

THE GENETICS OF COTTON.

PART XI. FURTHER EXPERIMENTS ON THE INHERITANCE OF CHLOROPHYLL DEFICIENCY IN NEW WORLD COTTONS.

BY SYDNEY CROSS HARLAND.

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

CONTENTS.

| | PAGE |
|---|------|
| Introduction | 181 |
| Material | 182 |
| Methods | 182 |
| Results of crosses of New World species with chlorophyll deficient | 183 |
| (1) <i>G. hirsutum</i> L. | 183 |
| (2) <i>G. barbadense</i> L. | 183 |
| (3) <i>G. purpurascens</i> Poir. | 183 |
| (4) <i>G. taitense</i> Parl. | 184 |
| (5) <i>G. Darwinii</i> Watt | 184 |
| Identification of factors in New World species. Inter-relationships | 186 |
| (1) Monomeric <i>hirsutum</i> and monomeric <i>barbadense</i> | 186 |
| (2) Monomeric <i>barbadense</i> and dimeric <i>hirsutum</i> | 187 |
| (3) Monomeric <i>barbadense</i> and dimeric <i>purpurascens</i> | 188 |
| (4) Monomeric <i>purpurascens</i> and monomeric <i>barbadense</i> | 189 |
| (5) Monomeric <i>taitense</i> and monomeric <i>hirsutum</i> and <i>barbadense</i> | 189 |
| (6) Monomeric <i>Darwinii</i> and monomeric <i>hirsutum</i> and <i>barbadense</i> | 189 |
| (7) Dimeric <i>tomentosum</i> and dimeric <i>purpurascens</i> | 190 |
| Discussion | 191 |
| Summary | 194 |
| References | 195 |

INTRODUCTION.

IN a previous paper (1932*a*) it was shown that a chlorophyll-deficient type frequently occurred in the second generation of the interspecific hybrid *G. barbadense* L. (Sea Island or Egyptian) × *G. hirsutum* L. (Upland), usually in the ratio 15 green : 1 deficient. By selection in the chlorophyll-deficient group, a chlorophyll deficient was isolated which could be reproduced from seeds, whereas most of the chlorophyll deficiencies occurring in the F_2 of such crosses were not capable of surviving the cotyledon stage. Viability of the extracted pure line of deficient, in which, although the cotyledons were almost devoid of chlorophyll, the

adult plant was normal green, rendered it possible to make direct crosses between a representative series of types from all the species of New World cottons, and thus the elucidation of their genetic constitution in terms of the pair of duplicate genes:

$$\begin{aligned} &C_{ha}-c_{ha} \text{ (green deficient),} \\ &C_{hb}-c_{hb} \text{ (green deficient).} \end{aligned}$$

The existence of a third factor, C_{hc} , was thought to be demonstrated by the occurrence of the ratios 63 green : 1 chlorophyll deficient in the F_2 of the cross Upland \times Sea Island white. Further experiments have shown that there are only two factors, viz. C_{ha} and C_{hb} , and that the ratio 63 green : 1 deficient can be explained by the discovery that many of the chlorophyll deficient in F_2 have extremely minute embryos and do not germinate. In back-crosses of heterozygotes with standard chlorophyll deficient (type 5) no ratios have been encountered indicating the existence of more than two factors. In the present experiments is presented a full account of the distribution of the factors C_{ha} and C_{hb} in all the known species of New World cottons with 26 pairs of chromosomes.

MATERIAL.

As a result of both genetic and taxonomic observations, it has been concluded (*vide* 1932*b*) that the New World cottons fall into the following groups:

| Group | Species | Geographical distribution |
|-------------------|------------------------------|-------------------------------------|
| Upland | <i>G. hirsutum</i> L. | Mexico, Guatemala, Southern U.S.A. |
| Peruvian | <i>G. barbadense</i> L. | Peru, Ecuador, Caribbean area |
| Bourbon | <i>G. purpurascens</i> Poir. | Central and South America, Antilles |
| Polynesian Wild 1 | <i>G. tomentosum</i> Nutt | Hawaiian Islands |
| Polynesian Wild 2 | <i>G. taitense</i> Parl. | Fiji and other Polynesian Islands |
| Galapagos Wild | <i>G. Darwinii</i> Watt | Galapagos Islands |

Of the above six species, the last three occur in a truly wild state, and are apparently endemic in the regions where they occur. In the discussion of the experiments, it will be convenient to refer to the species by their specific, and not by their popular names, *e.g.* Upland will be referred to throughout as *G. hirsutum* or *hirsutum*.

METHODS.

Several representative types from each of the above New World species were crossed with standard chlorophyll deficient. In general four F_1 plants were selected of each cross and back-crossed to chlorophyll deficient.

