THE MODIFIER CONCEPT. A DEVELOPMENTAL ANALYSIS OF LEAF-SHAPE 'MODIFICATION' IN NEW WORLD COTTONS

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(With Ten Text-figures)

I. The general problem

The modifier concept of speciation as applied to the genus *Gossypium* has been clearly stated by Harland (1937, 1939). It is as follows:

'Different species in the genus *Gossypium* are characterized by what may be termed differences in genetical architecture. It may be assumed that each species has a large number of genes, most of which have only a minute physiological or morphological effect; that these genes constitute a harmoniously working system as a result of natural selection and that the particular association of genes in two species may be so different as to lead to disharmonious combinations as a result of crossing' (1937). '...the genetical architecture of species...may be viewed as great systems of co-ordinated modifiers' (1939).

This concept has proved to be extraordinarily useful in the genetic analysis of the genus. A direct result has been the adoption of the 'transference technique' which is a process of repeated backcrossing with the purpose of transferring an unknown gene from one species to another where it can be tested against standard alleles. Genetic analyses which transcend the limits of a single species are thus facilitated, providing the cytological limitations are borne in mind (Stephens, 1944*b*). From the practical point of view the transference technique has been used by Knight (1939) to introduce special characters from one species of *Gossypium* into economic strains of another in which these characters are absent. In its widest aspect the modifier concept has been used in detailed determinations of degree of speciation (Harland, 1939; Silow, 1944) and for testing Fisher's theory of the evolution of dominance (Fisher, 1930; Harland, 1932, 1934; Hutchinson & Ghose, 1937).

More recently Mather (1943*a*, *b*) has developed a general theory of inheritance from what was initially a similar concept. He draws a distinction between 'oligogenes' (main genes) which have large effects and 'polygenes' (modifiers) 'the effects of which are so small as to be individually unrecognizable'. Waddington (1943) has criticized the advisability of this distinction on the ground that one and the same gene may be regarded as an oligogene in so far as it affects one particular character while it may behave polygenically in effects on others. The distinction would appear to lie in the type of character studied rather than in the type of gene concerned. Furthermore, since so little is yet known about the physiological mechanism of gene action it would seem dangerous to assume that the magnitude of a gene's effect on any single character gives an indication of its importance to the genotype as a whole. One may be observing only a minor pleiotropic expression. The position has perhaps been stated most clearly by Dobzhansky (1941):

'Detailed studies tend to show that modifiers are not a class of genes subsidiary to

others, but merely genes with manifold effects which influence, *among other things*, the expression of certain mutants at other loci' (italics inserted).

These differences of opinion only serve to emphasize the need for a new approach to what is a fundamental problem in genetics. Developmental studies of gene action furnish a possible line of attack, and these will be considered in this paper.

II. The particular problem

In the case of most allelomorphic character differences in *Gossypium* it is found that crosses within the limits of a single species give clear segregations in F_2, but that crosses involving parents from different species do not, owing to increased variability and overlapping of the main segregating classes. In such crosses, unless the parental characters are very widely different, F_2 segregations cannot be analysed. According to Harland's conception of speciation in *Gossypium* which has been quoted at length in the previous section, the increased variability in F_2 is due to segregation of modifiers—the different species having accumulated widely different modifier combinations during their evolution. As a further consequence, a 'shift'* in expression of a character is frequently observed when that character is transferred by repeated backcrossing from one genotype to another. For example, Harland (1935) showed that the large petal spot of *G. arboreum* became reduced when transferred to *G. hirsutum*, and Silow (1944) finds in general that the level of expression of *G. herbaceum* lint-colour genes becomes intensified on transference to *G. arboreum*. According to the modifier concept, each species has a characteristic modifier level associated with each 'main' gene locus. Change of species background therefore brings about a plus or minus modification of the 'main' gene under test. It will be seen later that although shift is more typical of interspecific crosses, it can also occur when the parents belong to the same species.

It is clear that a mere recording of the direction and amount of shift, or of the extent of blurring exhibited by the main classes in F_2 segregations provides little evidence as to the nature of modifiers and how they work. What is required is a developmental study of 'main' genes on different modifier backgrounds in order to find out *how* their development is affected. Suitable material for such a study is provided in *Gossypium* by the leaf shape alleles, since it has been shown (Stephens, 1944*a*) that the development of leaf shape, i.e. the progressive change in shape from node to node of the main stem, is characteristic for each leaf-shape allele and can be represented graphically by a 'developmental track'. By comparing tracks of the same alleles on different genotypic backgrounds, modifications of the course of development can be readily observed.

