THE GENETICS OF JASSID RESISTANCE IN COTTON

IV. TRANSFERENCE OF HAIRINESS FROM *GOSSYPIUM HERBACEUM* TO *G. BARBADENSE*

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CONTENTS

Introduction

The commercial annual cottons of the Old World (*Gossypium arboreum* and *G. herbaceum*) often combine high resistance to blackarm disease with an equally strong resistance to jassid. This latter resistance is attributable to long dense hairs on the under-surface of the leaves. The research described in this paper was initiated with the object of transferring any major genes in either of these resistances, from *G. herbaceum* to Sakel. The blackarm resistance aspect of the work will be covered separately; this paper deals with the transfer of a main hairiness gene from *herbaceum*. It was not intended to transfer jassid resistance as such, since the inheritance of this would almost certainly be too complex to be handled in crosses between the **A** and (**AD**) genoms. The intention was to transfer one or more major hairiness genes with a view to seeing whether adequate jassid resistance could be synthesized by adding together two or three hairiness genes of different origin. Wagad 8 was chosen as donor parent primarily for its excellent blackarm resistance; its hairiness status, though fairly good, is below the optimum obtainable in *herbaceum* cottons.

Previous work

Knight (1952) showed that the hairiness gene H_1 (identical with Harland's H^{TAN} and H^B) provides the core of jassid resistance in the *G. barbadense* types Tanguis and Carpulla, in the *G. hirsutum* variety MU 8*b* and in the *G. hirsutum* var. *marie-galante* cotton, St Ignatius.

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In the *barbadenses* $\mathbf{H}_1$ was accompanied by a number of minor genes with direct effect, whereas in the *hirsutums* resistance was achieved mainly by intensification of $\mathbf{H}_1$ by length modifiers. A major **H** gene, closely linked with a chlorophyll-deficiency gene, was found to be the basis of jassid resistance in the *hirsutum* type, Kapas Purao, and the results indicated that here again resistance was largely dependent on intensifying genes acting on the basic **H**. Knight & Sadd (1954) showed this Kapas Purao gene to be allelic to $\mathbf{H}_1$ and gave it the symbol $\mathbf{H}_1^k$. They also showed the jassid resistance of Philippines Ferguson (*G. hirsutum*) to be controlled by $\mathbf{H}_1^k$ accompanied by minor genes (largely intensifiers) and that $\mathbf{H}_1^k$ from Ferguson, Kapas Purao and Kawanda *punctatum* is closely linked (possibly inverted) with the chlorophyll deficiency gene $\mathbf{chl}_1$. $\mathbf{H}_1$ from *barbadense* is associated with $\mathbf{Chl}_1$, the normal allele of $\mathbf{chl}_1$, and in MU 8*b* and St Ignatius $\mathbf{H}_1$ and $\mathbf{chl}_1$ are associated but are not closely linked.

A hair density gene $\mathbf{H}_2$ (identical with Harland's $\mathbf{H}^{TO}$) was shown to be responsible for the dense tomentum of *G. tomentosum* (Knight, 1952) and the gene controlling hairiness in the *hirsutum* variety Pubescent T 611 was shown to be identical with this (Knight & Sadd, 1953). Lint length and plant height were reduced in plants carrying $\mathbf{H}_2$.

Description of strains

Wagad 8 (G. herbaceum). This variety was originally obtained in 1941, through the courtesy of the Secretary of the Indian Central Cotton Committee, for inclusion in a blackarm resistance survey.

Domains Sakel (G. barbadense). Evelyn's Selected Domains Sakel was used as the backcross parent, since this variety has all the quality of commercial Domains Sakel coupled with the advantage of greater purity. After the first four crosses to Sakel, a blackarm-resistant Sakel was substituted as the recurrent parent and finally a blackarm and leafcurl-resistant strain was used. These strains, like Domains Sakel, have almost glabrous leaves.

