

# THE GENETICS OF 'CORKY'

## I. THE NEW WORLD ALLELES AND THEIR POSSIBLE ROLE AS AN INTERSPECIFIC ISOLATING MECHANISM

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(With Plate 4 and One Text-figure)

### 1. INTRODUCTION

Harland (1915, 1939) first noted in crossing certain types of Bourbon (*Gossypium hirsutum* var. *marie-galante* Hutchinson) with Sea Island cotton (*G. barbadense* L.) that the hybrid obtained was an abnormal stunted plant with leaves 'showing yellow spotting of the mosaic type' and the stem 'streaked with a rough corky outgrowth'. Repeated back-crossing of the abnormal 'corky' type to *G. barbadense* gave clear 1 'corky' : 1 normal segregations, which suggested that complementary genes were responsible for abnormal cork production. These he named provisionally  $Ck^P ck^B$  (carried by Bourbon) and  $ck^P Ck^B$  (carried by Sea Island) respectively.

Since 1939 data have been collected which do not confirm Harland's interpretation but suggest that abnormal cork is due to the interaction of alleles at a single locus, i.e. that all corky plants are heterozygotes. Critical analysis has proved to be surprisingly difficult owing to the complicating factors of female sterility, differential effects of modifier complexes and differential response to environmental conditions. It is the purpose of this paper to give an account of abnormal cork production in certain *barbadense* × *marie-galante* hybrids, and to consider the geographic distribution of its occurrence.

### 2. THE CORKY COMPLEX

Since cork production is only one symptom of a complex abnormality, it will be convenient at the outset to describe more fully the abnormal characters which behave as a genetic unit. The first deviation from the normal appearance is seen prior to flowering, sometimes as early as the first foliage leaf. The leaves become yellow in the neighbourhood of the veins, and patches become 'cleared' of chlorophyll. Later a yellowish mottling spreads over the whole leaf. The edges of the leaves tend to roll inwards so that the leaf surface becomes trough-shaped instead of flat. Internodes are shortened, and in extreme cases the main axis of the plant is greatly compressed so that it becomes dwarfed with crowded leaves. This dwarfing is most noticeable prior to flowering. Also there is a tendency for an excess production of lateral branches which enhances the crowded appearance of the vegetative parts. Cork production is very variable and is often suppressed when the plants are shaded or grown under exceptionally humid conditions. Under normal field conditions high-grade corky types have the whole of the stems, petioles and leaf midribs covered with a thick greyish layer of cork. The cork usually makes its first appearance as thin streaks running longitudinally along the still rapidly elongating stem internodes; hence it occurs prematurely in comparison with the time of normal cork production. In low-grade types only faint traces of cork may be apparent.

and even these are sometimes absent from the main stem but just discernible on late-formed monopodial branches. Scoring for cork is unreliable until the peak of flowering has been reached. As a rule the general vigour of the corky plant does not seem to be impaired and it usually flowers freely. In all corky plants, however, female fertility tends to be reduced. High-grade corky types fail completely to set seed by self- or cross-pollination, although the flowers are externally indistinguishable from normal. Microscopic examination of the pollen of these extreme types showed that it was normal in appearance, and its viability was confirmed by the fact that it was capable of fertilizing Sea Island ovules. Stigmas of these female sterile plants were pollinated with Sea Island pollen. Twenty-four hours after pollination pollen-tube growth was examined using a modification of Nebel's (1931) method. The tubes grew satisfactorily in the style. However, it is unlikely that fertilization had taken place, since examination of the ovaries of newly shed pollinated flowers showed that none of the ovules had enlarged or developed lint hairs. It seems probable that sterility of these extreme corky types is due to the failure of fertilization to be effected before flower abscission occurs. Whether the failure is due to premature formation of an abscission layer in the flower stalk which might possibly be an extreme manifestation of premature cork formation has not yet been investigated. Low-grade types usually set bolls, but a variable proportion of the seeds fails to germinate. This elimination appears to be progressive, since inviable fertilized ovules ranging from small 'motes' to empty seeds are found when immature bolls are opened. The general appearance of a high-grade corky type is compared with a normal type in Pl. 4. Throughout this paper the term 'Corky' designates the whole complex of abnormal characters which has been described.

