

THE GENETICS OF COTTON.

PART V. REVERSAL OF DOMINANCE IN THE INTERSPECIFIC
CROSS *G. BARBADENSE* LINN. × *G. HIRSUTUM*
LINN. AND ITS BEARING ON FISHER'S
THEORY OF DOMINANCE.

BY S. C. HARLAND.

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

INTRODUCTION.

THE Crinkled Dwarf mutation of Sea Island cotton was described, and its mode of inheritance in relation to the normal type worked out by the present writer (1918*a, b*). Briefly, normal and Crinkled behaved as a simple pair of allelomorphic characters, normal being completely dominant. The only exception was a normal which showed a certain degree of crinkling. This plant behaved as a strict normal in F_3 , producing 3 normal to 1 Crinkled.

The present paper describes the results of crosses between Crinkled Dwarf and Upland, and references are also made to the results of crosses with other types.

MATERIAL.

The Crinkled Dwarf used in these experiments occurred in a plot of Sea Island cotton grown from St Vincent seed in 1926. When selfed it bred true to Crinkled, and the original Crinkled has been maintained by grafting since that date.

When crossed with Sea Island the same results were obtained as in former experiments.

THE EXPERIMENTAL RESULTS.

(1) *Crosses of Crinkled Dwarf with other Peruvian types.*

(a) Crinkled Dwarf × Red Kidney.

Red Kidney is a tree Peruvian which has been used extensively in genetic experiments at this Station (Harland, 1929).

It is a type of *G. brasiliense* Macf., though this species is now,

according to our classification, considered as not being specifically distinct from *G. barbadense* Linn.

F_1 . Slight traces of crinkling were exhibited.

$F_1 \times$ Crinkled. Segregation occurred into normal and Crinkled in the usual 1:1 ratio. An occasional normal showed slight signs of crinkling.

(b) Crinkled Dwarf \times G.W.P.

G.W.P. (Grenadines white pollen) is a Peruvian type of Marie-Galante, again not specifically distinct from *G. barbadense* Linn.

F_1 . Very faint traces of Crinkled were apparent, particularly in old and badly grown plants.

F_2 . Segregation took place into normal and Crinkled in the 3:1 ratio. A few of the normals showed traces of crinkling and these behaved as heterozygotes in F_3 . It is unnecessary to present the results in detail, since they are merely confirmatory of those already obtained with Sea Island.

(c) Crinkled Dwarf \times Enan's Brown Egyptian.

The results of this cross were similar to those of (a) and (b). A few of the normal plants of F_2 were slightly crinkled and behaved as heterozygotes in F_3 .

(d) Egyptian Wrinkled Leaf \times Sea Island.

Wrinkled Leaf is reported to occur in Egyptian cotton in Egypt, and from its appearance it was suspected to be identical with Crinkled Dwarf in respect of the Crinkled-normal pair of factors. This proved to be the case, since the cross Crinkled Dwarf \times Wrinkled Leaf gave nothing but Crinkled in F_1 .

The F_1 of the cross Wrinkled Leaf \times Sea Island exhibited faint signs of crinkling to about the same degree as in the cross Red Kidney \times Crinkled Dwarf.

Conclusions. The broad conclusion may be drawn from the above experiments that Crinkled behaves as a simple recessive to normal in other members of the Peruvian group, though absolutely complete dominance was only found in crosses between Crinkled and the type from which it originated by mutation. The fact that dominance was slightly affected, in Crinkled by Egyptian, and Wrinkled Leaf by Sea Island, seems to indicate that each varietal type within the species has its own particular association of factors for normality, and that the slight variations in dominance resulted from the transference of Crinkled

to a different genetic background. It was therefore decided to see what would happen, if Crinkled were transferred to another species in the genus *Gossypium*, and crosses were therefore made of Crinkled with *G. hirsutum* Linn. (Upland). This species is markedly different from *G. barbadense* Linn. in almost all characters, although fully fertile hybrids are possible.

(2) *The cross Upland × Crinkled Dwarf.*

F_1 . Uniform and practically intermediate between the parents. Crinkling was not apparent until three or four leaves had unfolded, whereas in Crinkled Dwarf the first leaf after the cotyledons is characteristically crinkled.

F_2 . The plants showed complete gradation from normal to Crinkled of a type more extreme than the original type. No classification was possible.

The first back-cross ($F_1 \times$ Upland).

Segregation occurred as follows:

Family	Normal	Crinkled
1	118	77
2	13	1
3	35	20
Total	166	98
<i>Expected</i>	<i>132</i>	<i>132</i>

Here there is a considerable excess of normals, and the distinction between normal and Crinkled was not always easy to make. Some of the Crinkleds were more crinkled than the F_1 type, others resembled the F_1 , while a number exhibited only slight traces of crinkling. It is probable that some of the plants classified as normal were really heterozygotes.

