THE GENETICS OF BLACKARM RESISTANCE

VIII. *GOSSYPIUM BARBADENSE*

By R. L. KNIGHT, D.Sc. (Lond.)
Senior Economic Geneticist, Empire Cotton Growing Corporation and Sudan Government

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Introduction

This investigation of the genetic nature of resistance to *Xanthomonas malvacearum* in *Gossypium barbadense* is complementary to previously published studies of resistance in other species of cotton (Knight & Clouston, 1939; Knight, 1944, 1947, 1948*a*, 1948*b*). In this series of papers an account is given of the method of testing for resistance, and the existence of four major resistance genes, $\mathbf{B}_1$, $\mathbf{B}_2$, $\mathbf{B}_3$ and $\mathbf{B}_4$, and a group of minor genes, is demonstrated. In two further contributions, Knight (1949) and Knight & Hutchinson (1950) discuss the distribution of resistance in Old and New World cottons, and the sources of the major resistance genes. In this paper an account is given of the behaviour of a fifth major gene, $\mathbf{B}_5$, found in perennial *G. barbadense* and of a minor gene group common in the annual Sea Island form of the same species.

Description of strains

BA 1–1. Harland's original V 135 Sea Island from St Vincent. This strain was carried on in Trinidad, by grafting, from 1928 to 1944, and was subsequently selfed each year in the C.R.S. collection. Sprayed with blackarm inoculum it showed grade '7'–'8' resistance in 1946–7 season and '5' ranging to an occasional '12' in 1947–8. In the latter season almost all of the plants gave grades '7'–'10'.

BA 1–5. Commercial Montserrat Sea Island selfed in the C.R.S. collection since 1937. It gave grade '6'–'7' resistance in 1946–7 and '7'–'10' in 1947–8.

BA 1–14. Barbados superfine Sea Island. Gave blackarm grades ranging from '6' to '8'

with an average grade of 7·2 in 1946, and a range from '7' to '12' with an average grade of 9·9 in 1947.

Grenadines White Pollen (BP 1–1) is a perennial *barbadense* from the Grenadines, B.W.I. It shows marked blackarm resistance and typically ranges from grade '5' to '7'.

Sakel is an established Egyptian commercial type which needs no further description here. Like all 'Egyptian' cottons it shows full (*barbadense*) susceptibility to blackarm, i.e. grade '12'.

Crosses between Sea Island types and Sakel

Plants showing maximal resistance in BA 1–1, BA 1–5 and BA 1–14 were crossed with Sakel in 1946 season and the F_1's of these crosses were grown, sprayed with blackarm inoculum and graded in 1947 season. The results are shown in Table 1.

Table 1. *Blackarm grading of Sea Island × Sakel* F_1

	Blackarm grade	
	'10'	'12'
BA 1–1 × Sakel	3	29
BA 1–5 × Sakel	4	16
BA 1–14 × Sakel	6	23
Sakel Control	8	22

In these F_1 families, grade '10' plants were selected for selfing and these gave the F_2 results shown in Table 2.

Table 2. *Blackarm grading of Sea Island × Sakel* F_2

	Blackarm grade	
	'10'	'12'
BA 1–1 × Sakel	—	12
	—	29
BA 1–5 × Sakel	—	35
	—	21
BA 1–14 × Sakel	2	86
Sakel Control	—	37

The resistance shown by these three strains (BA 1–1, BA 1–5 and BA 1–14) may be taken as representative of the resistance typical of the Sea Island group of cottons. The figures given above show that this resistance was not recovered in the rather small F_2 progenies examined, from which it may be argued that no major gene is involved. This is supported by an examination made recently by J. B. Hutchinson (unpublished) of a resistant rogue found in Stirling Rivers Sea Island; here again it was shown that no major resistance gene was involved. Furthermore, Sea Island types have for many years been grown at Shambat and sprayed with blackarm inoculum, and it has been noted that there is often considerable variation from one season to the next in their degree of resistance, depending on the environment in each particular season. Grown in an area exposed to high winds, especially hot dry winds, Sea Island will show fairly marked resistance, whereas in a sheltered spot they will be almost fully susceptible. It is considered that the Sea Island resistance is the result of the plant's capacity to harden its leaves quickly in response to certain climatic factors, notably high winds. Such a resistance does not result from the selective impact

of the disease but from the selective effect of the climate. High winds are common in the West Indies and rapid leaf hardening is probably the plant's natural protection against them.