RESULTS OF CROSSES OF NEW WORLD SPECIES WITH CHLOROPHYLL
DEFICIENT(1) *G. hirsutum* L.

It was previously found that *hirsutum* types gave either monohybrid or dihybrid ratios when tested with standard chlorophyll deficient. Several types proved to be homozygous for one of the green factors, but heterozygous for the other. A further series of types of *G. hirsutum* has given the results placed in Table I.

TABLE I.

Results of crossing various types of G. hirsutum with standard chlorophyll deficient. Back-crosses of $F_1 \times$ recessive, or recessive $\times F_1$.

| Type | Origin | Green | Deficient | Ratio | Remarks |
|-------|--------------|-------|-----------|-------|------------------|
| G 152 | South Africa | 649 | 195 | 3 : 1 | Cambodia variety |
| G 153 | " | 509 | 147 | 3 : 1 | " |
| G 154 | " | 416 | 308 | 1 : 1 | U 4 (S. Africa) |
| G 155 | " | 297 | 297 | 1 : 1 | " |
| G 156 | " | 531 | 165 | 3 : 1 | " |
| G 162 | U.S.A. | 30 | 32 | 1 : 1 | King type |

The results of Table I confirm those previously put forward, and indicate that even in the standard U 4 variety of South Africa, there occurs a mixture of monomeric and dimeric plants, with respect to the two factor pairs for green. Discussion of the genetic constitution of *hirsutum* types will be deferred to a later stage.

(2) *G. barbadense* L.

This species is now made to include not only cultivated Sea Island and Egyptian but also a series of wild and semi-wild tropical tree cottons formerly assigned to *G. brasiliense* (Kidney cotton), *G. peruvianum* and *G. vitifolium* (Harland, *loc. cit.*). The genetic constitution of eleven further types, comprising forms from the West Indies, Gambia, Nigeria, Ecuador and Peru, has been investigated. The results are placed in Table II.

The results show that all types of *G. barbadense* L. exhibit monofactorial inheritance in crosses with standard chlorophyll deficient.

(3) *G. purpurascens* Poir.

A number of representative types of this species (Bourbon group) were worked with. The results are presented in Table III.

These results show that of twenty-five types tested, twenty-one exhibit the dihybrid ratio of 3 : 1 in back-crosses. Two types, one from the island of Nevis and the other from the Gambia, were heterozygous

for one of the factors for green and homozygous for the other, since sister F_1 plants produced both 3 : 1 and 1 : 1 ratios in the back-cross. Two¹ types only gave monohybrid ratios, one a truly wild type from the small uninhabited island of Patos a few miles from Trinidad, and the other a semi-wild form from the Gambia, undoubtedly introduced from some unknown region of the New World. These two types resemble each other in many respects and also exhibit many points of similarity to the Polynesian wild species *G. taitense*, which it has been found convenient to separate from *G. purpurascens* principally on ecological grounds.

TABLE II.

Results of crossing various types of G. barbadense with standard chlorophyll deficient. The back-cross $F_1 \times$ recessive, or recessive $\times F_1$.

| Type | Origin | Green | Do- ficient | Ratio | Remarks |
|---------------|-------------|-------|----------------|-------|--|
| 3 | Egypt | 168 | 202 | 1 : 1 | Commercial Egyptian |
| 10 | " | 60 | 78 | 1 : 1 | " |
| Gambia 15 | Gambia | 262 | 373 | 1 : 1 | Semi-wild " |
| 14 | West Indies | 203 | 237 | 1 : 1 | Cultivated tree type |
| Mart. 10 | " | 404 | 357 | 1 : 1 | Semi-wild |
| Tobago, Braz. | " | 267 | 259 | 1 : 1 | Semi-wild kidney (= <i>G. brasiliense</i> Macf.) |
| E.C. 1 | Ecuador | 52 | 62 | 1 : 1 | Cultivated by Indian tribes. Tree type |
| Tanguis | Peru | 112 | 136 | 1 : 1 | Cultivated Peruvian |
| Ishan | Nigeria | 312 | 287 | 1 : 1 | Cultivated commercial variety |
| 15 | West Indies | 356 | 379 | 1 : 1 | Cultivated Sea Island (white flower) |

(4) *G. taitense Parl.*

Two types of this species from Fiji and Vahuka respectively were available for experiment. Both may be regarded as truly wild species, since the seeds are very tiny and the lint covering them is so short and sparse that it cannot possibly have been employed at any time for spinning purposes. The results are presented in Table IV.

These results indicate that both types investigated are monomeric, though it is realised that a further series of plants might reveal the existence of dimery in this species.