III. The mechanism of leaf-shape modification

A genetic analysis of leaf shape inheritance in New World cottons (Stephens, 1944*b*) led to the conclusion that crosses within a single species gave clear leaf-shape segregations in F_2 with little or no modifier disturbances. A typical example is provided by the leaf

* This term was first used by Engledow (1920, 1923) to describe the behaviour of certain interspecific F_2 segregations in *Triticum*. In crosses which exhibit shift, one or both of the parental types can only be recovered in a modified form in F_2 and subsequent generations. Darlington (1928) attributed this phenomenon to autosyndetic pairing in polyploids, but there is some evidence to show that this mechanism cannot apply universally. Shift is of very general, not sporadic occurrence in segregations of quantitative characters in cereals and is found in the diploid *Hordeum* as well as in the polyploid genera, *Triticum* and *Avena* (Bell & Carson, 1941). In the writer's opinion recombination of modifiers as found both in diploid and 'tetraploid' *Gossypium* species furnishes a mechanism of more general applicability.

index correlation in Table 1. It was also noticed in such crosses, that when the flowering habits* of the parents differed appreciably, leaf-shape segregation remained clear *but one or both of the extracted parental types exhibited shift*. In interspecific crosses variability in F_2 was increased (cf. Tables 1 and 2), and as a result, if the parental alleles did not differ greatly in effect, integradation occurred in the segregating classes, rendering analysis by this method impossible. In interspecific crosses, therefore, shift could not always be detected.

Since shift in leaf shape is known to be in some way associated with parental differences in flowering habit, a comparison of the developmental track of a standard allele on an early-flowering background with the corresponding track on a late-flowering background is of special interest. A case of shift suitable for investigation is provided by the 'Jamaica Xerophytic' and '*darwinii*' leaf shapes which have been described in an earlier paper (Stephens, 1944*b*). On their original, late-flowering backgrounds their climax leaf shapes are distinct, Jamaica Xerophytic carrying a broader leaf than *darwinii* (cf. Fig. 1*a*, *c*). Transference to a common early-flowering (Upland) background narrows the Jamaica Xerophytic leaf appreciably, but slightly broadens the *darwinii* leaf. As a result of these

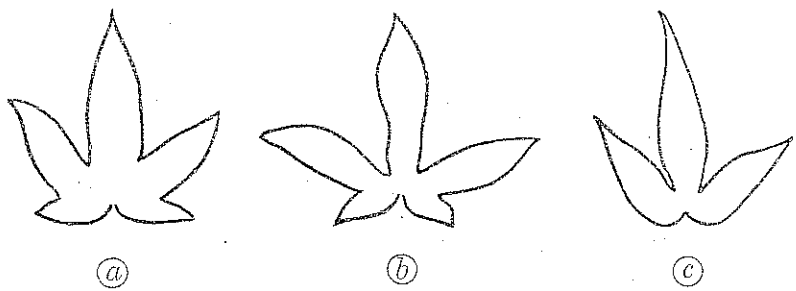

Fig. 1. Leaf outlines of (*a*) Jamaica Xerophytic, (*b*) Okra, (*c*) *darwinii*. Transferred to an early-flowering background the late-flowering types (*a*) and (*c*) closely resemble (*b*) in leaf shape.

shifts the transferred leaf types very closely resemble each other and also a third leaf type, Okra (Fig. 1*b*). In fact the three types are probably determined by the same leaf shape allele, L^0 (Stephens, 1944*b*).

Plants with the original and transferred leaf types were available for developmental analysis. In each type measurements were based on the leaves of twenty-four plants grown in replicated and randomized plots. Developmental tracks of Jamaica Xerophytic and *darwinii* are shown in Figs. 2 and 3 respectively. In each case the total length of track plotted includes development from the first to the climax leaf. Unfortunately, when the climax leaf was reached in the transferred types at node 13, measurements of the untransferred types were discontinued and the only further measurements available were the dimensions of their climax leaves. The dotted portions of the tracks can therefore only be regarded as approximate, though measurements of the same types available from other experiments confirm that the course of development shown is reasonably accurate. In both figures it can be seen that though the course of the track is not altered appreciably, transference from early- to late-flowering background has accelerated the rate of leaf

* It should be explained that early- versus late-flowering habit in *Gossypium* is determined by the serial number of the node on the main axis at which the first flowering branch (sympodium) is produced. In early-flowering (annual) types the first sympodium may be produced as early as node 4.

Table 1. *Correlation table obtained by plotting climax leaf indices* of an F_2 segregation from the cross Upland* (ll) × '*transferred*'† darwinii (L^0L^0)

Index D \ Index C	0·02	0·04	0·06	0·08	0·10	0·12	0·14	0·16	0·18	0·20	0·22	0·24	0·26	0·28	0·30	0·32	0·34	0·36	0·38	0·40	0·42	0·44	0·46	0·48	0·50	0·52	0·54	0·56	0·58	0·60	Total
0·60																													1		1
0·58																										1		1	1		3
0·56																								1		2					3
0·54																															
0·52																							1			2		1	1		6
0·50																									1	1					2
0·48																										1			1		1
0·46												2	3	3	2	1														11
0·44												1		2	1	1														5
0·42										1	2	2	1			2														8
0·40										2	1	2	3	1																9
0·38												1	1																	2
0·36								2		1																				3
0·34							1	3				1																		5
0·32						1	3		1																					5
0·30						1	1																							2
0·28						3																								3
0·26																														
0·24																														
0·22																														
0·20																														
0·18																														
0·16																							1	1	2		6		3	3	69
Total						5	5	5	1	4	3	9	8	6	3	4															

* Index C = sinus length/leaf length. Index D = lobe width/leaf length. For further details see Stephens (1944 *b*).
† I.e. the *darwinii* leaf shape transferred to an Upland (*hirsutum*) background. The cross is therefore intraspecific.

