THE GENETICS OF BLACKARM RESISTANCE

IX. THE GENE $\mathbf{B}_{6m}$ FROM *GOSSYPIUM ARBOREUM*

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CONTENTS

Previous work

Five genes controlling resistance to *Xanthomonas malvacearum* (blackarm) in cotton have so far been isolated and identified, viz.

$\mathbf{B}_1$ is a weak, fully dominant gene which occasionally occurs in *Gossypium hirsutum* (American Upland).

$\mathbf{B}_2$ is a strong, fully dominant gene which is the basis of all effective resistance in Old World races of American Upland and *punctatum* cottons.

$\mathbf{B}_3$ is a strong, partially dominant gene found in some *punctatum* cottons. $\mathbf{B}_2$ and $\mathbf{B}_3$ are linked and show a 32% cross-over value in early crosses with *G. barbadense*. In later generations recombination approaches free assortment.

$\mathbf{B}_4$ is a strong, partially dominant gene which occurs in *G. arboreum*.

$\mathbf{B}_5$ is a strong, partially dominant gene which has been found in one strain of perennial *G. barbadense*.

These genes have been discussed in detail in parts I–VIII of this series, whilst the whole question of the evolution of blackarm resistance has been discussed by Knight & Hutchinson (1950).

Knight (1948*b*) showed the immunity of Multani cotton (*G. arboreum* race *bengalense*) to depend on $\mathbf{B}_4$ accompanied by a strong complex of minor genes. This gene was successfully transferred to Sakel (*G. barbadense*) (Knight, 1948*a*).

Description of strains

Multani (Sanguineum), strain NT 12/30, belongs to *G. arboreum* race *bengalense*, which has 26 somatic chromosomes belonging to the **A** genom. It is a red-leaved, sympodial type which, even after repeated spraying with inoculum, is usually immune to blackarm disease. In certain seasons a small proportion of plants seemed to show grade '1', '2' and even '3' symptoms, but, owing to the way in which anthocyanin pigment increases the apparent size both of small lesions and insect punctures, it has never been certain that these plants were actually attacked by blackarm. The tetraploid strain used as donor parent in the

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crosses recorded here arose from the single tetraploid plant reported by Knight (1948*a*, p. 361).

Sakel (*G. barbadense*) is the commercial crop of the northern irrigated areas of the Sudan (except for Northern Province, where a certain amount of American Upland (*G. hirsutum*) cotton is grown). Both *G. barbadense* and *G. hirsutum* have 52 somatic chromosomes belonging to the (**AD**) genom. Two types of Sakel are cultivated in the Sudan—Domains Sakel in the northern Gezira and parts of the Gash, and X1730A in the southern Gezira, White Nile irrigation schemes, Tokar and the Gash. Synthetic X1730A carrying $\mathbf{B}_2$ transferred from American Upland and named XL1 has replaced X1730A in the White Nile areas and in parts of the Gash and Gezira. BLR14/16, a Domains Sakel derivative carrying $\mathbf{B}_2$, was used in some of the crosses recorded here, but the final commercial crosses were made to BAR4/16, an X1730 type carrying $\mathbf{B}_2$ and $\mathbf{B}_3$, and to BAR14/21, its Domains Sakel counterpart.

THE ORIGIN OF THE GENE $\mathbf{B}_{6m}$

The transference of the *arboreum* gene $\mathbf{B}_4$ to Sakel has been described elsewhere (Knight, 1948*a*). During the course of this work a 'natural' progeny of a single second Sakel backcross plant was grown, and in this progeny a number of grade '3' male plants appeared. Check crosses with $\mathbf{B}_2$ Sakels showed that these plants were outcrosses carrying $\mathbf{B}_2$. However, their degree of resistance seemed so promising that, despite their obscure ancestry from open pollination, it was decided to use them for breeding. Accordingly, they were crossed with X1730A and with Domains Sakel and backcrossed to these two Sudan Sakel strains, using as parents in each hybrid generation plants showing the maximum resistance.

In the first Sakel backcross the following distributions were obtained:

	Blackarm grade*									
Family no.	'2'	'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA119/47	8	20	—	11	16	8	—	—	—	58
BA120/47	3	26	2	5	20	10	—	—	—	70
Totals	11	46	2	16	36	18	—	—	—	128
Grouped totals		59			70					128
Expected (1:1:2)		$64\frac{1}{4}$			$64\frac{1}{4}$					$128\frac{1}{2}$

These figures clearly suggest the presence of a strong intensifying gene which fortifies the resistance of a major **B** gene (in this case $\mathbf{B}_2$). Subsequent backcross progenies gave distributions proving this hypothesis, and this strong modifying gene was given the symbol $\mathbf{B}_{6m}$.