VARIABLE NATURE OF RESISTANCE OF GRENADINES WHITE POLLEN

A small self-bred bulk of Grenadines grown in 1946 gave the following blackarm grades:

Blackarm grade			
'4'	'5'	'6'	'7'
1	18	19	5

Two plants with grade '5' symptoms and three with grade '7' symptoms were selfed to see whether the difference represented fluctuation or a genetic difference. The results are given in Table 3.

Table 3. *Progenies of Grenadines from plants of different grade*

Family no.	Parent grade	Blackarm grade		
		'4'	'5'	'6'
BA127/47	'5'	—	26	20
BA128/47	'5'	2	53	16
BA129/47	'7'	—	31	19
BA130/47	'7'	—	32	14
BA131/47	'7'	—	93	15
Totals		2	235	84

Clearly plants from either end of the resistance range of Grenadines are genetically similar with regard to their blackarm resistance.

CROSSES BETWEEN GRENADINES WHITE POLLEN AND SAKEL

F_1 of Grenadines × Sakel

Two F_1 families were grown in 1946, sprayed with inoculum 6 weeks after sowing, and subsequently graded (Table 4).

Table 4. *Blackarm grading of Grenadines × Sakel F_1.*

Family no.	Blackarm grade							
	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
Grenadines	1	18	19	5	—	—	—	—
Sakel	—	—	—	—	—	—	1	24
BA472/46	—	—	12	30	17	1	—	—
BA473/46	—	—	6	42	17	—	—	—
Totals	—	—	18	72	34	1	—	—

In these two families, plants of grades '6' and '8' were selected for backcrossing to Sakel and for selfing.

First Sakel backcross

The F_1 plants suffered severely from leaf-curl disease, making it difficult to obtain large first backcross progenies. Seven first backcross families were raised in 1947 and these gave the distributions shown in Table 5.

Table 5. *Blackarm grading of first Sakel backcross*

Family no.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Resistant	Susceptible	Totals	Ratios*
Grenadines	—	2	235	84	—	—	—	—	—				
BA143/47	'6'	—	—	3	8	18	12	17	31	58	31	89	1·9:1
BA146/47	'6'	—	—	—	1	11	6	9	17	27	17	44	1·6:1
BA147/47	'6'	—	—	—	8	18	11	13	10	50	10	60	5·0:1
BA144/47	'8'	—	—	—	14	24	14	20	28	72	28	100	2·6:1
BA145/47	'8'	—	—	6	24	23	9	25	17	87	17	104	5·1:1
BA148/47	'8'	—	—	13	26	28	13	20	33	100	33	133	3·0:1
BA149/47	'8'	—	—	1	7	28	8	23	57	67	57	124	1·2:1
Totals		—	—	23	88	150	73	127	193	461	193	654	2·39:1

* I.e. grade '10' and under to grade '12'.

Second Sakel backcross

The backcross progenies of two grade '6' plants, one in BA472/46 and one in BA473/46 (Table 4), were grown out-of-season in 1946–7 winter. Exact grading of out-of-season material is not always possible; but plants showing maximal resistance were selected for further backcrossing to Sakel, and the families resulting from these crosses gave the distributions shown in Table 6.

Table 6. *Blackarm grading of second Sakel backcross*

Family no.	Blackarm grade '7'	'8'	'9'	'10'	'12'	Resistant	Susceptible	Totals	Ratios
BA150/47	2	18	15	25	60	60	60	120	1·0:1
BA151/47	1	25	14	21	54	61	54	115	1·1:1
BA156/47	—	—	2	—	1	2	1	3	2·0:1
BA157/47	—	—	6	9	28	15	28	43	0·5:1
Totals	3	43	37	55	143	138	143	281	0·97:1

Third Sakel backcross

A number of plants covering the full resistance range of BA150/47 (Table 6) were selected for further backcrossing. In addition, the two grade '9' plants in BA156/47 were also selected. The grades shown by the backcross progenies of these plants are given in Table 7.