The progeny of Crinkleds from the first back-cross.

Five Crinkleds were selfed and a small progeny row grown from each. The results were as follows:

Family	Normal	Crinkled	Condition of parent
128	6	9	Less crinkled than F_1
129	18	28	About F_1 type
130	6	17	More crinkled than F_1
131	0	8	More crinkled than F_1
132	16	17	About F_1 type

It will be seen that family 130 gives a ratio of 3 Crinkled to 1 normal. Distinction between normal and Crinkled in this family was readily effected. Some of the Crinkleds, presumably homozygotes, were of the

extreme type which appeared in F_2 . The leaves were very small (about one-quarter the normal size and excessively crinkled). The other families 128, 129, 132 segregate irregularly. Since in these plants the Upland genetic background tends to produce a dominant Crinkled and a Peruvian background a recessive Crinkled, it is not surprising that a normal Mendelian ratio fails to appear. Probably a family such as 132 consists of both pure and heterozygous normals as well as homozygous and heterozygous Crinkleds.

The progeny of family 130.

A number of plants of family 130 were grown on to the next generation. The results were as follows:

Family	Parent	Crinkled	Normal
2	Normal	0	164
4	Normal	0	34
5	Normal	0	36
6	Normal	0	79
3	Crinkled (less than F_1)	19	18
7	Crinkled (more than F_1)	52	9
8	Crinkled (more than F_1)	18	10
10	Crinkled (more than F_1)	10	4
12	Crinkled (strong)	22	10
13	Crinkled (less than F_1)	57	27
17	Crinkled (very strong)	38	12
22	Crinkled (about F_1)	45	13
14	Crinkled (very strong)	14	0
18	Crinkled (very strong)	54	0
21	Crinkled (about F_1)	27	0

In the above families it is seen that normal bred true (4 families) while Crinkled bred true in 3 families and split into Crinkled and normal in 8 families. The proportion of Crinkled to normal deviates considerably from 3 : 1 in some families (*e.g.* nos. 3 and 8), but is close to expectation in others (nos. 10, 17 and 22).

Close examination of the abnormal families showed that some at least of the normals were probably crinkled, and the distinction between normal and Crinkled was as impossible to make as in the original F_2 . Segregation of modifying factors affecting the expression of Crinkled readily accounts for the results.

It may be noted that the Crinkled parents which proved to be homozygous were more viable than the extreme Crinkled which appeared in F_2 .

Some of the latter were practically sterile and produced minute flowers with only two or three anthers. It is evidently possible to produce a viable Crinkled dominant by a combination of modifiers from Upland and Peruvian.

In the above series of families it was not possible to distinguish

between homozygous and heterozygous Crinkled by inspection, although homozygous Crinkled was in general more strongly crinkled than heterozygous. Families breeding true to Crinkled showed much variability in the development of the crinkled character.

Second back-cross with Upland.

Six of the Crinkled plants in the first back-cross were back-crossed again with Meade. The results were as follows:

Family	Normal	Crinkled
11	0	3
13	7	3
21	7	8
23	6	7
117	1	0
125	6	3
Total	27	24
<i>Expected</i>	<i>25.5</i>	<i>25.5</i>

The Crinkleds still showed a good deal of variation, but in two plants only was there any difficulty in classification. The ratio of normal to Crinkled now approaches the ordinary 1:1 type, and most of the Crinkleds were more crinkled than the original F_1 . Evidently the replacement of Peruvian genes by their Upland allelomorphs is progressively converting Crinkled into a dominant.

Third back-cross with Upland.

Three Crinkleds were again back-crossed with Upland with the following results:

Family	Normal	Crinkled	Remarks
300	61	50	Some strongly crinkled but grading to F_1 type or less
312	73	69	Classification occasionally difficult
322	52	52	Some variability in crinkled class but mostly strongly crinkled
Total	186	172	
<i>Expected</i>	<i>179</i>	<i>179</i>	

The plants in these families showed no traces of Peruvian genes with the exception that segregation still occurred in Family 300 into Y (yellow corolla) and y (cream corolla), the Y being derived from the original Crinkled parent.

Fourth back-cross with Upland.

A single Crinkled from the third back-cross was back-crossed with Upland and again gave a ratio of 1 Crinkled : 1 normal (10 : 9). There was sharp segregation and the Crinkleds were almost uniform, with the exception of one plant which was less crinkled than the rest.

(3) *Crosses between Crinkled and 13-chromosome species.*(a) Crinkled \times *G. sturtii*.

The fact that crosses are readily made between the wild Australian species *G. sturtii* F. v. M. and cultivated New World cottons made it possible to observe the F_1 of Crinkled \times *G. sturtii*.

Several plants were grown and *all were uniform and strongly crinkled*. The investigation could not be followed further owing to the complete sterility of the hybrid.