(5) *G. Darwinii Watt.*

Some taxonomic notes on *G. Darwinii* will be presented elsewhere. It may suffice to state that this species shows affinities both to *G. barbadense*, to the more primitive wild types of *G. purpurascens*, such as the

¹ Shull (1918) found among a number of plants investigated two heterozygotes for one member of a pair of duplicate genes for leaf shape in *Bursa bursa-pastoris*.

TABLE III.

Results of crossing various types of G. purpurascens Poir. with standard chlorophyll deficient. Back-cross $F_1 \times$ recessive, or recessive $\times F_1$.

| Type | Origin | Green | De- ficient | Ratio | Remarks | |
|-------------------|-------------------|-----------------|----------------|-------|-----------------------------|--|
| Antilles | 1 | Trinidad | 569 | 169 | 3 : 1 | Semi-wild |
| | 2 | " | 731 | 211 | 3 : 1 | " |
| | 3 | " | 612 | 179 | 3 : 1 | " |
| | 4 | " | 298 | 137 | 3 : 1 | " |
| | 5 | Island of Patos | 540 | 623 | 1 : 1 | Wild |
| | 6 | Trinidad (T 11) | 978 | 327 | 3 : 1 | Semi-wild |
| | 7 | " (T 12) | 653 | 195 | 3 : 1 | " |
| | 8 | Martinique | 178 | 52 | 3 : 1 | " |
| | 9 | Nevis | 12 | 5 | 3 : 1 | } ? Semi-wild, four sister F_1 plants |
| | | | 13 | 18 | 1 : 1 | |
| | | | 56 | 22 | 3 : 1 | |
| | | 22 | 13 | 1 : 1 | | |
| 10 | Jamaica (T 24) | 251 | 70 | 3 : 1 | Semi-wild | |
| 11 | Grenadines (T 13) | 240 | 67 | 3 : 1 | Cultivated Marie Galante | |
| Moco | 1 | N. Brazil | 194 | 48 | 3 : 1 | Cultivated |
| | 2 | " | 183 | 44 | 3 : 1 | " |
| | 3 | " | 140 | 49 | 3 : 1 | " |
| | 4 | " | 201 | 48 | 3 : 1 | " |
| | 5 | " | 198 | 52 | 3 : 1 | " |
| | 6 | " | 127 | 33 | 3 : 1 | " |
| Mexico | 2 | Mexico | 882 | 294 | 3 : 1 | Cultivated (=G. <i>Morelli</i> Cook) |
| Ecuador | 3 | Ecuador | 128 | 42 | 3 : 1 | " |
| | 5 | " | 168 | 43 | 3 : 1 | " |
| | 6 | " | 93 | 25 | 3 : 1 | " |
| | 9 | " | 195 | 53 | 3 : 1 | " |
| | 10 | " | 113 | 20 | 3 : 1 | " |
| | 11 | " | 103 | 25 | 3 : 1 | " |
| Colombia | 1 | Colombia | 198 | 58 | 3 : 1 | Semi-wild |
| Gambia | 1 | Gambia | 657 | 777 | 1 : 1 | Semi-wild |
| | 2 | " | 197 | 65 | 3 : 1 | } Semi-wild, four sister F_1 plants |
| | | | 75 | 73 | 1 : 1 | |
| | | | 83 | 74 | 1 : 1 | |
| | | | 175 | 162 | 1 : 1 | |
| Port Essington | 1 | N. Australia | 48 | 15 | 3 : 1 | Semi-wild. Intro- duced from un- known source. Re- sembles Gambia type |

TABLE IV.

Results of crossing two types of G. taitense Parl. with standard chlorophyll deficient. Back-cross recessive $\times F_1$.

| Type | Origin | Green | Deficient | Ratio | Remarks |
|------|--------|-------|-----------|-------|---------|
| 77 | Fiji | 219 | 284 | 1 : 1 | Wild |
| 200 | Vahuka | 452 | 422 | 1 : 1 | " |

Patos type, and to *G. waltense* Parl. The results of crosses with T 5 are presented in Table V.

TABLE V.

Results of crossing G. Darwinii Wall (No. 2127) *with standard chlorophyll deficient. Back-cross recessive* $\times F_1$.

| Family | Green | Deficient | Ratio | Remarks |
|------------------|-------|-----------|-------|------------------------|
| 5 \times G 950 | 26 | 15 | 1 : 1 | Sister F_1 plants |
| G 951 | 36 | 35 | 1 : 1 | |
| G 953 | 28 | 37 | 1 : 1 | |
| G 954 | 53 | 41 | 1 : 1 | |
| Total | 143 | 128 | | |
| Expected | 135.5 | 135.5 | | |

Here it is seen that the only plant tested behaves in monohybrid fashion with standard chlorophyll deficient.