These backcrosses are summarized below:

	Parent grade	Blackarm grade								
		'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
2nd backcross (BA123–124/48)	'3'	13	15	2	8	8	—	—	—	40
3rd backcross (BA54–55/49)	'3'	4	9	1	—	22	—	—	—	28
4th backcross (BA121, 184–196/50)	'3'	20	19	15	33	2	—	—	—	91
5th backcross (BA51, 56–59/51)	'3'	18	34	2	3	51	—	—	—	136
Totals		55	77	20	44	83	—	—	—	295
Grouped totals			142		137					295
Genotypes			$\mathbf{B}_2\mathbf{B}_{6m}$		$\mathbf{B}_2\mathbf{b}_{6m}$					$\mathbf{b}_2\mathbf{B}_{6m}$ and $\mathbf{b}_2\mathbf{b}_{6m}$

* Grade '0' represents immunity and '12' full (Sakel) susceptibility. This system of grading is defined and illustrated by Knight (1944).

The grouped totals of 142:137:295 (obtained by splitting the minimum frequency group at grade '5' equally) compare with expectation on a 1:1:2 basis of $143\frac{1}{2}:143\frac{1}{2}:287$. Clearly the fit is excellent.

In view of the complex of minor resistance genes known to be present in *G. arboreum* (Knight, 1948*b*), it seemed likely that this strong modifying gene had originated from *arboreum* rather than from the open-pollination parent. In order to obtain proof of the origin of $\mathbf{B}_{6m}$, a retransference of this gene from *arboreum* to Sakel was initiated.

Retransference of $\mathbf{B}_{6m}$ to Sakel

F_1 of tetraploid arboreum × *Sakel and the first Sakel backcross*

A bulk of tetraploid Multani (*G. arboreum* race *bengalense*) was crossed with Domains Sakel, using the latter as male parent. From this cross eighty-nine F_1 plants were raised in 1946. These were sprayed with blackarm inoculum and, on grading, gave the following distribution:

	Blackarm grade			
Family no.	'2'	'3'	'4'	'5'
BA105/46	42	41	5	1

This F_1 was grown in complete isolation, and it was regularly pollinated with Domains Sakel pollen without being emasculated (because of its self-sterility). From this hybridization seventy-five first backcross plants were raised in 1947. They were graded as follows:

	Blackarm grade								
Family no.	'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA126/47	2	3	9	6	11	20	6	10	8

Second and third Sakel backcrosses

All the plants in the first Sakel backcross were crossed again with Domains Sakel. Only eight plants gave progenies from this crossing. These progenies were sprayed with inoculum and graded in 1948. Their distributions are given in Table 1.

Table 1. *Blackarm grading of second Sakel backcross*

		Blackarm grade						
Family no.	Parent grade	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA101/48	'5'	—	1	—	—	—	—	—
BA102/48	'10'	—	—	—	1	—	—	1
BA104/48	'12'	—	—	—	—	—	—	2
BA106/48	'8'	—	—	—	3	—	—	—
BA108/48	'7'	—	—	2	1	—	—	1
BA109/48	'6'	—	—	—	2	—	—	—
BA110/48	'8'	—	—	—	—	—	1	1
BA112/48	'8'	1	—	2	5	1	—	4
Totals		1	1	4	12	1	1	9

All the plants in these progenies were again crossed with Domains Sakel, and this hybridization gave ten viable progenies having a total population of 107 plants. These third backcross progenies were graded as shown in Table 2.

Extraction of the intensifying gene $\mathbf{B}_{6m}$

The distributions given in Table 2 show that minor resistance genes have been almost eliminated by backcrossing to Sakel, although the grade '10' plant in BA14/49 probably indicates the presence of a minor element of resistance in this family, apart from the major

gene $\mathbf{B}_4$. The elimination of minor resistance genes was considered advisable, before attempting to pick out the gene $\mathbf{B}_{6m}$, since such minor factors would obscure the issue.

$\mathbf{B}_2$ is a strong gene having full dominance. For this reason it was chosen as the background on which $\mathbf{B}_{6m}$ could be most easily identified. It was assumed that some of the fully susceptible plants in the third Sakel backcross progenies would be of $\mathbf{B}_{6m}\mathbf{b}_{6m}$ genotype. Accordingly, sixty-four of these grade '12' plants were selected for crossing individually

Table 2. *Blackarm grading of third Sakel backcross*

Family no.	Parent grade	Blackarm grade '6'	'7'	'8'	'9'	'10'	'12'
BA 3/49	'2'	—	—	—	—	—	3
BA 4/49	'8'	—	—	2	—	—	2
BA 5/49	'12'	—	—	—	—	—	8
BA 7/49	'12'	—	—	—	—	—	6
BA 8/49	'7'	1	1	—	—	—	1
BA 9/49	'8'	—	2	—	—	—	2
BA 10/49	'12'	—	—	—	—	—	1
BA 12/49	'8'	1	10	7	—	—	25
BA 13/49	'12'	—	—	—	—	—	3
BA 14/49	'8'	—	6	9	—	1	17
Totals		2	20	18	—	1	68

