

THE GENETICS OF JASSID RESISTANCE IN COTTON
 III. THE KAPAS PURAO, KAWANDA *PUNCTATUM* AND PHILIPPINES
 FERGUSON GROUP

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INTRODUCTION

Two of the three cotton varieties discussed in this paper, Kapas Purao and Philippines Ferguson, show marked jassid resistance, due to a covering of hairs of excellent length and reasonable density on the undersides of the leaves. The investigation of the genetics of the resistance of these varieties was undertaken in parallel with a breeding programme designed to transfer their resistance to blackarm- and leafcurl-resistant Sakel. In this work the full hairiness of the Ferguson parent has now been recovered from sixth Sakel backcross material and further backcrosses have been made (Knight, 1952). An account of the transference methods employed will be published when the work is complete.

Kawanda *punctatum* was included in this programme, not on account of any outstanding jassid resistance, but solely because crosses made between it and Sakel indicated the presence of a major hairiness gene. Throughout this investigation an important objective has been to locate any additional major hairiness genes, in the hope of being able to build up jassid resistance by adding one or two such major genes to Sakel strains, which have already been synthesized, carrying H_1 .

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The present system of breeding for jassid resistance is intricate, since it involves transferring a whole complex of genes to Sakel; if resistance could be achieved with a strictly limited number of additive major genes, the process would be simplified.

PREVIOUS WORK

Knight (1952) showed that the hairiness gene H_1 provides the core of jassid resistance in the *Gossypium barbadense* types, Tanguis and Carpulla, and in the *G. hirsutum* varieties MU8b and St Ignatius. In the *barbadenses* H_1 was accompanied by a number of minor genes with direct effect, whereas in the *hirsutums* resistance was achieved mainly by intensification of H_1 by modifiers acting on hair length. An unidentified H gene, phenotypically similar to H_1 , was found to be the basis of jassid resistance in the *hirsutum* type Kapas Purae. H_2 was shown to control the pubescence of *G. tomentosum*, and Knight & Sadd (1953) showed this gene to be responsible for the pilosity of Simpson's (1947) mutant *hirsutum* strain T 611.

DESCRIPTION OF STRAINS

Sakel (*G. barbadense*). Evelyn's Selected Domains Sakel was used for some of the earlier crosses, but for the later ones blackarm resistant, and eventually blackarm- and leafcurl-resistant, strains were used. For the purposes of this paper all these strains have been called Sakel.

Kapas Purae UA7-48 and Philippines Ferguson UA7-49 (*G. hirsutum*). Two jassid-resistant American Upland types from the Philippines, via the Empire Cotton Growing Corporation's Type Collection. These varieties both have excellent hair length.

Kawanda punctatum. This is a strain of *G. hirsutum* var. *punctatum* of unknown origin, obtained from Kawanda, Uganda, in 1942.

THE GENETICS OF THE LAMINA HAIRINESS OF KAPAS PURAO

This section is a continuation of the work reported on in Part I of this series. There it was shown that in Kapas Purae length and density of lamina hairs are controlled by a major H gene fortified by intensifying genes, minor H genes being almost negligible. This major H gene was shown to be linked with, or identical with, a gene for chlorophyll deficiency.

The linkage of Kapas Purae H with chlorophyll deficiency

Knight (1952) transferred the Kapas Purae H to Sakel. At the third backcross F_2 stage, he selected five plants with maximum hairiness (and hence likely to be HH) for growing as F_3 progeny rows. None of these five F_3 rows bred true for hairiness. Fourteen plants showing maximum hairiness were selected in the F_2 of the fourth Sakel backcross; again none of these bred true in F_3 . It was suggested that the Kapas H is closely linked with one of the two genes governing chlorophyll deficiency, with the result that Sakel plants homozygous for H would also be homozygous for both deficiency factors. Such plants normally die in the seedling stage, and this would explain the absence of HH plants in the backcross F_2 's.

Harland (1939) gives the genetic constitution of *G. barbadense* and *G. hirsutum*, with regard to chlorophyll deficiency genes. Harland's data were expanded by Hutchinson (1946) as given on p. 188 below.

