

# THE GENETICS AND TAXONOMIC DISTRIBUTION OF SOME SPECIFIC LINT QUANTITY GENES IN ASIATIC COTTONS

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## I. INTRODUCTION

THE glabrous lintless mutation  $h_a$  was originally found in a Burmese strain of Asiatic cotton (Kottur, 1927). Afzal & Hutchinson (1933),<sup>1</sup> Hutchinson (1935) and Hutchinson & Gackari (1937) found that, in the crosses with normally linted strains which they studied, extracted recessives were always like the original mutant, and they concluded that the gene affects the entire hairiness mechanism of the plant.

In this paper it will be shown that this behaviour is a constant feature of crosses involving the original mutant and closely related linted strains. Glabrousness and lintlessness are pleiotropic effects of the same gene, as is evident from the fact that no breakdown of this association has been found in over one thousand  $h_a$  segregates examined in such crosses. The genetic behaviour of the mutant has also been studied in wide interspecific and intervarietal combinations, and in certain of these some of the glabrous recessive segregates were found to be linted, usually to a lesser degree, but occasionally as heavily as, the normal hairy fully linted plants in the same families. Were the effect on lint the only characteristic by which the "lintless" gene could be identified it would not have been easy to carry the analysis much further than to say that the segregation was obscured by modifiers, as so frequently occurs in

<sup>1</sup> Afzal & Hutchinson (1933) refer to this gene as  $h^f$ , but in Hutchinson & Silow's recent revision of gene nomenclature in cotton (1939) the symbol  $h_a$  is assigned to it.

wide crosses in cotton, but it was always possible to recognize members of the  $h_a$  class by their glabrousness, which was not observed to be affected by any other genes.

Evidence will be brought forward that the modifiers of lintlessness are members of a gene complex controlling number of lint hairs on the seed, a highly important component of ginning out-turn in cotton. In addition to the modifiers, which are effective in both phases of the lintless gene, this complex also comprises a number of factors which are only effective in the dominant phase of the lintless gene. It is proposed to refer to the modifiers as the "epistatic series" with reference to  $h_a$ , and to those which are ineffective on  $h_a$  as the "hypostatic series". In the fully linted genotype straightforward multiple factor action occurs, the members of both series acting together as quantity genes without distinction. The taxonomic distribution of members of these two series will be discussed.

In this investigation the degree of lint development is expressed as lint percentage, the weight of lint per 100 g. of seed. In certain tables ginning percentages are also indicated, as these figures, showing the percentage of lint obtained from seed cotton (seed + lint), are of greater commercial significance. Seed weight, the weight in grams of 100 seeds, is used as an index of seed size. Lint length estimates were obtained by the maximum halo length method. Taxonomic references are based on Hutchinson & Ghose's (1937) recent reclassification of Indian and African cottons.

## 2. ESTABLISHMENT OF A LINTED $h_a h_a$ LINE

A partially linted  $h_a h_a$  line was established from a cross between the original glabrous lintless strain, N 19, and a multiple heterozygote. The four following strains had entered into the ancestry of the latter plant:

- C.W., a strain of *G. arboreum* var. *neglectum* forma *bengalensis*.
- B.L., a strain of *G. arboreum* var. *neglectum* forma *burmanica*.
- A 16, a strain of *G. arboreum* var. *neglectum* forma *burmanica*.
- H 3, a strain of *G. herbaceum*.

Subsequent investigations have shown that C.W. and B.L. do not contain any of the epistatic lint genes, whilst both A 16 and H 3 do. Hutchinson (1935) presented some preliminary data which suggested that A 16 carried one of these epistatic lint genes.

Twenty-four plants of the  $F_1$  N 19  $\times$  the multiple heterozygote were selfed. In six of the  $F_2$  families all  $h_a$  segregates were completely lintless.

In the other eighteen families some of the glabrous-stemmed  $h_a$  progeny were linted. The range in amount of lint on the latter varied in different families. In some only a small amount of lint was present, and the partially linted  $h_a$  plants were quite distinctly less intensely linted than the fully linted  $H_a$  segregates in the same families. In other families some of the  $h_a$  plants were heavily linted, and on this basis alone it would not have been possible to differentiate them with any confidence from the dominant phenotype, but even the most heavily linted of them were as completely glabrous-stemmed as the original lintless mutant. Lint percentage estimates were obtained on all plants of which sufficient material had been harvested in the eighteen families segregating for epistatic lint genes. Data for two of these families are shown in Table I. In family number 428 there is a clear demarcation between the  $H_a$  and  $h_a$  phenotypes in lint percentage, whilst in family 415 the two phenotypes overlap, a few members of the  $h_a$  class having more lint than some of the fully linted class.

