

THE GENETICS OF BLACKARM RESISTANCE

X. THE GENE B_7 FROM STONEVILLE 20

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INTRODUCTION

This paper describes the transference of resistance to blackarm (*Xanthomonas malvacearum*) from the Upland variety, Stoneville 20 (*Gossypium hirsutum*), to Sudan Sakel (*G. barbadense*), and the testing of the Stoneville gene against established blackarm resistance genes to determine its homology.

PREVIOUS WORK

Simpson & Weindling (1946) reported resistance to blackarm in Stoneville 20, a derivative of Stoneville 2A. Although these writers made no attempt to determine the genetic factors involved in this resistance, they nevertheless recovered it from backcrosses to a susceptible Upland by selfing and selection, indicating that the resistance was unlikely to be genetically complex.

Blank (1949) crossed Stoneville 20 with a number of blackarm susceptible Uplands and showed its resistance to be inherited as a single recessive factor.

TRANSFERENCE OF RESISTANCE FROM STONEVILLE 20 TO SUDAN SAKEL

F₁ of Stoneville 20 \times Sakel and the Sakel backcross progenies

Stoneville 20 (19358) was crossed with Sudan Sakel and the F_1 was backcrossed to the Sakel parent. These and subsequent backcross progenies were sprayed with blackarm inoculum and graded on the system defined and illustrated by Knight (1944) in which grade '0' represents immunity of the leaves and '12' full susceptibility. The F_1 of Stoneville 20 \times Sakel gave a range from grade '7' to '9' with the bulk of plants showing grade '8' symptoms. The Sakel control showed grade '12' lesions on nearly all plants, although a few were graded as '10' (grade '11' was omitted from this scale in the early years as being superfluous (Knight & Clouston, 1939).

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The blackarm grading of the five Sakel backcrosses is summarized in Table 1. Of these progenies, the second and fourth were grown out of season, but in both cases their Sakel controls gave full grade '12' symptoms, as in in-season progenies. Grade '12' can therefore be confidently accepted as representing the 'fully susceptible' class in Table 1, although plants grown out of season at Shambat are usually more resistant than comparable plants grown in season. The difference is due to lower temperatures and humidity.

F₂'s of the various Sakel backcrosses

F₂ progenies were grown from the second, third and fourth Sakel backcrosses. These were sprayed with inoculum and graded, and their distributions are summarized in Table 2.

A control of Stoneville 20 grown near the fourth Sakel backcross *F₂* progenies ranged from grade '6' to '7' with the bulk of the plants in grade '6'. Clearly four backcrosses to Sakel have resulted in a marked loss in resistance.

Table 1. *Summary of blackarm grading of backcross progenies*

	Blackarm grade			
	'8'	'9'	'10'	'12'
1st backcross	6	3	—	11
2nd backcross	74	42	6	132
3rd backcross	—	3	—	5
4th backcross	2	4	—	4
5th backcross	1	4	10	7
Totals	83	56	16	159
Grouped totals	155			159
Expected 1:1	157			157

Table 2. *Summary of blackarm grading of F₂'s of Sakel backcrosses*

	Blackarm grade				
	'7'	'8'	'9'	'10'	'12'
2nd backcross <i>F₂</i>	14	28	5	—	14
3rd backcross <i>F₂</i>	—	39	9	—	8
4th backcross <i>F₂</i>	—	7	68	27	26
Totals	14	74	82	27	48
Grouped totals	197				48
Expected 3:1	183 $\frac{1}{2}$				61 $\frac{1}{2}$

F₃ results from the second and third Sakel backcrosses

To obtain lines homozygous for the Stoneville gene, a number of resistant plants in the second and third backcross progenies were selfed. Progenies from these plants were grown in 1951-2 season and graded for blackarm symptoms with the results shown in Tables 3 and 4.

GENE HOMOLOGY TESTS

Five synthetic Sudan Sakel strains were used as parents for gene homology tests. These were BAR 2/11 (homozygous for **B₁**), BLR 14/16 (**B₂ B₂**), BAR 14/9 (**B₃ B₃**), BAR 14/19 (**B₄ B₄**) and BAR 14/20 (**B₅ B₅**). Each of these five strains was crossed with Stoneville 20, and the *F₂*'s of these crosses were sprayed with blackarm inoculum and graded (Table 5).