### 3. THE INHERITANCE OF CORKY IN *MARIE-GALANTE* × SEA ISLAND CROSSES

The genetics of Corky was studied in two crosses:

- G. barbadense*                      *G. hirsutum* var. *marie-galante*
- (1) St Vincent Sea Island (V135) × St Thomas' Bourbon  
 (2) St Vincent Sea Island (V135) × Bourbon Intense

St Thomas' Bourbon is a native semi-wild type from the island of St Thomas (Virgin Islands), and Bourbon Intense is a type similar to those cultivated in the Grenadines and having a flower characterized by an intensely red petal spot. The  $F_1$  plants obtained from both crosses were medium-grade Corky, i.e. they exhibited the characteristic leaf abnormality and the stems were streaked with cork, but dwarfing was not pronounced. First and second backcrosses to Sea Island were carried out, using the Sea Island as female parent. It was apparent that the Corky symptoms were greatly intensified by backcrossing to Sea Island. In all cases only one type of segregation was obtained—1 Corky : 1 Normal—which confirmed Harland's earlier results. Data are presented below:

	Corky	Normal	Total
First backcross:			
Sea Island × St Thomas' → Sea Island	91	88	179
Sea Island × Bourbon Intense → Sea Island	49	46	95
Combined families	140	134	274
Second backcross:			
Sea Island × St Thomas' → Sea Island	57	50	107
Sea Island × Bourbon Intense → Sea Island	16	21	37
Combined families	73	71	144

In order to test critically Harland's hypothesis that complementary genes are responsible for Corky,  $F_2$ 's,  $F_3$ 's and selfings of Corky first backcross plants were grown. On a complementary (2-factor) hypothesis it should be possible to demonstrate the presence of three types of Corky which, according to Harland's terminology, should have the following genetic constitutions:

- |   |  |
|---|--|
| (1) $Ck^P Ck^P Ck^B Ck^B$                             | True-breeding Corky,                       |
| (2) $Ck^P ck^P Ck^B Ck^B$ or<br>$Ck^P Ck^P Ck^B ck^B$ | Segregating 3 Corky : 1 Normal on selfing, |
| (3) $Ck^P ck^P Ck^B ck^B$                             |  |

$F_2$ : data are given below:

	Corky	Normal	Total	$\chi^2$ (9 : 7)
Sea Island $\times$ St Thomas' Bourbon	43	45	88	1.95
Sea Island $\times$ Bourbon Intense	90	66	156	0.13
Combined families	133	111	244	0.30
	$n$	$\chi^2$		$P$
Combined families	1	0.30		0.50-0.70
Heterogeneity	1	1.78		0.10-0.20
Total	2	2.08		0.30-0.50

The  $F_2$  Sea Island  $\times$  Bourbon Intense fitted very well the 9 Corky : 7 Normal expected on a complementary gene hypothesis. Segregation in the  $F_2$  Sea Island  $\times$  St Thomas' Bourbon showed a deficiency of Corky types, but the deficiency was not significant ( $\chi^2 = 9 : 7$ ,  $P = 0.10-0.20$ ). It is important to note, however, that the families were not large enough to distinguish critically between 9 : 7 and 1 : 1 ratios, and furthermore the number of plants reared to maturity represented only 70% of the total seeds sown—due chiefly to elimination prior to the seedling stage as has been explained above.

$F_3$ . Two high-grade and three medium-grade Corky  $F_2$  plants in each of the crosses were selected for selfing. A high proportion of inviable seeds was obtained ( $45 \pm 9.5\%$ ), but no significant difference in viability was found on comparing progenies from high- and medium-grade parents. The  $F_3$  segregations obtained are shown below:

		$F_3$ segregations		
	Parent ( $F_2$ ) plant	Corky	Normal	Total
Sea Island $\times$ St Thomas' Bourbon	High-grade Corky*	—	—	—
	High-grade Corky*	—	—	—
	Medium Corky	5	16	21
	Medium Corky	9	24	33
	Medium Corky	15	24	39
Sea Island $\times$ Bourbon Intense	High-grade Corky	18	9	27
	High-grade Corky	20	19	39
	Medium Corky	4	11	15
	Medium Corky	6	29	35
	Medium Corky	6	19	25

\* Female sterile.

Two high-grade plants proved to be female sterile. Using them as male parents in crosses with Sea Island gave progenies which segregated for Corky and Normal in approximately equal numbers. They were therefore both heterozygotes. All the remaining progenies segregated for Corky and Normal, so that no true-breeding Corky types were extracted as would have been expected on a complementary factor hypothesis. In the segregating families the numbers of Corky types were deficient from the expected 9 : 7 and 3 : 1 segregations. However, none of this evidence was critical, since ten Corky selections

are too few to ensure definitely the inclusion of a homozygote (expected 1 in 9 selections), and the deficiency of Corky types in the segregating families might have been due to differential elimination in the seedling stage. This latter possibility was checked by carrying out reciprocal crosses. Since Normal (♀) × Corky (♂) invariably gives 1 Corky : 1 Normal segregation, any deviation from this ratio in the reciprocal cross would indicate differential elimination of the two classes. An examination of five families totalling 213 plants showed that the proportion of inviable seeds varied with the Corky female parent used, but that there was no differential elimination of Corky zygotes. It seems, therefore, that although certain Corky parents limit the development of the seeds, possibly through poor nutrition, Corky zygotes are not at a selective disadvantage. An additional factor which complicated interpretation of the  $F_3$  data was the variable cork expression. It was frequently found that plants classified at the first grading as Normal developed Corky symptoms later, on one or more lateral branches, so that the possibility that some mild Corky plants were mis-classified as Normal could not be ruled out.

