THE GENETICS OF LINTLESSNESS IN ASIATIC COTTONS

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I. Introduction

During the last decade a number of lintless mutants in the cultivated Asiatic species of *Gossypium* have been observed by different workers in India. The present investigation was started with the object of studying their genetic behaviour and their interrelations. The data presented here are incomplete with regard to the *G. herbaceum* lintless types. These are late at Indore, and the incidence of frost has prevented the completion of studies with their hybrids. The information at present available, however, is complete for the *G. arboreum* types studied.

II. Lintless types

The lintless types used were of two kinds, glabrous lintless and hairy lintless.

The glabrous lintless types are completely devoid of any kind of hair on the plant body. Four of these have been studied:

(1) *Dharwar glabrous lintless.* This was reported by Kottur (1927) and its genetic behaviour has been studied by Afzal & Hutchinson (1933). Hutchinson (1935) refers to it as N 19 in his further studies on the type. The seed is slightly fuzzy.

(2) *Mollisoni glabrous lintless.* Afzal & Singh (1932) reported this mutant, and its genetics were further studied by Afzal & Hutchinson (1933). The seed is slightly fuzzy.

(3) *Punjab glabrous lintless.* In 1933 Afzal discovered a second glabrous lintless mutant in a field of *Mollisoni* (*G. arboreum* var. *neglectum*). It differs from the above lintless types in having seeds entirely devoid of fuzz.

(4) *Nagpur glabrous lintless.* A glabrous lintless mutant discovered in the experimental cultures at Nagpur. Phenotypically it is identical with the Dharwar glabrous lintless.

The hairy lintless types have the same kind and distribution of hair on the vegetative parts of the plant as other members of the populations in which they occurred.

The following three hairy lintless types have been reported:

(5) *Punjab hairy lintless.* Afzal & Hutchinson (1933) reported this type and studied its genetic behaviour.

(6) 1027 *A.L.F. lintless.* This lintless mutant appeared in a pure culture of 1027 A.L.F. at Surat. The mutant is identical in appearance with 1027 A.L.F. (*G. herbaceum* var. *frutescens*), except for the entire absence of lint. The seeds are fuzzy.

(7) (1027 *A.L.F.* × *Wagad*) *lintless.* At the cotton-breeding station, Surat, another lintless mutant was observed in an F_2 progeny of the cross 1027 A.L.F. × Wagad 8. This also was vegetatively normal. It differed from the 1027 A.L.F. lintless in having naked seeds with only occasionally a few fuzz hairs.

III. Previous work

Genetic studies of "lintlessness" in *G. hirsutum* were reported by Griffee & Ligon (1929), where they found that lintless differed from fuzzy linted in a single factor.

In the Old World Cottons Kottur (1927) and Afzal & Singh (1932) reported the occurrence of glabrous lintless types. Afzal & Hutchinson (1933) studied the genetics of the three lintless mutants, Dharwar G.L.[1] (Kottur, 1927), Mollisoni G.L. (Afzal & Singh, 1932) and Punjab H.L. They found that glabrous lintless was a simple recessive to the normal. Though they did not demonstrate the identity of the gene in the two strains, they concluded from the similarity of the phenotypes that only one gene, which they designated $\mathbf{h^G}$, was concerned. The H.L. type was shown to be a heterozygote, $\mathbf{H^L h^L}$, the homozygote $\mathbf{H^L H^L}$ being lethal. A cross between Mollisoni G.L. and Punjab H.L. gave independent segregation in F_2 showing that the two genes are distinct.

[1] Hereafter "G.L." will be used to denote the phenotype glabrous plant body and lintless seed, and "H.L." the phenotype hairy plant body and lintless seed.

Hutchinson (1935) made further studies on the Dharwar G.L. under the name N 19. He could not get any satisfactory evidence of linkage of h^G with leaf shape, anthocyanin, corolla colour and leaf nectaries.

IV. EXPERIMENTS

Dharwar G.L. × Mollisoni G.L. The F_1 was glabrous and lintless like either parent. A large F_2 population consisted entirely of glabrous lintless plants identical in all respects with their parents and grandparents. Afzal & Hutchinson's assumption that the same gene is responsible for the lintlessness of both types is therefore justified.

Mollisoni G.L. × Nagpur G.L.

The F_1 was glabrous lintless, and though no F_2 data are yet available, it may be concluded that the same gene is responsible for lack of lint in both strains.