<i>G. barbadense</i>	Chl_1chl_2
var. <i>darwinii</i>	Chl_1chl_2
var. <i>brasiliense</i>	Chl_1chl_2
<i>G. hirsutum</i>	Chl_1Chl_2 or chl_1Chl_2 (rarely Chl_1chl_2)
var. <i>punctatum</i>	Chl_1Chl_2 , chl_1Chl_2 or Chl_1chl_2
var. <i>marie-galante</i>	Chl_1Chl_2 or chl_1Chl_2
<i>G. tomentosum</i>	Chl_1Chl_2

Chlorophyll-deficient plants are of $\text{chl}_1\text{chl}_1\text{chl}_2\text{chl}_2$ genotype. These symbols are not those originally used by Harland; his symbols have been changed for those suggested by Hutchinson & Silow (1939).

On this basis, the Kapas **H** must be closely linked with chl_1 . Thus Kapas Pura, though of **HH** composition, shows normal growth, being of $\text{H}/\text{chl}_1\text{H}/\text{chl}_1\text{Chl}_1\text{Chl}_2$ genotype. The transfer of **H** to Sakel (homozygous for chl_2) can only, except for cross-overs, result in chlorophyll-deficients when the **H** is selfed-out to make it homozygous.

Table 1. F_2 of the seventh Sakel backcross: hairiness and chlorophyll deficiency

Family no.	Hairy	Glabrescent	Chlorophyll-deficient*
J 1364/50	49	16	11
J 1365/50	38	12	6
J 1366/50	27	13	10
J 1367/50	24	13	8
J 1368/50	36	12	12
J 1369/50	48	12	13
J 1370/50	31	15	6
J 1371/50	44	22	13
J 1372/50	48	22	10
J 1373/50	46	20	21
J 1374/50	36	9	7
J 1375/50	15	6	6
J 1376/50	25	11	6
J 1377/50	17	9	5
J 1378/50	34	16	12
J 1379/50	51	21	6
Totals	569	229	152

* In this and all subsequent tables the chlorophyll-deficients have not been included under 'hairy' or 'glabrescent' because of the difficulty of classification.

To check this hypothesis, forty-four hairy plants in the F_3 of the fourth Sakel backcross (Knight, 1952, p. 63, table 26) were selfed. These plants were chosen from the three families whose ratio of 'hairy' : 'glabrescent' plants was closest to 3 : 1 (J 1261, 1263 and 1269/49), it being presumed that such families might derive from cross-over plants of $\text{H}/\text{Chl}_1\text{hChl}_1\text{chl}_2\text{chl}_2$ composition. All forty-four backcross F_4 progenies contained chlorophyll-deficient plants. Twenty one of these families were not carried beyond the seedling stage. The remainder were retained till fully grown, for hairiness classifications; all split for hairiness.

To ascertain whether this association between **H** and chl_1 still obtained in later backcrosses, sixteen hairy plants in the seventh Sakel backcross were selfed. It will be seen from Table 1 that each of the resulting sixteen progenies contained chlorophyll-deficient plants.

Twelve hairy plants selected in the eighth Sakel backcross progeny were selfed; all gave a proportion of chlorophyll-deficients in their progenies (Table 2).

Twenty-two plants were selected for selfing in the F_2 of the eighth Sakel backcross. These plants were chosen as displaying the maximum hairiness, in the hope of obtaining a progeny homozygous for **H**. It will be seen from the classification of the resulting progenies (Table 3) that none of these twenty-two plants bred true.

Table 2. F_2 of eighth Sakel backcross: hairiness and chlorophyll deficiency

Family no.	Hairy	Glabrescent	Chlorophyll-deficient
J1435/51	37	17	14
J1436/51	36	16	10
J1437/51	27	6	9
J1438/51	30	9	11
J1439/51	26	10	4
J1440/51	19	7	9
J1441/51	17	6	3
J1442/51	15	11	7
J1443/51	13	3	4
J1444/51	13	6	5
J1445/51	25	11	7
J1446/51	14	3	7
Totals	272	105	90