(b) (Crinkled \times Peruvian Normal F_1) \times *G. sanguineum* Hassk.

The Peruvian parent was a hybrid between Crinkled Dwarf and normal Egyptian, and showed very slight traces of crinkling. The cross between one of these plants and *G. sanguineum*, a red-flowered Asiatic, produced *one slightly crinkled plant* which showed the crinkled character rather more strongly than the female parent.

The difference in reaction of Crinkled to two different 13-chromosome types suggests that *Sanguineum* is closer taxonomically to Peruvian than is *Sturtii*.

Since the pollen of the *Sanguineum* hybrid is partly fertile on Peruvian, it may be possible to study the question further with different chromosomal combinations.

FISHER'S THEORY OF DOMINANCE—DISCUSSION.

In a series of papers, Fisher (1928, 1929) has brought forward a new theory of dominance. A summary of Fisher's theory is given by Wright (1929 *a*) as follows:

“Assuming that the pristine character of heterozygotes is intermediate, his suggestion is, in brief, that the observed gene mutations, however rare in laboratory experience, have nevertheless had opportunity to recur a very large number of times in the evolutionary history of the species; that such mutations are usually deleterious; that natural selection plays with much greater force on the heterozygotes than on the homozygous mutants (because of the enormously greater relative abundance of the former); that the character of the heterozygote is subject to the action of modifying factors, and that in consequence of all these facts there will be a gradual drift of the heterozygote toward the wild type, not necessarily involving the homozygous mutant type to any great extent. In the course of geologic time this may bring about dominance of the wild type, or dominance so nearly complete that the heterozygote is no longer subject to adverse selection.”

Wright (*loc. cit.*) calculated a selection rate so extremely slow that he believed its efficacy highly questionable. He considers that the hypothesis of a selection pressure of the order which he calculates, being "the general factor making for the dominance of the wild type depends on the assumption that modifiers of dominance (assumed to be sufficiently abundant) are in general so nearly indifferent to selection on their own account that a force of the order of mutation pressure is the *major* factor controlling their fate."

Wright doubts whether there are many such genes, and concludes: "it seems that in the hypotheses that mutations are most frequently in the direction of inactivation and that for physiological reasons inactivation should generally behave as recessive, at least among factors with major effects, may be found the explanation of the prevalence of recessiveness among observed mutations."

The preliminary results of the Crinkled Dwarf by Upland cross were communicated privately to Dr R. A. Fisher, who used them in support of his theory of dominance.

The experimental data are now carried to a further stage, and it will be convenient to examine their bearing on the Fisher theory. The salient facts may be briefly summarised as follows:

1. The Crinkled Dwarf mutation occurs in Peruvian relatively frequently, but not in Upland.

2. Enquiries have been made and all workers with Upland cotton are unanimous in stating that they have never seen it. If it does occur in Upland it must do so with far less frequency than in Peruvian. We thus have a clear demonstration of a fact of great importance, namely that the mutability of given locus is conditioned by the genotype as a whole. Transference of the Crinkled gene to the Upland genotype by continued back-crossing has the following results:

- (a) The heterozygous type (Aa phase) is Crinkled but less so than the homozygous Crinkled of Peruvian. The first few leaves are normal.

- (b) Homozygous Crinkled (aa phase) from first back-cross is a very weak type which may be classed as a semi-lethal and often a fully lethal dominant.

Crinkled may now be regarded as a dominant, since classification is most readily effected by grouping heterozygote and Crinkled together.

If the phenotypic appearance of the heterozygote in Upland represents the pristine appearance of the Crinkled gene in a species where it has not previously occurred, it may be concluded on the Fisher theory that on its first appearance in Peruvian the Crinkled heterozygote was

intermediate, and the homozygote semi-lethal. Factors promoting viability have been acquired, and these have converted the intermediate into a phenotypic normal, and the semi-lethal homozygous Crinkled into a type which can compete with a fair degree of success with the normal or wild type.

So far the experimental data are fully in accord with the Fisher theory, but it becomes pertinent to enquire how the modifying factors have been spread throughout the whole Peruvian group, for we have seen that any member of the Peruvian group gives clear segregation in crosses with Crinkled. The very slight variations in dominance which occur doubtless indicate that the genotypes differ in one or more minor factors only, and the absence of blending in F_2 makes it evident that all members of the Peruvian group are homozygous for most of the modifiers.

It may be assumed that at the time of the first appearance of the mutant in Peruvian a number of genes capable of promoting the viability of the **Aa** phase were present in the stock. This assumption may be made because of the differences in reaction shown by different Upland stocks to the newly introduced mutant. The **Aa** types, occurring in about 1 in 50,000 times, would be subjected to a stringent selection in which the most viable only would survive. At this stage, the **aa** type would not survive at all in nature, since the corresponding Upland type requires careful pot culture to flower at all.

