THE GENETICS OF BLACKARM RESISTANCE XII. TRANSFERENCE OF RESISTANCE FROM *GOSSYPIUM HERBACEUM* TO *G. BARBADENSE*

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Introduction

The previous eleven papers in this series on the genetics of resistance to *Xanthomonas malvacearum* were published in the Journal of Genetics between 1939 and 1954. Together with the present paper, they give abundant support for the conclusion reached by Knight and Hutchinson (1950) that "the foundation of effective resistance has proved to be a major gene in all the cottons tested. The value of minor genes alone is strictly limited, but wherever there has been prolonged selection under epidemic attack, the main gene has been fortified by lesser genes. Effective resistance can, in fact, only be built around a main gene".

In the course of the work reported in this series and by Knight (1957) ten major resistance genes have been identified—$\mathbf{B}_1$, $\mathbf{B}_2$ and $\mathbf{B}_7$ from *Gossypium hirsutum*, $\mathbf{B}_2$, $\mathbf{B}_3$ and $\mathbf{B}_{10}$ from *G. hirsutum* var. *punctatum*, $\mathbf{B}_4$ and $\mathbf{B}_{6m}$ from *G. arboreum*, $\mathbf{B}_5$ from a perennial *G. barbadense*, the recessive gene $\mathbf{b}_8$ from *G. anomalum*, and the gene $\mathbf{B}_9$ from *G. herbaceum*, discussed in the present paper. All these genes with the exception of $\mathbf{b}_8$ have been transferred to Sudan Sakel (*G. barbadense*) strains to ascertain their potential value for breeding purposes; several of them have been transferred to commercial Sudan varieties of American Upland cotton (*G. hirsutum*) also.

The value of a number of these genes, both individually and combined, in conferring leaf and stem resistance and in reducing spread of the disease has been examined and confirmed by Last (1958, 1959a, 1959b), by Last and Dransfield (1959) and by Cross and Innes (1963).

In 1941 all the varieties of cotton grown in the Sudan were susceptible to *X. malvacearum*. By contrast, by 1962-63 the whole of the Sudan rain-grown crop of Upland (*hirsutum*) cotton, amounting to some 330,000 acres, carried the resistance genes $\mathbf{B}_2$ and $\mathbf{B}_3$. In that season the Sudan crop of irrigated *barbadense* cottons amounted to over 763,000 acres; of this about 94,000 acres were sown with a strain carrying $\mathbf{B}_2$ and $\mathbf{B}_3$ and over 582,000 were sown with a $\mathbf{B}_2$ strain. The total value of the crop from blackarm resistant *barbadense* and *hirsutum* varieties amounted to over £50 million in 1961-62 and over £41 million in 1962-63. Very highly resistant types carrying $\mathbf{B}_2\mathbf{B}_{6m}$ and $\mathbf{B}_2\mathbf{B}_3\mathbf{B}_{6m}$ are now on test (Rose, Low and Faulkner, 1961).

Previous work on resistance in Old World cottons

Knight (1948a, 1948b, 1953) showed that blackarm (*Xanthomonas malvacearum*) resistance in Multani cotton, a variety of *Gossypium arboreum* race *bengalense* depends on a partially dominant major gene $\mathbf{B}_4$, accompanied by a strong intensifier $\mathbf{B}_{6m}$ and also by a constellation of minor genes. He transferred both $\mathbf{B}_4$ and $\mathbf{B}_{6m}$ to Sudan Sakel, *G. barbadense*, and $\mathbf{B}_{6m}$ is now being used in commercial breeding work on both Sakel and Upland (*G. hirsutum*) cottons.

Resistance in the African wild 'cotton' species, *G. anomalum*, was shown to depend on a recessive gene $\mathbf{b}_8$. The resistance conferred by $\mathbf{b}_8$ is increased to near-immunity in *anomalum* by factors for rapid leaf hardening evolved in response to the requirements of the xerophytic environment of this species. The gene $\mathbf{b}_8$ is closely linked with the $\mathbf{R}_2$ petal spot locus with a crossover value of about 1·4% (Knight, 1954b).

Knight and Hutchinson (1950), in a survey of blackarm resistance in both Old and New World cottons, show that India is the major centre of blackarm resistance. Indian races of *G. arboreum* and *G. herbaceum* are almost without exception immune. Immunity and high resistance predominate in the commercial Asiatic cottons of the surrounding countries, but the general level of resistance is lower in the more peripheral areas and in perennial types.

Kulkarni and Patel (1951) in crosses between resistant and susceptible *herbaceum* cottons, obtained F_2 and backcross results which "agree very closely on the basis of a single gene difference with susceptibility partially dominant". The resistant *herbaceum* in these crosses was Kumpta Farm cotton and the susceptible parent was a Russian strain, R. 22. While the results reported by Kulkarni and Patel are suggestive of single factor inheritance, they are not conclusive. These workers used only three grades in their classification: susceptible, mildly susceptible, and resistant. They give no indication as to whether these classes merged or were sharply defined, no F_2 results are given, nor are the backcrosses carried to F_2 and F_3.

All the material discussed in the present paper was sprayed with blackarm inoculum prepared and applied as described by Knight (1946). Grading of blackarm symptoms was done on the '0'—'12' scale defined by Knight and Clouston (1939) and re-defined and illustrated by Knight (1944). On this scale '0' represents complete absence of blackarm lesions on the leaves and '12' represents the attack typical of fully susceptible Egyptian type (*G. barbadense*) cottons when sprayed with inoculum. This scale was found to be too full at the susceptible end of the range and the use of grade '11' was discontinued (Knight, 1944).

TRANSFERENCE OF RESISTANCE FROM *Gossypium herbaceum* TO *G. barbadense*

Description of strains

Wagad 8 (*G. herbaceum*; $\mathbf{A}_1$ genome, $n = 13$). This is a standard commercial variety; it was imported from India in 1941 through the courtesy of the Secretary of the Indian Central Cotton Committee and was subsequently maintained by selfing.