IDENTIFICATION OF FACTORS IN NEW WORLD SPECIES.

INTER-RELATIONSHIPS.

(1) *Monomeric hirsutum and monomeric barbadense.*

From the fact that chlorophyll deficiencies occur in the F_2 of crosses between *hirsutum* and *barbadense*, we may assume the following facts regarding their genetic composition:

- (a) All *barbadense* are C_{ha} .
- (b) All single factor *hirsutums* are C_{hb} .

It is naturally impossible to test all types of *barbadense* against all single factor *hirsutums*, but six single factor *hirsutums* were tested against single factor *barbadense*, and all except one gave deficiencies either in F_2 or in back-crosses with T 5. The F_2 's gave the following results:

| Family | Green | Deficient | Seeds sown |
|----------------------|-------|-----------|------------|
| 4 \times 23 | 32 | 1 | 36 |
| 4 \times 19 | 40 | 1 | 46 |
| 4 \times G 163 | 51 | 0 | 54 |
| G 171 \times G 593 | 41 | 1 | 47 |

The number of deficiencies is below expectation in all the families, but as previously mentioned, the extreme form of deficient is characterised by a very small and weak embryo and does not germinate. In the above cultures, seeds were preliminarily germinated in wet blotting paper, and all exhibited radicles. If it is assumed that some of the ungerminated seeds represent deficiencies, the deviations from the expected 15 : 1 ratio are accounted for. Reference to the data on *hirsutum-barbadense* crosses in the writer's previous paper (1932 *a*) should also be made.

(2) *Monomeric barbadense and dimeric hirsutum.*

Since in back-crosses no ratios higher than the 3 : 1 type have been encountered, it seemed probable that all the *hirsutum* and *purpurascens* types exhibiting bifactorial inheritance contained both C_{ha} and C_{hb} . This assumption has proved to be correct and the experimental evidence is presented below:

The cross G. hirsutum (var. Guatemala Khaki) × G. barbadense (var. Enan's Brown Egyptian).

TABLE VI.

The second back-cross of G. hirsutum (dimeric) × G. barbadense (monomeric) × standard deficient.

| Family | Green | Deficient | Ratio |
|-----------|--------|-----------|-------|
| 5 × 18077 | 33 | 37 | 1 : 1 |
| 18179 | 31 | 26 | 1 : 1 |
| 18225 | 26 | 19 | 1 : 1 |
| 18195 | 28 | 16 | 1 : 1 |
| 18054 | 18 | 23 | 1 : 1 |
| 18070 | 42 | 60 | 1 : 1 |
| 18107 | 53 | 47 | 1 : 1 |
| 18108 | 45 | 51 | 1 : 1 |
| 18145 | 41 | 33 | 1 : 1 |
| 18154 | 16 | 20 | 1 : 1 |
| 18185 | 104 | 89 | 1 : 1 |
| 18189 | 40 | 35 | 1 : 1 |
| Total | 477 | 456 | |
| Expected | 466.5 | 466.5 | |
| 5 × 18156 | 28 | 8 | 3 : 1 |
| 18165 | 86 | 38 | 3 : 1 |
| 18173 | 43 | 10 | 3 : 1 |
| 18222 | 53 | 14 | 3 : 1 |
| 18061 | 39 | 12 | 3 : 1 |
| 18072 | 49 | 21 | 3 : 1 |
| 18078 | 80 | 33 | 3 : 1 |
| 18122 | 95 | 28 | 3 : 1 |
| 18162 | 45 | 19 | 3 : 1 |
| Total | 518 | 183 | |
| Expected | 525.75 | 175.25 | |

Guatemala Khaki was previously (1932*a*) demonstrated to be dimeric, while Enan's Brown (T 3) is established to be monomeric (see Table II).

F_1 . Green.

F_1 × *standard deficient*. Gave sixty-nine plants *all green*. This indicates that the two parents possess one gene in common (C_{ha}).

Second back-cross. Several plants of the first back-cross were back-crossed with standard deficient and gave the results in Table VI.

Table VI shows that of twenty-one families which are the result of a further back-cross to standard deficient, twelve are monohybrid and

nine dihybrid. The results establish conclusively that the genetic constitution of the types involved is:

$$\begin{aligned} G. \textit{hirsutum} \text{ (Guatemala Khaki)} & \mathbf{C}_{ha} \mathbf{C}_{hb}, \\ G. \textit{barbadense} \text{ (Enan's Brown)} & \mathbf{C}_{ha} \mathbf{c}_{hb}. \end{aligned}$$

This means that these two types both possess \mathbf{C}_{ha} (or an allelomorph of it with the same phenotypic effect).