Table 3. *Blackarm grading of the cross* (*tetraploid* arboreum × *Domains Sakel*[4]) × *BLR* 14/16 F_1

Family no.	Parent grade	Blackarm grade '3'	'4'	'5'	'6'	'7'	'8'
BLR 14/16	Control	—	1	58	17	3	—
BA 102/50	'12'	—	—	—	3	3	—
BA 103/50	'12'	—	—	1	11	5	—
BA 104/50	'12'	—	—	—	5	3	—
BA 105/50	'12'	—	1	3	42	11	—
BA 106/50	'12'	—	6	13	13	5	—
BA 107/50	'12'	—	10	7	7	3	—
BA 108/50	'12'	—	1	—	12	8	2
BA 109/50	'12'	—	16	4	12	7	—
BA 110/50	'12'	—	—	5	36	15	2
BA 111/50	'12'	3	11	6	10	3	—
BA 112/50	'12'	—	3	—	2	2	—
BA 113/50	'12'	—	—	—	16	8	—
BA 114/50	'12'	—	—	—	6	—	—
BA 115/50	'12'	6	6	1	3	4	—
BA 116/50	'12'	—	—	—	5	10	—
BA 117/50	'12'	—	—	3	20	5	—
BA 118/50	'12'	—	—	—	6	7	—
BA 119/50	'12'	—	3	—	2	1	—
BA 120/50	'12'	—	2	8	99	23	—
Totals		9	59	51	309	123	4
Totals of BA 106, 107, 109, 111, 112, 115 and 119/50		9	55	31	49	25	—
Totals of remainder		—	4	20	260	98	4

with BLR 14/16, a synthetic leaf-curl resistant Sakel carrying the Upland gene $\mathbf{B}_2$. The object of this cross was to make the gene $\mathbf{B}_{6m}$ phenotypically evident if present, since being an intensifying factor, it could only show in the presence of a major resistance gene. The resulting progenies, grown in 1950, gave the following distributions (Table 3).

An examination of the figures in Table 3 suggests that two types of distribution appear in these progenies. Most of the families fall within the range of, and have a similar

distribution to, the BLR14/16 control. Seven families, however, namely, BA106, 107, 109, 111, 112, 115 and 119/50 carry too high a proportion of plants at the grade '4' end of the range. These distributions indicate the presence of the gene $\mathbf{B}_{6m}$ in these seven families. Two plants with maximal resistance in BA111/50 and four plants in BA115/50 were chosen for crossing with Domains Sakel. The classification of the blackarm resistance of the resulting progenies is given in Table 4.

Table 4. *Blackarm grading of the cross* ((*tetraploid* arboreum × *Domains Sakel*[4]) × *BLR*14/16) × *Domains Sakel* F_1

		Blackarm grade								
Family no.	Parent grade	'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA9/51	'3'	—	2	—	—	1	—	—	—	3
BA10/51	'3'	1	2	1	1	6	—	—	—	10
BA11/51	'3'	—	3	—	—	1	—	—	—	13
BA12/51	'3'	—	2	—	—	2	—	—	—	8
BA13/51	'3'	—	3	—	2	2	—	—	—	3
BA14/51	'3'	3	10	1	4	16	—	—	—	33
Totals		4	22	2	7	28	—	—	—	70
Grouped totals			27		36					70
Expected 1:1:2			$33\frac{1}{3}$		$33\frac{1}{3}$					$66\frac{1}{2}$
Genotype			$\mathbf{B}_2\mathbf{B}_{6m}$		$\mathbf{B}_2\mathbf{b}_{6m}$					$\mathbf{b}_2\mathbf{B}_{6m}$ and $\mathbf{b}_2\mathbf{b}_{6m}$

From these figures it is clear that the gene $\mathbf{B}_{6m}$ has been successfully transferred from *arboreum* to Domains Sakel and that the *arboreum* parent was in fact the source from which the original $\mathbf{B}_{6m}$ was obtained in the earlier crosses recorded in this paper.

Economic utilization of the gene $\mathbf{B}_{6m}$

Judged by comparison with controls of Sakel homozygous for $\mathbf{B}_2$, the new gene $\mathbf{B}_{6m}$ increases the resistance of $\mathbf{B}_2$ by approximately two grades. This is of considerable importance since $\mathbf{B}_2\mathbf{B}_2$ Sudan Sakel (variety XL1) is being grown on about 65,000 acres in the Sudan this season (1951–2). Clearly a gene capable of so greatly increasing the resistance conferred by $\mathbf{B}_2$ would be of commercial importance. On the other hand, the final objective for the two main Sudan Sakel varieties and for the rain-grown Upland (*G. hirsutum*) crop of the Sudan has been to produce $\mathbf{B}_2\mathbf{B}_3$ strains, and these types are now on trial. It is to this material that $\mathbf{B}_{6m}$ is being added to give types which should be effectively immune under Sudan conditions.

