

# THE GENETICS OF COTTON

## PART XVI. SOME OBSERVATIONS ON THE INHERITANCE OF FORM AND SIZE IN ASIATIC COTTONS<sup>1</sup>

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(With Four Text-figures)

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### INTRODUCTION

IN any project for improvement in commercial cottons problems of inheritance of form and size must play a large part. Agricultural suitability depends largely on leaf form and plant habit, and it is proposed to give an account in what follows of studies of the inheritance of these two characters.

### FACTORS AFFECTING FORM OF LEAF

The genetic behaviour of a multiple allelomorph series of five members controlling the shape of the leaf in Asiatic cottons has been described in a previous paper (Hutchinson, 1934).

Between the three members of this series giving intermediate heterozygotes ( $L^L$ ,  $L$ , and  $l$ ), practically the whole of the difference is accounted for by differences in the amount of growth at right angles to the main leaf veins. Exact comparison of the length of leaf with different allelomorphs is only possible in material differing genetically in  $L$  genes only, since independent genes exist affecting leaf length. A comparison of leaf length of homozygous  $L^L L^L$  with homozygous  $ll$  derived from it by mutation gave

$L^L L^L$	71.2 mm. long,
$ll$	66.1 mm. long,

<sup>1</sup> Read before the Genetics Section, 6th International Botanical Congress, Amsterdam, September 2, 1935.

showing a difference of 5 mm. between them, or about 8 per cent. A similar comparison can be made by inspection of leaves which are bilateral chimaeras. In Fig. 1 are shown two leaves from a sectorial

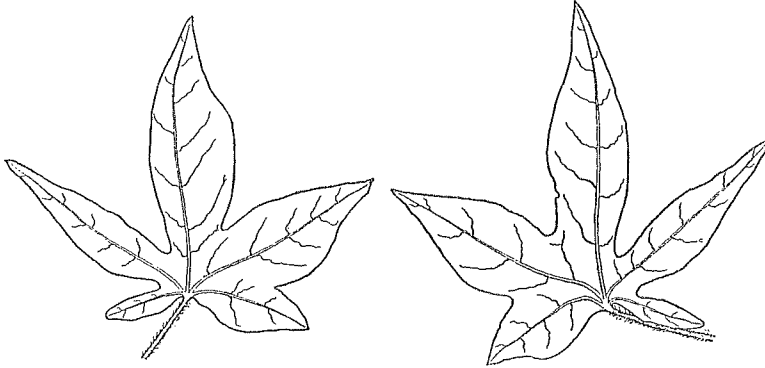


Fig. 1. Curvature of main vein due to differential growth rates in bilateral leaf chimaeras from  $L^L 1$  heterozygotes.

chimaera of  $L^L 1$  and  $ll$  tissue. One half of each leaf is broad ( $ll$  or  $L^B 1$ ) and the other half lacinated ( $L^L 1$ ). The slight curvature of the main vein of each leaf towards the broad side indicates that growth in length is somewhat less on that side, but the difference is small.

The areas of lacinated, narrow, and broad leaves are in approximately the proportion 1 : 1.5 : 2.2. The form of the leaf, therefore, has a very large effect upon its size.

The existence of leaf chimaeras is of importance in the study of the mode of action of genes. In Fig. 2 are shown outlines of three types of



Fig. 2. Three types of leaf chimaeras from  $L^L 1$  heterozygotes.

leaf chimaera observed in cultures of  $L^L 1$  heterozygotes. Since mutant tissue may alter the relation between longitudinal and lateral development in so small an area as a single lobe of a leaf, or on one side of the leaf and not on the other, control must be localised in the developing region, and the co-ordination between neighbouring regions of the same leaf depends upon uniformity of genetic constitution.

Of the Asiatic species of *Gossypium*, only *G. arboreum*<sup>1</sup> carries the genes for laciniated and narrow leaf. In *G. arboreum* these genes have spread widely. Laciniated leaved types form a large proportion of the mixed crop of Assam and Bengal and occur sporadically in the Punjab and the Central Provinces of India where unselected cottons are grown. In the Bombay Presidency a laciniated leaved type of hybrid origin (probably a cross with an Assam type) is being distributed.