Table 7. *Blackarm grading of third Sakel backcross*

Family no.	Parent grade	Blackarm grade '6'	'7'	'8'	'9'	'10'	'12'	Resistant	Susceptible	Totals	Ratios
Sakel		—	—	—	—	—	76				
BA244/48	'7'	—	5	9	9	14	24	37	24	61	1·5:1
BA245/48	'7'	1	11	29	13	19	69	73	69	142	1·1:1
BA246/48	'8'	—	4	25	8	16	47	53	47	100	1·1:1
BA247/48	'8'	—	2	8	9	1	22	20	22	42	0·9:1
BA252/48	'8'	—	—	8	10	6	24	24	24	48	1·0:1
BA248/48	'9'	1	18	34	17	21	63	91	63	154	1·4:1
BA249/48	'9'	—	5	32	21	20	59	78	59	137	1·3:1
BA274/48	'9'	2	13	23	12	2	55	52	55	107	0·9:1
BA275/48	'9'	2	9	17	6	2	23	36	23	59	1·6:1
BA250/48	'10'	—	3	17	13	6	45	39	45	84	0·9:1
BA251/48	'10'	—	4	17	23	13	50	57	50	107	1·1:1
Totals		6	74	219	141	120	481	560	481	1041	1·16:1

It is noteworthy that families BA274 and 275/48 in Table 7 are derived from the two grade '9' plants in BA156/47 (Table 6).

F_2 of Grenadines × Sakel

The F_1 of Grenadines × Sakel showed a range in blackarm response from grade '6' to '9' (one plant only showed grade '9' attack). Five F_1 plants showing grade '6' resistance and five with grade '8' resistance were selfed and sown in progeny rows in 1947. The blackarm response of these families is shown in Table 8.

Table 8. *Blackarm grading of F_2 of Grenadines × Sakel*

Family no.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals
Grenadines		2	235	84	—	—	—	—	—	
BA 132/47	'6'	—	—	6	20	12	6	11	3	58
BA 133/47	'6'	1	13	53	64	39	10	23	19	222
BA 134/47	'6'	—	—	8	49	29	4	19	17	126
BA 135/47	'6'	—	1	29	51	24	5	14	21	145
BA 136/47	'6'	—	—	6	35	32	6	15	18	112
BA 137/47	'8'	—	—	13	45	21	4	15	17	115
BA 138/47	'8'	—	—	9	48	49	11	23	12	152
BA 139/47	'8'	—	—	12	60	50	25	21	35	203
BA 140/47	'8'	—	—	25	95	78	26	36	39	299
BA 141/47	'8'	—	—	4	15	15	6	7	10	57
Totals		1	14	165	482	349	103	184	191	1489
Ratio of 'Resistant' to 'Susceptible'							1298:191 6·80:1			

F_2 of first Sakel backcross

Six F_2 families of first backcross origin were grown in 1947 and a further eight in 1948. The 1947 families are descended from progenies grown out-of-season in 1946–7 winter and for this reason the parental blackarm grades have not been recorded in Table 9.

Table 9. *Blackarm grading of F_2 of first Sakel backcross*

Family no.	Parent grade	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Resistant	Susceptible	Totals	Ratios
Grenadines (1947)		2	235	84	—	—	—	—	—				
Grenadines (1948)		—	30	12	—	—	—	—	—				
BA 152/47		—	—	—	4	42	24	17	34	87	34	121	2·6:1
BA 153/47		—	—	—	11	48	26	16	27	101	27	128	3·7:1
BA 158/47		—	—	—	—	4	4	3	3	11	3	14	3·7:1
BA 159/47		—	—	—	2	18	24	17	22	61	22	83	2·8:1
BA 160/47		—	—	—	—	2	3	8	4	13	4	17	3·3:1
BA 161/47		—	—	—	—	11	33	45	40	89	40	129	2·2:1
BA 253/48	'6'	—	—	6	11	13	6	1	21	37	21	58	1·8:1
BA 254/48	'6'	—	—	2	4	2	2	—	4	10	4	14	2·5:1
BA 255/48	'7'	—	—	—	—	8	7	5	4	20	4	24	5·0:1
BA 256/48	'7'	—	—	—	—	3	6	7	5	16	5	21	3·2:1
BA 257/48	'7'	—	—	7	24	19	3	4	21	57	21	78	2·7:1
BA 258/48	'8'	—	—	—	4	17	9	2	14	32	14	46	2·3:1
BA 259/48	'8'	—	—	—	1	15	14	8	13	38	13	51	2·9:1
BA 260/48	'8'	—	—	4	17	23	5	2	17	51	17	68	3·0:1
BA 261/48	'9'	—	—	—	10	7	2	—	7	19	7	26	2·7:1
BA 262/48	'9'	—	—	—	8	13	7	5	19	33	19	52	1·7:1
Totals		—	—	19	96	245	175	140	255	675	255	930	2·65:1

