THE GENETICS OF BLACKARM RESISTANCE

VI. TRANSFERENCE OF RESISTANCE FROM *GOSSYPIUM ARBOREUM* TO *G. BARBADENSE*

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Introduction

Despite a fairly comprehensive survey of the various cotton species of the world, complete immunity to blackarm disease (*Bact. malvacearum*, Sm.) has been found only in the two species of 'Old World' ($n=13$) cottons, *Gossypium arboreum* and *G. herbaceum*. Of these, *G. arboreum* includes many immune types, and, since the advantages of immunity over resistance are obvious, an investigation of the genetic nature of this immunity was undertaken, (1) to identify the gene or genes responsible, (2) to transfer any such genes to Sakel (*G. barbadense*), and (3) to determine the relationship between the *arboreum* gene or genes and the 'New World' resistance genes B_1, B_2 and B_3.

This paper deals with the transference of the Asiatic resistance gene B_4 to Sakel. The genetics of resistance within *G. arboreum* will be published in due course.

Previous work

Knight & Clouston (1939, 1941) and Knight (1944*a*) have shown that, in the New World allotetraploid cottons, resistance to blackarm, where present, is due, in *G. hirsutum*, to the gene B_2 very occasionally accompanied by a weak gene B_1, and in *G. hirsutum* var. *punctatum* (= *G. punctatum*, Sch. & Thon.) either to B_2 or to B_3, or to both genes acting additively. It was further shown that B_2 and B_3 are linked and have a 32% crossover value. Finally, B_1 is closely linked with (or possibly identical with) the allele of one of a pair of duplicate genes which together control normality of growth as opposed to a dwarfing described under the name 'dwarf-bunched' (Knight, 1947*a*). On a system of grading in which '0' = immunity and '12' full (Sakel) susceptibility, but from which grade '11' is missing, B_1b_1 and B_1B_1 confer '10·1' resistance when transferred to Sakel,

B_2b_2 and B_2B_2 confer grade '7', B_3b_3 gives '7·1'–'8·1' and B_3B_3 '4·1'–'7·1' resistance. This system of grading resistance is fully defined in Part I of this series and is redefined and illustrated in Part IV.

In Part I of this series, over 160 varieties of cotton are classified on their blackarm resistance and this number is further extended by Knight (1943, 1944*a*, *b*, 1946*a*, 1947*b*). These results and further data hitherto unpublished are summarized in tabular form below:

Species*	Reaction to blackarm disease
(*a*) Diploid ($n=13$) types:†	
Gossypium thurberi	Susceptible
G. harknessii	Resistant to susceptible
G. klotzschianum	Resistant
G. klotzschianum var. *davidsonii*	Resistant
G. armourianum	Resistant
G. raimondii	Resistant
G. aridum	Resistant
G. stocksii	Susceptible
G. somalense	Resistant
G. herbaceum	Immune to susceptible
G. arboreum	Immune to susceptible
G. anomalum	Highly resistant
G. sturtii	Susceptible
(*b*) Allotetraploid ($n=26$) types:	
G. hirsutum	Resistant to susceptible
G. hirsutum var. *punctatum*	Highly resistant to susceptible
G. hirsutum var. *marie-galante*	Susceptible
G. barbadense	Mainly susceptible
G. barbadense var. *darwinii*	Susceptible
G. tomentosum	Susceptible

* The nomenclature adopted throughout this paper is that used by J. B. Hutchinson in Part I of *The Evolution of 'Gossypium'*, Oxford University Press; by Hutchinson, J. B., Silow, R. A. and Stephens, S. G.

† It should be borne in mind that many of the samples of the wild species of cotton have originated at some stage from single plants, consequently these results do not necessarily apply to the species as a whole since this has not in all cases been adequately sampled.

G. barbadense var. *darwinii* has previously been reported as resistant (Knight, 1944*b*, 1946*b*) but this record was made on an accession received from abroad under the name *G. darwinii* and subsequently identified as *G. hirsutum* var. *punctatum* (Knight, 1947*b*).