Accordingly, $\mathbf{B}_2\mathbf{B}_{6m}$ plants were crossed with BAR14/21 and BAR4/16 (the former being a Domains Sakel type and the latter an X1730 type both carrying $\mathbf{B}_2$ and $\mathbf{B}_3$). These F_1's were backcrossed to BAR14/21 and BAR4/16 respectively, and the first backcross progenies gave the distributions shown in Table 5.

In the above families BA52–55/51 belong to the group of crosses involving BAR4/16. These progenies presumably contained $\mathbf{B}_2\mathbf{B}_3\mathbf{B}_{6m}$ and $\mathbf{B}_2\mathbf{B}_3\mathbf{b}_{6m}$ plants in equal proportions. A comparison of the totals for BA52–55/51 with the BAR4/16 control thus shows that the addition of $\mathbf{B}_{6m}$ has moved the degree of resistance nearly a full grade, on an average, towards complete immunity. Similarly, a comparison of the totals for BA64–65/51 with the control BAR14/21 shows a comparable increase of resistance brought about by $\mathbf{B}_{6m}$. This gene is therefore likely to be of considerable value in the Sudan in making the

end-products of the Sakel blackarm resistance breeding programme effectively immune under field conditions.

$\mathbf{B}_{6m}$ is being used at Shambat in the breeding programme for blackarm resistance in rain-grown Upland types. It is being added to BAR12/9·2, BAR7/8 and BARNT96. BAR12/9·2 is a Uganda BP52 strain which has been rendered homozygous for $\mathbf{B}_2$ and which is now being reselected for higher resistance by minor gene accumulation. BAR7/8 is a synthetic Upland type carrying $\mathbf{B}_2$ and $\mathbf{B}_3$ which is being expanded commercially in the Sudan, and BARNT96 is a commercial Sudan Upland carrying $\mathbf{B}_2$.

Table 5. *Blackarm grading of progenies obtained by crossing* $\mathbf{B}_2\mathbf{b}_2\mathbf{B}_{6m}\mathbf{b}_{6m}$ *plants twice on to* $\mathbf{B}_2\mathbf{B}_2\mathbf{B}_3\mathbf{B}_3$ *Sakel*

Family no.	Parent grade	Blackarm grade '2'	'3'	'4'	'5'	'6'	
BA52/51	'3'	—	2	10	2	—	BAR 4/16 crosses
BA53/51	'3'	1	9	13	6	—	
BA54/51	'3'	—	3	8	1	—	
BA55/51	'3'	—	7	11	1	—	
Totals		1	21	42	10	—	
Control BAR4/16		—	—	27	5	1	
BA64/51	'2'	16	33	17	—	—	BAR14/21 crosses
BA65/51	'2'	9	51	29	3	—	
Totals		25	84	46	3	—	
Control BAR14/21		—	15	21	—	—	

The utilization of $\mathbf{B}_{6m}$ in increasing the resistance of Upland varieties carrying $\mathbf{B}_2$, or $\mathbf{B}_2\mathbf{B}_3$, is likely to be of considerable value outside the Sudan. It is known that in parts of Uganda the value of $\mathbf{B}_2$ is much reduced, probably by climatic factors. For this reason the writer sent a range of material, carrying the known resistance genes, to Dr J. B. Hutchinson for trial at Namulonge. Dr Wickens's (1952) report on the marked resistance of material carrying $\mathbf{B}_2$ and $\mathbf{B}_{6m}$ suggests that this gene combination will be of great value under Uganda conditions.

SUMMARY

A blackarm resistance-intensifying gene, $\mathbf{B}_{6m}$, has been transferred from *Gossypium arboreum* to Sakel (*G. barbadense*). By itself, $\mathbf{B}_{6m}$ confers no resistance, but in *G. arboreum* it is associated with the gene $\mathbf{B}_4$.

The *G. hirsutum* resistance gene, $\mathbf{B}_2$, is stronger than $\mathbf{B}_4$ when both are transferred to Sakel background. For this reason the new gene $\mathbf{B}_{6m}$ is being transferred to commercial synthetic blackarm-resistant Sudan Sakel and Upland (*hirsutum*) types carrying $\mathbf{B}_2$ and $\mathbf{B}_3$. In these combinations $\mathbf{B}_{6m}$ confers in the Sudan a resistance closely approaching immunity, and this resistance appears to be retained under Uganda conditions.

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