Dharwar G.L. × Punjab G.L. and Mollisoni G.L. × Punjab G.L.

Since Dharwar G.L. and Mollisoni G.L. have been shown above to carry the same gene for lintless, these two crosses may be expected to behave alike, and are treated together.

The F_1's were normal hairy linted.

The F_2's segregated into hairy linted and glabrous lintless as follows:

Cross	Hairy linted	Glabrous lintless	Total
D.G.L. × P.G.L.	121	99	220
M.G.L. × P.G.L.	20	7	27
Total	141	106	247
Expected	138·9	108·1	247

The 9 : 7 ratio to be expected with complementary genes for hairy linted was closely realized, and it is clear that the glabrous lintless gene of Punjab G.L. is different from and complementary to that of Dharwar G.L. and Mollisoni G.L.

F_3 families were grown from hairy linted individuals of the F_2 of the cross Dharwar G.L. × Punjab G.L. Out of sixty-one families, four bred true and fifty-seven segregated, as against an expectation of 6·8 : 54·2, a satisfactory fit.

Of the segregating families, half should give 9 : 7 and half 3 : 1. Owing to the small numbers in many families it was difficult to divide them into two classes. Since equal numbers of each type of family were to be expected, summation over all segregating families should give the two classes in the proportions obtained by summing the two ratios, or

9 + 12 : 7 + 4 = 21 : 11. Adding all segregating families together the following result was obtained:

	Hairy linted	Glabrous lintless	Total
Observed	816	436	1252
Expected (21 : 11)	821	431	1252

Agreement is good.

Confining attention to families with twenty plants or more, the results obtained leave no doubt regarding the type of segregation. The data are summarized in Table I.

Three families bred true to hairy linted. Twelve families gave approximately 9 hairy linted : 7 glabrous lintless, and twelve gave approximately 3 hairy linted : 1 glabrous lintless. There are therefore two independent, complementary factors controlling the difference between normal and glabrous lintless. They may be designated $\mathbf{H_a}$–$\mathbf{h_a}$ and $\mathbf{H_b}$–$\mathbf{h_b}$.

TABLE I

F_3 of Dharwar G.L. × Punjab G.L.

(Families with less than 20 plants omitted)

Family no.	Homozygous hairy linted	9 : 7			3 : 1		
		Hairy linted	Glabrous lintless	Total	Hairy linted	Glabrous lintless	Total
292	56	—	—	—	—	—	—
293	—	7	13	20	—	—	—
298	—	19	10	29	—	—	—
299	—	16	10	26	—	—	—
300	—	—	—	—	20	8	28
301	—	—	—	—	44	12	56
302	—	—	—	—	37	10	47
306	—	—	—	—	34	12	46
307	—	25	21	46	—	—	—
309	—	18	23	41	—	—	—
310	—	—	—	—	20	5	25
313	—	—	—	—	35	13	48
314	—	—	—	—	17	3	20
315	—	—	—	—	19	8	27
319	33	—	—	—	—	—	—
320	—	—	—	—	19	8	27
323	—	—	—	—	20	5	25
324	—	34	24	58	—	—	—
325	—	11	12	23	—	—	—
328	—	18	14	32	—	—	—
329	—	—	—	—	18	7	25
331	—	12	9	21	—	—	—
338	—	—	—	—	44	14	58
340	33	—	—	—	—	—	—
343	—	17	14	31	—	—	—
345	—	10	10	20	—	—	—
349	—	27	15	42	—	—	—
Observed	122	214	175	389	327	105	432
Expected	—	218·8	170·2	389	324	108	432
	3 Families		12 Families			12 Families	

Dharwar G.L. × 1027 *A.L.F. lintless*

The F_1 was hairy linted. In F_2 three classes were recorded, hairy linted as in the F_1, hairy lintless as in the 1027 A.L.F. lintless parent, and glabrous. Glabrous plants were very weakly and scarcely flowered, but they would no doubt have been lintless as in the Dharwar G.L. parent if they had produced seed. Owing to the influence of the late *herbaceum* parent, most of the F_2 plants were late in maturing and frost in the first week of January destroyed a large proportion of the plants before they had produced seed. The classification of the hairy class into linted and lintless was consequently incomplete. The F_3 segregated as follows:

Hairy				
Linted	Lintless	Unclassified	Glabrous	Total
208	49	194	137	588

There were in all 451 hairy : 137 glabrous, a satisfactory fit to 3 : 1. Among those of the hairy class which produced seed, however, there were 208 linted : 49 lintless. χ^2 for the deviation from 3 : 1 is 4·8, for which P is between 0·05 and 0·02, so the deviation cannot be regarded as due to chance. The most likely explanation of the deviation is that the hairy lintless gene, derived from the late 1027 A.L.F. parent, was linked with genes causing lateness, and that an excess of the hairy lintless class was included in the unclassified group. The main facts are, however, clear. Hairy lintless in 1027 A.L.F. lintless results from the action of a simple recessive gene which is complementary to $\mathbf{H_a}$–$\mathbf{h_a}$ in the production of lint. A completely classified F_2 may be expected to approximate to 9 hairy linted : 3 hairy lintless : 4 glabrous lintless.

Punjab G.L. × 1027 *A.L.F. lintless*

The parent used as the Punjab G.L. was actually a glabrous lintless segregate in the F_2 of Punjab G.L. × Burma laciniated.

The F_1 hybrids were hairy linted.

A small F_2 was grown from the seed obtained from a single plant in the greenhouse. Of nine plants, eight were hairy and one glabrous. Four of the hairy plants gave seed. Three were linted and one lintless. The data, though inadequate, are sufficient to show that the gene for lintless in 1027 A.L.F. is distinct from that in Punjab G.L.

Dharwar G.L. × (1027 × *Wagad*) *lintless*

The F_1 plants were hairy linted. F_2 data are not yet available.

Punjab G.L. × (1027 × Wagad) lintless

F_1 was hairy linted. Germination in F_2 was bad, and only nineteen plants were obtained. Of these seventeen were hairy and two glabrous. All plants were very late and set badly, and at the time of their destruction by frost seed had been obtained from only three of the hairy class. Of these two were linted and one lintless.

1027 *A.L.F. lintless* × (1027 × *Wagad*) *lintless*

The F_1 hybrids were hairy linted, showing thereby that the lintless gene of (1027 × Wagad) lintless is different from that of 1027 A.L.F.

Linkage studies

The glabrous lintless types were crossed with strains differing from them in a number of simply inherited genes in the hope of discovering linkages with the genes for lintless. The following strains were used:

	Constitution				
Strain	Corolla colour	Anthocyanin pigment	Leaf shape	Lint colour	Leaf nectaries
Burma laciniated	Y	R^s	L^L	K	Ne
H 9	Y	R^L	l	k	Ne
1056	Y	R	L	k	Ne
Narrow kokati	Y	R^s	L	K	Ne

As the gene for lintless has been proved to be the same in Dharwar G.L. and Mollisoni G.L., the two factor ratios are summarized below for crosses involving both strains. For each two-factor ratio χ^2 is partitioned into three components, each with one degree of freedom. The first two show the extent of the deviations in the single factor ratio and the third the deviations from free assortment.

Segregation into linted and lintless was normal in all crosses. Significant deviations (χ^2 more than 3·8) occur in the lintless segregation in Table II (above) in the lintless-flower colour and lintless-lint colour classifications, as most lintless plants produced no flowers and none produced lint. The only significant deviation from 3 : 1 in other factors was in the data on leaf nectaries in Mollisoni G.L. × Burma laciniated, where there was a serious deficiency in the no-nectary class, for which no reason can be ascribed.

There were significant deviations from free assortment in a small family involving lintless and anthocyanin and in two small families involving lintless and leaf nectaries. Free assortment occurred between lintless and anthocyanin in another cross (Dharwar G.L. × 1056) and there was no evidence for linkage between leaf nectaries and lintless in

Mollisoni G.L. × Burma Laciniated. Direct evidence concerning linkage between lint colour and lintless is unobtainable, since the lintless class produces no lint to be classified for colour. From the fact that there was no departure from the expected 3K : 1k ratio in the linted class, however, it may be concluded that free assortment occurs.

TABLE II

Two-factor ratios in crosses involving Dharwar G.L. and Mollisoni G.L.