Domains Sakel (*G. barbadense*; $(\mathbf{AD})_2$ genome, $n = 26$). Strains derived directly from commercial Sudan Domains Sakel were used as recurrent parents. All such Domains Sakel derivatives are fully susceptible to blackarm (grade '12' leaf symptoms).

F_1 of Tetraploid Wagad 8 × Sakel and the first four Sakel backcrosses

Details of the treatment of Wagad 8 seed with 0·05% colchicine to obtain tetraploid plants and of the crossing and backcrossing of these with Sakel are given by Knight (1954a).

Sixty-seven F_1 plants were grown and sprayed with blackarm; all were graded as '0'. From pollinating these with Sakel pollen five first backcross plants were raised; four of these showed grade '3'—'4' symptoms and one proved fully susceptible (grade '12'). Only one of these five plants proved fertile in crosses with Domains Sakel using the latter as male parent. This was one of the grade '4' plants and it yielded 66 backcross seeds from which 21 mature plants were raised. Their classification following blackarm spraying is given in Table 1.

Table 1. *Blackarm grading of second Sakel backcross*

Family No.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA114/48	'4'	1	4	2	1	..	1	2	10

All of these twenty-one plants were used as female parents for backcrossing to Domains Sakel. Thirteen of them yielded backcross seed but only eight of these seed lots proved viable. The blackarm classification of these eight families is given in Table 2.

Table 2. *Blackarm grading of third Sakel backcross*

Family No.	Parent grade	Blackarm grade '5'	'6'	'7'	'8'	'9'	'10'	'12'
BA25/49	'4'	1	..	..	1	..	3	8
BA17/49	'5'	..	..	..	..	..	..	2
BA20/49	'5'	..	..	..	..	..	..	4
BA15/49	'6'	..	..	..	..	..	..	1
BA19/49	'12'	..	..	..	..	..	6	30
BA21/49	'12'	..	..	..	..	..	5	33
BA22/49	'12'	..	..	..	..	..	1	28
BA26/49	'12'	..	..	..	..	..	..	15

The two plants of grades '5' and '8' in BA25/49 (Table 2) were backcrossed to Domains Sakel using the latter as male; only the grade '5' plant yielded backcross seed (Table 3). From this single plant in the third backcross stems the remainder of the work described here.

Fifty-six of the grade '10' and '12' plants in the third backcross (Table 2) were crossed with BLR14/16, a synthesized Sakel carrying the blackarm resistance gene $\mathbf{B}_2$ transferred from *G. hirsutum*. None of the resulting 56 progenies differed significantly in their resistance distribution from the BLR14/16 control. This shows that the Asiatic intensifying gene $\mathbf{B}_{6m}$ was not present, since $\mathbf{B}_2\mathbf{B}_{6m}$ plants are very markedly more resistant than plants carrying $\mathbf{B}_2$ alone.

Table 3. *Blackarm grading of fourth Sakel backcross*

Family No.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA122/50	'5'	9	4	..	..	3	3	1	17
Sakel control		..	..	..	..	..	..	..	34

BA122/50 derives from BA25/49 (Table 2).

The distribution of resistance grades in the fourth Sakel backcross (Table 3) suggests the presence of two genes, there being 13 plants of grade '4'—'5', 7 of grade '9'—'10' and 17 grade '12'. The obvious divergence of this ratio from expectation on a 2:1:1 or 3:1 basis cannot be regarded as meaningful. Ratios in early backcrosses between Asiatic (**A** genome, $n=13$) cottons and New World (**AD** genome, $n=26$) cottons are often widely different from expectation on the number of genes involved (Knight, 1948a).

Fifth Sakel backcross

Eight grade '4' plants in BA122/50 (Table 4) and two grade '8' plants were backcrossed to Sakel, four of them being used as males (Families BA23-26/51) and the remainder as females (BA28-32/51). The grading of these progenies is given in Table 4.

In addition, two grade '3' plants in BA15/51 (an F_2 family of fourth backcross origin, deriving from the same parent plant in BA122/50 (Table 3) as did BA23/51 (Table 4): see Table 8) were crossed with Sakel. These gave families BA60 and 61/52 containing 39 and 40 plants respectively, ranging from grade '3' to '4'. These families have not been included in Table 4 because, although of fifth backcross 'blood' they could not be expected to segregate as backcrosses.

Sixth Sakel backcross

Two grade '4' plants in each of BA60 and 61/52 (effectively fifth backcrosses) were selected as males for further backcrossing to Domains Sakel. These gave rise to families BA88-91/53 (Table 5); plants selected from BA27 and 29/51 (Table 4) backcrossed to Sakel gave the remaining families.

Table 4. *Blackarm grading of fifth Sakel backcross*

Family No.	Parent grade	Blackarm grade '3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA23/51	'4'	..	..	..	..	..	..	..	..	1
BA24/51	'4'	..	..	..	1	..	..	..	..	14
BA25/51	'4'	..	..	2	..	1	..	..	..	9
BA26/51	'4'	..	..	1	4	2	..	..	..	17
BA27/51	'4'	..	..	5	..	1	..	2	7	6
BA27/51 OS	'4'	3	3	1	1	1	3	3	..	11
BA28/51	'4'	..	..	..	..	..	..	..	..	3
BA29/51	'4'	..	..	..	7	6	..	..	..	17
BA30/51	'4'	..	..	..	..	..	..	..	..	1
BA31/51	'8'	..	..	..	..	..	1	4	13	16
BA32/51	'8'	..	..	..	..	..	..	3	20	38
Sakel Control		..	..	..	..	..	..	..	..	30

BA23-30/51 derive from BA122/50 (Table 3).
BA27/51 OS was from the same parentage as BA27/51 but was grown out-of-season, its grading is therefore unreliable.