Transference of hairiness from *Gossypium herbaceum* to *G. barbadense*

F_1 of Wagad 8 × Sakel

In 1945, seed of Wagad 8 was soaked in 0·05 % colchicine for 48 hr. Six plants survived this treatment and all showed signs of polyploidy, but no cytological examination was made because no facilities were available. These six plants were used as female parents in crossing with Sakel and three of them set hybrid seed readily. This seed was sown in 1946 and sixty-seven F_1 plants were raised. These all looked alike and all showed great vigour; they were all, however, self-sterile.

First and second Sakel backcrosses

By using the sixty-seven F_1 plants as female parents, and pollinating them regularly with Sakel pollen, ten seeds were produced, five of which grew to adult plants. The reciprocal cross yielded thirteen seeds, none of which germinated. Of the five first backcross plants raised, only one (BA 368/47·2) proved fertile; fortunately, this plant was hairy, the others were all glabrous. By using this hairy first backcross plant as female and pollinating it with Domains Sakel, sixty-six hybrid seeds were produced, from which twenty-one healthy plants were grown. These were classified for hairiness as shown in Table 1.

In family BA114/48 the degree of hairiness ranged from a maximum expression rather stronger than that associated with H_1 when heterozygous down to weak hairiness, still, however, clearly distinguishable from the glabrescent condition of Sakel. Chromosome counts made by Dr H. Douwes on six of these second backcross plants showed somatic numbers ranging from 53 to 58.

Table 1. *Second Sakel backcross*

Family no.	Hairy	Glabrescent
BA114/48	17	4

Third Sakel backcross

Ten hairy plants in the second Sakel backcross were selected as female parents for further backcrossing to Sakel. Seven of these yielded progenies, the hairiness classification of which is shown in Table 2.

Table 2. *Third Sakel backcross*

Family no.	Parent	Parent chromosome no.	Hairy	Glabrescent
BA19/49	BA114/49·7	58	8	26
BA20/49	BA114/49·10	56	1	3
BA21/49	BA114/49·11	53	15	23
BA22/49	BA114/49·14	?	4	19
BA23/49	BA114/49·15	?	—	1
BA25/49	BA114/49·17	54–55	3	8
BA26/49	BA114/49·20	?	8	7
Totals			39	87

Many of these third backcross plants showed excellent fertility. In appearance they were close to Sakel though still distinguishable from it.

Fourth Sakel backcross

Thirty-eight of the hairy plants in the third Sakel backcross were chosen as female parents for crossing with blackarm-resistant Sakel. The classification of the resulting progenies is given in Table 3.

Subsequent Sakel backcrosses

A number of selections was made in the fourth backcross progenies so as to cover any variability in the expression of hairiness. These plants were all backcrossed to blackarm-resistant Sakel using the hybrid plants as male parents. The resulting progenies from this and the sixth and seventh backcrosses are summarized in Table 4.

There was only slight variation in the degree of hairiness within the 'hairy' group in the fifth backcross, but this variation was no longer evident in the sixth and seventh backcrosses.

From the 1 : 1 ratios obtained in these backcrosses, it is clear that a major hairiness gene has been transferred from Wagad 8. In the heterozygote this gene appears indistinguishable from H_1.

F_2 and F_3 of fourth Sakel backcross

No attempt was made to self out a line homozygous for hairiness until reasonably complete fertility had been obtained. It was found that four backcrosses to Sakel re-established fertility approximating to that of the recurrent parent. The hairy plants in some of the fourth backcross families (Table 3) were bulk selfed, in other families individual plants were selfed. The classification of these F_2's is given in Table 5.