From this material an attempt was made to establish a linted  $h_a h_a$  line. Selfed seed of six of the most heavily linted  $h_a$  plants available was sown. Germination was poor, and only from two of the most heavily linted plants selected from family 415 (Table I), with lint percentages of 26 and 18 respectively, were families of reasonable size raised. All of the plants in these two families were glabrous-stemmed, and all appeared to be more or less equally heavily linted. The lint percentages of these two families are shown in Table II.

Again selfed seed of three of the most heavily linted plants, P 2417, P 2418, and P 2424, was sown. These plants are indicated by asterisks in Table II, and the amount of lint on their progeny in Table III.

One of these three plants, P 2417, was also crossed to a completely lintless  $h_a$  plant. The progeny, shown in Table IV, were almost as heavily linted as the selfed progeny of P 2417 (Table III).

Referring again to Table III, it is obvious that three  $h_a$  lines constant for lint development had been established. In subsequent investigations plant P 2417 was used as standard, primarily on account of its homozygosity for several major genes, a point of importance in connexion with some other investigations into which this plant entered. In the selfed progeny of P 2417, shown in Table III, and in its backcross to the lintless  $h_a$  plant, shown in Table IV, no lintless segregates appeared. Further, P 2417 has been very extensively used in connexion with the investigation of the linkage of a light brown lint colour gene with  $h_a$ . In this experiment many  $H_a h_a$  heterozygotes known to be without epistatics



have been backcrossed to P 2417. Several hundred  $h_a$  plants in such families have been examined, and all have, to the eye, as much lint as P 2417 itself. P 2417 must therefore be homozygous for at least one of the epistatic genes it contains.

Of the twenty-four  $F_2$  progenies derived from the cross N 19  $\times$  the multiple heterozygote, six were completely lacking epistatic lint genes, all the  $h_a$  plants in these families being quite lintless. This indicated that only very few epistatic lint genes were concerned. Since the original N 19  $h_a$  strain was completely lintless, the cross N 19  $\times$  the multiple heterozygote may be regarded as a backcross for the epistatic lint genes, and the segregation into eighteen plants carrying them and six plants lacking them suggested that only two of these modifiers were concerned. Segregation in the eighteen progenies carrying epistatic genes was difficult to interpret on account of small numbers and absence of a sharp distinction between lintless and partially linted. The fact that the range of the linted  $h_a$  plants went higher in some of the eighteen  $F_2$  families than in others (see Table I) showed also that these epistatic genes were cumulative in effect.

In this material it is obvious to the eye that the range in lint percentage in the partially linted  $h_a$  class is due primarily to variation in the number of lint hairs, that is, in density of hairs per unit area of testa. The epistatic lint genes are ones which determine the outgrowth of epidermal cells on the testa into lint hairs. They are not lint length genes since, as soon as there is a measurable quantity of lint on the seed, its length is within the range of variability of this character shown by the fully linted segregates in the same family (see Table V).

### 3. THE EFFECT OF THE EPISTATIC LINT GENES IN THE $H_a$ GENOTYPE

To determine whether the genes epistatic to  $h_a$  act as lint quantity genes in the normal fully linted  $H_a$  genotype, P 2417, the  $h_a h_a$  plant with 22% of lint, was crossed with an  $H_a H_a$  plant already known to be lacking  $h_a$  modifiers. The latter plant was chosen from a strain of *G. arboreum* var. *cernuum* grown under the type number A 7. This strain, with a lint percentage of 96, was the most heavily linted one available at this Station.

A single  $F_1$  plant of this cross, P 2417  $\times$  A 7, was backcrossed to a single lintless plant of the N 19 strain. The expected genotypic segregation is shown below, where the symbol + is used to denote epistatic lint

genes present, with no implication as to the actual number of these epistatic genes.

Parents	P 2417		A 7	
	$h_a h_a + +$		$H_a H_a 00$	
$F_1$			$H_a h_a + 0$	
Backcross to N 19			$h_a h_a 00$	
Backcross family	$H_a h_a + 0$	$H_a H_a 00$	$h_a h_a + 0$	$h_a h_a 00$
	Both classes hairy lintered, genetically separable only by progeny test		Glabrous partially lintered	Glabrous linterless

The backcross family, which was raised in the greenhouse under as uniform cultural conditions as possible, consisted of 78 hairy ( $H_a h_a$ ) and 92 glabrous ( $h_a h_a$ ) plants (expected 1 : 1). Lint percentage and lint length records are shown in Table V.