*First backcross to Sea Island selfed.* Five Corky and five Normal plants from the first backcross to Sea Island were selected for selfing. Seed viability was even worse than in the  $F_3$ , so no reliable information on the type of segregation occurring could be obtained. However, in the small progenies raised, it was noted that while all Corky plants on selfing gave Corky and Normal in approximately equal numbers, no Corky plants were found in selfed progenies of Normal plants.

It is clear that the above data provide no positive evidence supporting a complementary factor hypothesis. The fact that no true-breeding Corky families were isolated and that the rather unsatisfactory data from selfed Corky plants were not inconsistent with 1 : 1 segregations suggested that Corky plants might all be heterozygotes. On this interpretation the constitution of Bourbon, Sea Island, and Corky hybrids should be respectively  $ck^X ck^X$ ,  $ck^Y ck^Y$ , and  $ck^X ck^Y$ . Normal plants occurring in selfed progenies of Corky plants should therefore consist of two types: (1)  $ck^X ck^X$  giving all Normal progenies on crossing with the Bourbon parents and all Corky progenies with the Sea Island parent, (2)  $ck^Y ck^Y$  giving all Corky progenies with Bourbons and all Normal progenies with Sea Island. Both Normal types on crossing with Corky should give only 1 Corky : 1 Normal segregations. Several Corky plants obtained in the selfed progeny of a first backcross family were again selfed and their progenies raised carefully in the greenhouse. One such family segregated as follows:

Total no. of seeds sown	No. of surviving plants		
	Corky	Normal	Total
20	9	7	16

The seven Normal plants were crossed with (1) Sea Island, (2) Bourbon Intense, (3) Corky, and the progenies obtained are shown in Table 1. The data show quite clearly that the complementary allele hypothesis offers a satisfactory interpretation.

#### 4. THE CONSTITUTION OF 'NON-CARRIERS'

For convenience of discussion, types carrying one or other of the complementary alleles producing Corky will be termed 'carriers', and types carrying neither of the alleles, 'non-carriers'. Harland (1939) noticed that only certain *marie-galante* types were carriers, and further investigation has shown that in *barbadense*, too, both carriers and non-carriers occur. The constitution of non-carriers will now be discussed.

Non-carrier *marie-galante* types and non-carrier *barbadense* types could be readily detected by crossing them with Sea Island and Bourbon Intense, respectively, since the  $F_1$  hybrids obtained showed no Corky symptoms. The constitution of two non-carriers was examined in detail, viz.:

- (i) BA8-4—an Egyptian (*barbadense*) type.
- (ii) RP5-6—a Colombian tree-cotton (*marie-galante*) type.

Table 1. Segregations obtained on crossing Normals (extracted by selfing a Corky type, GB349/5) with (1) Bourbon Intense, (2) Sea Island, (3) Corky

Normal extracts	Constitution	(1) × Bourbon Intense ( $ck^x$ )		(2) × Sea Island ( $ck^y$ )		(3)* × Corky ( $ck^x ck^y$ )	
		Corky	Normal	Corky	Normal	Corky	Normal
		GB349/5-2	$ck^y$	5	0	0	62
-3	$ck^y$	9	0	0	16	14	20
-4	$ck^y$	12	0	0	51	20	21
-5	$ck^y$	—	—	0	3	52	50
-6	$ck^x$	0	15	14	0	52	48
-7	$ck^y$	—	—	0	11	6	6
-8	?	—	—	—	—	12	9

\* The figures given in this column represent the pooled data from three Corky, male parent plants, showing mild, medium, and extreme expression of Corky characters respectively. The three plants, despite their phenotypic differences, were homogeneous in their breeding behaviour.