Table 3. F_3 of eighth Sakel backcross: hairiness and chlorophyll deficiency

Family no.	Hairy	Glabrescent	Chlorophyll-deficient
J1360/52	10	8	1
J1361/52	7	1	1
J1362/52	16	11	4
J1363/52	19	11	7
J1364/52	22	11	6
J1365/52	13	13	8
J1366/52	27	9	8
J1367/52	19	13	4
J1368/52	18	7	7
J1369/52	12	9	8
J1370/52	20	12	4
J1371/52	14	16	3
J1372/52	18	11	4
J1373/52	26	13	3
J1374/52	26	15	7
J1375/52	21	16	5
J1376/52	28	16	3
J1377/52	29	21	2
J1378/52	28	22	4
J1379/52	33	17	4
J1380/52	29	16	6
J1381/52	38	13	3
Totals	473	281	102

Check crosses with $H_1 H_1$ Sakel

Twenty-nine hairy (**Hh**) plants in the fifth backcross F_1 were bulk crossed with JR 14/5.* The F_1 of this cross, sown in 1949-50, consisted of 25 'more hairy': 17 'less hairy' plants. The plants in the former group were individually selfed. The 1949-50 season was one in which *Rhizoctonia* wilt was abnormally severe at Shambat, and only one of these selected plants survived. Seed of this, sown in the following season as family J 1021/50, gave 64 hairy : 0 glabrescent : 18 chlorophyll-deficient plants.

To repeat this gene homology test, three plants with maximum hairiness in the F_2 of the eighth Sakel backcross (Table 2) were crossed with BLJR 14/23 (a synthesized

* JR 14/5 is Domains Sakel to which H_1 has been transferred from Tanguis.

blackarm- and leafcurl-resistant Sakel homozygous for H_1 from Tanguis). In the F_1 's of these crosses, plants with maximum hairiness were selfed. The progenies of these plants, sown in 1952-3 winter, gave the ratios shown in Table 4.

In these families, those having no glabrescent plants but containing chlorophyll-deficients must have arisen from plants combining H Kapas with H_1 . Three families, J 1041, 1042 and 1044/53, all contain glabrescent plants. These three families total 62 hairy: 24 glabrescent: 0 chlorophyll-deficient plants, and clearly they must spring from plants with h Kapas combined with H_1 —hence the absence of chlorophyll-deficients. From this it follows that H Kapas and H_1 are allelic, but that the H_1 from Tanguis is associated with Ch_1 , whereas the H_1 from Kapas Purao is very strongly linked with ch_1 . Except for chlorophyll-deficient dwarfed plants, it has not been possible to obtain the Kapas Purao H_1 in homozygous condition on a Sakel background. For this reason it is not known whether Kapas Purao H_1 and ordinary H_1 are identical in their effects. Accordingly the symbol H_1^k is proposed for the Kapas Purao hairiness gene.

Table 4. F_2 of eighth backcross Hh plants \times H_1H_1 Sakel

Family no.	Hairy	Glabrescent	Chlorophyll-deficient
J 1036/53	14	0	2
J 1037/53	46	0	9
J 1038/53	32	0	5
J 1039/53	27	0	6
J 1040/53	37	0	7
J 1041/53	23	6	0
J 1042/53	28	11	0
J 1044/53	11	7	0
J 1046/53	29	0	3
J 1047/53	26	0	1
J 1048/53	27	0	6
J 1049/53	28	0	3
J 1050/53	63	0	12

THE GENETICS OF THE LAMINA HAIRINESS OF *KAWANDA PUNCTATUM*

F_1 of *Kawanda punctatum* \times Sakel and the first Sakel backcross

The original strain of *punctatum* used in these crosses was of interest from the blackarm resistance point of view, and only records of resistance to this disease were made in the F_1 and the first Sakel backcross. It was noted, however, that a major hairiness gene appeared to be present in the first backcross material, and steps were taken to isolate this gene with a view to its utilization in the jassid resistance breeding work.

Second Sakel backcross

Six hairy plants from the first backcross were again crossed with Sakel, yielding the progenies shown in Table 5.