Table 2. *Correlation table obtained by plotting climax leaf indices of an interspecific F_2 segregation Upland* (ll) × darwinii (L^0L^0). (*Compare with Table* 1, *where an* intra-*specific segregation of the same alleles is shown*)

Index D \ Index C	0·02	0·04	0·06	0·08	0·10	0·12	0·14	0·16	0·18	0·20	0·22	0·24	0·26	0·28	0·30	0·32	0·34	0·36	0·38	0·40	0·42	0·44	0·46	0·48	0·50	0·52	0·54	0·56	0·58	0·60	Total
0·60	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
0·58	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
0·56	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
0·54	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1
0·52	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	2
0·50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	.	.	1	1	.	.	5
0·48	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	1	5
0·46	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	2
0·44	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	3
0·42	.	.	.	.	.	.	.	.	.	.	1	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
0·40	.	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	5
0·38	.	.	.	.	.	.	.	.	1	1	1	3	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11
0·36	.	.	.	.	.	.	1	.	.	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
0·34	.	.	.	.	1	.	2	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
0·32	.	.	.	1	2	.	2	2	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
0·30	.	.	.	.	.	1	.	1	1	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
0·28	.	.	.	.	1	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
0·26	.	.	.	.	1	1	3	1	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9
0·24	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
0·22	.	.	1	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
0·20	.	.	.	1	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
0·18	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
0·16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Total	.	.	1	2	8	4	9	5	5	11	5	13	2	5	.	.	.	.	1	2	2	2	2	2	.	2	1	2	.	1	87

shape development considerably. In Fig. 2, for example, the position on the track corresponding to the 13th node on the late-flowering background (*a*) is reached at the 6th node on the early-flowering background (*b*). However, the shape of the climax leaf is not solely determined by the rate at which development proceeds, but is also dependent on the number of nodes over which it continues. Evidence has been presented elsewhere (Stephens, 1944*a*) that leaf-shape development under normal conditions of growth does not continue indefinitely, but is arrested soon after the plant enters the flowering phase. This seems likely to be connected with the deflexion of food material from the apical

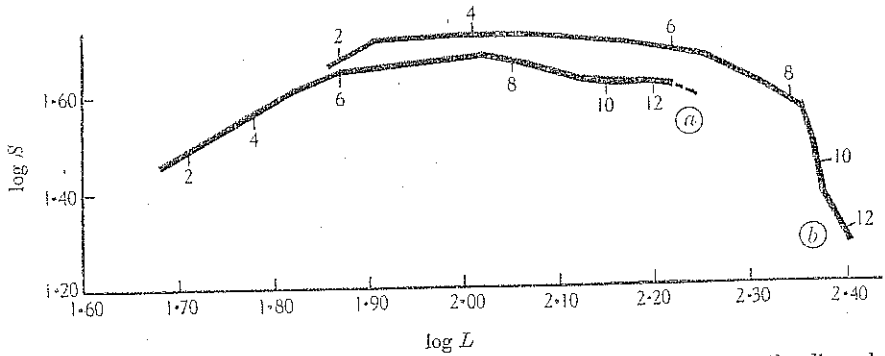

Fig. 2. Developmental tracks of the Jamaica Xerophytic leaf-shape allele from the first to the climax leaf (*a*) on its own late-flowering background, (*b*) transferred to Upland (early-flowering) background. The figures indicate nodes.

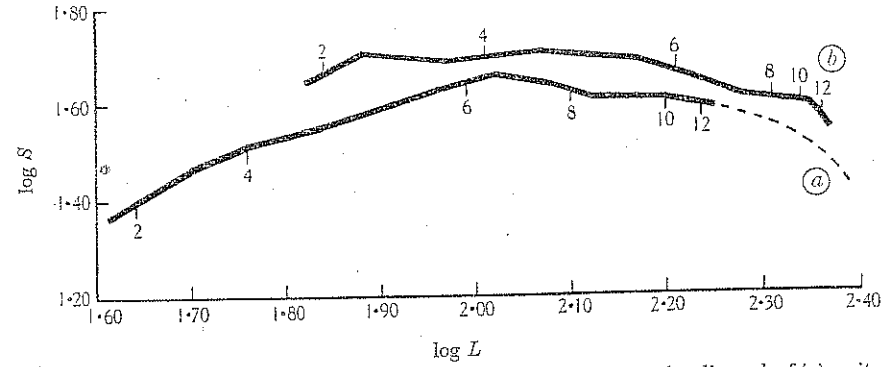

Fig. 3. Developmental tracks of the *darwinii* leaf-shape allele from the first to the climax leaf (*a*) on its own late-flowering background, (*b*) transferred to Upland (early-flowering) background. The figures indicate nodes.

meristem to the rapidly forming flower buds which was observed by Mason (1922). At this stage the climax leaf occurs,* and leaves produced subsequently show only minor and random fluctuations in shape. It is clear then that although leaf-shape development will proceed more rapidly on an early-flowering background, it will be arrested at an earlier node, since genes which accelerate flowering accelerate leaf-shape development but by the same process arrest that development at an earlier stage. *In other words, an 'automatic' compensation exists which tends to buffer the shape of the climax leaf against changes in flowering habit.*

* This has since been confirmed independently by examining a first backcross family, Upland (early flowering) →Bourbon (late flowering). It was found that the numbers of the nodes at which the climax leaf and the first flowering branch were formed were highly correlated ($r = 0{\cdot}6736$, significance at 1 %).