Table 5. *Blackarm grading of sixth Sakel backcross*

Family No.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Totals Sus.	Expected Res.	Expected Sus.
												(1 : 1)	
BA45/51	'5'	..	1	1	..	..	..	..	2	2	2	2	2
BA72/52	'6'	..	10	3	..	..	..	3	7	13	10*	$11\frac{1}{2}$	$11\frac{1}{2}$
BA89/53	'4'	..	4	10	2	..	..	..	14	16	14	15	15
Totals			15	14	2	..	..	3	23	31	26	$28\frac{1}{2}$	$28\frac{1}{2}$
												(3 : 1)	
BA88/53	'4'	2	27	20	11	4	..	..	20	64	20	63	21
BA90/53	'4'	9	14	12	6	13	..	..	22	54	22	57	19
BA91/53	'4'	3	17	12	10	14	..	..	28	56	28	63	21
Totals		14	58	44	27	31	..	..	70	174	70	183	61

*The 3 grade '10' plants have been included with the susceptibles because the Sakel control (normally grade '12') of this family ranged in grade from '9' to '12'.
BA45/51 and BA72/52 derive from BA27 and 29/51 respectively (Table 4); BA88-91/53 derive from BA60 and 61/52 (above).

The data in Table 5 strongly suggest the presence of two dominant genes, one being stronger than the other.

Seventh Sakel backcross

In BA45/51 (Table 5) two plants, grades '5' and '6', and in BA72/52 three grade '5' plants were backcrossed to Domains Sakel; in addition all grades of resistant plants in Family BA88/53 were backcrossed in order to isolate these two resistance genes. The grading of the progenies is given in Table 6.

Table 6. *Blackarm grading of seventh Sakel backcross*

Family No.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Totals Sus.	Expected Res.	Expected Sus.
BA101/52	'5'	..	1	2	4	8	7	13	2	?		?	
BA102/52	'6'	2	3	6	4	7	5	7	1	?		?	
												(1 : 1)	
BA80/53	'5'	..	15	21	..	..	..	..	42	36	42	39	39
BA81/53	'5'	..	34	19	..	..	..	..	34	53	34	43½	43½
BA82/53	'5'	..	14	23	3	..	..	..	46	40	46	43	43
BA166/54	'5'	..	7	4	..	..	..	..	11	11	11	11	11
BA167/54	'6'	..	2	..	..	..	..	..	3	2	3	2½	2½
BA168/54	'6'	..	1	3	..	..	..	..	15	4	15	9½	9½
BA169/54	'6'	..	1	1	2	..	..	..	1	4	1	2½	2½
BA170/54	'7'	..	2	12	..	..	..	..	14	14	14	14	14
Totals			76	83	5	..	..	..	166	164	166	165	165
												(1 : 1)	
BA171/54	'7'	..	..	..	..	..	..	4	25	4	25	14½	14½
BA172/54	'7'	..	..	..	..	4	9	15	39	28	39	33½	33½
BA173/54	'8'	..	..	..	..	..	..	5	15	5	15	10	10
BA174/54	'8'	..	..	..	..	..	1	8	14	9	14	11½	11½
BA175/54	'8'	..	..	..	..	..	1	5	21	6	21	13½	13½
Totals		..	..	..	..	4	11	37	114	52	114	83	83
												(3 : 1)	
BA162/54	'4'	..	10	11	..	..	7	6	12	34	12	34½	11½
BA163/54	'4'	..	14	12	..	2	7	6	12	41	12	39¾	13¼
BA164/54	'5'	..	5	7	2	..	2	3	11	19	11	22½	7½
BA165/54	'5'	..	5	2	..	..	3	..	4	10	4	10½	3½
Totals			34	32	2	2	19	15	39	104	39	107¼	35¾
				68			36		39				
Expected 2 : 1 : 1				71½			35¾		35¾				

BA101-102/52 derive from BA45/51; BA80-82/53 are from BA72/52; BA162-175/54 are from BA88/53 (Table 5).

Families BA101 and 102/52 suffered a climatic spell most unfavourable to blackarm disease such that the normally fully susceptible Domains Sakel controls, instead of being grade '12', gave a range down to grade '9' (see Table 10). For this reason the grading of these families is dubious. The remaining families in Table 6 developed the disease under normal conditions.

With the exception of BA101 and 102/52 the seventh backcross progenies have been grouped in Table 6 according to their presumed gene content. The first eight families (deriving from grade '5'—'6' and one '7' parents) show good agreement with expectation on a 1:1 basis and clearly carry a strong resistance gene conferring grade '5'-'7' resistance in the heterozygous state. Families BA162-165/54 (deriving from grade '4'-'5' parents) presumably carry two genes for resistance—one conferring grade '5'-'7' resistance as in the first group and the other conferring a weaker resistance ranging from grade '8' to '10' or even to full susceptibility ('12'). Families BA171-175/54 (from grade '7'-'8' parents) presumably carry the weaker resistance gene; their poor agreement with expectation on a 1:1 basis is discussed later (p. 339).

Eighth Sakel backcross

In view of the wide distribution of resistance grades in BA101 and 102/52 (Table 6) which was presumed to be due to unsuitable climatic conditions, plants were selected covering the range from grade '4' to '9' in these two families for further backcrossing. The classification of these progenies (Table 7) conclusively confirms the presence of a single resistance gene.

Table 7. *Blackarm grading of eighth Sakel backcross*

Family No.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Sus.	Expected Res.	Sus.
												(1 :	1)
BA58/53	'4'	..	..	2	..	..	..	..	2	2	2	2	2
BA59/53	'4'	..	..	2	..	..	..	..	7	2	7	4½	4½
BA50/53	'5'	..	..	..	16	10	..	..	41	26	41	33½	33½
BA60/53	'5'	..	..	..	11	7	..	..	20	18	20	19	19
BA61/53	'5'	..	..	..	2	6	..	..	13	8	13	10½	10½
BA51/53	'6'	..	..	1	15	9	..	..	34	25	34	29½	29½
BA52/53	'6'	..	..	1	8	4	..	..	14	13	14	13½	13½
BA53/53	'7'	1	3	11	40	7	..	..	58	62	58	60	60
BA54/53	'7'	..	..	..	12	15	..	..	24	27	24	25½	25½
BA55/53	'8'	..	..	..	4	10	..	..	24	14	24	19	19
BA62/53	'8'	..	..	4	9	4	..	..	15	17	15	16	16
BA63/53	'8'	..	..	..	25	21	..	..	32	46	32	39	39
BA57/53	'9'	..	..	..	7	9	..	..	15	16	15	15½	15½
Totals		1	3	21	149	102	..	..	299	276	299	287½	287½

BA50-57/53 derive from BA101/52 and the remaining families from BA102/52 (Table 6).