Table 3. *Fourth Sakel backcross*

Family no.	Parent	Hairy	Glabrescent
BA 123/50	BA 19/49·2	3	2
BA 124/50	BA 19/49·3	4	3
BA 125/50	BA 19/49·6	17	13
BA 126/50	BA 19/49·7	3	4
BA 136/50	BA 20/49·1	8	8
BA 137/50	BA 21/49·1	10	7
BA 138/50	BA 21/49·2	7	6
BA 139/50	BA 21/49·6	3	5
BA 140/50	BA 21/49·7	4	9
BA 141/50	BA 21/49·8	11	17
BA 142/50	BA 21/49·9	7	4
BA 143/50	BA 21/49·12	30	30
BA 144/50	BA 21/49·13	13	10
BA 145/50	BA 21/49·14	16	22
BA 146/50	BA 21/49·15	14	17
BA 159/50	BA 22/49·1	15	5
BA 160/50	BA 22/49·3	11	12
BA 171/50	BA 26/49·1	2	2
BA 172/50	BA 26/49·2	5	5
BA 173/50	BA 26/49·4	13	10
BA 174/50	BA 26/49·5	4	6
BA 175/50	BA 26/49·6	12	21
BA 176/50	BA 26/49·7	4	4
Totals		216	222
Expected (1 : 1)		219	219

Table 4. *Subsequent Sakel backcrosses*

Backcross no.	Actual		Expected (1 : 1)	
	Hairy	Glabrescent	Hairy	Glabrescent
5th	167	133	150	150
6th	39	47	43	43
7th	11	23	17	17
Totals	217	203	210	210

Within the fourth backcross F_2 families, thirty-two plants were chosen showing maximum hairiness. These were selfed and the classification of their progenies is shown in Table 6. In families J 1563/51 and J 1566/51, where the classification into 'hairy' and 'glabrescent' was not sharp, thirty-one plants were chosen covering the complete range of hairiness from nearly glabrescent to the maximum expression of the character. Of the resulting progenies, nine contained only more or less glabrescent plants (i.e. some plants carried a very weak degree of hairiness), four families gave good approximations to 3 : 1 ratios with sharp segregation, and four families were pure for hairiness. Two families showed only weak hairiness and clearly carried no major **H** gene. The remaining twelve families gave no clear segregation but all appeared to carry the main **H** gene; phenotypic grouping in these progenies had presumably been obscured by minor **H** genes. One of the families, J 1618/51, which had a clear 3 : 1 segregation (81 : 26), contained plants with

better hair length than was shown by any of the homozygous F_3 lines, showing that intensifying genes, acting on the main **H** gene, were present.

F_2 and F_3 of subsequent Sakel backcrosses

Three hairy plants in the fifth backcross F_1 were selfed; their progenies segregated into clear groups (Table 7), and it was evident from the nature of the hairiness in the 'hairy' group that the **H** gene concerned is only partially dominant.