In the F_2 of Stoneville 20 \times BAR 2/11 a number of 'dwarf-bunched' plants appeared. The presence of these plants proves that Stoneville 20 carries the gene \mathbf{d}_b and thus provides strong presumptive evidence that it does not carry \mathbf{B}_1 (Knight, 1947).

Table 3. *Blackarm grading of second Sakel backcross F_3*

Family no.	Parent grade	Blackarm grade						Totals	
		'6'	'7'	'8'	'9'	'10'	'12'	Res.	Sus.
BA 70/51	'7'	—	1	4	6	1	3	12	3
BA 71/51	'7'	—	—	13	23	4	—	40	—
BA 72/51	'7'	—	1	10	17	1	—	29	—
BA 73/51	'8'	—	1	5	4	1	—	11	—
BA 74/51	'8'	2	5	16	5	—	—	28	—
BA 75/51	'8'	—	—	7	20	4	9	31	9
BA 77/51	'8'	—	2	19	15	—	—	36	—
Totals of BA 70 and 75/51		—	1	11	26	5	12	43	12
Totals of remainder		2	9	63	64	6	—	144	—

Table 4. *Blackarm grading of third Sakel backcross F_3*

Family no.	Parent grade	Blackarm grade					Totals	
		'7'	'8'	'9'	'10'	'12'	Res.	Sus.
BA 78/51	'8'	—	1	11	4	6	16	6
BA 79/51	'8'	—	—	12	5	—	17	—
BA 80/51	'8'	—	3	10	3	7	16	7
BA 81/51	'8'	—	3	13	7	9	23	9
BA 82/51	'8'	1	4	12	15	9	32	9
BA 83/51	'8'	—	6	30	7	—	43	—
BA 85/51	'8'	2	8	23	5	6	38	6
BA 86/51	'8'	—	5	27	5	7	37	7
BA 87/51	'9'	—	5	16	4	8	25	8
BA 88/51	'9'	—	8	27	5	—	40	—
BA 89/51	'9'	—	1	14	2	—	17	—
BA 90/51	'9'	—	1	3	7	6	11	6
BA 91/51	'9'	1	7	19	2	—	29	—
Totals of BA 78, 80–82, 85–87 and 90/51		3	30	115	50	58	198	58
Totals of remainder		1	32	102	21	—	146	—

Table 5. *Blackarm grading of F_2 's of check crosses*

Type	Blackarm grade								
	'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
Control Sakel	—	—	—	—	—	—	—	—	38
Control Stoneville 20	—	—	—	29	5	—	—	—	—
Control BAR 2/11	—	—	—	—	—	12	22	2	—
Stoneville 20 \times $\mathbf{B}_1 F_2$	—	—	3	10	28	25	14	1	3
Control BLR 14/16	—	—	21	17	—	—	—	—	—
Stoneville 20 \times $\mathbf{B}_2 F_2$	—	59	88	50	12	27	22	10	2
Control BAR 14/9	—	—	1	28	—	—	—	—	—
Stoneville 20 \times $\mathbf{B}_3 F_2$	—	11	63	56	17	34	6	13	—
Control BAR 14/19	—	1	22	18	—	—	—	—	—
Stoneville 20 \times $\mathbf{B}_4 F_2$	3	13	39	18	14	17	4	3	1
Control BAR 14/20	—	—	—	—	5	32	1	—	—
Stoneville 20 \times $\mathbf{B}_5 F_2$	—	—	3	7	9	5	5	4	2

The distribution of blackarm grades in all five F_2 progenies indicates that in each cross the two resistance genes were non-allelic. There is, however, a distinct deficit of fully susceptible (grade '12') plants in each progeny, as compared with expectation on a 15:1 basis of resistant to susceptible. This is presumably due to the minor resistance genes of

Stoneville 20 origin. These would confer slight degrees of resistance on segregates not carrying a major **B** gene.

B₂ is the major gene which usually controls blackarm resistance in American Upland. For this reason it seemed likely that Stoneville resistance would be allelic to it, both being strong genes of *G. hirsutum* origin. Additional check crosses were therefore made involving **B**₂. With this object some of the *F*₁ plants of Stoneville 20 × BLR14/16 were crossed with ordinary blackarm-susceptible Sakel, and the classification of the progenies is given in Table 6.