TABLE VII.

Second back-crosses. Chlorophyll deficient \times (*barbadense* \times *purpurascens*).

| Cross | Family | Green | Deficient | Ratio | |
|-----------------------------|-----------------------------|---------------|-----------|---------|---------|
| 5 \times (1 \times 12) | 21 \times 5 | 46 | 32 | 1 : 1 | |
| | 24 \times 5 | 14 | 8 | 1 : 1 ? | |
| | 25 \times 5 | 15 | 17 | 1 : 1 | |
| | 27 \times 5 | 42 | 28 | 1 : 1 ? | |
| | 23 \times 5 | 26 | 10 | 3 : 1 | |
| | 26 \times 5 | 81 | 24 | 3 : 1 | |
| | 28 \times 5 | 45 | 19 | 3 : 1 | |
| | 29 \times 5 | 28 | 9 | 3 : 1 | |
| | 30 \times 5 | 18 | 5 | 3 : 1 | |
| | 5 \times (13 \times 14) | 31 \times 5 | 14 | 10 | 1 : 1 |
| | | 32 \times 5 | 34 | 27 | 1 : 1 |
| | | 33 \times 5 | 20 | 18 | 1 : 1 |
| | | 34 \times 5 | 47 | 22 | 1 : 1 ? |
| | | 39 \times 5 | 17 | 24 | 1 : 1 |
| 40 \times 5 | | 33 | 31 | 1 : 1 | |
| 35 \times 5 | | 60 | 15 | 3 : 1 | |
| 36 \times 5 | | 17 | 6 | 3 : 1 | |
| 5 \times (15 \times 35) | 52 \times 5 | 25 | 33 | 1 : 1 | |
| | 54 \times 5 | 36 | 39 | 1 : 1 | |
| | 56 \times 5 | 7 | 13 | 1 : 1 | |
| | 58 \times 5 | 3 | 7 | 1 : 1 | |
| | 60 \times 5 | 13 | 12 | 1 : 1 | |
| | 51 \times 5 | 68 | 14 | 3 : 1 | |
| | 53 \times 5 | 56 | 23 | 3 : 1 | |
| | 55 \times 5 | 50 | 15 | 3 : 1 | |
| 57 \times 5 | 18 | 8 | 3 : 1 | | |

(3) *Monomeric barbadense and dimeric purpurascens.*

A cross was studied between three types of *G. barbadense* and three types of *G. purpurascens*.

The parent types had been established by direct experiment to give monohybrid and dihybrid ratios respectively in crosses with chlorophyll deficient.

F_1 . Green.

$F_1 \times$ standard deficient. All green.

Second back-cross \times deficient. Gave the results given in Table VII.

In very few cases in the results given in Table VII is there any doubt as to the type of ratio produced, whether 1 : 1 or 3 : 1. If \mathbf{C}_{ha} is common

to both the *barbadense* and *purpurascens* types under investigation, as was the case with the dimeric *hirsutum* type, we should expect equal numbers of 1 : 1 and 3 : 1 ratios.

Actually fifteen families behave in monohybrid and eleven in dihybrid fashion—a close approximation to expectation.

Although the relation between dimeric *hirsutum* and *purpurascens* has not been directly studied, it appears from the above results that all three of the *purpurascens* types tested have one factor in common with *barbadense*, viz. C_{ha} , and since no deficient appear in the F_2 of monomeric *hirsutum* by dimeric *purpurascens*, numerous families of which have been recorded, the latter must also contain C_{hb} and thus be identical in genetic composition with dimeric *hirsutum*.

Conclusion. Genetic composition of dimeric types of *G. purpurascens* Poir. is $C_{ha} C_{hb}$.

(4) *Monomeric purpurascens and monomeric barbadense.*

| Family | Green | Deficient | |
|------------------------|-------|-----------|-----------|
| 15 × Patos G 960 × 5 | 63 | 19 | |
| G 961 | 57 | 17 | |
| G 962 | 71 | 6 | |
| G 964 | 58 | 13 | |
| | 249 | 55 | Total 304 |
| Expected (3 : 1 basis) | 228 | 76 | |

This is clearly the 3 : 1 type of ratio, and the Patos type of *purpurascens* is thus identical in composition with monomeric *hirsutum* ($C_{ha} C_{hb}$).