BA8-4 crossed with Bourbon Intense gave a Normal  $F_1$  hybrid which on selfing produced an all Normal  $F_2$  of 150 plants. It is clear, therefore, that BA8-4 does not carry the  $ck^y$  allele, and since its hybrid with Sea Island is also Normal it does not carry  $ck^x$ . That it carries a Normal allele (Ck) at the same locus is suggested by data from the following crosses:

- (1) (Sea Island × BA8-4) × Bourbon Intense—6 Corky : 6 Normal.
- (2) (BA8-4 × Bourbon Intense) × Sea Island—68 Corky : 59 Normal.
- (3) BA8-4 was crossed with a Corky selection ( $ck^x ck^y$ ) from the first backcross, St Thomas' Bourbon → Sea Island. A progeny of forty-five plants was obtained, all of which were Normal.

Colombian Bourbon (RP5-6) was tested by similar methods and found to have a similar constitution to BA8-4. (Sea Island × Bourbon Intense) × RP5-6 and (Sea Island × St Thomas' Bourbon) × RP5-6 gave all Normal progenies of seventeen and thirty-five plants respectively. Ten plants from each of these Normal progenies were selfed and none of the families (totalling 412 plants) segregated for Corky. Finally, RP5-6 was crossed with twenty-seven *barbadense* (both carrier and non-carrier) types. The  $F_1$  hybrids were all Normal. Sea Island was crossed with twenty non-carrier *marie-galante* types. All hybrids and their  $F_2$  progenies were completely Normal.

It may be concluded from these data that *barbadense* and *marie-galante* types have the following constitutions:

Carriers:	<i>marie-galante</i>	$ck^x ck^x$
	<i>barbadense</i>	$ck^y ck^y$
Non-carriers:	<i>marie-galante</i>	Ck Ck
	<i>barbadense</i>	Ck Ck

## 5. THE GEOGRAPHIC DISTRIBUTION OF CARRIERS AND NON-CARRIERS

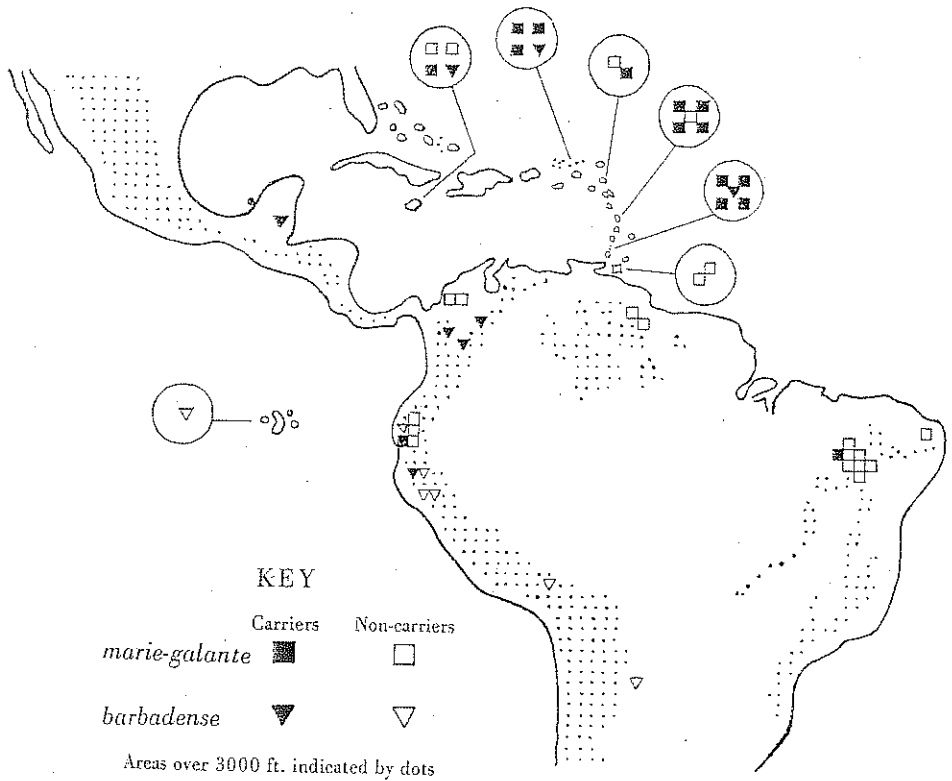
In order to appreciate the significance of the geographic distribution of carriers and non-carriers it is necessary to consider first the centres of origin of the two species concerned and their distribution under natural and cultural conditions. The centres of maximum variability, and hence probably the centres of origin of *G. hirsutum* and *G. barbadense*, are (i) Mexico-Guatemala and (ii) Peru, respectively (Vavilov, 1935; Hutchinson, 1938). The variety *marie-galante* of the former species is now found along the northern coast and hinterlands of South America from Ecuador eastwards and extending through all the islands bordering the Caribbean Sea (Hutchinson, 1943*a*). The most northerly limit to this extension which has so far been recorded is Cuba (Silow, cited Hutchinson, 1943*a*). Evidence presented by Hutchinson & Silow (1945) suggests that it reached these islands from the mainland of South America and not by a northerly route around the Gulf of Mexico. To what extent the present distribution of *marie-galante* cottons is due to man is problematic, but there is no sharp discontinuity between strains now grown under peasant cultivation and those which are supposedly 'wild types'. Similar types are found throughout the Lesser Antilles: in some islands forming part of a commercial crop as in the Grenadines, in others occurring as semi-wild types, i.e. not cultivated but encouraged in the neighbourhood of dwellings on account of their usefulness for minor household purposes. Hutchinson (1943*b*) brings forward evidence from a detailed survey which suggests that in Trinidad these cottons only survive in areas which are kept clear of the dominant vegetation. Since it is known that cotton was grown as a crop in Trinidad at the close of the eighteenth century and was later discontinued, it is probable that these semi-wild types are relics of former cultivations (Stephens, 1944). They are all perennial types.