Cross	Lintless and	Hairy linted		Glabrous lintless		Total	χ^2 (lintless)	χ^2 (X : x)	χ^2 (L)
		X	x	X	x				
D.G.L. × B.L.	Y–y	53	11	16	0	80	5·4	0·7	1·1
M.G.L. × B.L.	Y–y	504	161	104	24	793	33·2	1·2	0·8
D.G.L. × H. 9	R^L–R^S	21	3	3	6	33	0·1	0·1	8·1
D.G.L. × 1056	R–R^S	29	9	6	4	48	0·4	0·1	0·9
D.G.L. × B.L.	L^L–l	62	19	19	6	106	0·1	0·1	0·0
M.G.L. × B.L.	L^L–l	502	184	171	63	920	0·1	1·7	0·0
D.G.L. × B.L.	K–k	46	13	—	—	59	—	0·3	—
M.G.L. × B.L.	K–k	422	148	—	—	570	—	0·3	—
D.G.L. × B.L.	Ne–ne	70	11	16	9	106	0·1	2·1	5·1
M.G.L. × B.L.	Ne–ne	487	202	158	77	924	0·1	13·3	1·2
D.G.L. × H. 9	Ne–ne	16	6	2	6	30	0·0	0·0	7·8

With none of the factors studied is there any satisfactory evidence of linkage of lintless. With two factors, however (anthocyanin and leaf nectaries), the data are conflicting. Similar conflicting results were reported by Hutchinson (1935), but studies of F_3 material at Indore led to the conclusion that the deviations were probably due to chance only, and it appears safe to conclude that there is no linkage with lintless in either case.

Linkage data involving Punjab G.L. are summarized in Table III.

TABLE III

Two-factor ratios in Punjab G.L. × Burma Laciniated

Lintless and	Hairy linted		Glabrous lintless		Total	χ^2 (lintless)	χ^2 (X : x)	χ^2 (linkage)
	X	x	X	x				
Y–y	109	29	48	8	194	1·5	3·6	1·4
L^L–L	118	41	47	16	222	1·4	0·1	0·0
K–k	105	31	—	—	136	—	0·4	—
Ne–ne	129	42	38	15	224	0·2	0·0	0·9

All single-factor segregations were normal, except that there was a considerable deficiency in the white flowered lintless class. This may be ascribed to the poor growth and flowering of lintless segregates. White flowers are always smaller than yellows in the same family (Hutchinson, 1931) and on lintless plants they were so small as frequently to be overlooked.

Free assortment occurred in all cases.

Punjab hairy lintless

Afzal & Hutchinson (1933) showed that this type was a heterozygote, one homozygote being lethal and the other normal linted. In the early generations of the strain some families gave a 2 : 1 ratio and others a significant excess of normal linted, suggesting that in some families the heterozygote also was lower in viability than the normal. Their description of the lintless type is not quite accurate. It carries a full coat of lint, but the lint hairs are very little longer than normal fuzz hairs, so that the seed appears to be lintless, but with a heavy fuzz coating. The heterozygote termed "hairy lintless" by Afzal & Hutchinson will be called "short lint" in this paper.

The strain was first grown in Indore in 1934. It did not grow well, and in that and the two following seasons only small progenies were raised. The 1935 short lint plants failed to mature seed and the 1936 progeny was raised from reserve seed from the 1934 crop. In this progeny ten plants were grown and classified as follows:

Normal linted	3
Short linted	5
Lintless	2
Total	10

The lintless plants were hairy on the plant body, but their seeds were entirely naked, and they were considerably smaller than plants of the other two classes. It was suspected that this new class represented the homozygote which had previously been recorded as lethal. Accordingly, germination tests were carried out on four plants from which sufficient seed was obtained. Two of these were short linted and two normal.

Class	Plant no.	No. of seeds	No. germinated	Germination %
Normal	823	26	21	81
	831	42	28	67
Short lint	825	83	67	81
	289	71	48	68

There were great differences between plants of the same class, but the difference between classes to be expected on the lethal factor theory has disappeared. The data are, of course, inadequate for a proper study. Data are available, however, from a large F_2 population of Punjab H.L. × Narrow kokati. The cross was between Narrow kokati and a short linted plant. The F_1 segregated, as was to be expected, and gave 4 short linted : 6 normal. F_2 families were grown from four short linted F_1 plants. Germination was good. All plants segregated into normal, short

linted, and lintless plants. In Table IV are given frequency arrays of plant height at maturity in the three classes for each F_2 and the parental family. Plants with tops damaged by stem borer have been omitted.

