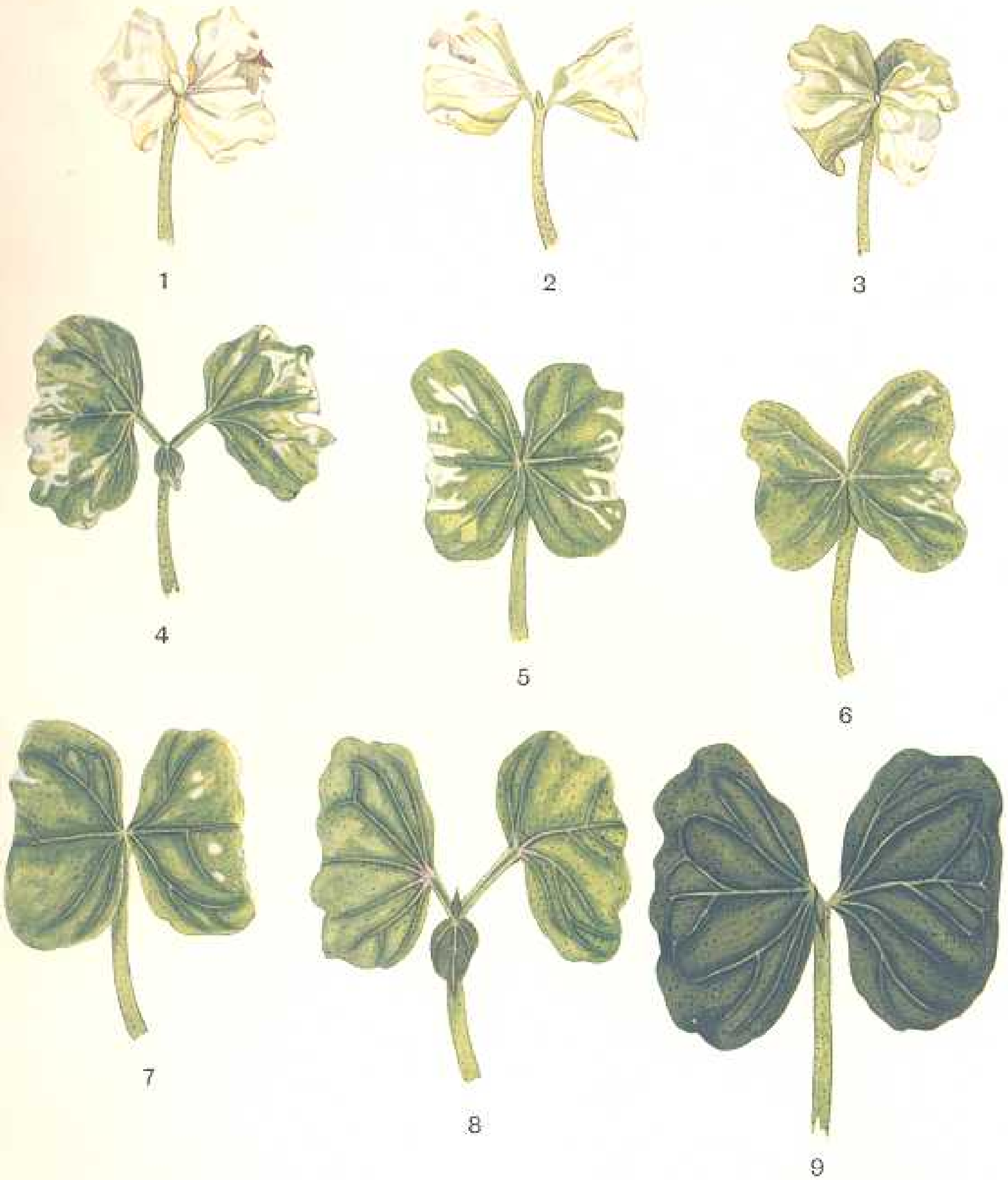
EXPLANATION OF PLATE VII.

The plate illustrates variation in the degree of chlorophyll deficiency in the F_2 of *G. hirsutum* Linn. × *G. barbadense* Linn. Grades 1 to 8 are deficients. Grade 9 is the normal growth.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