Narrow leaf occurs in Assam and Bengal types, increasing in proportion as laciniated decreases, and in Burmese types from the Chin and Pakokku hill tracts (Stock, 1927) which form a natural extension of the Assam cotton tracts. Narrow leaf is rare in, or absent from, other parts of Burma. It is known in China, but appears from the Chinese samples examined to be uncommon there.

In India tracts are known where narrow leaf does not occur (*e.g.* some of the South Indian areas which grow those types of *G. arboreum* usually known as *G. indicum* and *G. obtusifolium*), but there are no areas where narrow leaf occurs to the exclusion of broad leaf. In general, narrow-leaved types predominate in areas of low rainfall and short monsoon, where the crop has to withstand a rapid onset of dry conditions at the time of ripening. Where soil moisture is better maintained at the latter end of the crop season, and where the climate is less extreme, broad-leaved types predominate.

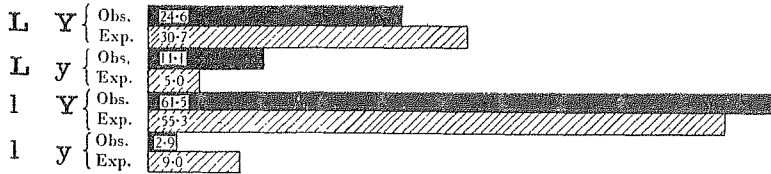
That the distribution of narrow and broad leaf among *arboreum* cottons in India is due to selective influences is shown by the results obtained from a crop analysis study carried out on the Malwa plateau, and in the Nimar valley in Central India. In Fig. 3 are given percentages of narrow- and broad-leaved plants in samples of the cotton crop (excluding introduced American types) taken on the Malwa plateau, the intermediate region of the Vindhya escarpment, and in the Nimar valley. The proportion of narrow-leaved plants rises from about 36 per cent. in Malwa to 63 per cent. in Nimar. In neither area has there been any organised distribution of pure seed, and in both areas, both narrow- and broad-leaved types are known to have been present for a long period, so that it may safely be assumed that the existing proportions fairly represent a condition of equilibrium. It is thus clear that according to conditions, either narrow or broad leaf may have a selective advantage.

A striking feature of the census data is the association which exists between leaf shape and corolla colour. In Fig. 3 are given data for corolla colour as well as leaf shape, and also the figures which would have been

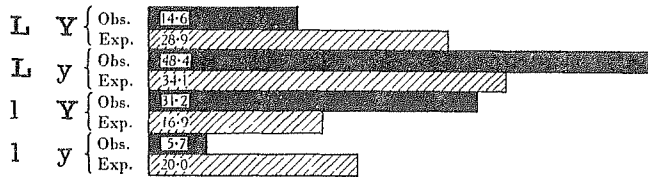
<sup>1</sup> Species and variety names are those given in Harland's (1932) "Genetics of *Gossypium*".

obtained if leaf shape and corolla colour were not associated. It has been shown (Hutchinson, 1934) that there is no linkage between leaf shape and corolla colour. In both areas the association is strong ( $\chi^2=13.5$ , 35.4 and 45.8 in the three examples), the yellow broad and white narrow classes being in excess.

## MALWA



## VINDHYA ESCARPMENT



## NIMAR

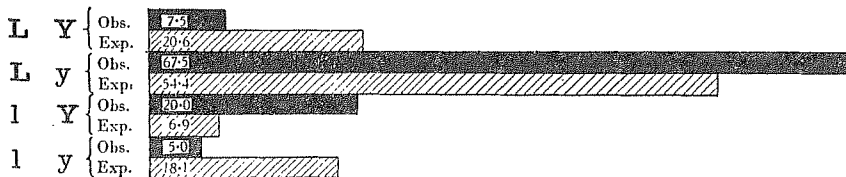


Fig. 3. Observed proportions of leaf shape and corolla colour types in the crops of Malwa and Nimar, and proportions expected on the assumption of independence.

These results are of considerable genetical interest. The great majority of species of *Gossypium*, and practically all primitive types, are broad-leaved, and it may be confidently assumed that broad leaf is a primitive character. In *G. arboreum* two allelomorphous genes have arisen causing progressive narrowing of the leaf lobes. Neither of these genes is as stable as well-established genes of positive selective value might be expected to be, yet both are now widely distributed in the species, and evidence

is presented to show that under certain conditions one of them is at a very considerable selective advantage over the primitive gene.