The lintless classification gave

	Normal	Short lint	Lintless	Total
Obs.	80	154	71	305
Exp. (1 : 2 : 1)	76·25	152·50	76·25	305·00

A very close approach to 1 : 2 : 1. In height normal plants averaged 35·8 in. and lintless plants only 11·7 in. Short lint plants were very nearly intermediate, averaging 25·6 in. The normal and short lint plants were much more variable in height than the lintless plants. The lintless plants were quite easy to distinguish in the field. They were dwarf, but did not appear to be lacking in vigour. They did not fruit very freely.

In order to prove beyond doubt that the lethal effect had disappeared, germination tests were carried out with seed from the three classes. Results are summarized below:

Class	Plant no.	No. of seeds	No. germinated	Germination %
Normal	29	99	86	86
	982	50	49	98
	984	50	47	94
	990	100	96	96
Short lint	755	100	95	95
	756	103	97	94
	988	100	90	90
	991	100	99	99
	999	98	93	95
Lintless	18	27	23	85
	24	35	34	97
	32	22	21	95
	33	39	39	100

In all cases germination was practically complete, so that the disappearance of the lethal effect of the homozygote is decisively proven. The newly emerged lintless type may be taken to be the now viable homozygote.

Corolla colour, leaf shape, lint colour, and leaf nectaries segregated in the Punjab H.L. × Narrow kokati cross. Sixfold classifications for lintless with corolla colour and leaf nectaries and a fourfold classification with lint colour are given below:

Lintless and	Normal		Short lint		Lintless		Total	χ^2 (lintless)	χ^2 (X : x)	χ^2 (linkage)
	X	x	X	x	X	x				
Y–y	62	18	118	36	54	16	304	0·7	0·0	0·0
Ne–ne	65	15	111	43	35	15	284	0·7	0·2	2·8
K–k	13	8	42	9	—	—	72	0·6	0·1	2·7

There was no deviation from free assortment of any magnitude.

TABLE IV

Punjab H.L. × Narrow kokati. Height (inches) of linted and lintless classes

Family	Class	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Punjab H.L.	Lintless	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Short lint	—	—	—	—	—	—	1	1	—	—	1	—	1	—	—	—	—	—	—	1	—	—	—	—
	Normal	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—
F_2 891	Lintless	—	4	4	8	3	2	1	3	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
	Short lint	—	—	—	—	—	2	1	—	—	1	1	—	6	1	1	2	6	—	6	2	2	3	2	3
	Normal	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	1	—	2	2	—	3	—
F_2 893	Lintless	—	1	—	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Short lint	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—	—	—	—	—	—
	Normal	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F_2 899	Lintless	3	3	4	5	6	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Short lint	—	—	—	—	—	1	1	1	—	3	7	3	3	6	4	4	6	7	4	1	5	3	6	1
	Normal	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—	2	—	—	1	1	2	3	1	1
F_2 898	Lintless	—	—	—	3	1	3	4	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Short lint	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	4	2	2	1	2	1	3	4
	Normal	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	1	1
Total F_2	Lintless	3	8	8	17	10	12	7	4	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
	Short lint	—	—	—	—	—	3	2	1	1	5	8	3	9	8	5	6	16	9	12	4	6	7	11	8
	Normal	—	—	—	—	—	—	—	—	1	—	—	—	3	1	—	2	1	1	1	3	4	4	5	2

Family	Class	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	58	Total
Punjab H.L.	Lintless	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
	Short lint	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
	Normal	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
F_2 891	Lintless	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26
	Short lint	3	1	—	—	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	47
	Normal	2	—	1	1	—	—	2	—	—	—	1	—	1	—	1	—	—	—	—	—	—	—	—	19
F_2 893	Lintless	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
	Short lint	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
	Normal	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
F_2 899	Lintless	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	28
	Short lint	2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	71
	Normal	1	1	5	1	1	1	3	1	—	1	—	2	1	1	—	2	—	2	3	—	—	—	1	41
F_2 898	Lintless	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13
	Short lint	1	1	3	1	1	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32
	Normal	—	—	—	1	3	1	—	1	1	—	—	—	1	2	—	—	1	—	—	—	2	1	—	18
Total F_2	Lintless	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	71
	Short lint	6	4	4	2	4	4	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	149
	Normal	3	1	6	4	5	2	5	2	1	1	1	2	3	3	1	2	1	2	3	—	2	1	1	80

The Narrow kokati parent proved to be heterozygous for leaf shape and one of the four F_1 plants carried on to F_2 was homozygous broad. In Table V below are given frequency arrays of mean leaf index (see Hutchinson, 1934) for the three lint classes, for the sum of three segregating F_2's.