Considering next the distribution of perennial *barbadense* types in the New World, it is found that they are practically confined to the northern half of the South American continent, the West Indies, and the Galapagos Islands. The most striking exception is the presence of 'kidney' cotton (*G. barbadense* var. *brasiliense* Hutchinson) in British Honduras. Ancient historical records suggest that cottons in the West Indies have been to a large extent distributed by man; in the first place by the Caribs and other Indian tribes who already understood the arts of spinning and weaving when discovered by Columbus, and later by European colonists and travellers who introduced 'kidney' cotton from Brazil (Watt, 1907; Lewton, 1920). It is probable that the 'kidney' cotton of British Honduras was carried there by man in historical times, since, according to the West Indies Committee's Handbook of that colony, its present Carib population is for the most part descended from Caribs exported by the British from St Vincent to the north coast of Honduras in 1796. They spread from there into British Honduras, and since 'kidney' cotton was formerly common in St Vincent before eradication measures were introduced,\* it is almost certain that these cottons would be carried with them.

A search was made for carriers, as described previously, and both in *barbadense* and *marie-galante* it was found that there was a marked association between frequency of occurrence and geographical distribution. The result of the crossing programme which involved 36 *marie-galante* and 15 *barbadense* types is illustrated in Text-fig. 1. Carrier

\* As a measure for controlling pests in the Sea Island crop. Perennial semi-wild cottons are permanent sources of infection if not eradicated.

types occur most frequently in the West Indies. This is the region where the geographical distributions of *marie-galante* and *barbadense* not only overlap, but where the two species have been grown in close contact as will now be shown. In the Grenadines, where mixed cultivation of *marie-galante* and *barbadense* is still practised under a system which has persisted probably unchanged for two centuries, all types examined have proved to be carriers, and Corky 'rogues' occur frequently in the fields. In the other West Indian islands the great majority of perennial cottons are also carriers, and old records suggest that there, too, mixed cultivation was practised, as in the Grenadines now, until the end of the eighteenth century (Stephens, 1944). In the West Indies at the present day there



Text-fig. 1. Map showing distribution of carriers and non-carriers of the corky complementary alleles.

is a tendency for *marie-galante* and *barbadense* types to occur in different ecological situations (Hutchinson, 1943 a, b). This is more marked in Jamaica, where cotton cultivation was abandoned at the end of the eighteenth century, than in Trinidad, where it was continued on a small scale until the end of the American Civil War (1863-5) and where the ecological situation is less varied. In Jamaica true feral (secondarily wild) types occur, while, in Trinidad, cottons are only found associated with native dwellings or at the edges of cultivated areas. The situation, in fact, is much what would be expected if the two species, formerly restricted to the same area by mixed cultivation, were gradually recovering their normal ecological niches after being abandoned as crop plants. That the two species are naturally adapted to rather different ecological conditions is shown conclusively by Mauer's (1930) survey of cottons in Colombia. The mesophytic

*G. barbadense* is rarely found below an altitude of 1000 m., while the xerophytic *G. hirsutum* var. *marie-galante* is rare above 1500 m. Both wild types and types under 'home-  
stead cultivation' occur, and since, according to Mauer, there is an overlap in distribution  
of the species between 1000 and 1500 m. altitude, it seems likely that mixed cultivation  
frequently occurs in the overlapping zone. In fact, Harland (1939) states that the Indians  
of north Brazil, Guiana, Venezuela, Colombia and Ecuador 'use cotton from both  
*purpurascens* (= *marie-galante* Hutchinson) and *barbadense*—often from mixed popula-  
tions of both species'. Text-fig. 1 shows that in Colombia carrier *barbadense* types occur  
just in the region where mixed cultivation would be expected, while the *marie-galante*  
types at a lower altitude near the coast are non-carriers. Similarly, in British Guiana and  
Brazil,\* the *marie-galante* types occurring at low altitudes are non-carriers, while in Peru  
and Ecuador, on the western slopes of the Andes, where there is a rapid change in  
altitude over relatively small areas, both carriers and non-carriers are found. Outside  
the *marie-galante* range—in the Argentine, Bolivia and the Galapagos Islands—the three  
*barbadense* samples examined were non-carriers. The presence of a carrier *barbadense* in  
British Honduras has already been explained.