The degree of resistance shown by these families indicates that they carry the weaker of the two resistance genes and this was subsequently confirmed in self-bred progenies (Table 15).

F_2 and F_3 results from fourth Sakel backcross

From the fourth Sakel backcross (Table 3) five plants showing grade '4' resistance and two with grade '8' symptoms were selfed. The classification of these progenies is shown in Table 8.

Table 8. *Blackarm grading of fourth Sakel backcross F_2*

Family No.	Parent grade	Blackarm grade '3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA15/51	'4'	2	7	5	..	..	..	2	1	2
BA17/51	'4'	..	..	1	1	..	..	..	..	6
BA18/51	'4'	..	..	..	1	1	..	..	..	1
BA19/51	'4'	..	5	16	4	2	..	15	24	6
BA20/51	'4'	..	..	1	4	..	..	..	..	5
BA21/51	'8'	..	..	..	..	..	1	3	26	7
BA22/51	'8'	..	..	..	..	..	..	8	9	8
Sakel control		..	..	..	..	..	..	..	..	30

BA15-22/51 derive from BA122/50 (Table 3).

Five plants in BA15/51 (Table 8), showing maximal resistance, were selfed; the classification of their progenies is shown in Table 9.

Table 9. *Blackarm grading of fourth Sakel backcross F_3*

Family No.	Parent grade	Blackarm grade '2'	'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA62/52	'3'—'4'	3	20	15	..	..	..	..	..	..	..
BA63/52	'3'—'4'	..	13	17	..	..	..	..	..	..	..
BA65/52	'3'—'4'	1	19	10	..	..	..	4	1	1	..
BA64/52	'3'—'4'	..	12	12	4	..	..	..	2	..	3
BA66/52	'3'—'4'	..	13	18	2	..	..	..	1	2	3

BA62-66/52 derive from BA15/51 (Table 8).

In these progenies, BA62 and 63/52 are presumably homozygous for the stronger of the two major resistance genes but there is no evidence as to the presence or absence of the weaker gene. The parent of BA65/52 was presumably heterozygous for the stronger gene and homozygous for the weaker, and BA64 and 66/52 appear to be segregating for both. As noted earlier, ratios cannot be expected to be meaningful in transferences between **A** and **AD** cottons until more advanced backcrosses are reached.

F_2 and F_3 results from fifth Sakel backcross

Little confidence can be placed on blackarm grading of out-of-season crops, but in the out-of-season sown family BA27/51 (Table 4) plants of all blackarm grades from '3' to '6' were selfed. The progenies of these plants were grown in 1951 at normal crop time and their blackarm grading is shown in Table 10. In this table are included, also, families BA74-79/52, sown in 1952 and derived from the in-season sowing of BA27/51. The 1951 and 1952 figures for Domains Sakel controls are included in Table 10 because, owing to unfavourable climatic conditions, the 1952 fully susceptible controls ranged from grade '9' to '12'.

Table 10. *Blackarm grading of fifth Sakel backcross F_2*

Family No.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA34/51	'3'	..	2	2	..	..	1	3	1
BA41/51	'3'	1	6	1	1	..	1	2	3
BA33/51	'4'	..	..	..	1	..	..	1	2
BA40/51	'4'	..	4	1	1	..	..	..	8
BA43/51	'5'	..	1	..	1	..	..	..	..
BA39/51	'6'	..	1	..	3	..	..	..	6
Sakel control 1951		..	..	..	..	..	..	..	46
BA74/52	'5'	..	3	8	10	..	..	1	28
BA75/52	'5'	..	5	..	1	..	..	3	2
BA76/52	'5'	..	6	..	..	3	6	2	9
BA77/52	'5'	1	2	1	3	..	..	1	14
BA78/52	'6'	9	20	6	1	..	..	1	9
BA79/52	'6'	1	4	1	1	..	..	..	3
Sakel control 1952		..	..	..	..	..	5	9	24
BA92/53	'4'	..	2	2	..	..	..	..	10
BA93/53	'4'	..	13	2	..	..	..	..	2
BA94/53	'4'	..	8	5	..	..	..	..	2
Sakel Control 1953		..	..	..	..	..	..	..	41

BA33-44/51 derive from BA27/51 OS, BA74-77/52 are from BA27/51, and BA78-79/52 are from BA29/51 (Table 4). BA92-94/53 derive from BA60 and 61/52 (p. 331).

Twenty resistant plants were selfed in the 1951 sowing of the fifth backcross F_2 (BA34-43/51, Table 10). One of these plants was grade '4', eleven were grade '5' and the remainder were grade '6' and '7'. Of the 20 resulting progenies only one (BA100/52) proved pure for a high level of resistance; this family came from a grade '5' parent. The detailed grading of these F_3 progenies is not given because, owing to climatic conditions in the 1952 plot, no clear ratios were obtained, Sakel controls grading from '12' down to '9'. However, comparison of the homozygous progeny, BA100/52, with a nearby control of BAR14/19 (a synthesized Domains Sakel carrying the *G. arboreum* gene $\mathbf{B}_4$) showed markedly greater resistance in the material of Wagad 8 origin.

A further nine fifth backcross F_3 progenies were sown in 1953 (Table 11).