F_2 of second Sakel backcross

Twelve plants covering the resistance range of the second Sakel backcross (Table 6) were selected for selfing. The progenies of these plants, grown in 1948, showed the following distributions (Table 10).

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

Family no.	Parent grade	Blackarm grade '5'	'6'	'7'	'8'	'9'	'10'	'12'	Resistant	Susceptible	Totals	Ratios
Grenadines		30	12	—	—	—	—	—				
Sakel		—	—	—	—	—	—	120				
BA 236/48	'7'	—	1	30	75	6	10	18	122	18	140	6·8:1
BA 237/48	'7'	—	—	9	90	17	4	33	120	33	153	3·6:1
BA 238/48	'8'	—	—	5	43	5	2	23	55	23	78	2·4:1
BA 239/48	'8'	—	—	—	23	10	4	13	37	13	50	2·8:1
BA 240/48	'9'	—	—	12	90	20	3	34	125	34	159	3·7:1
BA 241/48	'9'	—	6	25	32	22	23	27	108	27	135	4·0:1
BA 270/48	'9'	2	15	34	25	7	4	24	87	24	111	3·6:1
BA 271/48	'9'	4	31	51	10	2	—	28	98	28	126	3·5:1
BA 272/48	'10'	7	46	41	14	—	—	22	108	22	130	4·9:1
BA 273/48	'10'	3	20	46	24	—	—	28	93	28	121	3·3:1
BA 242/48	'10'	—	5	38	40	12	9	32	104	32	136	3·3:1
BA 243/48	'10'	—	8	34	51	13	13	29	119	29	148	4·1:1
Totals		16	132	325	517	114	72	311	1176	311	1487	3·78:1

F_3 of Grenadines × Sakel

In the F_2 progenies of Grenadines × Sakel (Table 8) thirty-three plants covering the full range from grade '5' to '12' were selected for selfing. The progenies of these plants have been arranged in Table 11 in two groups according to whether they are homogeneous or heterogeneous for resistance. The heterogeneous families have again been divided into two groups on the basis of whether or not they appear to carry a major resistance gene. In two cases, BA 179 and 187/48, the progeny size is rather small for assessing parental homozygosity, but a family of nine plants would, on a 3:1 expectation, allow about a 93% chance of the recessive susceptible appearing, and ten plants give more than a 95% chance.

In addition to the progenies listed in Table 11, three families from grade '12' parents contained only grade '12' plants.

F_3 of first Sakel backcross

Twenty four plants in BA 153/47 (Table 9) were selected for selfing as being representative of the full range of blackarm response found in the family. The progenies of these plants, grown in 1948, yielded the distributions shown in Table 12.

Check crosses between Grenadines White Pollen and Sakel types carrying $\mathbf{B_1}$, $\mathbf{B_2}$, $\mathbf{B_3}$ *and* $\mathbf{B_4}$

Crosses were made between Grenadines White Pollen and four Sakel strains carrying respectively the genes $\mathbf{B_1}$, transferred from *G. hirsutum*, $\mathbf{B_2}$, also from *hirsutum*, $\mathbf{B_3}$, transferred from *G. hirsutum* var. *punctatum* and $\mathbf{B_4}$, from *G. arboreum*. In F_2 these hybrids gave the distributions shown in Table 13.