TABLE V

Mean index frequency arrays in F_2 of Punjab H.L. × Narrow kokati

	Mean index													
Class	1·9	2·0	2·1	2·2	2·3	2·4	2·5	2·6	2·7	2·8	2·9	3·0	3·1	3·2
Normal	—	—	1	—	—	2	1	3	3	4	1	4	5	2
Short lint	—	—	—	1	2	2	3	3	5	2	2	9	5	6
Lintless	1	1	6	4	4	4	4	6	2	3	2	—	3	1
Total	1	1	7	5	6	8	8	12	10	9	5	13	13	9

	Mean index												
Class	3·3	3·4	3·5	3·6	3·7	3·8	3·9	4·0	4·1	4·2	4·3	4·4	4·5	Total
Normal	1	2	2	2	1	1	1	—	2	1	—	—	1	40
Short lint	8	11	6	3	3	5	3	1	2	—	—	1	—	83
Lintless	1	—	1	—	—	—	—	—	—	—	1	—	—	44
Total	10	13	9	5	4	6	4	1	4	1	1	1	1	167

The division between the narrow and broad classes is not very sharp, but a fair approximation will be made by dividing at 2·9. Omitting plants with a mean index of 2·9 there were:

		Normal	Short lint	Lintless	Total
Narrow:	Obs.	25	63	7	95
	Exp.	22·9	47·5	24·6	95·0
Broad:	Obs.	14	18	35	67
	Exp.	16·1	33·5	17·4	67·0

There were 95 narrow : 67 broad, a large and significant excess of broads over the expected 3 : 1. The lintless segregation agreed closely with expectation. The excess of broad leaved plants may safely be ascribed to mutation from narrow to broad, and accordingly, to enquire whether there is linkage between lintless and leaf shape, the expected frequencies assuming free assortment have to be calculated from the actual marginal totals. The figures are given above, and it will be seen that there are very large deviations from free assortment in the short lint and lintless classes, while in the normal class the proportions are approximately the same as in the totals. Such a result cannot be ascribed to linkage, since with linkage large deviations would occur in the normal and lintless classes and only a relatively small deviation in the short lint class. There is clearly some large disturbing element present, but it can only be identified by further work.

V. Discussion

The occurrence of lintless in Asiatic cottons has been recorded on seven separate occasions. Of these, three (Mollisoni G.L., Dharwar G.L. and Nagpur G.L.) have been shown to represent independent mutations at the same locus. Modifying Afzal & Hutchinson's (1933) terminology this allelomorphic pair may be designated $\mathbf{H_a}$–$\mathbf{h_a}$. The other types have each been recorded once only. The factor pair represented by the difference between Punjab G.L. and normal may be called $\mathbf{H_b}$–$\mathbf{h_b}$. These two lintless types are glabrous lintless and result in complete loss of hair from all parts of the plant. The appearance of the seed differs slightly in the two types, but not sufficiently to allow of classification with confidence in a segregating family. The two genes are complementary.

The two hairy lintless types from *G. herbaceum* have been shown to be distinct from the two glabrous lintless types and to be complementary to each other. They may be designated as follows:

1027 A.L.F. lintless : $\mathbf{Li_a}$–$\mathbf{li_a}$
1027 × Wagad lintless : $\mathbf{Li_b}$–$\mathbf{li_b}$

In these two cases normal is completely dominant, and may be assigned the capital letter.

Punjab H.L. has not yet been crossed with $\mathbf{h_2^2}$ or with $\mathbf{li_a}$ and $\mathbf{li_b}$, but it is hairy and therefore distinct from $\mathbf{h_2^2}$, while the nature of the heterozygate makes it very probable that it is distinct from both $\mathbf{li_a}$ and $\mathbf{li_b}$. Pending critical tests, Afzal & Hutchinson's $\mathbf{H^L}$–$\mathbf{h^L}$ may be altered to $\mathbf{li_c}$–$\mathbf{Li_c}$.