Table 11. *Blackarm grading of fifth Sakel backcross* F_3

Family No.	Parent grade	Blackarm grade '3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Totals Sus.	Expected Res.	Expected Sus.
													(3 : 1)	
BA95/53	'4'	4	34	5	..	..	..	..	..	..	43	..		
BA96/53	'4'	..	..	13	13	..	..	..	..	13	26	13	29¼	9¾
BA97/53	'4'	..	..	40	2	..	..	..	..	..	42	..		
BA98/53	'4'	..	1	24	..	..	..	..	..	..	25	..		
BA99/53	'4'	..	..	14	13	..	..	..	..	13	27	13	30	10
BA100/53	'6'	..	..	6	21	..	..	..	..	9	27	9	27	9
BA101/53	'6'	..	..	14	13	..	..	..	..	10	27	10	27¾	9¼
BA102/53	'6'	..	..	14	12	..	..	..	..	16	26	16	31½	10½
BA103/53	'6'	..	..	10	20	..	..	..	..	11	30	11	30¾	10¼
Totals (hets. only)		..	..	71	92	..	..	..	..	72	163	72	176¼	58¾

BA95-103/53 derive from BA78/52 (Table 10).

F_2 *and* F_3 *results from sixth Sakel backcross*

Two small sixth backcross F_2 families (BA103 and 104/52) were grown in 1952 from grade '5' and '6' plants respectively in BA45/51 (Table 5). These gave no clear ratios. In 1953, five sixth backcross F_2 families were grown; these gave clear ratios showing reasonable agreement with expectation on a 3:1 basis (Table 12).

A single sixth backcross F_3 family was grown in 1953 from a grade '4' parent in BA103/52 (above). This gave the distribution shown in Table 13.

Presumably the grade '4' parent was homozygous for the weaker gene and heterozygous for the stronger one. This interpretation was confirmed by crossing three grade '5' plants and three grade '8' plants with Sakel. The grade '5' plants gave a total of 52 grade '4'-'6' : 66 grade '8'-'10' in good agreement with an expectation

Table 12. *Blackarm grading of sixth Sakel backcross F_2*

Family No.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Sus.	Expected Res.	Sus.
												3 : 1	
BA83/53	'5'	2	27	20	..	..	..	..	18	49	18	$50\frac{1}{4}$	$16\frac{3}{4}$
BA84/53	'5'	1	12	9	..	..	..	..	12	22	12	$25\frac{1}{2}$	$8\frac{1}{2}$
BA85/53	'5'	..	19	19	..	..	..	..	18	38	18	42	14
BA86/53	'5'	..	11	16	1	..	..	..	12	28	12	30	10
BA87/53	'5'	..	9	16	..	..	..	..	9	25	9	$25\frac{1}{2}$	$8\frac{1}{2}$
Totals		3	78	80	1	..	..	..	69	162	69	$173\frac{1}{4}$	$57\frac{3}{4}$

BA83-87/53 derive from BA72/52 (Table 5).

Table 13. *Blackarm grading of sixth Sakel backcross F_3*

Family No.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA78/53	'4'	1	7	..	5	10	..	..	..
Sakel control		..	..	..	..	..	..	..	42

BA78/53 derives from BA103/52 (p. 337).

of 59 very resistant: 59 weakly resistant. The grade '8' plants gave a total of 32 plants ranging from grade '8' to '10'; no grade '12' plants were present.

These same six plants in BA78/53 were selfed, and the classification of their progenies is given in Table 14.

Table 14. *Blackarm grading of sixth Sakel backcross F_4*

Family No.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA156/54	'5'	15	14	1	..	..	..	..	..
BA157/54	'5'	..	..	1	..	..	5	..	..
BA158/54	'5'	8	33	9	..	1	18	12	..
BA159/54	'8'	..	..	..	..	..	25	97	..
BA160/54	'8'	..	..	..	..	..	22	70	9
BA161/54	'8'	..	..	..	..	2	33	47	3
Sakel control		..	..	..	..	..	..	..	15

BA156-161/54 derive from BA78/53 (Table 13).

Presumably BA156/54 came from a parent homozygous for both genes whereas the parents of BA157 and 158/54 were homozygous for the weaker gene and heterozygous for the stronger one. The parents of BA159-161/54 were presumably homozygous for the weaker gene and these families show that in certain seasons plants carrying this gene in the heterozygous phase can be expected to grade from '8' to '12' with the bulk of the plants in grade '10'. This presumably accounts for the poor agreement with expectation on a 1:1 basis in Families BA171-175/54 in Table 6.

F_2 and F_3 results from seventh Sakel backcross

A number of plants were selected in the seventh backcross covering the range of resistance in BA101 and 102/53 (Table 6). Self-bred seed of these was sown in 1953 and the resulting progenies were classified for blackarm resistance (Table 15). In addition, two families BA103 and 104/54, self-bred from BA81/53 (Table 6), have been included in the table.

Two of the seventh backcross plants, graded at '8' and '9' respectively, were found to give only grade '12' progenies and so presumably had been in reality 'fully susceptible' plants which did not develop the disease fully under the adverse climatic conditions of 1952.

Clearly in this material the two genes have been isolated independently; the first group of families in Table 15 carry the strong gene and the second group the weak gene.

Eleven resistant plants in BA73/53 (Table 15) were selfed in order to establish lines homozygous for the stronger of these two genes. The grading of the resulting progenies is shown in Table 16(i); clearly 5 progenies were homozygous and 6 were from heterozygous parents. The distributions in these two groups suggest that this gene is not fully dominant.

In addition 15 resistant plants in Family BA69/53 and 15 in Family BA77/53 (Table 15) were selfed to establish lines homozygous for the weaker gene. The grading of the resulting 30 progenies is shown in Table 16. Families containing no grade '12' plants are classed as homozygous, in addition families with only a very low proportion of grade '12' plants are included as presumably homozygous. It is considered that even in the homozygous phase this weak gene is not always phenotypically distinguishable from full susceptibility (grade '12'). The ratio of 362 plants of grade '10' and under: 163 grade '12' in the heterozygous group (Table 16 (ii, b)) suggests that the expression of the weaker gene when heterozygous frequently ranges into full susceptibility. Seventh backcross F_2 families carrying this weaker gene, however, gave clear cut segregations (Table 15); clearly this gene is subject to marked seasonal variation in its expression, the degree of resistance conferred varying with climatic conditions. Other blackarm resistance genes are known to show similar variation though this is usually less marked.