DISCUSSION

The first Sakel backcross of Grenadines White Pollen (Table 5) shows no segregation into distinct phenotypes though there is a clear bimodality with a minimum frequency at grade '9'. Since Sakel types are fully susceptible (grade '12') it is reasonable to consider

Table 11. *Blackarm grading of F_3 of Grenadines × Sakel*

Family no.	Parent grade	Blackarm grade '5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals
Grenadines		30	12	—	—	—	—	—	
Sakel		—	—	—	—	—	—	76	
		(*a*) Homogeneous families							
BA176/48	'5'	1	13	6	—	—	—	—	20
BA178/48	'5'	—	4	10	5	—	—	—	19
BA179/48	'5'	—	3	7	—	—	—	—	10
BA182/48	'6'	—	1	9	7	—	—	—	17
BA184/48	'6'	—	4	14	2	—	—	—	20
BA187/48	'7'	—	—	5	4	—	—	—	9
BA191/48	'8'	—	3	15	2	—	—	—	20
Totals		1	28	66	20	—	—	—	115
		(*b*) Heterogeneous families carrying a major resistance gene							
BA175/48	'5'	—	7	16	3	2	4	2	34
BA177/48	'5'	—	—	4	3	—	—	1	8
BA180/48	'6'	1	1	8	8	1	1	1	21
BA181/48	'6'	—	16	15	8	5	1	3	48
BA186/48	'7'	—	—	—	6	1	—	1	8
BA188/48	'8'	—	1	2	3	—	1	1	8
BA190/48	'8'	—	—	1	4	—	1	7	13
BA192/48	'8'	—	—	4	9	1	2	5	21
BA193/48	'8'	—	1	—	28	7	2	17	55
BA194/48	'9'	—	10	38	18	2	3	8	79
BA196/48	'9'	—	1	10	14	5	1	7	38
BA201/48	'9'	—	1	9	41	3	1	24	79
Totals		1	38	107	145	27	17	77	412
		Ratio of 'Resistant' to 'Susceptible'				335:77 4·35:1			
		(*c*) Families carrying only minor resistance genes							
Four families	'9'	—	—	—	—	7	20	114	141
Six families	'10'	—	—	—	1	3	33	111	148
One family	'12'	—	—	—	—	1	—	25	26
Totals		—	—	—	1	11	53	250	315

grades '10' and under as representing a resistant group. Dividing the distributions in the first backcross in this way gives 461 resistant and 193 susceptible plants—a ratio of 2·39:1.

The second Sakel backcross (Table 6) gives a ratio of 0·97:1 if divided in this way, suggesting the presence of a major resistance gene. The third backcross (Table 7) with its ratio of 1·16:1 supports this view. It is suggested that minor resistance genes were sufficiently powerful in the first backcross to confer some slight resistance on a number of plants not carrying the major resistance gene, thereby distorting the expected 1:1 ratio to 2 39 resistant: 1 fully susceptible. Though markedly different from a 1:1 ratio, this difference is phenotypically slight since it consists solely in a shift of a proportion of the grade '12' plants into grade '10'. The total number of plants of grade '9' and under is 334 as against 320 plants in grades '10' and '12'.

The F_2 data support the suggestion of the presence of a major resistance gene. The ratio of 6·80 resistant: 1 susceptible obtained in the straight F_2 of Grenadines × Sakel (Table 8)

is considered to be a 3:1 ratio weighted by the presence of minor resistance genes. Such minor genes would be reduced in the backcross progenies, and the F_2's of the first and second backcrosses (Tables 9, 10) show ratios of 2·65:1 and 3·78:1 respectively, both being reasonably close to expectation on a 3:1 basis.