Now there is no reason to suppose that this compensation will be exact, i.e. that acceleration of leaf-shape development will be *proportional* to acceleration of flowering. In the present instance the first flowering branches in Jamaica Xerophytic, *darwinii* and Upland (early-flowering background) were produced at nodes 16, 22 and 7 respectively. Transference of the Jamaica Xerophytic leaf shape to Upland background therefore involved a smaller change in flowering habit than did transference of the *darwinii* leaf shape. But, on the other hand, acceleration of leaf-shape development was much greater in the former than in the latter transference (cf. Figs. 2, 3). It may be concluded that in the Jamaica Xerophytic transference, change in flowering habit was *over*-compensated by acceleration in leaf-shape development, with the result that the developmental track was extended and the climax leaf consequently narrowed. In the case of the *darwinii* transference *under*-compensation occurred, so that the developmental track was diminished in length and the climax leaf broadened. On this interpretation shift is a measure of failure of adjustment between stage of leaf-shape development and initiation of flowering.

Table 3. *F_2 segregations in flowering habit scored by recording 1st flowering node number. The figures represent the percentage frequency in each class. The original parental classes are indicated by bold type.*

EF = early-flowering type; MF = medium-flowering type; LF = late-flowering type.

Type of crosses and parents	1st flowering node number classes in F_2														Size of family
	−6	−8	−10	−12	−14	−16	−18	−20	−22	−24	−26	−28	−30	30+	
(A) Intra-*hirsutum*:															
Upland (EF) × *punctatum* (EF)	2	77	19	2	.	.	.	.	.	.	.	.	.	.	93
Upland (EF) × *laitense* (MF)	.	7	**31**	37	14	5	4	**1**	.	1	.	.	.	.	183
m. galante (MF) × *m. galante* (LF)	.	.	.	1	3	12	**20**	17	14	9	6	2	5	**11**	65
(B) Intra-*barbadense*:															
V135 (EF) × MSI (EF)	.	1	**30**	**64**	5	.	.	.	.	.	.	.	.	.	250
V135 (EF) × Ecuador wild (LF)	.	2	**11**	22	28	16	7	6	4	1	.	1	1	**1**	178
(C) *hirsutum* × *barbadense*:															
Upland (EF) × V135 (EF)	3	**52**	**42**	2	1	.	.	.	.	.	.	.	.	.	200
laitense (MF) × V135 (EF)	.	2	6	18	26	11	8	7	11	4	2	2	1	2	99
m. galante (LF) × V135 (EF)	.	.	1	2	4	12	20	13	15	9	3	3	3	15	117
m. galante (LF) × Grenadines Naked (MF)	.	.	.	.	1	5	18	**26**	20	6	5	5	1	13	147

It will be remembered that in crosses within the same species, shift occurs in F_2 unaccompanied by any large increase in the variability of the segregating classes. At first sight it would be expected that the segregation of genes controlling flowering habit would provide an array of different backgrounds, in each of which a different degree of adjustment could occur, and hence a different climax leaf shape. The main segregating leaf-shape classes should therefore show increased variability. In Table 3, sections A and B, flowering habit data from intra-*hirsutum* and intra-*barbadense* F_2's are presented. It can be seen that when both parents are early flowering, practically no habit segregation occurs, and even when the parental habits differ considerably, the late-flowering class is rarely recovered. Owing to this dominance of early- over late-flowering habit the leaf-shape classes in F_2, whether shifted or not, will not show greatly increased variability.

On the other hand, in crosses between species (Table 3, section C) the early-flowering habit is far less dominant, and transgressive segregation often occurs. This should contribute to the increased leaf-shape variability which is characteristic of interspecific crosses, and the question arises as to whether it is a source of major importance. As has been seen, variation in flowering habit does not alter the course of leaf-shape development but only the rate at which it occurs (Figs. 2, 3). If, therefore, variation in habit is the

chief source of modification in interspecific crosses, the intergrading classes in F_2 which are obtained by leaf index measurements or visual examination, should be amenable to analysis by developmental methods, because the tracks corresponding with each class should have a distinct form although the end-points (determined by rate of development) vary. Accordingly, a test was carried out on a small F_2 family, *hirsutum* (Guatemala Khaki (ll)) × *barbadense* (Sea Island (L^EL^E)), consisting of twenty plants grown in large buckets. Five plants of each or the parental strains were grown alongside under similar conditions. The Guatemala Khaki and Sea Island parents produced flowering branches at nodes 4 and 5 respectively, without variation. Flowering habits of the F_2 plants showed the following range:

Node number	4	5	6	7	8	9	10	11	Total
Frequency	3	10	2	4	—	—	—	1	20

In all plants flower buds were removed as fast as they were formed—the normal restriction on leaf-shape development thus being avoided. Even under these favourable conditions for vegetative growth, no clear separation into the three leaf-shape classes, ll, L^El, L^EL^E,

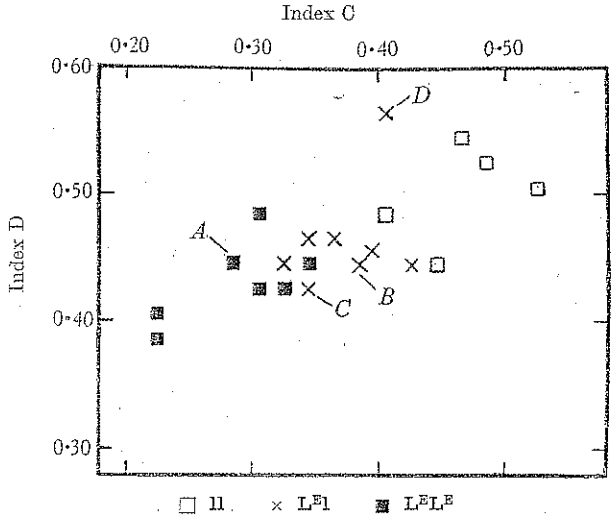

Fig. 4. Correlation diagram of leaf indices obtained from leaves at the 14th node in the F_2 Guatemala Khaki (ll) × Sea Island (L^EL^E). The classes integrade and, as explained in the text, can only be distinguished by developmental analysis. The lettered entries, *A*, *B*, *C* and *D*, correspond to the tracks shown in Fig. 10.

could be made either by visual classification or by plotting leaf indices (Fig. 4). However, by plotting* developmental tracks for each plant individually, separation was facilitated. Developmental tracks of the parents and of the F_2 plants are shown in Fig. 5, 6 and 7–10 respectively. To aid comparison the approximate limits of the parental tracks are indicated by broken lines in the appropriate F_2 figures.

Comparison of the parental tracks shows that they are clearly distinct and, bearing in mind that they are plotted from single plant data, remarkably uniform in each case. The important distinction between the parents is that the Guatemala Khaki (ll) tracks are linear, those of V 135 (L^EL^E) non-linear. On examining the tracks or the F_2 plants it was found that five were readily classified as ll since they were approximately linear (Fig. 7). All the other tracks were markedly non-linear. By 'matching' them with the tracks of

* The tracks were smoothed by plotting running means of leaf dimensions at consecutive nodes.

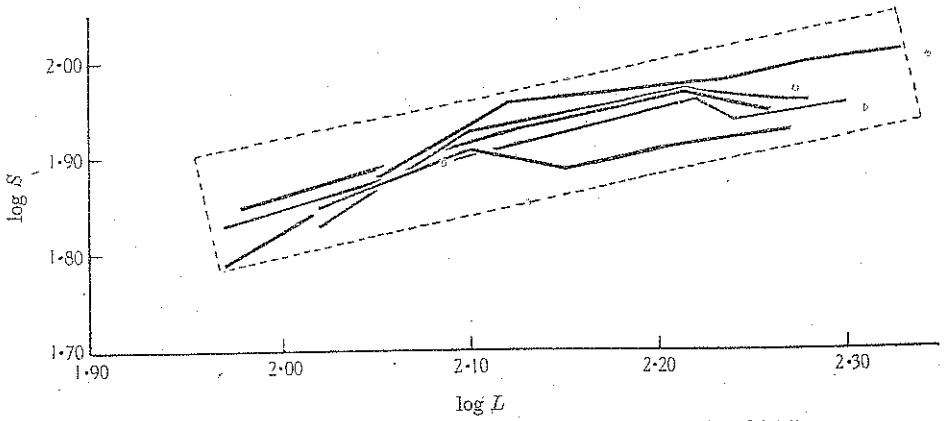

Fig. 5. Developmental tracks of individual plants of Guatemala Khaki (11).

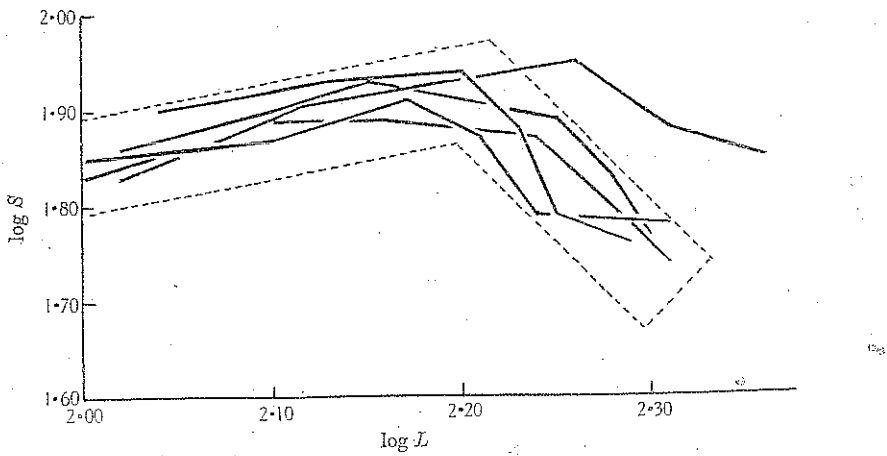

Fig. 6. Developmental tracks of individual plants of Sea Island ($L^E L^E$).