Table 15. *Blackarm grading of seventh Sakel backcross F_2*

Family No.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Totals Sus.	Expected Res.	Expected Sus.
												(3 : 1)	
BA72/53	'4'	..	..	1	..	..	..	..	1	1	1	$1\frac{1}{2}$	$\frac{1}{2}$
BA73/53	'4'	9	13	3	..	..	..	..	8	25	8	$24\frac{3}{4}$	$8\frac{1}{4}$
BA103/54	'5'	6	34	31	6	..	..	..	17	77	17	$70\frac{1}{2}$	$23\frac{1}{2}$
BA104/54	'5'	10	20	23	5	..	..	..	32	58	32	$67\frac{1}{2}$	$22\frac{1}{2}$
Totals		25	67	58	11	..	..	..	58	161	58	$164\frac{1}{4}$	$54\frac{3}{4}$
BA74/53	'5'	..	..	..	3	23	..	..	16	26	16	$31\frac{1}{2}$	$10\frac{1}{2}$
BA75/53	'5'	..	..	..	2	21	..	..	11	23	11	$25\frac{1}{2}$	$8\frac{1}{2}$
BA64/53	'6'	..	..	..	5	12	..	..	6	17	6	$17\frac{1}{4}$	$5\frac{3}{4}$
BA65/53	'6'	..	..	..	..	17	..	..	3	17	3	15	5
BA66/53	'7'	..	..	..	..	9	..	..	4	9	4	$9\frac{3}{4}$	$3\frac{1}{4}$
BA67/53	'7'	..	..	1	2	19	..	..	9	22	9	$23\frac{1}{4}$	$7\frac{3}{4}$
BA69/53	'8'	..	..	2	50	28	..	..	18	80	18	$73\frac{1}{2}$	$24\frac{1}{2}$
BA76/53	'8'	..	..	..	2	33	..	..	8	35	8	$32\frac{1}{4}$	$10\frac{3}{4}$
BA77/53	'8'	..	..	..	8	32	..	..	9	40	9	$36\frac{3}{4}$	$12\frac{1}{4}$
BA71/53	'9'	..	..	..	5	11	..	..	11	16	11	$20\frac{1}{4}$	$6\frac{3}{4}$
Totals		..	..	3	77	205	..	..	95	285	95	285	95

BA64-71/53 derive from BA101/52 (Table 6).
BA72-77/53 ,, ,, BA102/52 ,, .
BA103-104/54 ,, ,, BA81/53 ,, .

Table 16. *Blackarm grading of F_3 of seventh Sakel backcross*

Family No.	Blackarm grade '5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Totals Sus.	Expected Res.	Expected Sus.
(*i*) Families carrying the strong resistance gene											
(*a*) Homozygous											
BA120/54	6	8	..	..	..	..	..	14	0		
BA121/54	11	18	..	..	..	..	..	29	0		
BA122/54	4	9	..	..	..	..	..	13	0		
BA129/54	5	14	..	..	..	..	..	19	0		
BA130/54	1	12	..	..	..	..	..	13	0		
Totals	27	61	..	..	..	..	..	88	0		
(*b*) Heterozygous										3:1	
BA123/54	2	4	10	7	..	..	7	23	7	$22\frac{1}{2}$	$7\frac{1}{2}$
BA124/54	..	3	2	4	..	..	1	9	1	$7\frac{1}{2}$	$2\frac{1}{2}$
BA125/54	..	1	2	2	..	..	3	5	3	6	2
BA126/54	..	1	1	2	..	..	1	4	1	$3\frac{3}{4}$	$1\frac{1}{4}$
BA128/54	1	6	9	6	..	..	8	22	8	$22\frac{1}{2}$	$7\frac{1}{2}$
BA132/54	2	..	9	1	..	..	1	12	1	$9\frac{3}{4}$	$3\frac{1}{4}$
Totals	5	15	33	22	..	..	21	75	21	72	24

Table 16—(*Contd.*)

Family No.	Blackarm grade '5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Totals Sus.	Expected Res.	Expected Sus.
(*ii*) Families carrying the weak resistance gene											
(*a*) Homozygous											
BA113/54	..	..	..	..	13	23	..	36	0		
BA114/54	..	..	..	6	14	11	..	31	0		
BA115/54	..	..	..	8	25	8	..	41	0		
BA117/54	..	..	..	..	25	17	2	42	2		
BA118/54	..	..	..	..	10	16	1	26	1		
BA119/54	..	..	..	..	16	30	..	46	0		
BA135/54	..	..	..	..	10	18	..	28	0		
BA137/54	..	..	..	..	6	20	..	26	0		
BA138/54	..	..	..	..	4	19	1	23	1		
BA139/54	..	..	..	..	15	19	..	34	0		
BA140/54	..	..	..	..	12	24	..	36	0		
BA144/54	..	..	..	..	11	24	..	35	0		
BA149/54	..	..	..	1	11	26	..	38	0		
Totals	..	..	..	15	172	255	4	442	4		
(*b*) Heterozygous										3:1	
BA105/54	..	..	..	1	1	4	5	6	5	$8\frac{1}{4}$	$2\frac{3}{4}$
BA106/54	..	..	..	..	8	10	9	18	9	$20\frac{1}{4}$	$6\frac{3}{4}$
BA107/54	..	..	..	..	1	8	11	9	11	15	5
BA108/54	..	..	..	..	6	16	15	22	15	$27\frac{3}{4}$	$9\frac{1}{4}$
BA109/54	..	..	..	..	3	17	12	20	12	24	8
BA110/54	..	..	..	..	5	16	11	21	11	24	8
BA111/54	..	..	..	..	8	16	7	24	7	$23\frac{1}{4}$	$7\frac{3}{4}$
BA112/54	..	..	..	..	3	16	11	19	11	$22\frac{1}{2}$	$7\frac{1}{2}$
BA116/54	..	..	..	..	10	12	7	22	7	$21\frac{3}{4}$	$7\frac{1}{4}$
BA136/54	..	..	..	..	6	17	13	23	13	27	9
BA141/54	..	..	..	..	1	17	15	18	15	$24\frac{3}{4}$	$8\frac{1}{4}$
BA142/54	..	..	..	..	5	24	4	29	4	$24\frac{3}{4}$	$8\frac{1}{4}$
BA143/54	..	..	..	..	5	23	10	28	10	$28\frac{1}{2}$	$9\frac{1}{2}$
BA145/54	..	..	..	..	8	20	13	28	13	$30\frac{3}{4}$	$10\frac{1}{4}$
BA146/54	..	..	..	..	7	24	9	31	9	30	10
BA147/54	..	..	..	..	3	18	5	21	5	$19\frac{1}{2}$	$6\frac{1}{2}$
BA148/54	..	..	..	..	2	21	6	23	6	$21\frac{3}{4}$	$7\frac{1}{4}$
Totals	..	..	..	1	82	279	163	362	163	$393\frac{3}{4}$	$131\frac{1}{4}$