Table 5. Second Sakel backcross

Family no.	Actual		Expected (1:1)	
	Hairy	Glabrescent	Hairy	Glabrescent
BA 598/45	3	4	$3\frac{1}{2}$	$3\frac{1}{2}$
BA 599/45	4	9	$6\frac{1}{2}$	$6\frac{1}{2}$
BA 600/45	21	29	25	25
BA 601/45	41	46	$43\frac{1}{2}$	$43\frac{1}{2}$
BA 602/45	38	49	$43\frac{1}{2}$	$43\frac{1}{2}$
BA 603/45	33	19	26	26
Totals	140	156	148	148

Subsequent Sakel backcrosses

The results from subsequent Sakel backcrosses are summarized in Table 6.

Table 6. *Subsequent Sakel backcrosses*

Backcross no.	Hairy	Glabrescent
3rd	61	82
4th	34	35
5th	150	155
6th	29	50
7th	12	30
8th	18	15
9th	7	8
Totals	311	375
Expected (1 : 1)	343	343

Clearly a single major hairiness gene is involved.

The linkage of Kawanda punctatum H with chlorophyll deficiency

Three hairy plants in the third Sakel backcross were selfed and their seed sown in progeny rows. These gave respectively 144 : 64, 105 : 51 and 49 : 27 hairy to glabrescent plants. These figures total 298 : 142 compared with expectation on a 3 : 1 basis of 330 : 110. No F_2 was grown from the fourth Sakel backcross, but the fifth backcross F_2 totalled 111 : 66, and the sixth backcross F_2 also showed a deficit as compared with a 3 : 1 expectation, totalling 51 : 30 hairy to glabrescent plants.

These figures are summarized in Table 7, and it is clear from them that the ratios of 'hairy' : 'glabrescent' plants accord much more closely with expectation on a 2 : 1 than on a 3 : 1 basis. This suggests a similar mechanism to that observed in Kapas Purao crosses, but no counts of chlorophyll-deficient plants were made in the F_2 's listed in Table 7. This interpretation is strengthened by the fact that five hairy plants chosen at random in the F_2 of the third Sakel backcross all yielded progenies which segregated for hairiness and which totalled 219 hairy : 83 glabrescent plants.

Table 7. F_2 's of the third, fifth and sixth Sakel backcrosses

Backcross no.	Hairy	Glabrescent
3rd	298	142
5th	111	66
6th	51	30
Totals	460	238
Expected (3 : 1)	523½	174½
Expected (2 : 1)	465½	232½

Counts of chlorophyll-deficient plants were made on the F_2 's and F_3 's of later backcrosses, and these show that Sakel plants carrying the Kawanda *punctatum* H invariably throw chlorophyll-deficient plants in their progenies (Tables 8 and 9).

Forty-eight hairy plants were chosen at random within the ninth backcross F_2 families to see if any of them would give an HH line. None of these forty-eight plants bred true for hairiness in F_3 . Thirty of these F_3 progenies contained chlorophyll-deficient plants, and it is a fair inference that all forty-eight progenies would have thrown a proportion of chlorophyll-deficients had they been sown on better land and had the advantage of a good tilth in the seed bed. Chlorophyll-deficient plants, being weak, require optimum

conditions in the seed bed if their germination is to be ensured, whereas conditions were so inferior for the ninth backcross F_3 families that plant stands were poor throughout

Check crosses with H_1H_1 Sakel

Hairy plants (**Hh**) in the sixth Sakel backcross F_1 were 'bulk' crossed with JR14/5. The F_1 progeny of this cross consisted of twenty-three plants, all hairy. Five plants showing maximum hairiness were chosen as being likely to carry both the Kawanda *punctatum* **H** and H_1 . These were selfed and their progenies, grown in the following season, gave the ratios shown in Table 10.

Table 8. F_2 of eighth Sakel backcross

Family no.	Hairy	Glabrescent	Chlorophyll-deficient
J1481/50	24	8	6
J1482/50	25	16	7
J1483/50	41	21	22
J1484/50	23	13	9
J1485/50	38	22	18
J1486/50	34	15	10
J1487/50	44	24	22
J1488/50	12	10	8
J1489/50	31	17	8
J1490/50	27	16	17
Totals	299	162	127

Table 9. F_2 of ninth Sakel backcross

Family no.	Hairy	Glabrescent	Chlorophyll-deficient
J1113/51	103	39	15
J1114/51	56	25	22
J1115/51	29	18	10
Totals	188	82	47

Table 10. F_2 of sixth backcross **Hh** plants \times H_1H_1 Sakel

Family no.	Hairy	Glabrescent	Chlorophyll-deficient
J1492/50	103	0	41
J1493/50	98	30	0
J1494/50	41	13	0
J1495/50	83	44	0
J1496/50	89	0	32
J1497/50	75	32	0

In these families chlorophyll-deficients were counted shortly after germination was complete and checked again later.