Preparation of inoculum and technique of infecting the plants

Knight & Clouston (1939) described the method used for preparing inoculum and for infecting plants evenly with blackarm. Knight (1946*b*) has since simplified the original method and the following account is quoted from this source. 'Experience has shown, however, that perfectly even infection can be obtained by using an inoculum made by soaking 5 lb. of air-dried diseased leaves in 40 gal. of water, instead of the 10 lb. originally advocated. The infected leaves are soaked in water for 1 hr. and then continuously crushed and stirred for a further hour, after which the suspension is strained through sacking and used immediately. "Solo-sprayers" are used for spraying and the jet is directed at the plant from ground-level upwards. Spraying is done twice a day for two successive days so that, on the present technique, each plant receives four sprayings with suspension compared with the six previously advocated.'

Transference of resistance from *G. arboreum* to *G. barbadense*

Description of strains

Multani (Sanguineum), strain NT 12/30, belongs to *G. arboreum* race *bengalense*. 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 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.

Domains Sakel (*G. barbadense*) 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'.

F_1 *of Multani × Sakel*

In 1940–1 winter a number of Multani ($n=13$) plants were treated with colchicine in the cotyledon stage and later planted out in an isolated place. Although typical colchicine 'symptoms' were produced on the early leaves of some of these plants these abnormalities disappeared in the later leaves and the plants all appeared to be typical $n=13$ Multani.

During the coolest part of the season these plants were regularly pollinated, before sunrise, with Sakel ($n=26$) pollen. The Multani flowers were not emasculated, since setting of a reasonable quantity of seed per boll ensures against undue boll shedding. Seed from these 'hybrid' bolls was delinted with concentrated sulphuric acid. The largest seeds were then picked out, it being assumed that these would contain triploid ($2n=39$) embryos. These seeds proved, with one exception, to be of F_1 type and the exception gave rise to a tetraploid ($2n=52$) Multani plant.

This type of crossing has several times been repeated using various arboreum cottons, not previously treated with colchicine, as female parents. In no case were F_1 embryos found amongst the large seeds.* Furthermore, crosses between autotetraploid Multani female and Sakel male, yielded F_1 plants indistinguishable from those obtained in the original hybridization. It thus seems probable that some of the Multani plants used as female parents in 1940–1 winter contained mixoploid tissue of diploid/tetraploid type and that the resulting Multani × Sakel F_1 plants were autoallotetraploids of $2n=52$ composition carrying two Multani genoms and one Sakel genom, i.e. $2A_2+(AD)_2$. The actual composition of these F_1 plants must remain conjectural since the writer had, at the time, no facilities for making chromosome counts.

Twenty-five of these Multani × Sakel plants were raised. Only fifteen of them were graded for blackarm resistance since the remainder had been grown out-of-season when grading is difficult and often inaccurate. In the following season, a second F_1 family, consisting of four plants, was raised and examined for blackarm. This second F_1 was obtained by crossing tetraploid Multani female with Sakel male. Adding these two F_1's together gives the following distribution:

Blackarm grade							
'1'	'2'	'3'	'4'	'5'	'6'	'7'	'8'
5	5	2	3	3	.	.	1

* The writer has, however, twice seen F_1 plants from the reciprocal cross resulting from open pollination of 'Egyptian' types grown in isolated areas and belted by Multani.

First Sakel backcross

Using the F_1 of Multani × Sakel as male parent, 500 pollinations of emasculated Sakel flowers were made. No bolls set.

Using the F_1 plants as female parent, 15,000 pollinations with Sakel pollen were made. The F_1 proved self-sterile, hence its flowers were not emasculated, but pollination was carried out early in the morning during the coolest part of year. These pollinations yielded eighty-nine seeds, and these were sown in 1942–3 summer. Thirty-one plants were raised, two of which died as a result of ant attack. The remainder were graded for blackarm resistance with the following result:

Table 1. *Blackarm grading of first Sakel backcross*

Family no.	Parent grade	Blackarm grade								
		'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'
BA391/42	'2'	.	.	.	1	.	.	1	.	1
BA392/42	'4'	.	.	.	.	2	2	.	.	1
BA393/42	'5'	.	1	.	.	2	1	2	1	3
BA394/42	'1'	.	.	.	.	.	1	1	.	.
BA396/42	?	.	.	.	.	.	1	.	.	.
BA397/42	'2'	.	.	1	.	1	.	.	.	.
BA399/42	'5'	1	.	.	1	.	2	1	1	.
Totals		1	1	1	2	5	7	5	2	5

Second Sakel backcross

Using the first backcross plants as female parents, a large number of pollinations with Sakel pollen were made. Most of the plants in the first backcross progenies showed a high degree of sterility, but a small amount of second backcross seed was obtained and sown. Much of this seed failed to germinate, including, unfortunately, the seed from the only highly resistant (grade '3') plant which proved at all fertile.

The blackarm grading of these second backcross progenies is shown below (Table 2):

Table 2. *Blackarm grading of second Sakel backcross*

Family no.	Parent grade	Blackarm grade					
		'6'	'7'	'8'	'9'	'10'	'12'
BA61/43	'9'	.	.	1	.	.	.
BA289/43	'7'	.	1	.	.	.	1
BA290/43	'7'	1	.	1	.	.	4
Totals		1	1	2	.	.	5

BA61/43 is from BA391/42; BA289 and 290/43 are from BA393/42 (Table 1).

Third Sakel backcross

Of the four resistant plants in the second Sakel backcross, two showed moderate fertility, viz. those in families BA61/43 and BA289/43. All four were pollinated with Sakel pollen, but seed was obtained only from these two plants. The two resulting backcross progenies were examined for resistance with the following result (Table 3):

Table 3. *Blackarm grading of third Sakel backcross*

Family no.	Parent grade	Blackarm grade			
		'8'	'9'	'10'	'12'
BA61/44	'8'	5	.	.	5
BA416/44	'7'	1	.	.	1
Totals		6	.	.	6

BA61/44 is from BA61/43; BA416/44 is from BA289/43 (Table 2).

Fourth Sakel backcross

The third backcross plants showed reasonably good fertility and they were crossed in both directions with Sakel. The resistant plant in BA416/44 was equally effective in transmitting resistance whether it was the male or the female parent (in BA 90/45, below, it was the male parent and in BA 91/45, the female). One plant in BA 61/44 was used as female parent and this gave rise to family BA485/45, below. Three other plants were selected in BA 61/44 and these were used as male parents; they gave rise to families BA486/45, BA487/45 and BA414/44 (Table 4):

Table 4. *Blackarm grading of fourth Sakel backcross*

Family no.	Parent grade	Blackarm grade '6'	'7'	'8'	'9'	'10'	'12'
BA90/45	'8'	.	.	6	.	.	1
BA91/45	'8'	.	.	4	.	.	1
BA485/45	'8'	.	8	4	.	.	20
BA486/45	'8'	.	2	.	.	.	58
BA487/45	'8'	2	5	1	.	.	114
BA414/44	'8'	.	.	.	2	.	11

BA90 and 91/45 are from BA416/44; BA485–487/45 and BA414/44 are from BA61/44 (Table 3).

Since the reciprocal hybrids, BA 90/45 and BA 91/45, show a preponderance of resistant plants, it is evident that resistance did not, in this case, have any deleterious effect on the pollen carrying it. In the remaining four families, however, BA485/45 shows a distribution of twelve resistant plants to twenty susceptibles—a fair approximation to a 1 : 1 ratio in view of the small size of the family. BA486/45 and BA487/45 both show very distorted ratios, two resistant and fifty-eight susceptible in the one and eight resistant to 114 susceptible in the other. The female parent of BA485/45 was resistant whereas the resistant plants were the male parents of BA486/45 and BA487/45. The ratio, in the last family (BA414/44), of two resistant to eleven susceptible plants possibly represents a similar distortion, but the numbers are small and chance might equally well be the cause.