The demonstration that the lack of any one out of four or perhaps five independent genes results in complete loss of lint shows the extremely wide nature of the genetic basis of lint production. Two types of behaviour have been demonstrated. In the most extreme cases, the whole hairiness mechanism of the plant is disturbed, and the loss of lint is a secondary result of the failure to produce hairs of any kind. In the hairy lintless types, however, the plant hairs develop normally and all that is disturbed is the control of the extra development of seed coat hairs which results in lint.

Huskins (1935) has discussed the classification and nature of lethal factors and concludes as follows: "...the lethality of factors cannot really be measured or determined otherwise than in relation to the remainder of the genes they are associated with, to the other constituents of the cell, to the nature of the surrounding cells, and to the whole of the internal and external environment." The behaviour of the various lint-

less types provides an excellent illustration of Huskins' conclusion. In Trinidad, in a mild and humid climate, the Dharwar G.L. type, and hg_a segregates from its crosses, grew normally in the field and produced a moderate crop. Though probably less prolific than their normal allelomorphs, there was no suggestion of a lethal effect or even of seriously low viability. In the rigorous monsoon climate of Central India, when grown in ordinary black soil, the glabrous lintless types do so badly that a very large proportion of them set no seed, and considered from the point of view of their contribution to the next generation they may be regarded as semi-lethal.

The Punjab H.L. type affords a remarkable example of the modification of genic action. It is not possible at present to state with certainty the nature of the change that has occurred, but in the course of the eight generations that have been grown since the first heterozygous plant was discovered (in 1927) there has been a change in the homozygote from complete lethality to complete viability. Two possible causes of the change may be suggested. One is that a reverse mutation may have occurred bringing the homozygote up sufficiently towards normality to ensure its survival. The other is that the action of natural selection on the heterozygote has been sufficiently powerful to increase the viability of the homozygote up to complete survival in eight generations. Both suggestions involve changes which seem unlikely. Lethal factors have been studied so extensively and reverse mutations have been recorded so seldom that it is safe to say that the occurrence of such a change by mutation is contrary to all previous genetic experience.

That the homozygote should be raised to viability by natural selection for vigour among heterozygotes appears at first sight to be an extension of the theory of the improvement of the heterozygote by selection put forward by Fisher (1931) to account for the evolution of dominance. Apart from the exceedingly rapid improvement which would have to be postulated, the fact that the homozygote was fully viable in the F_2 of the cross with the unrelated Narrow kokati is difficult to explain on the selection theory. The selection theory on the whole seems the less improbable, and the behaviour in the Narrow kokati cross can only be ascribed at present to the chance selection for crossing of a type carrying a favourable set of modifying factors. If the selection theory is correct, there can be no development of dominance in such cases, since as the heterozygote is improved in the direction of normality, the homozygote is equally improved by the same modifying factors, and the heterozygote remains intermediate between the normal and the improved mutant

homozygote. In the present instance this is illustrated by the height data (Table IV) in which the heterozygote is almost exactly intermediate between the homozygotes. The efficiency of the Fisher effect for the development of dominance depends, in fact, upon the influence of the modifying factors being confined to the heterozygote for the modification of which they are selected, and not reaching the mutant homozygote, which is usually a more extreme variant in the same direction. That their influence should be so confined in most or all cases does not seem likely, and the $\mathbf{Li}_c$–$\mathbf{li}_c$ factor pair appears to be exceptionally suitable material on which to test the theory.

VI. Summary

Seven types of lintless occurring in Asiatic cottons are described. It is shown that at least four independent genes are involved. Two of these are complementary genes for glabrous lintless and two complementary genes for hairy lintless.

The relationship of the $\mathbf{Li}_c$ gene carried by Punjab H.L. to the rest has not been fully worked out, and it remains to be seen whether it is the same as one of the hairy lintless complementary pair. Data are presented to show that the hairy lintless homozygote $\mathbf{li}_c$–$\mathbf{li}_c$ shown by Afzal & Hutchinson (1933) to be a lethal is now fully viable both in the original strain and in a hybrid with Narrow kokati. The probable cause of the change and its bearings on Fisher's theory of the origin of dominance are discussed.

The linkage relations of the lintless genes were studied, but no satisfactory evidence of linkage was found. There was, however, a strong association between $\mathbf{Li}_c$ and leaf shape in segregating families in which considerable mutation from narrow to broad leaf had occurred. This association could not be ascribed to linkage.

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