Amongst the glabrous-stemmed  $h_a$  progeny, seven were completely devoid of lint and another thirteen had only the very minutest trace of a few hairs. The amount of lint on the remaining seventy-two glabrous plants ranged from 3 to 26%. The demarcation between the thirteen plants with a trace of lint and the least lintered of the seventy-two partially lintered plants was much clearer than the frequency table would suggest. In dealing with the establishment of the lintered  $h_a h_a$  line, it was pointed out that the data implied the presence of very few, probably only two, modifiers. Here again the backcross ratio of 72 lintered : 20 not lintered amongst the  $h_a$  progeny leads to a similar inference.

It will be seen from Table V that in this particular cross the  $H_a$  and the partially lintered  $h_a$  plants were quite distinct in lint percentage range. In lint length there was only a very slight difference, and the greater part of the slightly lower distribution of the  $h_a$  class was associated with the technical difficulty of measuring maximum halo length on a seed with relatively sparse lint. The modifiers appear to act solely as lint quantity genes in the  $h_a$  genotype, and in their presence lint length genes are able to exert their full and independent effect.

Subsequently it was necessary to treat the 78  $H_a$  and the 92  $h_a$  segregates independently.

(a) *The  $H_a$  plants*

To determine the "linterless" modifier content of the hairy plants, their selfed progenies were grown and the incidence of lint amongst their  $h_a h_a$  segregates observed. The seventy-eight progenies were grown in the field, a total of 4114 hairy and 1324 glabrous plants. The amount of lint on glabrous  $h_a$  segregates was estimated by eye in accordance with a series



of five arbitrary grades—3, 2, 1, trace and 0. The visual grading is well correlated with the actual weight of lint, as follows:

Visual grades	Lint percentage	
	Range	Mean
3	30-16	19.7
2	20- 8	11.8
1	11- 3	7.2

In the trace class only a few lint hairs are present, and there is a sharp distinction between this type and grade 1. As it was not possible to weigh individual plants this visual classification was very useful, but for the purposes of this investigation a more accurate estimate of lint development was required. Mean lint percentages for each progeny were therefore obtained on bulks consisting of equal numbers of seeds from all  $h_a$  plants within each progeny (Table VI).

In five of the progenies in the "0" class in the table all  $h_a$  segregates were completely devoid of lint; in the three other progenies in this class, and in all seven of those in class "1", a few of the  $h_a$  plants had a trace of lint. These fifteen progenies which lacked the epistatic genes were quite distinct from the other sixty-three families which segregated for them, and this proportion is very near to the expected in the case of a 3 : 1 backcross ratio indicating two modifiers. All three lines of evidence which have been discussed are therefore confirmatory in indicating the presence of two epistatic genes in this material.

Since it had already been observed that the epistatic genes were cumulative in effect, the above mean lint percentages of  $h_a$  plants were taken as indications of the epistatic lint gene content of the progenies, and were correlated with the lint percentage of their  $H_a$  parent plants. In the correlation, which is shown in Table VII, individuals which fell midway between classes have been entered in the higher class. For the calculation of the correlation coefficient the entries were halved or quartered as necessary.

The value of the correlation was +0.51, with a very high significance ( $P$  much less than 0.01). Since seed size has a considerable influence on lint percentage, the correlation between seed weight and lint percentage for the  $H_a$  plants was also calculated, in order to be sure that the apparent correlation between epistatic gene content and lint percentage was not due to association with changes in seed size. The seed weight-lint percentage correlation was not significant, being only -0.04.

The mean lint percentage of the  $h_a$  progeny was also compared with that of their  $H_a$  sibs within each family (Table VIII).

TABLE VII  
*Correlation between lint percentage of the 78 H<sub>a</sub> backcross plants  
 with mean lint percentage of their h<sub>a</sub> progeny*

Lint percentage of H <sub>a</sub> plants	Mean lint percentage of h <sub>a</sub> progeny																												Total			
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27		28		
59	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2		
58	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	
57	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	
56	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	
55	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	
54	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	
53	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	
52	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	
51	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	
50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	
49	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	
48	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	
47	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	
46	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	
45	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	
44	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	
43	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	
42	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	
41	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	
40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	
39	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
38	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Total	8	7	.	1	2	.	9	12	6	1	6	3	4	3	2	1	1	1	1	1	3	3	.	1	1	1	.	1	1	78		

TABLE VIII  
*Correlation between mean lint percentage of H<sub>a</sub> progeny with lint percentage of h<sub>a</sub> progeny of the 78 H<sub>a</sub> plants*

	Mean lint percentage of h <sub>a</sub> progeny																												Total	
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27		28
64	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
63	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
62	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
60	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
59	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
58	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
57	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
56	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
55	1	.	.	.	.	1	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
54	2	1	.	.	.	.	3	1	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	9
53	1	.	.	.	1	.	.	1	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
52	1	.	.	.	.	1	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
51	2	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	6
50	.	.	.	.	.	1	3	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	7
49	.	.	.	.	.	1	2	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
48	1	.	.	.	.	1	.	1	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
47	1	.	.	.	1	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
46	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
45	.	.	.	.	.	1	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
44	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
43	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Total	8	7	.	1	2	.	9	12	6	1	6	3	4	3	2	1	1	1	1	3	2	.	1	1	1	.	.	1	1	78

The value of the correlation was  $+0.275$  ( $P = 0.02$ ) with no significant contribution to variability from seed weight. This correlation is lower than the one found above but not significantly different from it on the  $z$  test. Both lines of evidence agree in indicating that the amount of lint on the  $H_a$  genotype is correlated with the presence of the  $h_a$  modifiers.