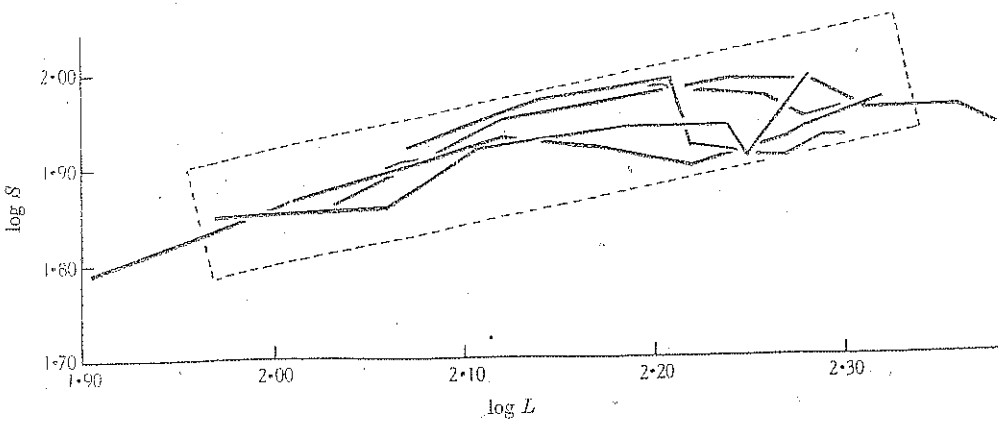

Fig. 7. Extracted 11 types in F_2 Sea Island × Guatemala Khaki.

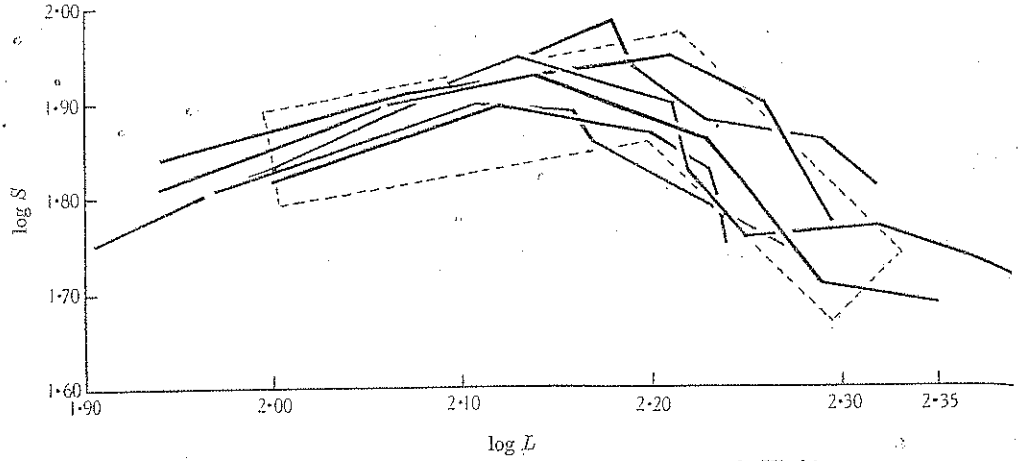

Fig. 8. Extracted $L^E L^E$ types in F_2 Sea Island × Guatemala Khaki.

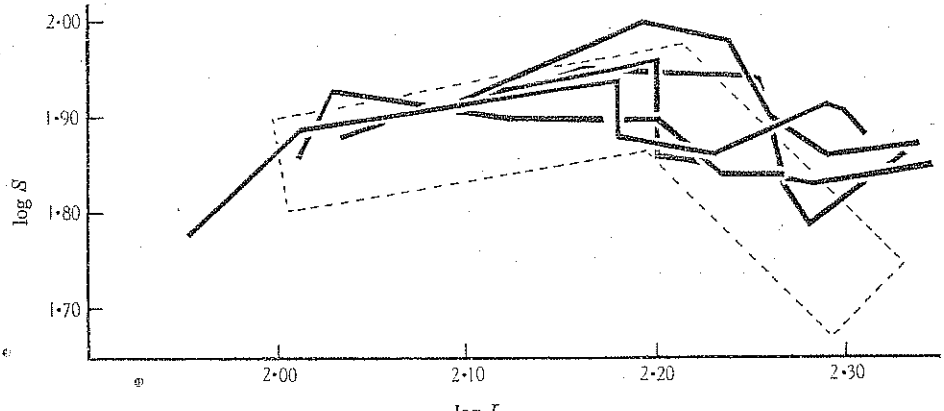

Fig. 9. $L^E l$ heterozygous types in F_2 Sea Island × Guatemala Khaki.