BA120-134/54 derive from BA73/53, BA105-119/54 are from BA69/53, and BA135-149/54 are from BA77/53 (Table 15).

Gene homology tests

Crosses were made between a number of synthesized Domains Sakel strains, each homozygous for one of the known blackarm resistance genes, and the fourth back-cross F_3 family BA62/52 (Table 9) homozygous for the stronger of the two *herbaceum* genes. The F_2s of these crosses were grown in 1953 and their grading is given below (Table 17).

Table 17. *Gene homology tests: blackarm grading of F_2 progenies*

Family No.	Blackarm grade '3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Totals Sus.	Expected Res.	Expected Sus.
(*a*) *BAR 14/11* ($\mathbf{B_1B_1}$) × *BA62/52* F_3												(15 : 1)	
BA120/53	2	47	39	13	5	19	13	..	17	138	17	145·3	9·7
BA121/53	1	49	44	18	3	20	25	..	11	160	11	160·3	10·7
BA122/53	2	72	34	24	1	16	6	..	13	155	13	157·5	10·5
BA123/53	..	21	10	2	1	3	4	..	2	41	2	40·3	2·7
BA124/53	..	54	49	12	3	12	22	2	16	154	16	159·4	10·6
BA125/53	..	82	30	16	2	18	10	2	8	160	8	157·5	10·5
Totals	5	325	206	85	15	88	80	4	67	808	67	820·3	54·7
Sakel control		..	..	..	..	..	..	..	38				
BAR14/11 control		..	..	..	..	3	21	8	..				
(*b*) *BAR 14/16* ($\mathbf{B_2B_2}$) × *BA62/52* F_2												(15 : 1)	
BA227/54	5	12	3	3	9	2	1	..	1	35	1	33·8	2·2
BA228/54	6	43	24	11	11	2	3	..	5	100	5	98·4	6·6
BA229/54	11	26	2	7	13	3	..	..	4	62	4	61·9	4·1
BA231/54	7	13	..	2	5	2	..	..	3	29	3	30·0	2·0
BA234/54	5	21	4	3	15	7	..	..	6	55	6	57·2	3·8
BA235/54	19	42	18	16	7	1	..	..	4	103	4	100·3	6·7
BA236/54	19	22	16	16	6	1	2	..	4	82	4	80·6	5·4
Totals	72	179	67	58	66	18	6	..	27	466	27	462·2	30·8
BAR14/16 control	..	..	..	37	8	..	..	..	..				

Table 17—(*Contd.*)

Family No.	'3'	'4'	'5'	Blackarm grade '6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Sus.	Expected Res.	Sus.
(*c*) *BAR 14/9* ($\mathbf{B_3B_3}$) × *BA62/52* F_2												(15 : 1)	
BA128/53	..	26	67	28	16	8	2	1	13	148	13	150·9	10·1
BA129/53	..	7	70	35	12	17	3	..	6	144	6	140·6	9·4
Totals	..	33	137	63	28	25	5	1	19	292	19	291·5	19·5
(*d*) *BAR 14/19* ($\mathbf{B_4B_4}$) × *BA62/52* F_2												(15 : 1)	
BA109/53	7	20	9	2	4	..	..	..	..	42	0	39·4	2·6
BA110/53	7	15	9	15	2	..	..	..	5	48	5	49·7	3·3
BA111/53	1	13	24	8	6	..	..	..	4	52	4	52·5	3·5
BA112/53	1	15	16	6	4	5	..	..	1	47	1	45·0	3·0
BA133/53	..	13	64	40	17	11	..	..	12	145	12	147·2	9·8
Totals	16	76	122	71	33	16	..	..	22	334	22	333·8	22·2
Sakel control	..	..	..	..	..	..	..	..	41				
(*e*) *BAR 14/20* ($\mathbf{B_5B_5}$) × *BA62/52* F_2												(15 : 1)	
BA242/54	..	..	37	19	2	9	7	1	5	75	5	75·0	5·0
BA243/54	..	2	35	3	2	7	..	3	6	52	6	54·4	3·6
Totals	..	2	72	22	4	16	7	4	11	127	11	129·4	8·6
BAR 14/20 control	..	..	..	..	6	23	5	..	..				
(*f*) *BAR 14/31* ($\mathbf{B_7B_7}$) × *BA62/52* F_2												(15 : 1)	
BA104/53	..	21	23	4	7	3	..	..	2	58	2	56·2	3·8
BA105/53	1	38	14	10	12	4	..	..	2	79	2	75·9	5·1
BA106/53	2	29	20	7	8	16	..	..	2	82	2	78·8	5·2
BA107/53	..	29	24	2	8	1	..	..	1	64	1	60·9	4·1
Totals	3	117	81	23	35	24	..	..	7	283	7	271·8	18·2

The divergence of some of the individual progenies in Table 17 from expectation on a 15:1 basis cannot be regarded as significant since these progenies all represent relatively early backcrosses in the transference of this resistance gene from an **A** genome to an **AD** genome background.