In addition to the perennial *barbadense* types which have been considered, the following  
twelve annual types were examined including American, West Indian, and Sind Sea  
Islands; Egyptians; and so-called 'indigenous' African types from French Sudan and  
Nigeria:

	Source	Name	Station no.
Sea Island	U.S.A.	Bleak Hall	BA2-5
	U.S.A.	Seabrook	BA2-6
	St Vincent (B.W.I.)	V135	BA1-1
	St Vincent (B.W.I.)	Sea Island White	BA1-4
	Nevis (B.W.I.)	Nevis Naked	BA1-18
	Sind (India)	Sind Sea Island	BA7-2
Egyptian	North Khartum	—	BA8-4
	El Giza (Egypt)	Sakel	BA8-8
	Shambat (Sudan)	—	BA8-15*
	Shambat (Sudan)	—	BA8-16*
African indigenous	Nigeria	Ishan	BA8-7
	Angola	—	BP8-4

\* Black-arm resistant types bred by Mr R. E. Knight.

All of these, with the exception of the four Egyptian types examined, proved to be carriers.  
It is of interest to consider this fact in relation to the origin of these annual types. All  
Sea Island cottons are known to have originated from a common stock developed in the  
'sea islands' off the Carolina coast in the late eighteenth century. From there they were  
introduced into the West Indies, various Polynesian islands, Egypt, India and Russia.  
It was formerly supposed that the original perennial stock was introduced into the  
southern States from the West Indies, but though this is possibly correct, there is little  
supporting evidence. Although there are numerous records of introductions into the  
southern States from the West Indies (as would be expected in the days when both were  
British colonies), there is no reliable information of the types so introduced (Hutchinson  
& Manning, 1945). The origin of the 'indigenous' African cottons is also obscure, but the  
most probable explanation of their presence in Africa is that they were introduced from  
the New World by the early Portuguese or French colonists in the sixteenth and seven-  
teenth centuries. It is known definitely that the Portuguese introduced other crops  
(e.g. maize) into Africa from Brazil at that time. If the perennial ancestors of Sea Island

\* See also later.



cottons and of the 'indigenous' African types were originally taken from regions in the New World where *marie-galante* and *barbadense* were grown in mixed cultivation by the Indian inhabitants, the prevalence of carriers among them would be expected. A more surprising feature, however, is that the four Egyptian types examined were found to be non-carriers. Balls (1919) suggested that Egyptian cottons are descended from hybrids between 'indigenous' perennials (Jumel's cotton) and Sea Islands known to have been introduced into Egypt in the early nineteenth century. If this is correct, it might be expected that Egyptian cottons would be carriers, since the six Sea Island and two 'indigenous' African types examined so far all carry the  $ck^x$  allele. A more extensive survey of Egyptian and 'indigenous' African types is clearly required and may possibly throw light on the relations between the different strains of *barbadense* now acclimatized in Africa.

The apparent association between mixed cultivation and the prevalence of carriers can scarcely be fortuitous, in which case it is probable that carriers have a selective advantage over non-carriers when *barbadense* and *marie-galante* are grown in close contact. The genetic basis of the Corky mechanism rules out a purely physiological explanation, though it is clearly of fundamental physiological interest. It is believed that the most probable interpretation lies in the effect of agricultural practice on a partially outcrossed population. It may be supposed that at an earlier stage of domestication of cotton in the New World, carriers and non-carriers were present in both species—their relative proportions depending (in the absence of differential selection) on the mutation pressures of the  $ck^x$  and  $ck^y$  alleles. When, however, the two species became cultivated as a mixed crop, a selective mechanism would come into operation. Historical records of cotton-growing in the West Indies show that the methods of cultivation from the middle of the seventeenth to the beginning of the nineteenth centuries varied little, and exhibited a high standard of agricultural practice (see Stephens (1944) for citation of general references). The seeds were sown in holes from 5 to 9 ft. apart and the seedlings subsequently thinned at each hole. To facilitate harvesting and to encourage boll development on the lower flowering branches the plants were repeatedly topped at a height of 4–6 ft. as a routine practice. Crops were taken from 3 to 5 years without replanting and then the plants were destroyed, or alternatively the plants were ratooned annually and mulched to encourage fresh growth. Under this standard of agriculture, which is comparable with the best existing in Europe during the same period, it is almost certain that seeds from the best plants would be selected for sowing the following crop and for 'supplying' gaps in the current one. This latter practice, in fact, is carried out to-day in the Grenadines under a far lower standard of agriculture.