A second test of gene homology was made, using hairy plants from the eighth Sakel backcross. These were crossed with BJR14/18 (a synthesized Sakel homozygous for B_2 from Upland and H_1 from Tanguis). The F_1 of this cross gave eighteen plants classed as 'more hairy' and sixteen classed as 'less hairy'. Four of the 'more hairy' plants were selfed. The classification of the F_2 progenies is given in Table 11.

Clearly the Kawanda *punctatum* **H** gene occupies the same locus as H_1 but, whereas H_1 from Tanguis is linked with $Ch1_1$, H_1 from Kawanda *punctatum* is linked with $ch1_1$. Thus Kawanda *punctatum* carries H_1^k .

Table 11. F_2 of eighth backcross Hh plants $\times H_1H_1$ Sakel

Family no.	Hairy	Glabrescent	Chlorophyll-deficient
J 1116/51	94	0	31
J 1117/51	142	0	53
J 1118/51	215	0	38
J 1119/51	118	0	27
Totals	569	0	149

THE GENETICS OF THE LAMINA HAIRINESS OF PHILIPPINES FERGUSON

 F_1 of *Philippines Ferguson* \times Sakel

In the F_1 of *Philippines Ferguson* \times Sakel, leaf hairiness showed partial dominance, the degree of hairiness being similar to that found in F_1 's of *MU8b* \times Sakel and of *Kapas Purao* \times Sakel. Leaf hairs appeared to be reduced both in length and density as compared with the hairy parent and the stems of the F_1 were almost glabrous.

First Sakel backcross

Four first Sakel backcross progenies were grown and it was found possible to classify the plants in these into the two phenotypes 'hairy' and 'glabrescent' with reasonable confidence (Table 12).

Table 12. *First Sakel backcross*

Family no.	Actual		Expected (1 : 1)	
	Hairy	Glabrescent	Hairy	Glabrescent
BA 98/46	11	12	$11\frac{1}{2}$	$11\frac{1}{2}$
J 1058/46	63	50	$56\frac{1}{2}$	$56\frac{1}{2}$
J 1058A/46	95	99	97	97
J 1059/46	60	50	55	55
Totals	229	211	220	220

Clearly a single major gene for hairiness is involved.

Subsequent Sakel backcrosses

Subsequent Sakel backcrosses gave good approximations to a 1 : 1 ratio of hairy to glabrescent plants. These distributions are summarized in Table 13 below.

Table 13. *Subsequent Sakel backcrosses*

Backcross no.	Hairy	Glabrescent
2nd	184	176
3rd	51	42
4th	17	18
5th	18	17
Totals	270	253

 F_2 results

Eight families of *Philippines Ferguson* \times Sakel F_2 composition were grown, and each gave a good approximation to a 3 : 1 ratio of hairy to glabrescent plants (Table 14). There was considerable variation within the hairy phenotype, with plants ranging up to, and beyond, the full hairiness of the hairy parent. The glabrescent class was kept fairly

distinct by including plants with rather more hair than Sakel, though definitely less than that of H_1h_1 Sakel.

Table 14. *Philippines Ferguson* × *Sakel* F_2

Family no.	Actual		Expected (3 : 1)	
	Hairy	Glabrescent	Hairy	Glabrescent
J 1060/46	69	21	$67\frac{1}{2}$	$22\frac{1}{2}$
J 1061/46	92	39	$98\frac{3}{4}$	$32\frac{3}{4}$
J 1062/46	42	18	45	15
J 1177/48	487	140	$470\frac{1}{2}$	$156\frac{3}{4}$
J 1178/48	78	31	$81\frac{3}{4}$	$27\frac{3}{4}$
J 1179/48	85	28	$84\frac{3}{4}$	$28\frac{3}{4}$
J 1180/48	62	22	63	21
J 1182/48	26	8	$25\frac{1}{2}$	$8\frac{1}{2}$
Totals	941	307	936	312

Within these eight families, about eleven plants were present with hair length and density equal to, or better than, that of the Ferguson parent. Another F_2 was grown in 1949–50 and gave 297 hairy : 67 glabrescent plants, but classification was not at all distinct. Eight plants were present with hair length and density as good as or better than Ferguson. A feature of all these F_2 plants having the maximum expression of hairiness was their marked sterility.