Selection could hardly be taking place among the normals, since the **AA** phenotype of Upland shows no sign of any selective effect. The ultimate end of the selection process is that in the absence of natural crossing a number of lines would be established—the descendants of Crinkled, with certain combinations of modifiers of viability. But these combinations need not be the same in all stocks, and it cannot be assumed that any one stock would be initially so heterozygous at the start that the **Aa** descendants of any one **Aa** plant could acquire them all by selection for viability. We find, however, that the modifiers are the same, or nearly the same in every member of the Peruvian group, and we are driven to the conclusion that selection could not produce this result. Mutation then must be invoked.

We have seen that all Uplands are not alike in their reaction to Crinkled, so that mutation in genes influencing dominance has already taken place.

If there are a large number of possible and mutually replaceable (polymeric) genes capable of acting as modifiers, it is possible that a sufficient number of these can be accumulated in a relatively short

period by mutation in the heterozygotes and their descendant lines to convert them to normal. It is further possible that every modifying gene has a definite rate of mutation, and if the most frequently mutating ones are made use of first, all the lines descended from heterozygotes may ultimately come to have the same or nearly the same combinations of modifiers.

The fact that genes modifying the **Aa** phase are nearly homozygous throughout the species means that every normal now in existence is descended from original heterozygotes. The strict application of this conception means that all members of any species showing a large number of recessive mutants to which the wild type is dominant, must have descended from the **Aa** phase of all these mutants.

This would require that an enormous number of mutations insensitive to selection on their own account become common to the whole species merely on account of their effect on the viability of heterozygotes which may not occur with greater frequency than once per million. Can it be granted that the viability genes accumulated by the **Aa** phase, under enormously stringent selection, give the **AA** descendants of such **Aa** plants an advantage over unmodified **AA** plants? It seems that such genes are not sensitive to selection on their own account in normal populations, but it is conceivable that the cumulative effect of a number of them might impart some slight advantage. Unless this be granted the writer is inclined to believe that it is some other process than that put forward by Fisher that we must look to for the explanation of complete dominance of the wild type.

The alternative theory put forward by Wright (1929 *a*), that there tends to be dominance of the active phase of a gene, is inapplicable to the phenomena observed when Crinkled is transferred to the Upland genotype, for here the physiological effect of the Crinkled gene is conditioned by whatever modifying genes happen to be present, and we cannot say *per se* whether the Crinkled gene or its allelomorph is physiologically the most active.

SUMMARY.

1. Crosses of Crinkled Dwarf \times Sea Island exhibit complete dominance of Sea Island, but in crosses with other Peruvian types, dominance is slightly disturbed, producing in F_1 normals with a slight trace of crinkling and some variation of the Crinkled class in F_2 .
2. A cross of Crinkled Dwarf \times Upland gave an intermediate F_1

with dominance becoming increasingly manifest in back-crosses of heterozygote to Upland.

3. Selfed heterozygotes from the first back-cross produced in one case a family indicating true reversal of dominance, the ratio 3 Crinkled : 1 normal being obtained. Reversal of dominance persisted in the next generation from this family.

4. Crosses involving Crinkled and *G. sturtii* gave F_1 strongly crinkled, but a heterozygous Crinkled \times *G. sanguineum* gave F_1 only slightly crinkled.

5. The bearing of the experiments on Fisher's theory of dominance is discussed, and it is concluded that while the behaviour of Crinkled in Upland crosses is in accordance with the Fisher theory, the process by which genes modifying dominance are thought to have become homozygous in Peruvian involves the assumption that normals descended from heterozygotes have replaced the original normal population. This assumption is thought to be improbable.

REFERENCES.

- FISHER, R. A. (1928 *a*). "The possible modification of the wild type to recurrent mutations." *Amer. Nat.* LXII, 115.
 — (1928 *b*). "Two further notes on the origin of dominance." *Ibid.* LXII, 571.
 — (1929). "The evolution of dominance; reply to Professor Sewall Wright." *Ibid.* LXIII, 553.
 HARLAND, S. C. (1918 *a*). "On the genetics of Crinkled Dwarf rogues in Sea Island cotton. Part 1." *West. Ind. Bull.* XVI, 82.
 — (1918 *b*). "On the genetics of Crinkled Dwarf rogues in Sea Island cotton. Part 2." *Ibid.* XVI, 353.
 — (1929) "The genetics of cotton. Part I. The inheritance of Petal Spot in New World cottons." *Journ. Gen.* XX, 365.
 WRIGHT, S. (1929 *a*). "Fisher's theory of dominance." *Amer. Nat.* LXIII, 274.
 — (1929 *b*). "The evolution of dominance." Comment on Dr Fisher's reply. *Ibid.* LXIII, 556.