Table 5. *F_2 of fourth Sakel backcross*

Family no.	Parent	Actual		Expected (3 : 1)		Phenotypic grouping
		Hairy	Glabrescent	Hairy	Glabrescent	
J1532/51	BA 123/50·1	81	31	84	28	FS
J1533/51	BA 124/50·1	19	10	21¾	7¼	FS
J1534/51	BA 125/50·1	59	20	59¼	19¾	FS
J1535/51	BA 125/50·2	81	38	89¼	29¾	S
J1536/51	BA 125/50·3	18	8	19½	6½	S
J1537/51	BA 125/50·4	27	12	29¼	9¾	S
J1538/51	BA 126/50·1	24	15	29¼	9¾	M
J1539/51	BA 126/50·2	23	13	27	9	M
J1540/51	BA 136/50·1	21	8	21¾	7¼	S
J1541/51	BA 136/50·2	62	11	54¾	18¼	S
J1542/51	BA 136/50·3	60	25	63¾	21¼	S
J1543/51	BA 136/50·5	95	25	90	30	S
J1544/51	BA 136/50·6	18	5	17¼	5¾	S
J1545/51	BA 137/50·1	108	29	102¾	34¼	S
J1546/51	BA 137/50·2	33	23	42	14	S
J1547/51	BA 137/50·4	15	9	18	6	S
J1548/51	BA 138/50·1	77	22	74¼	24¾	S
J1549/51	BA 138/50·2	11	2	9¾	3¼	S
J1550/51	BA 139/50·1	29	8	27¾	9¼	S
J1552/51	BA 140/50·1	19	5	18	6	S
J1553/51	BA 140/50·2	41	19	45	15	S
J1554/51	BA 141/50·1	67	20	65¼	21¾	S
J1555/51	BA 141/50·2	69	16	63¾	21¼	S
J1556/51	BA 141/50·3	67	19	64½	21½	S
J1557/51	BA 141/50·4	74	40	85½	28½	S
J1558/51	BA 141/50·5	49	18	50¼	16¾	S
J1559/51	BA 142/50·3	16	8	18	6	S
J1560/51	BA 145/50 bulk	105	29	100½	33½	S
J1561/51	BA 146/50 bulk	100	34	100½	33½	S
J1562/51	BA 159/50 bulk	111	57	126	42	S
J1563/51	BA 160/50 bulk	200	68	201	67	M
J1564/51	BA 172/50·1	34	6	30	10	M
J1565/51	BA 172/50·2	31	11	31½	10½	M
J1566/51	BA 173/50 bulk	188	92	210	70	M
J1567/51	BA 174/50 bulk	129	84	159¾	53¼	M
J1568/51	BA 175/50 bulk	143	46	141¾	47¼	FS
J1569/51	BA 143/50 bulk	130	52	136½	45½	S
J1570/51	BA 144/50 bulk	131	46	132¾	44¼	S
Totals		2565	984	2661¾	887¼	

Note: M = merging; FS = fairly sharp; S = sharp.

Within family J 1618/51, six plants showing maximal hairiness were chosen for selfing; three plants were likewise chosen in J 1619/51 and four in J 1620/51. The progenies of these plants are classified in Table 8.

Check crosses with H_1H_1 Sakel

Three homozygous hairy families in the F_3 of the fourth Sakel backcross were each bulk crossed with BLJR 14/23, a synthesized Sakel resistant to blackarm and leafcurl diseases and carrying H_1H_1 from Tanguis. The three F_1's resulting from these crosses were

Table 6. *F_3 of fourth Sakel backcross*

Family no.	Parent	Hairy	Glabrescent
J 1448/52	J 1532/51·2	28	—
J 1449/52	J 1532/51·3	14	3
J 1450/52	J 1535/51·1	34	—
J 1451/52	J 1535/51·6	38	—
J 1452/52	J 1540/51·1	24	—
J 1453/52	J 1541/51·1	39	—
J 1454/52	J 1541/51·2	40	—
J 1455/52	J 1541/51·4	39	—
J 1456/52	J 1543/51·1	39	—
J 1457/52	J 1544/51·1	24	—
J 1458/52	J 1544/51·2	31	—
J 1460/52	J 1554/51·1	40	—
J 1461/52	J 1554/51·2	38	—
J 1462/52	J 1556/51·1	36	—
J 1463/52	J 1557/51·1	34	—
J 1465/52	J 1561/51·1	40	—
J 1466/52	J 1561/51·2	32	—
J 1467/52	J 1561/51·3	40	—
J 1468/52	J 1562/51·1	27	4*
J 1469/52	J 1566/51·1	25	12
J 1470/52	J 1566/51·2	33	2*
J 1471/52	J 1568/51·3	32	—
J 1472/52	J 1568/51·4	31	1*
J 1473/52	J 1569/51·1	28	9
J 1474/52	J 1569/51·2	39	—
J 1475/52	J 1570/51·1	34	—
J 1476/52	J 1570/51·2	37	—
J 1477/52	J 1570/51·3	39	—
J 1478/52	J 1570/51·4	40	—
J 1479/52	J 1570/51·5	32	—
J 1480/52	J 1570/51·6	39	—
J 1481/52	J 1570/51·7	32	—

* Dwarfed, abnormal plants.