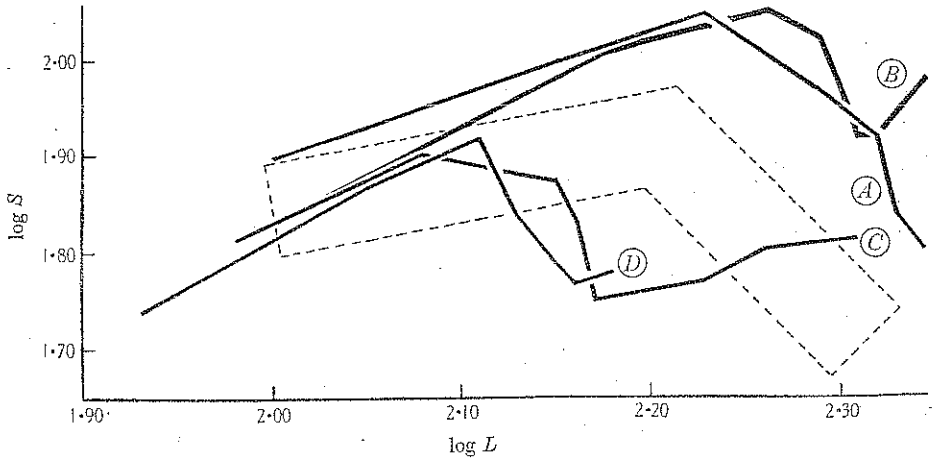

Fig. 10. Developmental tracks of four plants not readily classifiable in F_2 Sea Island × Guatemala Khaki. (Further explanation in text.)

the V135 parent, six could be selected with some confidence as belonging to the L^EL^E class (Fig. 8). Of the remaining nine tracks, five followed a course intermediate between those of the parents and could reasonably be classified as L^El (Fig. 9). Four tracks (Fig. 10) were not readily matched with either the L^EL^E or L^El classes and require special consideration. It can be seen that one of them (*A*) although lying outside the parental limits of the L^EL^E tracks has a very similar form, i.e. follows an approximately parallel course. In fact if one imagines the effect of shifting the track diagonally towards the left-hand bottom corner of the diagram, without altering its form, it would be practically contained within the parental L^EL^E limits. It is clear that this could be accomplished by reducing the values of log *S* and log *L* proportionately along the whole length of the track. In other words (*A*) may be regarded as an L^EL^E homozygote which is acting on a larger leaf than the other tracks belonging to the same class. The other three tracks (*B*), (*C*) and (*D*) run parallel to the L^El tracks in Fig. 9. Offering a similar interpretation it may be suggested that (*B*) is an L^El heterozygote acting on a large-scale leaf, while (*C*) and (*D*) are members of the same class but acting on small leaves. Provisionally therefore the complete F_2 segregation can be analysed into 5 ll:8 L^El:7 L^EL^E which for the small number of plants concerned is a reasonable enough approach to the expected 1:2:1 ratio.

Now although variation in size of leaf appears to be the chief complication in the above method of analysis, it will have little disturbing effect on classification either by eye or by plotting leaf indices, since it affects the leaf dimensions proportionately. It may therefore be discounted as an important source of leaf-shape variability and other possible causes of modification must be sought. Examination of the F_2 homozygous classes in Figs. 7 and 8 shows that the tracks vary considerably in length as compared with the corresponding parental tracks (Figs. 5, 6). While some of the F_2 tracks are contained within the parental limits, others show considerable overlaps, although within each class the tracks follow a similar course. Since leaves from corresponding nodes (1–14) were measured in each case it is clear that length of track is proportional to rate of leaf-shape development. This means that leaves at corresponding nodes of different plants will be at different stages of development and consequently will have a different shape, thus providing the principal source of variation in the leaf index measurements shown in Fig. 4.

Further evidence of the relation between rate of leaf-shape development and flowering habit is provided by data from the interspecific F_2, *hirsutum* (Okra), $L^OL^O \times$ *barbadense* (Pardo), L^EL^E. Thirty plants were grown in replicated plots of five plants each, with the parents as controls. Of the thirty plants only twenty-six provided complete samples of leaves for measurement. The *hirsutum* and *barbadense* parents had first flowering node numbers of 6 and 11 respectively, and these limits were not transgressed by the individual F_2 plants:

1st flowering node number	6	7	8	9	10	11	Total
Frequency	7	8	6	1	3	1	26

(Flowering node numbers of parents: Okra 6, Pardo 11)

As in the case of the Sea Island × Guatemala Khaki cross (Figs. 6–9), the F_2 could be classified by examination of the developmental tracks of individual plants into three genotypes: 6 L^OL^O, 12 L^OL^E, 8 L^EL^E, and the chief source of modification was seen to be due to segregation in rate of leaf-shape development. A convenient though approximate way of estimating this rate (*D*) was to calculate the difference in *Index C* (= sinus length/leaf length) between leaves at the 1st and 10th nodes. To reduce chance fluctuation, however,

D was actually calculated as the difference between the mean index of leaves at nodes 1 and 2 and the mean index of leaves at nodes 9 and 10. Investigation showed that D was negatively correlated with 1st flowering node number, as shown below:

F_2. *G. barbadense* (Pardo) × *G. hirsutum* (Okra)

Analysis of variance and co-variance in 1st flowering node number (N) and rate of leaf-shape development (D):

	DF	*N*	*D*	*ND*	*r*
Between L^0L^0, L^0L^E and L^EL^E	2	1·3493	0·0555	−0·2709	—
Within genotypes	23	50·6507	0·4655	−2·7491	−0·5661 (signif.) at 1 %
Total	25	52·0000	0·5210	−3·0200	—

It may be concluded therefore that within the limited scope of these experiments, modification of leaf shape is dependent to a major extent on variations in flowering habit.