Considerable differences in leaf shape exist between broad-leaved types of *G. arboreum* and *G. herbaceum*. While the differences between **L** allelomorphs are adequately expressed by measures of lacination, the species differences have comparatively little effect on depth of incision between lobes. The lobes of broad-leaved types of *G. arboreum* are broadly triangular, only slightly constricted at the base, and with acute tips. Those of *G. herbaceum* are rounded, usually constricted at the base, and with blunt or rounded tips. This difference in lobe shape shows typical multiple-factor inheritance, and only general observations on  $F_2$ 's have been made. Its chief interest lies, however, in the fact that a whole group of characters of foliar organs appears to be inherited as a unit. A summary of the characters concerned is given below:

Character	<i>G. arboreum</i>	<i>G. herbaceum</i>
Leaf lobes	Triangular, pointed, not constricted at the base	Rounded, blunt, constricted at the base
Bracteoles	Triangular, longer than broad, enclosing the boll	Rounded, or kidney shaped, broader than long, flaring away from the boll
Petals	Wedge shaped, longer than broad	Rounded, broader than long
Bolls	Tapering, pointed	Round, or parallel sided with prominent shoulders

The genes controlling these characters appear to have a similar effect on all foliar organs, no matter to what purpose they are adapted. This is in striking contrast to the **L** series of genes, the effect of which is confined to leaves only.

#### FACTORS AFFECTING PLANT HABIT

An important character of commercial cottons is branching habit. All cottons produce two types of branches, the main stem and main laterals, which are monopodial, and do not bear flowers; and the fruiting branches, which are sympodial, bearing a flower bud at every node. The length of the vegetative period of a cotton plant depends primarily on the number of nodes formed on the main stem before the development of lateral sympodia begins. The development of the first sympodium marks a sudden change in plant development, since all buds below that point develop, if stimulated, into monopodia, and above that point a sympodium is developed at every node. The number of the node at which the first sympodium is formed gives, therefore, a convenient and easily determined index of a major factor in plant habit.

In general, wild and semi-wild cottons have a high node number, are very late in flowering and are often perennial. The adaptation of cotton to monsoon areas with a short growing season necessitates a low node number, comparatively little vegetative growth, and early flowering.

Two general types of behaviour were observed in crosses segregating for plant habit. In crosses within a species, segregating families exhibited a complete range of habit between the parental types, and usually transgressed the parental limits, but the component characters of plant habit were highly correlated. Plants with high node number had many monopodia, and *vice versa*. Basal monopodia were long, and upper ones short, giving a pyramidal outline to the plant. With low node number, comparatively few monopodial buds developed, whereas with high node number, most of the monopodial buds developed. In interspecific crosses, on the other hand, habit correlations broke down, and plants were obtained with every possible combination of habit characters. Node number is equally easily studied in both types of cross, but while in crosses within a species it is an adequate index of plant habit as a whole, in interspecific crosses it is an index of no more than the initiation of development of flowering parts.

The inheritance of node number was studied in detail in the  $F_2$ 's of five crosses, and in a back-cross of one of the  $F_1$ 's to a parental type. The crosses Cawnpore White  $\times$  N 289 and Burma Ghost  $\times$  N 289 were interspecific. The rest were crosses within the species *G. arboreum*.

Data are given in Tables I and II.

All the  $F_2$ 's transgressed the parental limits at either the lower or the upper end of the frequency array, or both. Very large differences in variance exist between the different  $F_2$ 's, but the size of the variance bears no relation to the magnitude of the difference between the parental means. It must therefore be concluded that node number is controlled by a number of different sets of factors.

All crosses segregated for anthocyanin pigment, and in three crosses (G.S. 2  $\times$  B.G., B.G.  $\times$  C.W., and C.W.  $\times$  N 289) there were significant differences in mean node number between anthocyanin classes. Clearly, C.W., G.S. 2, and A.H. 1-9 carry a gene for low node number linked with the anthocyanin multiple allelomorph series, which is not carried by B.G. and N 289. The difference in mean node number between anthocyanin classes is about 0.8 in crosses giving evidence of segregation in a linked node number factor. As an estimate of the effect of the linked gene, this will be low in proportion to the amount of crossing-over.