Table 7. *F_2 of fifth Sakel backcross*

Family no.	Actual		Expected (3 : 1)	
	Hairy	Glabrescent	Hairy	Glabrescent
J 1618/51	81	26	80¼	26¾
J 1619/51	8	4	9	3
J 1620/51	42	10	39	13
Totals	131	40	128¼	42¾

Table 8. *F_3 of fifth Sakel backcross*

Family no.	Hairy	Glabrescent
J 1501/52	44	—
J 1502/52	37	—
J 1503/52	42	—
J 1504/52	38	—
J 1505/52	35	—
J 1506/52	43	—
J 1507/52	21	—
J 1508/52	39	—
J 1509/52	41	—
J 1510/52	37	—
J 1511/52	36	8
J 1512/52	39	—
J 1513/52	27	—

composed of plants all equally hairy and all similar to $\mathbf{H_1H_1}$ Sakel controls. Twenty F_2 families were grown from these crosses (Table 9).

Clearly the Wagad **H** gene occupies the same locus as $\mathbf{H_1}$. Furthermore, in view of the relationship between $\mathbf{H_1}$ and the chlorophyll-deficiency gene $\mathbf{chl_1}$ (Knight & Sadd, 1954), it is of interest to record that no chlorophyll-deficient plants appeared in these families. Of the families listed in Table 9, four (J 1052, 1053, 1054 and 1063/53) contained a proportion of 'Fragile' plants. These plants, presumably because of their poorer growth, appear semi-glabrous at first and do not develop their full hairiness until somewhat later than normal plants. Even when fully grown, these 'Fragiles' show a rather weaker development of hairiness than do normal plants.

Table 9. *F_2 of (Wagad 8 × Sakel[5] F_3) × BLJR 14/23*

Family no.	Hairy	Glabrescent
J 1052/53	36	—
J 1053/53	36	—
J 1054/53	36	—
J 1055/53	43	—
J 1056/53	49	—
J 1057/53	50	—
J 1058/53	33	—
J 1059/53	42	—
J 1061/53	34	—
J 1062/53	43	—
J 1063/53	40	—
J 1064/53	46	—
J 1065/53	23	—
J 1066/53	47	—

DISCUSSION

It is not to be expected that a full picture of the genetic control of hairiness in Wagad 8 should emerge from crosses between this and New World ($n=26$) cottons. Clearly, however, in this variety of *G. herbaceum*, as in New World cottons, jassid resistance has been built around a major gene. This gene, when transferred to Sakel, has been shown to occupy the same locus as the *hirsutum-barbadense* gene $\mathbf{H_1}$. Since to all appearance the two genes are phenotypically indistinguishable, the Wagad 8 **H** will be referred to as $\mathbf{H_1}$ in future.

The range of hairiness in the second Sakel backcross shows that minor hairiness genes are present in Wagad 8 in addition to $\mathbf{H_1}$. This conclusion is supported by the F_2 and F_3 observations on the fourth Sakel backcross, where minor hairiness genes were shown to exist and where the presence of intensifying genes acting on $\mathbf{H_1}$ was also inferred.

Thus hairiness in Wagad 8 depends on $\mathbf{H_1}$ plus minor and modifying genes, but there is not enough evidence to be certain that $\mathbf{H_1}$ is the only major hairiness gene present. Since $\mathbf{H_1}$ has already been proved to provide the core of jassid resistance in *G. hirsutum*, *G. hirsutum* var. *punctatum*, *G. hirsutum* var. *marie-galante* and in *G. barbadense* (Knight, 1952; Knight & Sadd, 1954), this fact is of considerable evolutionary significance.

The cultivated cottons of the Old World, *G. arboreum* and *G. herbaceum*, belong to the **A** genom and carry 13 haploid chromosomes. The New World linted cottons are allopolyploids carrying 13 **A** and 13 **D** chromosomes, the latter deriving from the **D** genom of the New World wild group of *Gossypiums*. Since $\mathbf{H_1}$ is of Old World origin (and hence belongs to the **A** genom), the New World chlorophyll-deficiency gene $\mathbf{chl_1}$, shown by Knight & Sadd (1954) to be closely linked with $\mathbf{H_1}$, must by inference be of Old World origin also.