IV. Discussion

A developmental analysis of leaf-shape modification suggests that it is caused by genes which are in no way minor or subsidiary to the leaf-shape alleles. On the contrary, they appear to be genes which have profound effects on the co-ordination of physiological processes which are fundamental to the growth of the plant. A purely formal conception of an array of 'plus' and 'minus' modifiers, each having a very small effect on any single chosen character, fails to give a correct impression of the mechanism involved, because it over-emphasizes the importance of that character in relation to the remainder of the genotype. The formal conception becomes more misleading when its relation to evolution and speciation is considered. For instance, in the present case, there is no good evidence that the shape of the *Gossypium* leaf has any appreciable selective value on its own account. What appear to be the only quantitative data on this question are provided by the work of Hutchinson (1936) and Gadkari (1941) who found in certain areas in India that white-flowered, narrow-leaved types had a selective advantage over yellow-flowered, broad-leaved types. This suggests either some obscure physiological interaction between flower colour and leaf shape or, more probably, that the leaf-shape and flower-colour loci mark certain chromosomes which carry balanced 'polygenic' combinations (Mather, 1943*b*). It gives no critical evidence of the relative values of the two leaf shapes *per se*. Furthermore, general considerations of the genus *Gossypium* as a whole suggest no well-marked correlation between leaf shape and habitat. On the other hand, some at least of the leaf shape modifiers, viz. genes which control flowering habit, have a selective value on their own account which during the evolution of cotton under domestication has been of the greatest importance (Watt, 1907; Balls, 1919; Hutchinson, 1938; Silow, 1944). It is possible that genes which exert the most fundamental influence on the growth and development of the plant may typically be incapable of analysis by non-physiological methods, and hence it may only be possible to appreciate them as yet, by their incidental modification of genes which affect striking but relatively superficial characters. In other words, Harland's statement that 'the modifier complex constitutes the species' may be merely another way of saying that genes which control the most fundamental processes in the plant are those which have the greatest selective value and hence are, for the most part, those which have accumulated differentially in the formation of species.

A second point of importance is that, although modifiers or 'polygenes' are undoubtedly very numerous, there seems to be no *a priori* reason to suppose that they have individually

small effects—except in *one* aspect of their action, viz. their incidental modifying effect upon some relatively localized genetic process under the control of a specialized gene. It is evident that until the genetic control of physiological process is properly understood, the magnitude of a gene's effect cannot be estimated.

Finally, the distinction between a 'main' gene (oligogene) and a modifier (polygene) may be a difference in degree only and not in kind. A gene which has a striking but rather localized (even superficial) effect on an organism will be naturally of a type likely to be selected for laboratory examination, since its effects will be clear cut and unlikely to be disturbed seriously by interaction with the remainder of the genotype. At the other extreme, genes which alter the normal course of growth and development so profoundly as to produce abnormal or sublethal types, will likewise tend to furnish suitable material for genetic analysis. Between these limits must be genes controlling physiological processes which are of first importance to the normal functioning of the organism. Since normal functioning depends on the efficient co-ordination of the ultimate unit processes, it is not expected that 'end-effects' can be easily traced to the individual genes concerned. Where, however, the characters under study are suitable for developmental analysis, the position may be clarified appreciably, and an insight gained into the mechanism of genetic interaction.

V. SUMMARY

1. Differences in opinion as to the role of modifiers (polygenes) in genetic mechanisms suggest that new methods of attack would be of value. Developmental studies provide a possible line of approach.

2. Leaf shape in New World cottons furnishes suitable material for developmental study. Analysis shows that the major source of modification in leaf-shape expression is the interaction of the leaf-shape alleles with genes controlling flowering habit.

3. On transference from a late- to an early-flowering background, the action of the leaf-shape alleles is accelerated, but, as a compensatory effect, the period of development is reduced. If compensation were exact the shape of the climax leaf would be unaffected by change in flowering habit. In the cases studied, however, *over*- and *under*-compensation occur, so that the shape of the climax leaf is 'shifted'.

4. In interspecific crosses involving different leaf-shape alleles, transgressive segregation in F_2 of genes controlling flowering habit is associated with transgressive segregation in rate of leaf-shape development. Consequently measurements of climax leaves show increased variability, frequently leading to intergradation of the 'main' leaf-shape classes.

5. The fact that flowering habit has been a character of undoubted selective value during the evolution of cotton under domestication, whereas any selective value of leaf shape *per se* has yet to be proved, shows that modifiers are not necessarily genes of minor importance—their modification of the expression of another gene being only one of several possible pleiotropic effects. Neither is there any *a priori* reason to suppose, in the absence of any understanding of the physiological processes which they control, that modifiers have individually small effects.

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