TABLE II

*Means, variances, and  $g_1$ 's of node number distributions*

Parents:	Family	Mean	Variance	$g_1$	$g_1/\sigma (g_1)$	$P (g_1)$
A.H. 1-9		17.00	2.80	-0.16	0.24	Large
B.G.		13.94	3.58	-0.50	0.93	0.35
G.S. 2		12.06	0.56	-0.10	—	—
C.W.		9.48	0.59	+0.46	—	—
N 289		7	—	—	—	—
$F_2$ 's:						
G.S. 2 × A.H. 1-9	R	15.65	16.40	—	—	—
	R <sup>s</sup>	15.59	23.09	—	—	—
	Total	15.63	17.96	+2.25	V. large	V. small
G.S. 2 × B.G.	R	14.43	8.75	—	—	—
	r <sup>s</sup>	15.16	8.16	—	—	—
	Total	14.60	8.67	+0.61	5.0	V. small
B.G. × N 289	R <sup>o</sup>	13.29	13.02	—	—	—
	r <sup>s</sup>	13.55	7.42	—	—	—
	Total	13.35	8.04	+0.67	2.73	0.01
B.G. × C.W.	R <sup>s</sup>	10.50	4.69	—	—	—
	r <sup>s</sup>	11.33	3.28	—	—	—
	Total	10.70	4.47	+0.57	3.71	V. small
C.W. × N 289	R <sup>o</sup>	9.40	7.82	—	—	—
	R <sup>s</sup>	8.50	4.15	—	—	—
	Total	9.18	7.03	+2.48	V. large	V. small
(C.W. × N 289) × C.W.	R <sup>o</sup>	8.17	3.34	—	—	—
	R <sup>s</sup>	7.81	3.12	—	—	—
	Total	7.98	3.19	+0.63	10	V. small

Similar information is provided by data for three crosses segregating for corolla colour.

Cross	M (Y)	M (y)	$d$	$P$
G.S. 2 × B.G.	14.63	14.04	+0.59	0.1
B.G. × N 289	12.83	15.05	-2.22	0.01
C.W. × N 289	8.61	10.53	-1.92	0.01
(C.W. × N 289) × C.W.	7.61	8.33	-0.72	0.01

Significant differences in mean node number exist between corolla colour classes in B.G. × N 289 and C.W. × N 289, but not in G.S. 2 × B.G. N 289, therefore, carries a gene for low node number in the same chromosome as corolla colour, which is not carried by B.G., C.W., or G.S. 2. The difference between corolla colour classes in B.G. × N 289 and C.W. × N 289 is about two nodes.

Differences between means of classes are about one-third as great in the back-cross as in the  $F_2$ , both in anthocyanin pigment and corolla colour. With no dominance they would be expected to be one-half as great, so that the effects of dominance cannot be very great.

Fisher's  $g_1$  (see Fisher, 1934) was calculated for the parental,  $F_2$  and back-cross distributions in order to give an estimate of asymmetry.



In the parental types there was no evidence of asymmetry. All the  $F_2$ 's and the back-cross gave large and significant positive  $g_1$ 's. Asymmetry of the  $F_2$  distribution may be caused either by dominance or by the interaction of factors being such that a given factor difference is greater at the upper end of the frequency distribution than at the lower end.

The best available evidence on dominance is afforded by a comparison of the  $F_2$  and back-cross of C.W.  $\times$  N 289. Below are given the variances,  $g_1$ 's, and the differences between the means of classes in the  $F_2$  and the back-cross:

Family	Variance	$g_1$	Mean	$R^o-R^s$	$Y-y$
$F_2$	7.03	+2.48	9.18	+0.90	-1.92
Back-cross	3.19	+0.63	7.98	+0.36	-0.72

The ratio of the genetic variance of  $F_2$  to that of a back-cross with different degrees of dominance is illustrated in Fig. 4. With complete dominance the genetic variance of a back-cross to the dominant parent is zero, and  $\frac{V(F_2)}{V(B.C.)}$  becomes infinity, while in a back-cross to the

recessive parent the genetic variance of the  $F_2$  will be three-quarters that of the back-cross. With no dominance the genetic variance of the  $F_2$  will be double that of the back-cross. In the present case  $\frac{V(F_2)}{V(B.C.)} = 2.20$ .