Table 12. *Blackarm grading of F_3 of first Sakel backcross*

Family no.	Parent grade	Blackarm grade '5'	'6'	'7'	'8'	'9'	'10'	'12'	Totals
Grenadines		30	12	—	—	—	—	—	
Sakel		—	—	—	—	—	—	120	
		(*a*) Homogeneous families							
BA212/48	'7'	2	20	31	4	—	—	—	57
BA213/48	'7'	3	40	31	3	—	—	—	77
BA214/48	'7'	—	12	28	1	—	—	—	41
BA216/48	'7'	—	26	42	1	—	—	—	69
BA218/48	'8'	—	29	50	2	—	—	—	81
BA221/48	'8'	—	7	33	8	—	—	—	48
BA225/48	'9'	—	1	23	48	2	—	—	74
Totals		5	135	238	67	2	—	—	447
		(*b*) Heterogeneous families carrying a major resistance gene							
BA215/48	'7'	—	—	28	19	1	—	10	58
BA217/48	'8'	—	6	30	30	4	1	17	88
BA219/48	'8'	—	12	29	18	5	11	7	82
BA220/48	'8'	—	—	16	9	—	—	7	32
BA222/48	'9'	1	9	25	20	3	8	6	72
BA223/48	'9'	—	1	24	25	3	1	19	73
BA224/48	'9'	—	—	4	33	11	7	19	74
BA226/48	'10'	—	—	12	42	9	2	17	82
BA227/48	'10'	—	—	—	18	17	29	16	80
BA228/48	'10'	—	—	4	45	9	3	19	80
BA229/48	'10'	—	—	1	46	12	8	10	77
BA230/48	'10'	—	—	—	39	14	4	19	76
Totals		1	28	173	344	88	74	166	874
		Ratio of 'Resistant' to 'Susceptible'				708:166 4·26:1			
		(*c*) Families carrying only minor resistance genes							
BA233/48	'12'	—	—	—	4	1	3	28	36
BA235/48	'12'	—	—	—	—	1	1	36	38
BA231/48	'12'	—	—	—	—	—	3	37	40
BA232/48	'12'	—	—	—	—	—	3	31	34
BA234/48	'12'	—	—	—	—	—	1	18	19
Totals		—	—	—	4	2	11	150	167

The F_3 ratios (Tables 11, 12) conclusively prove the presence of a major gene. Both in the straight F_3 of Grenadines × Sakel and in the F_3 of the first Sakel backcross, the progenies are readily divisible into three sharp groups: (*a*) families homozygous for a main resistance gene, (*b*) families heterogeneous for this major gene and (*c*) families carrying only minor genes.

In crosses with synthetic Sakel strains carrying $\mathbf{B}_1$, $\mathbf{B}_2$, $\mathbf{B}_3$ and $\mathbf{B}_4$ respectively (Table 13) grade '12' plants appeared in F_2 in every case showing that this major resistance gene is not allelic to any of the four genes previously known. The gene has accordingly been given the symbol $\mathbf{B}_5$.

A comparison of the grade of resistance shown by Grenadines White Pollen itself and homozygous F_3 lines from the first Sakel backcross (Table 12) shows a considerable reduction in resistance to have occurred. Grenadines showed a range from '5' to '6' whereas the first backcross F_3 homozygotes ranged from '5' to '9' and grade '5' appeared

in only two progenies. This difference in resistance between the Grenadines parent and the backcross F_3 progenies is attributed to the effect of minor resistance genes. The grading of family BA 225/48 (Table 12) suggests that in the absence of minor genes $\mathbf{B}_5$, when homozygous, confers resistance ranging from '6' to '9'. The families in the second group of Table 12 show that, when heterozygous, $\mathbf{B}_5$ confers resistance ranging from '6' to '10'.

Table 13. *Blackarm grading of F_2's of check crosses*

Family no.	Blackarm grade '3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Resistant	Susceptible	Totals	Ratios
						(*a*) Grenadines × $\mathbf{B_1B_1}$ Sakel							
$\mathbf{B}_1$ Control*	—	—	—	—	—	25	12	1	—				
BA 280/48	—	—	55	113	67	29	4	4	17	272	17	289	16·0:1
BA 281/48	—	—	3	8	11	8	1	—	2	31	2	33	15·5:1
BA 282/48	—	—	4	28	19	6	1	—	4	58	4	62	14·5:1
BA 283/48	—	—	6	30	15	10	—	—	4	61	4	65	15·3:1
BA 284/48	—	—	18	37	19	2	1	1	4	78	4	82	19·5:1
Totals	—	—	86	216	131	55	7	5	31	500	31	531	16·1:1
						(*b*) Grenadines × $\mathbf{B_2B_2}$ Sakel							
$\mathbf{B}_2$ Control	—	2	28	13	—	—	—	—	—				
BA 276/48	25	32	24	10	5	—	1	3	4	100	4	104	25·0:1
BA 277/48	5	14	12	5	2	2	—	—	2	40	2	42	20·0:1
BA 278/48	6	32	21	3	4	6	1	2	5	75	5	80	15·0:1
BA 279/48	—	15	17	3	2	5	2	1	5	45	5	50	9·0:1
Totals	36	93	74	21	13	13	4	6	16	260	16	276	16·3:1
						(*c*) Grenadines × $\mathbf{B_3B_3}$ Sakel							
$\mathbf{B}_3$ Control	—	—	33	9	—	—	—	—	—				
BA 285/48	27	111	65	30	28	6	—	—	14	267	14	281	19·1:1
BA 286/48	8	36	19	4	5	3	—	—	8	75	8	83	9·4:1
BA 287/48	5	17	13	2	7	4	2	—	4	50	4	54	12·5:1
BA 288/48	7	11	14	3	4	5	—	—	2	44	2	46	22·0:1
Totals	47	175	111	39	44	18	2	—	28	436	28	464	15·6:1
						(*d*) Grenadines × $\mathbf{B_4B_4}$ Sakel							
$\mathbf{B}_4$ Control	—	—	1	21	14	3	—	—	—				
BA 289/48	4	78	60	31	19	8	4	2	18	206	18	224	11·4:1
BA 290/48	4	94	70	27	30	8	1	2	12	236	12	248	19·7:1
BA 291/48	—	26	26	8	13	6	—	—	2	79	2	81	39·5:1
BA 292/48	—	100	106	13	16	18	—	—	22	253	22	275	11·5:1
BA 293/48	—	13	39	9	3	10	5	2	9	81	9	90	9·0:1
BA 296/48	—	11	58	19	16	17	4	1	6	126	6	132	21·0:1
Totals	8	322	359	107	97	67	14	7	69	981	69	1050	14·2:1