Fifth Sakel backcross

Five resistant plants in BA 90/45 and three in BA 91/45 (Table 4) were backcrossed to Sakel, using the latter as female parent. BA 90 and 91/45 were sown in 1944–5 winter and the fifth backcross progenies from them were sown in 1945 summer. The distributions obtained in these backcross progenies are shown below (Table 5):

Table 5. *Blackarm grading of fifth Sakel backcross*

Family no.	Parent grade	Blackarm grade '6'	'7'	'8'	'9'	'10'	'12'	Totals Res.	Sus.
BA490/45	'8'	.	6	3	.	.	14	9	14
BA491/45	'8'	1	5	6	.	.	10	12	10
BA492/45	'8'	4	27	6	.	.	31	37	31
BA493/45	'8'	1	13	4	.	.	19	18	19
BA494/45	'8'	5	12	2	.	.	14	19	14
BA495/45	'8'	.	8	2	.	.	6	10	6
BA496/45	'8'	3	18	4	.	.	20	25	20
BA497/45	'8'	.	1	1	.	.	3	2	3
Totals		14	90	28	.	.	117	132	117
						Expected	(1 : 1)	124·5	124·5

BA490–495/45 are from BA90/45, and BA495–497/45 are from BA91/45 (Table 4).

From these figures it is evident that a single factor for blackarm resistance has been transferred from Multani to Sakel.

F_2 of fourth Sakel backcross

In the two winter-sown families, BA90/45 and BA91/45 (Table 4), all the plants were selfed after they had been used for backcrossing to Sakel, and these self-bred fourth backcross F_2 progenies were grown in 1945 summer. As in the late backcross progenies, clear segregation into 'resistant' and 'susceptible' (grade '12') was obtained (Table 6):

Table 6. *Blackarm classification of F_2 of fourth Sakel backcross*

Family no.	Observed		Expected (3 : 1)	
	Res.	Sus.	Res.	Sus.
BA716/45	37	16	$39\frac{3}{4}$	$13\frac{1}{4}$
BA717/45	3	2	$3\frac{3}{4}$	$1\frac{1}{4}$
BA718/45	8	1	$6\frac{3}{4}$	$2\frac{1}{4}$
BA719/45	27	8	$26\frac{1}{4}$	$8\frac{3}{4}$
BA721/45	57	18	$56\frac{1}{4}$	$18\frac{3}{4}$
BA723/45	14	9	$17\frac{1}{4}$	$5\frac{3}{4}$
Totals	146	54	150	50

BA716–721/45 are from BA90/45; BA723/45 is from BA91/45 (Table 4).

In conjunction with the distributions found in the second, third, fourth and fifth Sakel backcrosses, the above figures clearly prove that a single factor for resistance has been transferred from Multani to Sakel.

F_3 of fourth and fifth Sakel backcrosses

Among the resistant plants in the F_2 progenies of the fourth and fifth Sakel backcrosses, selections were made from the extremes of the range. Grade '6'–'7' represented the maximum resistance obtained and '9' the minimum. Progenies of these plants were classified for resistance with the results shown in Tables 7 and 8.

It will be seen from the progenies shown in these two tables that out of a total of forty-three grade '6'–'7' parent plants, twenty-four were homozygous and nineteen heterozygous for resistance against an expectation on a 1 : 2 basis of $14\frac{1}{3}$ and $28\frac{2}{3}$ respectively. For these totals $\sigma = 3{\cdot}091$ and P is approximately 0·003. Thus there is a significant tendency for the more resistant plants in F_2 to be homozygous. Similarly, an examination of the progenies from grade '9' parents shows that nine of these were homozygotes whilst twenty-four of them were heterozygotes. These figures do not differ greatly from expectation on a 1 : 2 basis of eleven and twenty-two respectively.

Treating these figures as a contingency table gives the following result:

	Homozygotes	Heterozygotes	Totals
Grade '6'–'7'	24	19	43
Grade '9'	9	24	33
Totals	33	43	76

$\chi^2 = 6{\cdot}191$. P lies between 0·01 and 0·02.

Clearly dominance is incomplete.