Variance due to non-genetic causes may be assumed to be equal in  $F_2$  and back-cross, so that an allowance must be made for it in calculating dominance. Allowing 0.59 ( $=V$  of C.W. parent), the ratio is raised to 2.48. This is probably a fair estimate. As an upper limit, twice the variance of the C.W. parent may be allowed, giving a ratio of 2.91. Even with this allowance, dominance must be slight. Skewness due to dominance is to be expected in  $F_2$  only, a back-cross giving a symmetrical genetic distribution. In the present case skewness is much less in the back-cross than in the  $F_2$ , but it remains definitely significant. It is therefore probable that node number genes are geometric rather than additive in their effect.

Rasmusson (1935) has stressed the importance of interaction between factors in quantitative inheritance. In the back-cross of (C.W.  $\times$  N 289)  $\times$  C.W. the class numbers are large enough to make worth while the estimation of interaction between leaf shape and corolla colour, with which node number genes are linked. The means and class frequencies of the four classes were:

	Mean	Frequency		Mean	Frequency
$R^oY$	7.789	356	$R^sY$	8.524	374
$R^o y$	7.427	356	$R^s y$	8.144	403

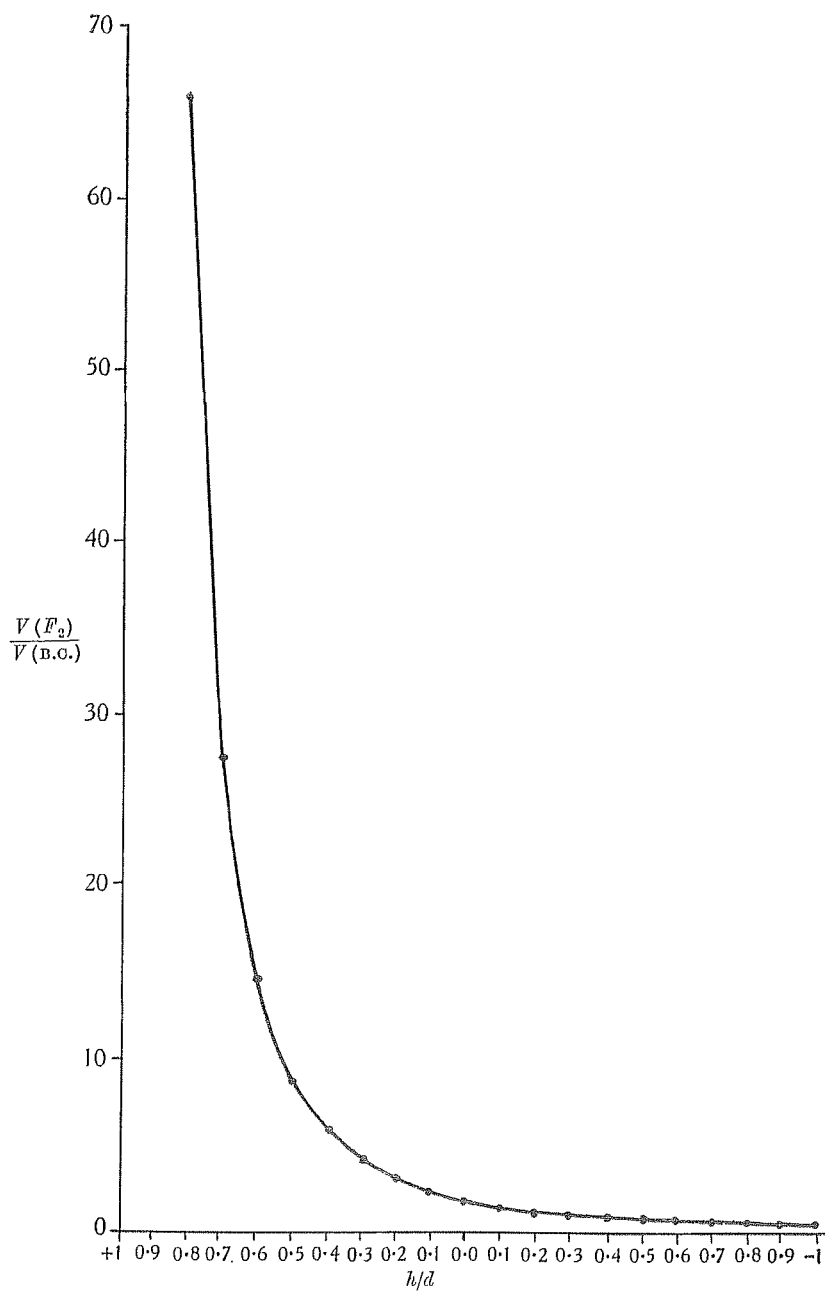


Fig. 4. Ratio of variance of  $F_2$  to variance of backcross with different degrees of dominance.