(5) *Monomeric taitense and monomeric hirsutum and barbadense.*

As previously mentioned, two types proved to contain a single factor when tested against standard deficient. When tested further against *barbadense* (C_{ha}) and *hirsutum* (C_{hb}) the following results were obtained:

| Cross | Green | Deficient | Ratio |
|------------------------|-------|-----------|-------|
| (Fiji Wild × S.I.) × 5 | 63 | 22 | 3 : 1 |
| (Vahuka × S.I.) × 5 | 17 | 6 | 3 : 1 |
| (Fiji Wild × 23) × 5 | 66 | 0 | — |
| (Vahuka × 23) × 5 | 183 | 0 | — |

From the above results, it is clear that the genetic constitution of both types of *taitense* is identical with that of monomeric *hirsutum*.

(6) *Monomeric Darwinii and monomeric hirsutum and barbadense.*

Two plants were worked with, Nos. 2127 and 2120.

(a) Cross with *G. hirsutum* (single factor): No. 2127 \times *hirsutum* T 57.

F_1 . Green.

F_2 . 44 green : 3 deficient.

This is clearly a 15 : 1 ratio and indicates that the single factor possessed by *Darwini* is not the same as that of *hirsutum*.

(b) Crosses with standard *hirsutum* (T 23) and *barbadense* (T 4).

| Cross | Green | Deficient | Ratio |
|--|-------------|-----------|-------|
| (23 \times 2127) \times 5 | 42 | 11 | 3 : 1 |
| (4 \times 2127) \times 5 | (All green) | | |
| (G 1545) \times 5, 2nd back-cross (<i>barbadense</i> \times <i>Darwini</i> \times 5) | 104 | 0 | |

Only one plant (No. 2127) has been tested against both C_{ha} and C_{hb} but since another type (No. 2130) also gave monohybrid ratios with standard deficient, it is probable that both are of the same genetic composition, viz. $C_{ha} c_{hb}$ —identical with *G. barbadense*.

(7) *Dimeric tomentosum and dimeric purpurascens.*

In the previous paper it was suggested that *G. tomentosum* had the genetic constitution $C_{ha} C_{hb}$. It has been shown that the dimeric forms of *hirsutum* and *purpurascens* are also $C_{ha} C_{hb}$. To confirm the identity of the genetic constitution of *tomentosum* and *purpurascens* a cross between *tomentosum* and a dimeric *purpurascens* was investigated. The results were as follows:

F_1 . Green.

F_2 . All green.

$F_1 \times$ deficient. All green.

Second back-cross \times deficient. Gave the results in Table VIII.

TABLE VIII.

The second back-cross, chlorophyll deficient \times (purpurascens \times tomentosum).

| Cross | Family | Green | Deficient | Ratio |
|-----------------------------|--------|-------|-----------|-------|
| 5 \times (12 \times 22) | 1271 | 13 | 13 | 1 : 1 |
| | 1272 | 57 | 15 | 3 : 1 |
| | 1273 | 8 | 2 | 3 : 1 |
| | 1274 | 51 | 13 | 3 : 1 |
| | 1275 | 49 | 13 | 3 : 1 |
| | 1276 | 38 | 12 | 3 : 1 |
| | 1278 | 55 | 12 | 3 : 1 |

Here, as expected, with the exception of one family, only 3 : 1 ratios are obtained in the second back-cross, and the constitution of *purpurascens* and *tomentosum* is clearly established to be identical ($C_{ha} C_{hb}$).

The aberrant family giving 13 green : 13 deficient does not affect the general validity of this conclusion since six families are clearly of the 3 : 1 type. It is possible that one of the members of the duplicate pair has mutated in the case of the parent plant 1271 which gave monohybrid segregation.

DISCUSSION.

In the foregoing pages, the genetic constitution of all the known species of 26-chromosome New World cottons in respect of the pair of chlorophyll-deficient factors C_{ha} and C_{hb} has been determined.

The distribution of a gene or genes in several species of a genus or even in geographical races of one species has not often been investigated, but from the evolutionary point of view it is of great importance. The data discussed in this paper may be summarised briefly in the form shown in Table IX.

TABLE IX.

Showing the genetic constitution of species of New World cottons, in respect of C_{ha} and C_{hb} .

| Species | Genetic constitution |
|------------------------------|------------------------------------|
| <i>G. barbadense</i> Linn. | $C_{ha} C_{hb}$ |
| <i>G. hirsutum</i> Linn. | $C_{ha} C_{hb}$ or $c_{ha} C_{hb}$ |
| <i>G. purpurascens</i> Poir. | $C_{ha} C_{hb}$ or $c_{ha} C_{hb}$ |
| <i>G. taitense</i> Parl. | $c_{ha} C_{hb}$ |
| <i>G. tomentosum</i> Nutt | $C_{ha} C_{hb}$ |
| <i>G. Darwinii</i> Watt | $C_{ha} C_{hb}$ |