(b) *The  $h_a$  plants*

The 92  $h_a$  segregates in the backcross, with varying amounts of lint presumably dependent upon their content of epistatic genes, were outcrossed with a single unrelated fully linted plant of an Indian strain of *G. arboreum*, N 14. This strain was known to lack epistatic lint genes, since 111  $h_a$  plants of the backcross ( $N 14 \times N 19$ )  $\times$   $N 19$  had all been observed to be completely lintless. Between ten and thirty plants of each outcross progeny were grown, and all were of course normal hairy linted plants. An estimate of the mean lint percentage of each progeny was obtained by weighing a bulk composed of an equal number of seeds from each plant within the progeny, and this was correlated with the mean lint percentage of the  $h_a$  parent plant of that progeny (Table IX).

The correlation was highly significant,  $+0.46$  ( $P$  much less than 0.01). Within this set of progenies there was however a strong negative correlation of 0.55 between seed weight and lint percentage, as is frequently encountered in cotton. Eliminating seed weight, the partial correlation lint percentage of  $h_a$  parent-lint percentage of outcross progeny was raised to  $+0.55$ .

The information derived from the  $h_a$  segregates therefore affords further confirmation of the conclusion that was reached as a result of the investigation of the  $H_a$  plants, that the "lintless" modifiers act as lint quantity genes effective on both the  $h_a h_a$  and  $H_a h_a$  phases of the main gene.

It has been stated above in Section 2, that the epistatic lint genes appear to control the outgrowth of epidermal cells of the testa to form lint hairs. This conclusion was reached primarily as a result of the direct visual observation of variation in amount of lint on  $h_a$  plants. The normal  $H_a$  fully linted plants in this section of the investigation give additional information on this point. The most important components of lint percentage are size of seed and weight of lint. The latter is dependent upon number of hairs per seed, the length of these hairs and their weight per unit length. It has been shown above that seed weight did not contribute to the variability of the lint percentages of the  $H_a$  backcross segregates—that in fact the differences in lint percentage really did

TABLE IX  
*Correlation between lint percentage of the 92 H<sub>a</sub> plants with mean lint percentage of their outcrosses with a single unrelated H<sub>a</sub> plant*

	Lint percentage of H <sub>a</sub> plants																										Total	
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25		26
64	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
63	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Mean lint percentage of outcross progeny

represent differences in lint quantity, as was believed to be the case. The differences in lint quantity were not due to changes in length of the lint hairs. There was actually a very slight but quite insignificant negative correlation between lint length and lint percentage in the 78  $H_a$  backcross plants. It is not easy to obtain reliable estimates of mean hair weight per unit length for single plants. The technique is extremely laborious, and there are no facilities in Trinidad for this type of work. Miss G. G. Clegg, of the Hair Testing Department of the Shirley Institute, very kindly undertook the examination of a limited number of plants, and performed hair weight tests on 100 hairs from four seeds of each of ten plants. Five of these plants were the most heavily linted amongst the seventy-eight  $H_a$  backcross plants, with a mean lint percentage of 56.7, and the other five were the least heavily linted, with only 41.3% lint. Analysis of variance of the results showed that the two groups of plants did not differ significantly in hair weight. Since neither lint length nor hair weight accounted for the differences in ginning out-turn, the genes under investigation must have acted upon the only other remaining variable, density of hairs on the seed coat.

#### 4. LINKAGE RELATIONSHIPS OF THE EPISTATIC LINT GENES

Whenever possible an attempt has been made to determine whether these modifiers of  $h_a$  are associated with major genes. Data available so far are rather fragmentary, since it is only amongst the  $h_a$  segregates in any family that linkage of the modifiers with other genes can be observed. In addition it is in very few families that only one modifier has been segregating, and where more than one was segregating, any association with other genes would in the small numbers available be difficult to detect unless very strong. It is not therefore proposed to present the data in detail, but only to mention that no striking association has been observed between  $h_a$  modifiers and the independent loci  $L$ ,  $Y_a$ ,  $R_2$ ,  $R_3$ ,  $Ne$ ,  $Fz$  affecting respectively leaf shape, petal colour, anthocyanin, leaf nectaries, and fuzz (see Hutchinson & Silow, 1939).