In the F_2 progenies from the second backcross material, it was again possible to divide the plants into the phenotypes ‘hairy’ and ‘glabrescent’, with little or no overlap between the two groups. There was, however, considerable variation within the hairy phenotype. The second backcross F_2 , grouped on this basis, gave a ratio of 148 ‘hairy’ : 51 ‘glabrescent’ plants as against an expectation of $149\frac{1}{4}$: $49\frac{3}{4}$ on a 3 : 1 basis. No search for chlorophyll-deficient plants was made.

The linkage of Ferguson H with chlorophyll deficiency

Twelve hairy plants in the fifth Sakel backcross were selfed. Their progenies, grown in 1951–2, all contained chlorophyll-deficient plants (Table 15).

Table 15. F_2 of fifth Sakel backcross

Family no.	Hairy	Glabrescent	Chlorophyll-deficient
J 1211/51	109	35	30
J 1212/51	19	7	11
J 1213/51	14	10	4
J 1214/51	28	19	18
J 1215/51	77	41	33
J 1216/51	27	11	10
J 1217/51	15	11	7
J 1218/51	25	8	8
J 1219/51	18	7	10
J 1220/51	17	6	14
J 1221/51	20	2	5
J 1222/51	13	7	6
Totals	382	164	156

Within these families, fifty hairy plants were chosen at random for selfing, in the hope of establishing lines homozygous for hairiness—that is, free from chlorophyll deficiency. The progenies of these fifty plants, grown in 1952–3, carried in every case a proportion of

glabrescent plants and every progeny contained chlorophyll-deficient plants. These families gave a total of 950 hairy : 508 glabrescent : 264 chlorophyll-deficient plants.

Check crosses with H_1H_1 Sakel and with Kapas Purao and Kawanda punctatum

Hairy plants (Hh) from the third Sakel backcross were bulk crossed with JR14/5. The F_1 progeny of this cross, consisting of twenty-three plants, could be roughly classified into two groups, thirteen 'more hairy' and ten 'less hairy' plants. The 'more hairy' plants were identical with H_1H_1 Sakel (JR14/5) in degree of hairiness. Six plants showing full hairiness were selfed and their progenies were grown in 1948-9 (Table 16). Unfortunately, no examination for chlorophyll-deficients was made, as it was not until 1949-50 season that the importance of chlorophyll deficiency in relation to hairiness began to be appreciated.

Table 16. F_2 of third backcross Hh plants $\times H_1H_1$ Sakel

Family no.	Hairy	Glabrescent
J 1335/48	25	0
J 1336/48	33	0
J 1337/48	6	0
J 1339/48	10	0
Totals	74	0

As a check on this, Ferguson was crossed with Kapas Purao. Five F_2 progenies, each of 30-50 plants, were grown. There was no variation in hairiness either within or between these progenies, strongly suggesting that Ferguson and Kapas Purao share the same main hairiness gene and at least approximately the same minor gene complex. No chlorophyll-deficient plants were present in these families.

Hairy plants from the fourth backcross of Ferguson to Sakel were crossed with plants from the eighth backcross of Kapas Purao to Sakel. The F_1 of this cross gave 50 hairy : 20 glabrescent : 21 chlorophyll-deficient plants.

Finally, a cross between fourth Sakel backcross Hh material of Ferguson origin and eighth Sakel backcross Hh plants of Kawanda *punctatum* origin gave 16 hairy : 11 glabrescent : 8 chlorophyll-deficient plants in F_1 .

Thus the main hairiness gene of Philippines Ferguson is allelic to H_1 and, like the H_1^{Φ} from Kapas Purao and Kawanda *punctatum* it is closely linked with chl_1 . Clearly, Philippines Ferguson carries H_1^{Φ} .