The distribution of the pair of factors under consideration is in accordance with the known facts respecting the relationship of the above species. The three species *hirsutum*, *purpurascens*, and *taitense* are genetically so closely allied, that they are probably not deserving of more than sub-specific rank. *Darwinii* and *barbadense*, although identical in composition in respect of chlorophyll deficiency, are certainly further removed from each other than *hirsutum* is from *taitense*, and the taxonomic affinities of *tomentosum* are still in doubt, though it has affinities to both *hirsutum* and *barbadense*. Further, only two types of *Darwinii*, two types of *taitense* and one of *tomentosum* have been investigated, and it is possible that the mode of distribution of the factors may be more variable than so far appears.

It is obvious that the distribution of one or two factors throughout a section of a genus cannot by itself afford much information regarding taxonomic relationship, and the modifiers affecting such factors are probably more important than the main genes themselves.

There is considerable reason for the belief that duplicate factors may often be a consequence of polyploidy, and according to the investigations of Dr Skovsted of this laboratory (1933) the New World species of *Gossypium* with 26 pairs of chromosomes are most probably allopolyploids with one set of 13 chromosomes homologous with cultivated Asiatics, and the other set derived from an undetermined 13-chromosome species.

Whether the duplication of factors in the present material took place through polyploidy cannot be said with certainty, but the data presented in this paper seem to point to the dimeric type as the original condition, and to a tendency for one or other of the factors to mutate to its allelomorph. In monomeric (single factor) types, the recessive could certainly not survive in nature, but when protected by the other factor, mutation of either factor could take place without injury to the species. It is possible that the widespread occurrence of monomeric forms in New World species of *Gossypium*, probably now greatly exceeding the dimeric types in total number, is merely a consequence of the fact that recurrent mutation has taken place unopposed by selection (*vide* Fisher, 1930, p. 80). On the other hand, it is conceivable that mutation to the recessive may confer a slight advantage since the pleiotropic nature of factors is well known.

An extensive survey of a representative group of *hirsutum*s taken from an ordinary commercial field where C_{ha} is known to be present in all three phases of the gene (AA , Aa and aa) would undoubtedly provide data of extreme interest.

The most complete account of the distribution of duplicate factors in the different geographical races of a species (*Bursa bursa-pastoris*) has been given by Shull (*loc. cit.*).

He found that the two factors B and B^1 exist in certain strains, that these two factors produce the same characteristic lobing of the leaves, and that they are independently inherited from each other.

Of special interest in connection with the present experiments is the fact that the biotypes having the B factor duplicated appeared to be less widely distributed than the monomeric types. No data are presented on the composition of the latter in respect of B and B^1 . The author draws a conclusion quite opposite to the one put forward in this paper, namely that duplication of the factor has taken place at a relatively recent date. This view, however, was expressed at a time when the possibilities of polyploidy in inducing the dimeric condition were not realised.

He envisages, however, the possibility that the dimeric condition may

also be in some cases "the primitive condition from which monomeric and recessive strains may have arisen... If wild bio-types almost universally possess the duplicated factors, it may be assumed that this condition is either primitive or at least relatively old."

Another pair of duplicate factors was also investigated by Shull (1914). He found that all the wild forms of *Bursa* tested by him possessed duplicate factors for capsule shape (triangular vs. round). Dahlgren however (1915) found a type which exhibited monohybrid inheritance with round. It appears therefore that the tendency for the dimeric condition to break down into the monomeric is probably fairly common. The chromosome number of this species ($n=16$) establishes with a fair degree of certainty its polyploid nature (Gaiser, 1930).

The present writer (1919) established the existence of duplicate factors for the Holstein pattern of the seed coat in *Vigna sinensis*. The genetic composition of four further types has been determined in subsequent experiments. Altogether, of six types, five have been shown to be monomeric and only one dimeric, though some complications in ratios occurred which are as yet unexplained. Here again it seems that the monomeric condition is much commoner than the dimeric.

A phenomenon similar to that found in cotton was observed by Trow (1916). In *Senecio vulgaris*, the F_2 of *praecox* \times *lanuginosus* segregated into 15 green : 1 white, and the genetic constitution of the two parental types was therefore represented as **AAbb** and **aaBB** respectively. Here again we have evidence of the tendency for the dimeric condition to break down into the monomeric.

If as a consequence of polyploidy a large number of genes become duplicated, and the characters governed by such genes are of importance to the species, one of the members may mutate, leaving the character unimpaired, with the further possibility that such mutation may be of benefit to the species. The duplication of all the genes in an autopolyploid should mean that a large number, possibly several hundred genes, are liberated for mutative purposes with concomitant augmentation of genetic variance and potentiality for evolution. Since even the two species from which allopolyploids probably arose also possess many genes in common (otherwise it may be imagined that they would fail to cross), the same process could also take place, inasmuch as mutations in many loci could take place and be unopposed by counter-selection.