* $\mathbf{B_1B_1}$ Sakel did not develop blackarm well and graded '8'–'9' instead of the usual '10'.

$\mathbf{B}_5$ is phenotypically similar to the Asiatic gene $\mathbf{B}_4$ when both are transferred to a Sakel background. $\mathbf{B_4B_4}$ Sakel shows a range in blackarm grade of '6'–'9', the bulk of the plants being at the more resistant end of the range (Knight, 1948*a*). $\mathbf{B_5B_5}$ Sakel shows a range from '5' to '9' (Table 12), but it is probable that the grade '5' plants carried minor resistance genes in addition to $\mathbf{B}_5$. In the heterozygous state $\mathbf{B}_4$ confers grade '6'–'9' resistance on Sakel, but the bulk of the plants are at the more susceptible end of the range. As judged from third Sakel backcross material, $\mathbf{B}_5$, when heterozygous, gives grades '6'–'10' resistance with the bulk of the plants in grades '8'–'10'.

From the results shown in Table 13, $\mathbf{B}_5$ appears to segregate independently of the other four resistance genes. In view of the obscure ratios obtained in the straight F_2's of Grenadines × Sakel (Table 8) too much reliance should not be placed on the good agreement

with 15:1 expectation obtained in the check crosses shown in Table 13. It should be pointed out, however, that 1947 was a bad year for working on blackarm resistance—it was a year in which ancillary resistance, due to rapid leaf hardening, was common, and this tends to obscure ratios where the gene concerned is variable in expression. Nevertheless, these check cross results show clearly that $\mathbf{B}_5$ is non-allelic to the other four genes and that in each case it is additive in effect.

Thus two types of resistance occur in *G. barbadense*: the weak and seasonally variable resistance of the Sea Island group and the major resistance found in Grenadines White Pollen. Sea Island resistance has been shown to depend on minor genes and is probably dependent on the plant's capacity to harden its leaves quickly, in response to winds and/or low humidity. Grenadines resistance is due to the gene $\mathbf{B}_5$ fortified by minor genes. Only two other cases of worthwhile resistance have been reported in *G. barbadense*; both were due to $\mathbf{B}_2$, and in both cases the $\mathbf{B}_2$ had become transferred from *G. hirsutum* by introgressive hybridization (Knight, 1942; Knight & Hutchinson, 1950).

SUMMARY

Two forms of resistance occur in *Gossypium barbadense*: weak resistance, due to leaf hardening, is found in the Sea Islands, and strong resistance, due to the gene $\mathbf{B}_5$ fortified by minor genes, occurs in the perennial variety Grenadines White Pollen. $\mathbf{B}_5$ is variable in expression but, in general, the homozygotes show stronger resistance than the heterozygotes. $\mathbf{B}_5$ is additive in conjunction with $\mathbf{B}_1$, $\mathbf{B}_2$, $\mathbf{B}_3$ and $\mathbf{B}_4$ respectively.

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