Table 7. *Blackarm classification of F_3 of fourth Sakel backcross*

(*a*) Progenies from heterozygotes

Family no.	Parent grade	No. of plants Res.	Sus.
BA71/46	'7'	20	8
BA76/46	'7'	27	9
BA78/46	'7'	25	10
BA82/46	'7'	23	5
BA85/46	'7'	32	4
BA86/46	'7'	23	5
BA88/46	'7'	21	10
BA90/46	'7'	22	7
BA504/46	'6'	24	6
BA658/46	'7'	22	5
BA660/46	'7'	30	5
BA72/46	'9'	22	8
BA73/46	'9'	26	11
BA74/46	'9'	17	5
BA75/46	'9'	27	11
BA499/46	'9'	31	9
BA500/46	'9'	33	6
BA502/46	'9'	31	11
BA527/46	'9'	32	8
BA528/46	'9'	33	9
BA530/46	'9'	31	10
BA661/46	'9'	16	6
BA662/46	'9'	14	4
BA663/46	'9'	22	4
Totals		603	176
Expected	(3 : 1)	$584\frac{1}{4}$	$194\frac{3}{4}$

(*b*) Progenies from homozygotes

Seven progenies from grade '6' parents, eleven from grade '7' parents and six from grade '9' parents proved to be homozygous for resistance. In size these homozygous families ranged from seventeen to forty-three plants.

Table 8. *Blackarm classification of F_3 of fifth Sakel backcross*

(*a*) Progenies from heterozygotes

Family no.	Parent grade	No. of plants Res.	Sus.
BA495/46	'7'	30	10
BA496/46	'7'	25	5
BA497/46	'7'	28	5
BA512/46	'7'	32	6
BA518/46	'7'	29	10
BA524/46	'7'	37	6
BA525/46	'7'	30	10
BA526/46	'7'	30	5
BA491/46	'9'	28	11
BA493/46	'9'	19	8
BA494/46	'9'	12	6
BA507/46	'9'	14	8
BA508/46	'9'	15	7
BA509/46	'9'	29	6
BA510/46	'9'	30	10
BA515/46	'9'	27	8
BA516/46	'9'	26	7
BA517/46	'9'	32	10
BA522/46	'9'	15	3
Totals		488	141
Expected	(3 : 1)	$471\frac{3}{4}$	$157\frac{1}{4}$

(*b*) Progenies from homozygotes

Six progenies from grade '7' parents and three progenies from grade '9' parents proved to be homozygous for resistance. In size these homozygous families ranged from twenty-eight to forty-two plants.

Check crosses with B_1, B_2 *and* B_3

Heterozygous resistant plants from the fifth Sakel backcross progenies were crossed with a Sakel strain homozygous for B_2, transferred from American Upland (*Gossypium hirsutum*). In F_2 the following distributions were obtained:

Table 9. *Blackarm grading of* F_2 *of check cross with* B_2B_2 *Sakel*

Family no.	Blackarm grade									Totals		Expected (15 : 1)	
	'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Res.	Sus.	Res.	Sus.
BA474/46	13	65	71	20	.	.	.	.	11	169	11	168·75	11·25
BA475/46	.	.	54	49	1	.	.	.	37	104	37	(B_2 only)	
BA476/46	7	49	60	26	1	.	.	.	15	143	15	148·12	9·88
BA477/46	.	.	106		.	.	.	.	27	106	27	(B_2 only)	
BA480/46	.	.	117		.	.	.	.	44	117	44	(B_2 only)	
Control 1	.	.	28	15	.	.	.	.	.	.	.	.	.
Control 2	.	7	61	13	1	.	.	.	.	.	.	.	.
Totals (BA474 and 476)	20	114	131	46	1	.	.	.	26	312	26	316·87	21·13

Note. Control 1 = B_2B_2 Sakel; Control 2 = Sakel of fifth backcross F_3 type homozygous for the Multani resistance gene.

Clearly B_2 and the transferred *arboreum* gene occupy different loci.

In these families blackarm development was poor for climatic reasons, and this explains the unduly high resistance of the control types. Nevertheless, neither control contained grade '3', and grade '4' only represented a low proportion of control no. 2. It is evident, therefore, from the distributions obtained in BA474 and 476/46, that the *arboreum* gene and B_2 show additive effect on a *barbadense* background.