#### 5. THE TAXONOMIC DISTRIBUTION OF LINT GENES EPISTATIC TO $h_a$

The crosses between the original glabrous lintless mutant N 19 and other normally linted strains reported by earlier workers gave clear-cut monofactorial segregation. The normal types which they used were all taxonomically closely related to N 19. When interspecific and inter-varietal crosses were performed it was found that in many of these a proportion of the glabrous-stemmed  $h_a$  segregates were partially linted.

Amount of lint on the  $h_2$  segregates was graded by eye in accordance with the arbitrary scale which has been described above. It should be pointed out that this grading gave no information as to the number of modifiers segregating, since it was not always possible accurately to delimit the partially linted from the completely lintless, though the relative frequency of the latter indicated that only very few modifiers were concerned. In some families the number of  $h_2$  plants investigated was rather low on account of the poor fruiting of some strains and their hybrids under Trinidad conditions. Nevertheless it was always possible to say whether the modifiers were present or absent in any particular family, as will be seen from the representative  $F_2$  segregations shown in Table X.

TABLE X  
*F<sub>2</sub> segregations in some representative crosses between N 19 and fully linted strains*

Cross	Lint % of linted strains	$H_2$ (hairy)	$h_2$ (glabrous)	Grading of amount of lint on $h_2$ segregates						Epistatic lint genes	
				3	2	1	0.5	Trace	0	Not scored	Present
N 19* × A 8†	22	286	78	.	.	.	.	.	78	.	0
N 19 × A 12‡	82	99	34	.	.	.	.	2	30	.	0
N 19 × A 7§	96	857	241	.	.	.	.	39	200	.	0
N 19 × N 3	52	34	14	.	.	.	.	.	11	3	0
N 19 × N 16¶	61	32	8	.	3	4	.	.	1	.	+
N 19 × N 24**	40	568	185	.	10	35	35	20	32	53	+
N 19 × H 17††	25	93	43	9	12	5	.	14	4	.	+

\* N 19, Wagale Lintless. *G. arboreum* v. *neglectum* f. *burmanica* (Burma).

† A 8, Burma Lacinated. *G. arboreum* v. *neglectum* f. *burmanica* (Burma).

‡ A 12, Bengal Commercial Khaki. *G. arboreum* v. *neglectum* f. *bengalensis*.

§ A 7, *G. arboreum* v. *cernuum*.

|| N 3, Nanking Million Dollars. *G. arboreum* v. *neglectum* f. *burmanica* (China).

¶ N 16, Kiangyin Million Dollars. *G. arboreum* v. *neglectum* f. *burmanica* (China).

\*\* N 24, Karungani. *G. arboreum* v. *neglectum* f. *indica*.

†† H 17, Persia. *G. herbaceum* v. *typicum*.

When it became evident that these modifiers of lintlessness act as lint quantity genes in the normal genotype their general taxonomic distribution was investigated. In all eighty-one representative *arboreum* and *herbaceum* strains have been investigated, and the results are presented in summary form in Table XI.

Two facts of considerable importance emerge from this survey:

(1) The ginning out-turn of the strain is no indication as to whether it does or does not carry the particular genes affecting ginning out-turn which have been identified by their epistasy to  $h_2$ .

(2) There is a marked differential varietal and specific distribution of the epistatic lint genes.

It is worth discussing the results in some detail. The original lintless mutation occurred in a Burmese strain of *G. arboreum* forma *burmanica*.

TABLE XI

Data on the taxonomic distribution of lint genes epistatic to  $h_a$  summarized with reference to the ginning out-turn of the strains examined.\*

Ginning percentage Lint percentage	10-16 11-20	17-23 21-30	24-29 31-40	29-33 41-50	34-37 61-60	38-41 61-70	42-44 71-80	45-47 81-90	48-50 91-100	No record	Total number of strains with epistatic genes	
											Present	Absent
<i>G. arboreum</i> v. <i>neglectum</i> f. <i>indica</i>	+	+	+	0	0	0	0	0	0	0	2	18
<i>G. arboreum</i> v. <i>neglectum</i> f. <i>bengalensis</i>	+	+	+	0	0	0	0	0	0	0	0	0
<i>G. arboreum</i> v. <i>cernuum</i>	+	+	+	0	0	0	0	0	0	0	0	2
<i>G. arboreum</i> v. <i>neglectum</i> f. <i>burmanica</i> (Burma)	+	+	+	0	0	0	0	0	0	0	0	8
<i>G. arboreum</i> v. <i>neglectum</i> f. <i>burmanica</i> (China)	+	+	+	+	+	+	+	+	+	+	14	18
<i>G. herbaceum</i> v. <i>typicum</i>	+	+	+	+	+	+	+	+	+	+	11	0
<i>G. herbaceum</i> v. <i>frutescens</i>	+	+	+	+	+	+	+	+	+	+	4	0
<i>G. herbaceum</i> v. <i>africanum</i>	+	+	+	+	+	+	+	+	+	+	4	0