Now it is known that the  $F_1$  *barbadense* × *marie-galante* (providing one or both parents are non-carriers) shows considerable hybrid vigour\* which is always accompanied by increased yielding capacity and often by an improved lint quality. Whenever such hybrids occurred by outcrossing in a plantation they would attract attention, and would stand a considerable chance of selection as seed parents for the following crop. This chance would be maximized in a perennial crop, since the performance of certain outstanding plants over several seasons would gain them a reputation—just as it does in orchard crops to-day. But selection of such plants would be disastrous, as the  $F_2$  of

\* 'The hybrid exhibits the phenomenon of hybrid vigour to such a high degree that the growing of the  $F_1$  on a commercial scale has been proposed several times' (Harland, 1939, p. 166).

interspecific crosses in *Gossypium* is known to give a medley of unthrifty and partly sterile types.\* Only a small proportion of the progeny would even approach the parent in yielding capacity and of these the majority would again break down into inferior types in subsequent generations.

On the other hand, when natural interspecific crossing occurred between two carrier parents, the hybrid obtained would be a Corky rogue, which would either be eliminated in competition with Normal seedlings in the same hole, or struck out subsequently as undesirable by the cultivator during the routine practice of topping. Even if it escaped attention at this stage, its appearance would later eliminate its chances of selection as a seed parent for the following crop, apart from the additional possibility that it would prove to be female sterile. As a result of mixed cultivation, therefore, it seems highly probable that crops of carriers would maintain their productive capacity and enhance the reputation of the cultivator, while crops of non-carriers would tend to degenerate. In the long run this could only result in the general, though unconscious, adoption of carrier strains for cultivation. Corky, on this interpretation, may be regarded as an interspecific isolating mechanism favoured by selection in a manner rather similar to that postulated by Dobzhansky (1941, pp. 285-8).

It is clear, on the selective mechanism outlined above, that the rate at which carriers would replace non-carriers would depend on the standard of agriculture and the length of time during which the two species were grown in contact. In the old plantation days of the eighteenth and nineteenth centuries the change could have proceeded rapidly in the West Indies since there is no reason to suppose that the initiative of the planters was inferior to that of the contemporary gentlemen farmers and estate owners in Europe among whom must be included Thomas Andrew Knight, Patrick Shirreff and Le Couteur. The situation has been greatly different in Brazil, however, where the standard of agriculture is low, selection by no means stringent, and where one of the chief criticisms by experts in the past has been the small attention paid to uniformity of product. The Brazilian *marie-galante* cottons whose distribution is indicated in Text-fig. 1 were all collected by Dr S. C. Harland during a tour of the cotton-growing areas in the Rio Grande do Norte. In a report of this tour Harland (1933) states that the cotton area falls into two main zones: a littoral belt of moderate rainfall and an interior (Sertao) region of about 1000 ft. elevation with an extremely arid climate. The littoral belt grows 'Verdao' cotton which consists of dilute hybrids of the indigenous cotton 'Moco' (*marie-galante*) with introduced American Uplands, while in the arid region 'Moco' is chiefly grown. With regard to the latter, however, Harland states that 'practically every field examined was contaminated by Kidney [*G. barbadense* var. *brasiliense*], and could virtually be described as a Kidney-Moco hybrid swarm'. It is evident from Harland's further descriptions that both carrier and non-carrier types occur (as has been confirmed here), since although he found 'loggerheads' (= Corky hybrids) in the fields, he was also able to find plants with the mixed characters of *brasiliense* and *marie-galante*, and sterile and physiologically unbalanced types which are characteristic results of selfing interspecific hybrids in *Gossypium*. The result of this hybridization has been 'a thorough degeneration of all qualities' (Pearse, 1937), which provides an interesting contrast with the situation in

\* 'Considerable trouble and disappointment have been experienced from time to time in these islands owing to selected (cotton) plants chosen to establish or carry on a special strain eventually turning out to be hybrids' (Imperial Dept. of Agriculture for the West Indies, Pamphlet 74 (1914)).

the Grenadines where Corky hybrids occur in the fields but the two species show no signs of blending and breakdown. Reference to Text-fig. 1 shows that the single *marie-galante* sample taken from the 'Verdao' area is a non-carrier as expected. Of the six types obtained from the interior only one was a carrier. This seems to be good evidence that in the Grenadines the two species are maintained as separate entities in mixed cultivation *because* they consist almost exclusively of carrier types, while in Brazil carrier types only occur sporadically and therefore the Corky mechanism is only partially effective.