Crosses between heterozygous resistant fifth backcross plants and a Sakel strain homozygous for B_3 were grown out-of-season. The F_1 plants ranged in resistance from grade '4' to '7'. Five plants showing maximal resistance were selfed and their progenies yielded the following distributions:

Table 10. *Blackarm grading of* F_2 *of check cross with* B_3B_3 *Sakel*

Family no.	Blackarm grade									Totals		Expected (15 : 1)	
	'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'12'	Res.	Sus.	Res.	Sus.
BA481/46	.	56	74	29	14	7	.	.	8	180	8	176·25	11·75
BA482/46	.	33	91	33	22	14	.	.	16	193	16	195·90	13·06
BA483/46	1	43	94	28	11	4	.	.	14	181	14	182·85	12·19
BA484/46			88				.	.	6	88	6	88·13	5·88
BA485/46			66				.	.	3	66	3	64·69	4·31
Control 3	.	.	18	22	3	.	.	.	.	.	.	.	.
Control 2	.	7	61	13	1	.	.	.	.	.	.	.	.
Totals										708	47	707·82	47·19

Note. Control 3 = B_3B_3 Sakel. Control 2 = Sakel of fifth backcross F_3 type homozygous for the Multani resistance gene. Families BA484 and 485/46 were not graded in detail.

Clearly, from the above figures, the transferred Multani resistance factor and B_3 occupy separate loci and show no linkage. Furthermore, these distributions indicate that the Multani gene has some additive value in conjunction with B_3.

In the F_1 progenies of crosses between the heterozygous Multani factor and B_1B_1 Sakel, approximately 50 % of the plants showed '10·1' (B_1) resistance and the remainder showed resistance similar to that conferred by the homozygous Multani gene. In F_2 the following distributions were obtained, in progenies derived from the more resistant plants:

Table 11. *Blackarm grading of F_2 of check cross with $\mathbf{B}_1\mathbf{B}_1$ Sakel*

Family no.	Blackarm grade '4'	'5'	'6'	'7'	'8'	'9'	'10·1'	'12'	Totals Res.	Sus.	Expected (15 : 1) Res.	Sus.
BA486/46	2	66	43	7	3	.	24	9	145	9	144·38	9·63
BA487/46	4	76	56	10	7	.	18	11	171	11	170·63	11·38
BA488/46				195				15	195	15	196·88	13·13
BA489/46				197				15	197	15	198·75	13·25
BA490/46				195				17	195	17	198·75	13·25
Control 2	7	61	13	1	.	.	.	.	.	.	.	.
Totals									903	67	909·39	60·64

Note. Families BA488–490/46 were not graded in detail.

Thus the transferred Multani gene and $\mathbf{B}_1$ are independent. Moreover, $\mathbf{B}_1$ adds little if anything to the resistance conferred by the homozygous *arboreum* gene.

Discussion

Two main points of interest arise out of this *arboreum-barbadense* transference of a blackarm resistance gene, viz. (*a*) the possible economic value of the gene itself, and (*b*) the economic possibilities of the method of transference used.

It has been shown that the new gene, $\mathbf{B}_4$, has additive properties in conjunction with either of the New World genes, $\mathbf{B}_2$ and $\mathbf{B}_3$. This is likely to be important since *immunity* (as distinct from *resistance*) has not as yet been either found or synthesized in the allotetraploid cottons. It is of considerable interest that this new gene, when transferred to the *barbadense* genom, segregates independently of the other three known genes. This fact cannot be regarded as evidence concerning the number of loci affecting blackarm resistance unless it is known that a high degree of gene homology exists between the Asiatic genom and the corresponding half of the New World genom. That gene homology exists in at least some cases is shown by Harland's (1935) successful transference of the *arboreum* gene $\mathbf{R}_2^{\mathbf{RS}}$ to *Gossypium hirsutum* from a type similar to Multani. Harland showed the transferred gene to be homologous with the New World anthocyanin gene series.