\* For purposes of record it may be stated that the following types were examined. In *forma indica*, Karunganni and Coconadas; in *bengalensis*, sixteen types of Bengalis from Central India, and Commercial Khaki and Bengal 5 from Bengal; in *cernuum* and *burmanica*, various types of taxonomic or genetic interest, mostly from unspecified varieties with the exception of five of "Million Dollars"; in *herbaceum frutescens*, 1027 A.L.F. and Jaywant; other *frutescens* and all *typicum* types tested were of taxonomic or genetic interest from unspecified varieties, and *africanum* types from the bushveld of South Africa.

Eight Burmese strains of *burmanica* tested were found to be lacking the epistatic lint genes, and this is also the case in all eighteen strains of the northern and central Indian forma *bengalensis* which were tested. The same mutation in its completely lintless condition has also been recorded independently in two other strains of *bengalensis* (Hutchinson & Gadkari, 1937). Two strains of var. *cernuum* which is very closely related to forma *bengalensis* also carried no epistatic genes. Within the species *G. arboreum* the most striking result of this survey is the finding that, whereas the northern and central Indian *bengalensis* and *cernuum* and the Burmese *burmanica* all lack the epistatics, the only two strains of the southern Indian forma *indica* tested both carried the epistatics. Agriculturally this is a point of fundamental importance, emphasizing the distinction which Hutchinson & Govande (1938) have already indicated in hair weight and spinning value. It may be mentioned here that the writer has also found (unpublished data) that *indica* strains differ from *bengalensis* and *burmanica* ones and resemble most *herbaceum* types in lacking lint colour modifiers.

There are historical records that cotton has several times been introduced into China from various distinct sources (Watt, 1907; Grumm-Gržimailo, 1934), with the result that a very wide range of types exists there, though all agree in being of very early maturity. Hutchinson & Ghose (1937) have classified the Chinese strains along with the Burmese representatives as forma *burmanica*, chiefly in this case on geographic grounds. There were even genotypic differences between different samples reputed to be of the same commercial strain "Million Dollars". Of five samples tested only one was found to carry the epistatic genes. "Million Dollars" is derived from a field selection of recent and vague origin, and was highly variable in its early stages when several different selections from it were established in various localities. Within the Chinese lots as a whole the occurrence of epistatics was not associated with geographic distribution. The historical records indicate that the two primary routes of importation were overland from Bengal-Assam to the Yellow river basin (presumably *bengalensis* types) and by sea from Indo-China to the Yangtse valley (presumably *burmanica* types, Hutchinson, 1938). The majority of present-day *bengalensis* and Burmese *burmanica* strains appear to lack epistatics, yet types carrying them are common in both the Yellow river and Yangtse basins. This may indicate that some of the Chinese cottons have originated from sources other than those so far suggested, such as the southern Indian *indica*, or the present distribution of epistatics may be the result of local selection trends from the original prototype. The

inclusion of both Burmese and Chinese cottons in forma *burmanica* is evidently not a natural grouping.

The situation in *G. herbaceum* is very distinct from that in *G. arboreum*. Nineteen strains representing the three varieties of *herbaceum* from its entire geographic range were tested, and eighteen of these gave clear indication of carrying epistatic genes. The other strain gave one  $h_a$  segregate classed as 0.5, and an unusually high proportion of "traces" for a family lacking modifiers, and in this case there is a very real possibility that a modifier of low potency was involved.

The arrangement of these strains with reference to their ginning value shows that there was no association between high ginning out-turn and presence of these epistatic genes, which are themselves positive genes affecting lint quantity. In this connexion it must be remembered that a great deal of the indicated differences in ginning out-turn is associated with variability in hair weight, and not necessarily with number of lint hairs.