The analysis of variance gave the following:

	Sum of squares	Degrees of freedom	Mean square	$\frac{1}{2} \log e$	$z$
Within classes	4505.24	1485	3.03	0.550	1.648
Between classes	243.42	3	81.14	2.198	
Total	4748.66	1488			

The individual factor effects have already been studied. The significance of interaction can be tested by comparing the difference of the differences between the class means with its standard error by the  $t$  method (see Yates, 1934). The difference of the differences is 0.0178, and its variance is the within classes mean square multiplied by a quarter of the sum of the reciprocals of the class numbers.

Difference	0.0178
$V$ (diff.)	0.0082
$\sigma$ (diff.)	0.0903
$d/\sigma$	0.2
$P$	0.8

Clearly, there is no interaction between node number genes linked with corolla colour and with anthocyanin pigment. The cross C.W.  $\times$  N 289 also segregated for the **L-1** leaf-shape factor pair. In  $F_2$  the mean node numbers of the **L** and **l** classes were

	$M$	$V(M)$
<b>L</b>	9.35	0.057
<b>l</b>	8.17	0.141
Diff.	1.18	$V$ (diff.) 0.198
$d/\sigma(d)$	2.65	
$P$	0.01	

The narrow-leaved class had a mean node number higher by one node than the broad-leaved class. The difference is significant. The back-cross was made to the **L** parent, and though the **Ll** heterozygote is intermediate in leaf shape between the homozygotes, it is not possible to separate the **LL** and **Ll** classes. The correlation between leaf shape and node number was therefore calculated in each of the four anthocyanin and corolla colour classes. The following correlations were obtained:

Class	$r$	$P$
<b>R<sup>c</sup>Y</b>	+0.134	0.01
<b>R<sup>c</sup>y</b>	+0.089	0.08
<b>R<sup>a</sup>Y</b>	-0.026	0.57
<b>R<sup>a</sup>y</b>	+0.041	0.42

Correlation only exists in **R<sup>c</sup>** classes. There was, therefore, interaction between the node number factors situated in the **R<sup>c</sup>** and **L-K** chromosomes.

#### DISCUSSION

The results described show clearly the many different types of inheritance involved in the control of form in cotton. Simple inheritance

of allelomorphic genes affecting only the rate of growth at right angles to the main leaf veins is matched by a group of genes of small individual effect influencing all foliar organs. In plant habit the controlling mechanism differs so greatly between species that the normal habit correlations are broken down in interspecific crosses, though individual genes, so far as they can be studied through their linkage with simply inherited characters, behave in the same way whether the cross is within or between species.

The work of Rasmusson (1935) is supported by the demonstration that there is a general interaction between individual genes affecting node numbers and the rest of the node number component of the genotype, so that the magnitude of the factor difference depends upon the position in the node number range at which it occurs.

The simple nature of the inheritance of the main leaf-shape difference, and the demonstration of widely different population compositions in neighbouring areas leads to the hope that valuable information can be gained concerning the selective values of form factors in crops at present untouched by the plant breeder.

#### ACKNOWLEDGMENTS

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For the data on gene distribution, I am indebted to Mr R. L. M. Ghose, of the Institute of Plant Industry, Indore, Central India.

#### REFERENCES

- FISHER, R. A. (1934). *Statistical Methods for Research Workers*, 5th ed. Oliver and Boyd.
- HARLAND, S. C. (1932). "The genetics of *Gossypium*." *Biblogr. genet.* **9**, 107.
- HUTCHINSON, J. B. (1934). *The Genetics of Cotton*, Part X. "The inheritance of leaf shape in Asiatic *Gossypiums*." *J. Genet.* **28**, 437.
- RASMUSSON, J. (1935). "Studies on the inheritance of quantitative characters in *Pisum*. I. Preliminary note on the genetics of time of flowering." *Hereditas*, **20**, 161.
- STOCK, T. D. (1927). "The indigenous cottons of Burma." *Mem. Dept. Agri. Ind. Bot.* **14**, 177.
- YATES (1934). "The analysis of multiple classifications with unequal numbers in the different classes." *J. Amer. statist. Ass.* March, 1934.