On the evidence presented in this paper it has been suggested that carrier types in a mixed *barbadense* and *marie-galante* population will have a selective advantage and will ultimately replace non-carriers. The history of cotton development in Brazil supports this suggestion. All the evidence available (see Edwards, 1793; Leriis, cited Watt, 1907; Lewton, 1920) leads to the conclusion that the common cotton of Brazil in the sixteenth to eighteenth centuries, and the species on which its export trade was based in colonial days, was Kidney (*G. barbadense* var. *brasiliense*). Harland (1933) says that 'the Moco industry succeeded an industry based on a rather short staple Kidney cotton'. Now the Moco cotton industry of to-day is a comparatively recent development. According to Pearse (1921) cotton spinning and weaving mills were first established in Brazil in 1775, but owing to conservative Portuguese legislation in colonial days the manufacture of any but the coarsest cloth was prohibited until 1846. Consequently, apart from a short period during the American Civil War, the Brazilian cotton industry never developed properly, and in 1888 when slavery was abolished 'all the large planters gave up cotton in the north and from then onwards cotton was only cultivated in small plots, often to supply the domestic needs of the village only'. The Moco cotton industry did not become important until the first decade of the twentieth century, and it seems certain that its desirable long staple has resulted in its adoption and dissemination over a much wider area than its original ecological range. This conclusion is borne out by the fact that its probable ancestor, 'Macaque' or 'Ganga' cotton, is found growing wild to-day and is restricted to the mountainous arid regions of the interior, i.e. away from the areas where cotton is now cultivated as a crop (Pearse, 1921; Harland, 1933). In short it appears that the Moco cotton has not yet been long enough in contact with Kidney, whose former territory it has overlapped, for carrier types to have replaced non-carrier types under human selection.

## 6. SUMMARY

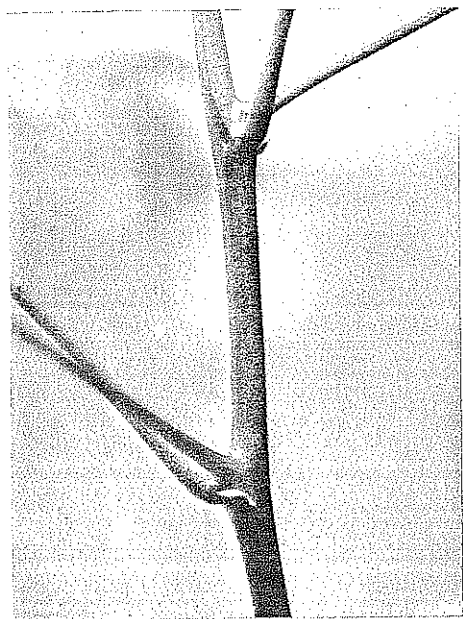
1. Interspecific hybrids between certain strains of *G. hirsutum* var. *marie-galante* and *G. barbadense* are abnormal.
2. The abnormal types have a characteristic bushy habit owing to their shortened internodes and excess production of lateral branches. Leaves are inrolled and exhibit a yellowish mottling; and stem, petiole, and leaf midribs tend to be covered with a thick layer of cork. Such 'Corky' types are more or less female sterile.
3. Corky symptoms depend on the interaction of complementary alleles,  $ck^x$  carried by the *marie-galante*, and  $ck^y$  carried by the *barbadense* parent. True breeding Corky types cannot therefore be isolated.
4. A geographic survey of the two species shows that the corky complementary alleles are most common in types occurring in, or originating from, areas where the geographical



(a)



(b)



(c)



(d)

ranges of *marie-galante* and *barbadense* overlap and where the two species have been grown in mixed cultivation.

5. It is unlikely that this association is fortuitous and it is suggested that it is the result of seed selection by man in a partially outcrossed population.

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## EXPLANATION OF PLATE 4

- (a) Normal (left) and extreme Corky (right) sibs growing as neighbouring plants. Note pronounced dwarfing of the Corky type.
- (b) Extreme Corky plant showing short internodes and crowded vegetative parts. It was not found possible to illustrate adequately by photograph the characteristic leaf mosaic, though the latter was easily seen in the living plant.
- (c) Details of 'Normal' stem.
- (d) Details of 'extreme Corky' stem. Note thick greyish layer of cork and excessive branching at the nodes.

(Photographs by Dr E. Phillis.)