DISCUSSION

Jassid resistance

Three types of gene appear to be concerned in the genetic control of hairs, of length and density sufficient to give jassid resistance, on the abaxial leaf surface: (1) Major and minor genes, the direct effect of which is to produce hairs—these have been referred to as H genes. (2) Modifying or intensifying genes which increase the length of hairs produced by the H genes. These lengthening genes act on any hairs present regardless of their density or sparseness. (3) Modifying genes which affect the density of the hairs produced by the H genes.

The genetic basis of the jassid resistance of Kapas Purao was covered in Part I of this series (Knight, 1952). Kawanda *punctatum* was only included in this work because of the presence in it of a major hairiness gene; apart from this it carries no true jassid resistance.

The resistance of Philippines Ferguson appears to be genetically very similar to that of Kapas Purao, except that minor hairiness genes with direct effect are of more importance in Ferguson. The relatively clear segregation in the straight F_2 of Ferguson \times Sakel shows that minor **H** genes with direct effect are of much less importance than H_1 , and the variation in hair length within the hairy class in these F_2 's is presumably attributable to intensifying genes. These genes do not act only on H_1 , but lengthen any hairs present no matter how sparse these may be. This is evident from the presence, in these F_2 's, of plants with hairs as sparse as those of Sakel (i.e. glabrescent) but with such hairs long, instead of short as in Sakel.

In the course of transference work with Ferguson \times Sakel hybrids it has been possible to self out lines with a high proportion of Sakel 'blood', yet carrying the bulk of the Ferguson minor gene and intensifier complex, though lacking H_1 . These lines carried hairs of good length and fair density. Other lines have been selfed-out having hair density as low or almost as low as Sakel, but having the length modifiers present so that all hairs were long.

Thus the jassid resistance of Ferguson is controlled by H_1^k supported by length modifiers and by minor **H** genes with direct effect. It will be seen later that other genes must be present having a negative effect on hair density.

The key gene

The evidence of the gene homology tests described in this paper, coupled with the close linkage of hairiness with chlorophyll deficiency in each of the three series of crosses, shows that Kapas Purao, Kawanda *punctatum* and Philippines Ferguson all carry the same key gene, H_1^k . Nevertheless, Knight & Sadd (1951) originally considered this gene to be distinct from H_1 and they tentatively called it H_3 . This was because crosses between Kapas Purao and H_1H_1 Sakel gave, in F_2 , a proportion of more or less glabrescent plants. These plants had more hair than Sakel, but definitely less than is associated with H_1 . Furthermore, the proportion of these 'semi-glabrescent' plants agreed well with expectation on a 15 : 1 basis, so that it seemed reasonable to conclude that H_1 and the Kapas **H** were independent genes.

In 1948, five F_2 's of Ferguson \times H_1H_1 Sakel were grown. No accurate classification into 'hairy' and 'glabrescent' was found to be possible, but, as in the Kapas Purao cross, more or less glabrescent plants were present. This supported the theory that the Ferguson-Kapas **H** was distinct from H_1 .

A comparison of leaf strips of Ferguson and BLJR 14/29,* prepared as recommended by Parnell, King & Ruston (1949), shows that, although the leaf-hairs of Ferguson are much longer than those of BLJR 14/29, they are less dense. Counts show that BLJR 14/29 has more than twice as many hairs per unit area as Ferguson. This suggests that Ferguson carries negative modifiers which reduce the hair density conferred in Ferguson by its quota of H_1^k plus minor **H** genes, to less than half the density associated with H_1 alone on a Sakel background (Sakel having very few minor **H** genes). Independent segregation of these negative density modifiers and of the minor **H** gene component of Ferguson, might explain the presence of the more or less glabrescent plants which appeared in

* BLJR 14/29 represents H_1 plus the minute amount of hair normally found in Sakel. The strain was selfed out after fifteen backcrosses of Tanguis to Sakel.

Ferguson \times H_1H_1 Sakel F_2 's. A similar explanation presumably holds for Kapas Purao.

The association of H_1 with chlorophyll deficiency

The gene H_1 occurs in three distinct types of association which, for convenience, may be called (1) the Tanguis group, (2) the MU8b group, and (3) the Ferguson group.