## 6. DISCUSSION

The particular genes which have been discussed in this paper have been shown to displace both the  $h_a h_a$  and the  $H_a h_a$  phases of the main gene, but their effect on the  $H_a H_a$  phase has not yet been investigated. That the latter phase does not represent full saturation, but is capable of displacement, is evident from the variability in density of lint hairs which exists amongst normal strains of Asiatic cottons. This is shown in the following figures, which have been summarized from Ahmad's (1937) technological report on standard Indian cottons:

Strains	Lint length mm.	Hair weight $10^{-5}$ mg./cm.	Seed weight mg.	Ginning %
Sind, N.R.	15.8-17.9	287-389	50	40
Aligarh, A 19	16.3-18.2	293-363	54	38
Mollisoni	17.4-19.0	271-374	53	32

These strains are all *bengalensis* types and have approximately the same lint length, hair weight and seed size. Since Mollisoni has a considerably lower ginning out-turn than the other two strains, it must have fewer hairs on its seeds. There is no reason to believe that the epistatic genes which are effective in the ranges covered by the  $h_a h_a$  and  $H_a h_a$  phases will not also be capable of exerting their effect in the range covered by the  $H_a H_a$  phase, and it is highly probable that they are in fact members of the gene complex controlling number of hairs on the cotton seed.

Since it has been shown that *bengalensis* types lack the epistatics, the above demonstration of variability in lint hair density within this taxonomic group indicates that there must also be other genes affecting this character. Since they have no effect on the  $h_n h_n$  phase, they may be termed the "hypostatic series".

Furthermore, not only are members of the epistatic series confined to certain taxonomic groups, but it is believed that the hypostatic series must also be synthesized differently in these groups. Most *herbaceum* strains, apart from the Indian strains of var. *frutescens*, are notoriously low ginnerers, and from the material it is obvious that this is more due to sparsity of lint on the seeds than to fineness of lint, though unfortunately figures are not available in support of this statement. These *herbaceum* types carry the epistatics, and their hypostatic component must therefore be much less effective than that of *arboresum* strains. Although it is well known that related strains may differ in their genotypic constitution with reference to quantitative characters, there has hitherto been no evidence that particular members of the complexes controlling such characters are of limited taxonomic distribution, though such an inference would have been justified from the results of Harland's (1936) investigations of the distribution of genes and modifier complexes, most of which concerned non-economic characters in New World cottons. Such information as this indicates that fairly wide crossing, probably with just sufficient but no more backcrossing than necessary to regain a viability balance may provide wide scope for the cotton breeder. As Mason (1938) has pointed out, direct selection in certain areas in very limited material is obviously approaching the limits of its effectiveness. Genetically we have not yet the knowledge that will enable us to say that certain crosses will lead to certain results, and it is probable that plant breeding will always remain a very largely empirical art, but there is abundant genetical support for the belief that wide crossing should provide valuable material for the cotton breeder. It may be countered that species crossing has not so far led to the appearance of any strikingly successful commercial variety, but the greater part of the comparatively rare interspecific hybridization which has so far been performed has been followed by immediate selfing, which, as Harland (1936) has pointed out, leads to the mutual disintegration of the viability balances of the parents. A certain amount of backcrossing would obviate this, but it must be remembered that excessive backcrossing is likely to render the retention of introduced genes of small effect difficult. This investigation has shown however that even varieties of the same species may be differently constituted, and

gives genetic support to Hutchinson & Govande's (1938) plea for the more extensive exploitation of intervarietal crossing in the improvement of Indian cottons. These varieties are not so distinct in their make-up as to lead to breakdown of fertility and viability in their progeny, but such crossing may be the means of bringing together particular genes which do not occur in combination in nature. Templeton (1938) has referred to the appearance, following interstrain crossing in cotton, of characters not obvious in either parent, and says that "as we find with almost all crosses, a character turned up in the new variety which is not found in either parent".

It is interesting that this investigation has confirmed in broad outline Hutchinson & Ghose's (1937) recent reclassification of the Indian and African cottons, which is based on morphological, geographic and agricultural grounds, though it does suggest that in separating the species into varieties primarily on habit and into forms on distribution the more fundamental genetic differences have been subordinated in importance to the acquisition of the annual habit, which is phylogenetically very recent. They refer to the fact that the *arboreums* of forma *bengalensis* are recent invaders of the northern and central Indian cotton-growing tracts, originating from the same stock as that which gave rise to var. *cernuum*. In general these are high ginning types with short coarse lint (Hutchinson & Govande, 1938). They are now shown to lack the epistatic series of lint genes. In all respects they present a striking contrast to the southern Indian forma *indica*, which are medium ginning types with moderately long fine lint. Their genotypic constitution with reference to factors affecting the outgrowth of epidermal cells of the testa to form lint hairs is also shown to be different from that of *bengalensis* and *cernuum* strains, though in this respect *indica* has not been as adequately sampled as other groups. These authors refer to the importance of *indica* types for the improvement of spinning quality of the northern and central Indian cotton strains. The demonstration that their content of genes affecting the density of hairs on the seed coat is distinct from that already present in the northern and central Indian strains suggests that the improvement in the spinning value of the latter need not necessarily be accompanied by an undue decrease in ginning out-turn, since an increased number of lint hairs may to some extent compensate for their reduction in weight.