This argument has already in its main form been put forward by Haldane. He mentions the fact (1932) that allopolyploids "possess several pairs of sets of genes, so that one gene may be altered without

disadvantage, provided its functions can be performed by a gene in one of the other sets of chromosomes," and further (1933), "The final result will be that most of the genes will return to the diploid condition."

It may be suggested that the extent to which conversion of the dimeric to the monomeric condition in autopolyploids will be an integration of (a) the age of the polyploid species, and (b) the rate of mutation of the loci involved. In old allopolyploid species of which the New World species of *Gossypium* probably provide examples, we should expect to find only a few cases of dimery—most of the pairs having broken up into the monomeric condition.

In *Gossypium* such breaking down appears to have taken place in most of the loci which have been tested. Thus there is no evidence of duplication in either the **Y** (yellow corolla) or **P** (yellow pollen) loci. These are monomeric throughout the group, though from the fact that the recessive **p** is unknown in the Asiatic group of cultivated cottons, it is likely that both of the original allopolyploid constituent species possessed yellow pollen. Decay of both these characters may have taken place however before the origin of the polyploid types, since the New World 13-chromosome species *G. lancoeforme* Miers is characterised only by **y** and **p**.

Cream pollen (presumably **p**) is characteristic also of the 13-chromosome species *G. Sturtii*, *G. africanum* Watt, and *G. Stocksii*.

Perhaps the most important point in connection with these experiments, however, is the fact that in an old polyploid species there may ultimately be no trace of the existence of duplicate genes, so far as single species are concerned, though in interspecific crosses duplication should be encountered fairly frequently through the here demonstrated tendency to mutate to a different member of a pair in different species.

SUMMARY.

1. Further experiments are described on the mode of inheritance and distribution in six species of New World cottons of a pair of duplicate factors for chlorophyll deficiency.

2. Duplication of factors is considered to have taken place through polyploidy with subsequent mutation of one or other of the members constituting the pair in some of the species. *Barbadense* and *Darwinii* have become monomeric through the loss of factor **C_{1b}** while *purpurascens*, *hirsutum*, and *latifolium*, when monomeric, are shown to have lost **C_{1a}**.

3. The experimental data support Haldane's view that in polyploid species one member of a pair of duplicate genes may mutate without

disadvantage, provided its functions can be performed by a gene in one of the other sets of chromosomes.

4. The taxonomic and evolutionary significance of the results is discussed and it is suggested that the extent to which the dimeric condition is converted to the monomeric in polyploid species may provide some indication of the age of the species. In an old series of allopolyploids such as the New World species of *Gossypium* are considered to be, cases of dimery might be expected only infrequently, and usually only in interspecific crosses.

REFERENCES.

- DAHLGREN, K. V. O. (1915). "Ein Kreuzungsversuch mit *Capsella Heegeri* Solms." *Svensk Bot. Tidsk.* **9**, 397.
- FISHER, R. A. (1930). *The genetical theory of Natural Selection*. Oxford: Clarendon Press.
- GAISER, L. O. (1930). "Chromosome numbers in Angiosperms. II." *Bibliogr. Genet.* **6**, 171.
- HALDANE, J. B. S. (1932). *The causes of Evolution*. London: Longmans, Green and Co.
- (1933). "The part played by recurrent mutation in evolution." *Amer. Nat.* **67**, 5.
- HARLAND, S. C. (1919). "Inheritance of certain characters in the cowpea (*Vigna sinensis*)." *Journ. Gen.* **8**, 101.
- (1932*a*). "The genetics of cotton. Part VI. The inheritance of chlorophyll deficiency in New World cottons." *Journ. Gen.* **25**, 271.
- (1932*b*). "The genetics of *Gossypium*." *Bibliogr. Gen.* **9**, 107.
- SHULL, G. H. (1914). "Duplicate genes for capsule form in *Bursa bursa-pastoris*." *Zts. ind. Abst. u. Verer.* **12**, 97.
- (1918). "The duplication of a leaf-lobe factor in the shepherd's purse." *Brooklyn Bot. Gard. Mem.* **1**, 427.
- SKOVSTED, A. (unpublished). "Cytological studies in cotton. Part 2. Two inter-specific hybrids between Asiatic and New World cottons."
- TROW, A. H. (1916). "On 'Albinism' in *Senecio vulgaris* L." *Journ. Gen.* **6**, 65.