There are three possible methods by which a gene (or genes) can be transferred from *G. arboreum* to *G. barbadense*: (*a*) the allotetraploid method, (*b*) the autotetraploid, and (*c*) straight transference via the triploid. In using the allotetraploid technique for transferring resistance to blackarm it would be necessary to start by crossing Multani with a fully susceptible diploid New World *Gossypium* such as *G. thurberi*. The F_1 of this cross would then have to be doubled with colchicine or another polyploiding agent.

The autotetraploid technique is illustrated by the transference of $\mathbf{B}_4$ recorded in this paper and the 'straight transference' method was used successfully by Harland (1935) when he transferred the *arboreum* gene $\mathbf{R}_2^{\mathbf{RS}}$ to *G. hirsutum*.

Using Beasley's (1942) symbols for the various genoms involved, the initial F_1's in these three techniques can be represented as follows:

$$(a)\ A_2D_1(AD)_2, \quad (b)\ A_2A_2(AD)_2, \quad (c)\ A_2(AD)_2.$$

Of these three F_1's only the first is approximately 'balanced', but it is known that gene transference to cultivated allotetraploid cottons is possible from the A_2 genom to the (AD) genom in all three.

A full discussion of the merits of method (*a*) must await a critical examination of this method of transference as compared with method (*b*). The outstanding point (to the pure geneticist) in favour of method (*a*) is that it is known that accurate studies of gene homology can be made by this means. The disadvantages are (1) that it is not always easy to synthesize the required *arboreum*-New World tetraploid, and (2) that the complication of a second foreign genom is introduced.

The disadvantage of method (*c*) is the extreme difficulty that is experienced in making the triploid F_1 of $A_2(AD)_2$ composition. The writer has many times unsuccessfully tried to make this F_1.

Method (*b*) has certain advantages of its own: (1) It is simple to make the original autotetraploid by soaking *arboreum* seeds in 0·05 % colchicine for 48 hr. (2) This tetraploid shows good fertility if used as a female parent in crosses with *barbadense*. (3) Although the F_1 with *barbadense* lacks fertility this is not a difficult obstacle to overcome since a large F_1 can readily be made.

The best system is to grow a large F_1 in an isolated place (to avoid contamination with foreign pollen) and to pollinate open F_1 flowers with *barbadense* pollen without emasculation. Thus, for example, an F_1 of tetraploid *arboreum* × Sakel, consisting of 89 plants, was grown at Shambat this season. A single boy, working $1\frac{1}{2}$ hr. a day throughout the cool season (4 months), was responsible for all pollination. From some 23,000 pollinations 209 seeds of first backcross type were obtained, but it should be noted that Pink and Egyptian bollworms had probably destroyed at least an equal number of seeds.

The use of a large F_1 population is essential in order to obtain a first backcross progeny of adequate size. In the present case, a backcross progeny of twenty-nine plants contained three plants showing a certain degree of fertility. There can be little doubt that by increasing the size of the backcross progeny one is automatically increasing the chance of finding fertile plants. Where a single known dominant (or partially dominant) gene is being transferred, the method is to grow a large first backcross progeny, eliminate all plants not carrying the required gene, and, in the remainder, to select the plants showing maximum fertility for further backcrossing.

It is of interest that hybridization between Asiatic and New World cottons seems to be less successful when American Upland is used than when *barbadense* is the New World parent. Thus the writer has crossed tetraploid Multani with two varieties of American Upland—XA 129 and BAR. SP 84. In both cases the F_1's died gradually, before the first flowers opened. Similarly, J. B. Hutchinson informs me that crosses between an *arboreum* × *thurberi* tetraploid and the American Upland type, U 4, do not grow more than a few inches high.

Summary

A strong, partially dominant gene governing resistance to blackarm disease (*Bact. malvacearum*) has been transferred from *Gossypium arboreum* to *G. barbadense* (Domains Sakel). The new gene, $\mathbf{B}_4$, segregates independently of $\mathbf{B}_1$, $\mathbf{B}_2$ and $\mathbf{B}_3$ and it shows additive effect in conjunction with $\mathbf{B}_2$ and with $\mathbf{B}_3$.

Three cytogenetically distinct techniques for transferring genes from Old World diploid to New World allopolyploid cottons are described and their relative merits discussed.

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