As a further check, Stoneville 20 was crossed with BAR7/1, an Upland homozygous for **B**₂. Five *F*₂ families were grown from this cross, and these gave the distributions of

Table 6. *Blackarm grading of (Stoneville 20 × B₂ B₂ Sakel) × Sakel F₁*

Family no.	Blackarm grade							
	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
Control BLR14/16	—	18	15	5	—	—	—	—
BA311/50	1	20	21	—	9	2	1	23
BA312/50	1	12	5	—	7	3	—	12
BA313/50	5	8	5	—	5	2	—	6
BA314/50	2	18	5	—	9	4	—	16
BA315/50	—	5	8	1	5	2	1	10
Totals	9	63	44	1	35	13	2	67
Grouped totals	117			50			67	
Expected (2:1:1)	117			58½			58½	

Table 7. *Blackarm grading of Stoneville 20 × BAR7/1 F₂*

Family no.	Blackarm grade							
	'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'
Control Stoneville 20	—	—	—	29	5	—	—	—
Control BAR7/1	—	1	23	1	—	—	—	—
Control SUS7/2	—	—	—	—	—	8	21	9
BA302/50	2	22	80	23	1	14	2	—
BA303/50	—	43	85	12	10	8	—	—
BA304/50	1	35	82	16	10	21	—	—
BA305/50	1	31	103	19	23	10	—	—
BA306/50	1	32	95	24	10	17	1	—
Totals	5	163	445	94	54	70	3	1
Grouped totals	761			73			52-1	
Expected (15:1)	781-9			52-1			52-1	

blackarm grade shown in Table 7. The control type, SUS7/2, included in this table is an Upland similar in all respects to BAR7/1 except that it does not carry **B**₂ nor any other major blackarm resistance gene. It will be seen that these inter-Upland *F*₂'s gave no sharp segregations, but since the more susceptible of the parents (Stoneville 20) showed no plants with more severe leaf attack than grade '7', plants with grade '8'–'10' attack may be regarded as susceptible segregates. This agrees with the grading of the susceptible Upland control, SUS7/2, with its range of from grade '8' to '10'. Grouping the *F*₂ distributions in this way gives 761 resistant: 73 susceptible—a fair approximation to expectation on a 15:1 basis.

DISCUSSION

The backcross progenies (Table 1), obtained by crossing Stoneville 20 with Sakel and backcrossing resistant plants to the susceptible (Sakel) parent, clearly show that a major resistance gene is present in Stoneville 20. This supports Blank's (1949) work except that in crosses involving Sakel the gene is clearly not recessive. An examination of Table 1, however, reveals that there has been a qualitative loss of resistance in the later backcrosses as compared with the earlier ones. Thus the first and second backcrosses showed a preponderance of plants in grade '8', whereas by the fifth backcross the mode had shifted to grade '10'. This loss of resistance is characteristic of the backcross F_2 's (Table 2) also, and it presumably indicates that Stoneville 20 resistance is due to the presence of a major gene accompanied by a number of minor resistance genes. It is these latter which have been lost in the later Sakel backcrosses.

The distributions shown by the backcross F_2 progenies (Table 2) indicate that there can be little difference between the degree of resistance conferred by the Stoneville gene when heterozygous and when homozygous. This is borne out by the F_3 results from backcrosses (Tables 3, 4), where selection of F_2 plants showing maximum resistance has failed to give an increased proportion of homozygous progenies in F_3 (BA 70-72 versus BA 73-77 in Table 3 and BA 78-86 versus BA 87-91 in Table 4).

Finally, the gene homology tests summarized in Table 5 show the Stoneville gene to be non-allelic to \mathbf{B}_1 , \mathbf{B}_2 , \mathbf{B}_3 , \mathbf{B}_4 and \mathbf{B}_5 . There is no proof that it is non-allelic to \mathbf{B}_{6m} , but since it is totally different from \mathbf{B}_{6m} in expression, non-homology has been assumed pending any proof to the contrary. The Stoneville 20 gene has accordingly been given the symbol \mathbf{B}_7 .

This gene may be of considerable economic significance, since Wickens (1952) has shown that Stoneville 20 carries marked boll and stem resistance to blackarm. This stem and boll resistance is probably an integral part of the \mathbf{B}_7 expression, but this has yet to be proved, and it is not impossible for it to be due to the minor genes which have been shown to fortify \mathbf{B}_7 in Stoneville 20.

SUMMARY

The blackarm resistance of the Upland variety Stoneville 20 is due to a major dominant gene, \mathbf{B}_7 , fortified by minor genes. This gene has been transferred to Sudan Sakel, on which background it is weaker in expression than the standard Upland resistance gene \mathbf{B}_2 .

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