Two Old World chlorophyll-deficiency genes are known, ***chl***$_1$ and ***chl***$_2$ (the italics have been used to distinguish between the Old World ***chl***$_1$ and the New World **chl**$_1$, now shown to be of Old World origin), but although it is a reasonable inference that one of these will prove allelic to the New World gene, **chl**$_1$, there is no direct evidence as yet to suggest which it will be. Balasubrahmanyan (1947) has referred to these Old World genes as 'albino' (***chl***$_1$) and 'xantha' (***chl***$_2$), the former being of *G. herbaceum* origin and the latter from *G. arboreum*. The linkage of the Asiatic 'xantha' gene, ***chl***$_2$, with the Asiatic anthocyanin gene $\mathbf{R}_2$ with a 9% c.o.v. (Yu, 1939), suggests one possible way of testing whether **chl**$_1$ is homologous with ***chl***$_1$ or with ***chl***$_2$ by making linkage tests between $\mathbf{H}_1$ and $\mathbf{R}_2$.

In the Sudan, Sakel (*G. barbadense*) lines have been separately synthesized carrying the Asiatic gene $\mathbf{R}_2$, the Tanguis gene $\mathbf{H}_1$ and the heterozygous closely linked combination $\mathbf{H}_1^k$/**chl**$_1$ from Kawanda *punctatum*. In these latter it is thought that the $\mathbf{H}_1^k$–**chl**$_1$ segment of chromosome is probably inverted. Crosses of these two forms of $\mathbf{H}_1$ Sakel with $\mathbf{R}_2$ Sakel should detect any linkage between $\mathbf{H}_1$ and $\mathbf{R}_2$. If such a linkage exists then the New World **chl**$_1$ will have been proved to be homologous with Feng's (1926) and Yu's (1939) gene for 'yellow seedling' (***chl***$_2$); it would also be linked with 'short branch', since this was shown to be linked with $\mathbf{R}_2$ in *G. herbaceum* (Patel, Munshi & Patel, 1947), and in New World cottons (Silow, 1946). In addition, in view of the results obtained by Ramiah & Paranjape (1947) in *arboreum* cotton it is probable that the $\mathbf{R}_2$ chromosome also carries a wilt resistance/susceptibility locus.

In the New World cottons, linkage has been established between 'cluster' (**cl**$_1$) and the anthocyanin locus, $\mathbf{R}_1$ (Harland, 1934; Neely, 1942), and Harland (1941) showed that $\mathbf{R}_1$ is located in the **D** genom. The New World $\mathbf{R}_2$ gene for anthocyanin pigmentation was shown by Harland (1935) to belong to the **A** genom. Since $\mathbf{R}_1$ is linked with 'cluster' and $\mathbf{R}_2$ with 'short branch', there can be little doubt that (as suggested by Silow, 1946) the $\mathbf{R}_1$ chromosome of the **D** genom is homologous in remote origin with the $\mathbf{R}_2$ chromosome in the **A** genom. If $\mathbf{H}_1$/**chl**$_1$ proves to be linked with $\mathbf{R}_2$ it will be interesting to see if the only other major hairiness gene so far found ($\mathbf{H}_2$) belongs on the $\mathbf{R}_1$ chromosome.

Summary

A major hairiness gene was transferred from *Gossypium herbaceum* (Wagad 8) to Sakel (*G. barbadense*) and shown to be identical with $\mathbf{H}_1$, the usual key gene in hairiness control in New World cottons. Since the $\mathbf{H}_1$ and **chl**$_1$ loci are linked in New World cottons it follows that both belong to the **A** genom. In addition to $\mathbf{H}_1$, Wagad 8 carries minor **H** genes and modifying genes affecting hair length.

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