The Tanguis group. Since *barbadense* cottons are $Chl_1Chl_1chl_2chl_2$ in genotype, H_1 when present in this species must be associated with Chl_1 .

The MU8b group. Crosses between MU8b and Sakel throw chlorophyll-deficient plants in F_2 in a ratio approximating to 15 : 1. Clearly, therefore, MU8b is of $chl_1chl_1Chl_2Chl_2$ composition and H_1 is thus associated with chl_1 in this variety. Nevertheless, Knight (1952, p. 57), using MU8b as donor parent, obtained very close agreement with expectation on a 3 : 1 basis of hairy : glabrescent plants in the F_2 's of the first three Sakel backcrosses. Similarly, in the St Ignatius crosses reported by Knight (1952, p. 59) good approximations to 3 : 1 were obtained in the F_2 's of the second, third and fourth Sakel backcrosses, and no difficulty was encountered in selfing out homozygous H_1 lines from the second Sakel backcross, although St Ignatius \times Sakel F_2 's contain chlorophyll-deficients. Thus, in this group, any linkage existing between H_1 and chl_1 must be such that crossing-over occurs frequently in the segment between these two loci.

The Ferguson group. This group covers the three strains Philippines Ferguson, Kapas Purao and Kawanda *punctatum*. From these varieties, despite numerous backcrosses to Sakel, no attempt to self out a Sakel homozygous for H_1^k has been successful. Furthermore, the numbers of attempts made are so large that it is evident that H_1^k and chl_1 are unbreakably linked in these types. Clearly the H_1^k/chl_1 chromosome in this group differs cytologically from its homologues in the other two groups and the difference is such as to render crossing-over impossible in the $H_1^k-chl_1$ zone. It seems likely that there is an inversion in this zone, and, in view of the total lack of crossing-over so far encountered, it seems probable that this inversion includes both the H_1^k and chl_1 loci.

Breeding policy. Transferences to Sakel of long and dense lamina hairs are carried out, at Shambat Station, on the cross-self-backcross-self-backcross-self principle. On this basis plants with the maximum expression of hairiness (typically greater than either parent) are selected in the straight F_2 for backcrossing to Sakel. F_3 lines from these hairy plants are also grown and backcrosses are discarded where the F_3 performance of the parent is below standard. A similar process is carried out with the backcross F_2 's.

In the Ferguson group, this process would be foredoomed because the end-product could never be made true breeding, since it would always be heterozygous for H_1^k , the homozygotes being chlorophyll-deficients. Had this fact been realized at the beginning of the transference programme, it would doubtless have been possible (though laborious) to transfer Chl_2 along with the H_1^k from Ferguson. By doing this, it would have been possible to synthesize Sakel plants of H_1^k/chl_1Chl_2 genotype, and these would not have given rise to chlorophyll-deficients.

The method being used to overcome the difficulty of the close association of H_1^k with chl_1 is to use H_1H_1 Sakel as the recurrent parent. This automatically eliminates the Ferguson H_1^k by random chance, and the Ferguson minor gene and modifier complex is added, by backcrossing and selfing, to a Sakel homozygous for Tanguis H_1 and carrying full blackarm-resistance factors transferred from Upland and *punctatum* cottons.

SUMMARY

Two Upland (*Gossypium hirsutum*) varieties (Kapas Puroo and Philippines Ferguson) and a *punctatum* cotton of unknown origin, were all shown to carry a key hairiness gene at the H_1 locus. This gene is so closely linked with chl_1 (one of the two complementary genes governing chlorophyll deficiency) that transferences of it to Sakel, which carries chl_2 , cannot produce strains homozygous for hairiness. This allele has been called H_1^k , and it is considered probable that the $H_1^k-chl_1$ segment of chromosome is inverted *vis-à-vis* the H_1-chl_1 segment in Sakel and in *G. barbadense* in general, and *vis-à-vis* the H_1-chl_1 segment in MU 8b and other *G. hirsutum* varieties.

In addition to H_1^k , Ferguson carries modifying genes which lengthen the hairs, minor H genes which can themselves directly confer hairiness, and modifying genes reducing the density of hair population.

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