As a further check, crosses were made in 1952 between Sakel lines homozygous for the various known resistance genes and BA100/52, which was homozygous for the strong resistance gene from Wagad 8. F_2s of these crosses were grown and graded in 1954. The data are summarized below:

	Observed		Expected (15:1)	
	Res.	Sus.	Res.	Sus.
BAR 14/11 ($\mathbf{B_1B_1}$) × BA100/52 F_2s	183	6	177·2	11·8
BAR 14/16 ($\mathbf{B_2B_2}$) × ,,	284	24	288·8	19·2
BAR 14/9 ($\mathbf{B_3B_3}$) × ,,	379	22	375·9	25·1
BAR 14/19 ($\mathbf{B_4B_4}$) × ,,	132	12	135·0	9·0
BAR 14/20 ($\mathbf{B_5B_5}$) × ,,	131	6	128·4	8·6
BAR 14/31 ($\mathbf{B_7B_7}$) × ,,	339	24	340·3	22·7

Clearly the strong gene from Wagad 8 is not allelic with any of the genes $\mathbf{B_1}$—$\mathbf{B_5}$ and $\mathbf{B_7}$. No homology tests have been made with the Asiatic intensifying gene $\mathbf{B_{6m}}$ from *G. arboreum*, nor with the recessive gene $\mathbf{b_8}$ found in *G. anomalum*, but the Wagad gene is so different in its action from either of these that it is assumed to be non-allelic.

Knight (1957) in a survey of work on blackarm resistance in the Sudan gave the symbol $\mathbf{B_9}$ to the stronger of the two genes transferred to Sakel from Wagad 8 and the gene homology tests detailed above confirm the validity of this. No symbol is suggested for the weaker gene as no homology tests have been made to determine its relationship with the other known blackarm resistance genes.

Discussion

It is clear from the data in Table 16 that two partially dominant resistance genes have been successfully transferred from *G. herbaceum* to *G. barbadense* through seven backcrosses. When homozygous, the stronger of these, $\mathbf{B_9}$, conferred resistance ranging from grade '6' down to '5' or even '4' (Tables 15 and 16). The weaker gene when homozygous gave a range from an occasional grade '12' plant down to '8', and when heterozygous showed a mode at grade '10' with a range from '8' to '12' there being assumedly far more heterozygotes ranging into grade '12' than homozygotes (Tables 14 and 16). In some seasons, however, the resistance conferred by this gene is considerably strengthened. The expression of all blackarm resistance genes appears to be somewhat subject to environment but this weaker gene shows a more marked environmental response than is common.

Because only two resistance genes were located and transferred in the course of this work, it cannot be argued that these are necessarily responsible for the whole of the near-immunity of Wagad 8; the writer's experience with a number of crosses within *G. herbaceum* suggests that greater complexity is common in this species.

In transferring characters from Old World ($n=13$) cottons to New World ($n=26$) species, the technique of doubling the chromosome number of the Old World parent has now been successfully used by the writer in moving blackarm resistance genes and hairiness genes from *G. arboreum* ($\mathbf{A}_2$ genome) and from *G. herbaceum* ($\mathbf{A}_1$ genome) to *G. barbadense* $(\mathbf{AD})_2$ genome (Knight, 1948a, 1953, 1954a, 1955).

From the plant breeding point of view this technique has much to recommend it compared with the theoretically more orthodox method of crossing the **A**-genome donor parent with a **D**-genome species, making a synthetic **AD** alloploid, and backcrossing this to the commercial **AD** cotton variety to which the required genes are to be transferred. The greatest disadvantage of the latter technique is that the plant breeder is faced with having to eliminate not only the unwanted portions of the original donor **A** genome, but also the whole of an unwanted wild species **D** genome. Other aspects of these alternative methods of transfer have been discussed elsewhere (Knight, 1948a, 1954a, 1955).

It has been the writer's experience that in transferences from *G. arboreum* ($\mathbf{A}_2$ genome) to Sakel (*barbadense*) the elimination of *arboreum* characters appears to be somewhat more rapid than is the elimination of *herbaceum* ($\mathbf{A}_1$ genome) characters in similar backcrosses. This supports Gerstel's (1953) finding that the **A** chromosomes of New World cottons appear to be more closely related to *G. herbaceum* than to *G. arboreum*. *G. herbaceum* appears to have originated in S. and S.W. Africa (Hutchinson, 1959); one is tempted to infer that the **A** genome, which reached the New World where it hybridized with a wild **D** genome *Gossypium* species to form the progenitor of New World cottons, achieved this crossing by way of the Atlantic rather than via the continent of Asia and thence via the Pacific. The race of humans that brought cotton with them to the New World would surely have brought with it a knowledge of the crafts of their own civilization. A trans-Atlantic crossing would account for the absence of a bronze age in the ancient New World cultures (there having been no real bronze age in southern Africa), whereas a trans-Pacific migration would have been likely to bring a knowledge of bronze in its train, since bronze making was established throughout Asia from very early times.

SUMMARY

Two partially dominant genes governing resistance to blackarm (*Xanthomonas malvacearum*) have been transferred from *Gossypium herbaceum* ($n=13$, $\mathbf{A}_1$ genome) to Sakel, *G. barbadense* ($n=26$, $(\mathbf{AD})_2$ genome). The stronger of these genes has been given the symbol $\mathbf{B}_9$; no symbol has been allocated to the weaker gene because gene homology tests have not been made between this and the other known genes.

I am grateful to Dr. S. O. S. Dark for supervising the grading in 1954 of progenies from crosses and selfs made by me in 1953 before I left the Sudan. I would also like to take this opportunity of thanking the many Sudanese members of the Cotton Breeding Section, Shambat, for all the help they so ably gave over the years—especially Mahmoud Abdel Nabi, Beshir Akashar, Abdel Wahid and Abdel Samad Hassan.

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