The genes which have been discussed form a very complex series. It is difficult to specify the exact role of the  $H_a-h_a$  factor pair. That they, like the epistatic and hypostatic series, act on or as hair number and not lint length genes is apparent from their dominance relationship, which has

been investigated by the genotypic testing of 270 plants in eleven related selfed progenies lacking the epistatic modifiers. Three of these progenies (series *a*) were derived from  $H_a h_a$  segregates in the backcross ( $A 7 \times N 19$ )  $\times N 19$ . The other eight (series *b*) were derived from  $H_a h_a$  segregates in the backcross ( $A 7 \times P 2417$ )  $\times N 19$ . Lint percentage and lint length data for the  $H_a H_a$  and  $H_a h_a$  genotypes are shown in Table XII.

TABLE XII  
*Dominance of  $H_a$*

Family no.	No. of plants		Lint percentage			Lint length (mm.)		
	$H_a H_a$	$H_a h_a$	$H_a H_a$	$H_a h_a$	Diff.	$H_a H_a$	$H_a h_a$	Diff.
3564	17	18	53.7	45.3	- 8.4	28.4	28.0	- 0.4
3566	17	31	48.3	39.6	- 8.7	28.4	27.9	- 0.5
3568	15	21	59.4	51.1	- 8.3	27.6	27.1	- 0.5
Total series <i>a</i>	49	70	53.5	44.6	- 8.9	28.1	27.7	- 0.4
3501	6	14	55.2	46.8	- 8.4	27.9	27.9	0.0
3503	2	10	50.5	43.0	- 7.5	28.2	28.0	- 0.2
3505	3	11	73.3	52.7	- 20.6	25.5	26.9	+ 1.4
3532	9	18	62.1	49.5	- 12.6	28.1	28.4	+ 0.3
3543	10	18	58.4	51.4	- 7.0	28.7	29.7	+ 1.0
3555	5	12	68.7	55.8	- 12.9	26.6	27.1	+ 0.5
3556	2	9	67.1	56.6	- 10.5	26.0	26.6	+ 0.6
3559	4	18	53.3	50.4	- 2.9	28.3	28.9	+ 0.6
Total series <i>b</i>	41	110	60.7	50.7	- 10.0	27.4	27.9	+ 0.5

Differences between the genotypes in lint length are very slight, and not consistently in one direction. In lint percentage however the heterozygotes are consistently less heavily linted in each family. The differences are highly significant, being 6.2 times their standard error in series *a*, and 7.2 in series *b*, indicating 83% dominance for  $H_a$ .

It is clear that  $H_a$ , the hypostatics, and the epistatics, all affect the same component of ginning out-turn, lint density. That genes which affect a single character in the same way will be expected to show reductive interaction has been discussed by the author elsewhere (Silow, 1939). Referring to the backcross family ( $A 7 \times P 2417$ )  $\times N 19$  (Table V) in which the epistatic lint genes were segregating, amongst the seventy-eight  $H_a$  segregates fifteen plants were lacking epistatic lint genes; their mean lint percentage was 45.53%. The mean lint percentage of the other sixty-three plants carrying epistatics was 48.09%, a mean increase over the plants lacking epistatics of 2.56%. The difference is reasonably significant, *P* lying between 0.03 and 0.04. Amongst the ninety-two  $h_a$  plants in this same backcross family, the seventy-two partially linted plants had a mean lint percentage of 13.8%. The  $H_a$  plants carrying epistatics and these partially linted  $h_a$  plants are directly comparable in their mean content of epistatic lint genes, being members of the same

backcross family. It may therefore be stated that the epistatic genes whose basal effect on a lintless genotype is 13.8%, have in the  $H_4$  range (40-60%) an effect of only 2.56%, clearly showing the lesser effect in the higher range which would be expected on the basis of reductive interaction. This material appears to be particularly suitable for the investigation of dominance and interaction effects of quantitative genes, and further experiments are in progress.

#### 7. SUMMARY

It has been possible to recognize particular members of the gene complex controlling number of lint hairs on the cotton seed by their effect on the glabrous lintless mutation. The latter was used as an analyser to separate the genes controlling lint development into two series, those hypostatic to it, and those epistatic to it and acting as modifiers. The basic lint percentage effect of a single epistatic gene in the heterozygous phase is about 6-10% on the lintless genotype. The epistatic genes show a reductive interaction with other genes working towards the same effect, so that in the fully linted genotype their effect is less than one-fifth of their basic value.

The epistatic genes are shown to have a clearly defined varietal and specific distribution, not associated with the ginning capacity of the strains in which they occur, showing that in different taxonomic groups a typical quantitative character may be controlled by quite distinct complexes of genes.

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