

# CANALIZATION OF GENE ACTION IN THE *GOSSYPIUM* LEAF-SHAPE SYSTEM AND ITS BEARING ON CERTAIN EVOLUTIONARY MECHANISMS

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(With Seven Text-figures)

## I. INTRODUCTION

Phenogenetic studies (Stephens, 1944*b*) have shown that the action of the *Gossypium* leaf-shape alleles may be represented as a branching track system (Waddington, 1940) in which the courses of the tracks are determined by the law of allometry (Huxley, 1932). The basic system is illustrated in Fig. 1, type 1. It has been shown also that speciation in the genus has been accompanied by modification of this basic leaf-shape system. Considering first the diploid ( $n=13$ ) species, it has been found that in Asiatic diploids the action of the leaf-shape alleles is 'telescoped' so that the first two phases illustrated in Fig. 1, type 1, are foreshortened on the developmental time scale, resulting in the modified system shown in Fig. 1, type 2. On the other hand, in various American diploid entire-leaved species a reverse process occurs—the first phase in type 1 becoming greatly prolonged until the system shown in Fig. 1, type 3, is attained. In lobed-leaved American diploid species and in certain wild Old World species, e.g. *G. anomalum* Wawra & Peyr., the unmodified (type 1) system is preserved. Considering next the New World amphidiploid ( $n=26$ ) species, a system resembling type 1 has also been found, but there is good reason to believe this to be a secondary system resulting from the interaction of type 2 with type 3 alleles (Stephens, 1944*a*).

Within any of the three systems, mutation may be represented as a switch from one track to another. It is easy to visualize such a mutation as a simple change in rate of whatever physiological process is involved (cf. Goldschmidt, 1938). The relation between members of different systems is not so readily understood. Since one of the type 1 alleles ( $L^A$  carried by *G. anomalum*) was shown by Silow (1939) to be a member of the Asiatic (type 2) series, it was at first supposed that differences between systems were also determined solely by changes at the leaf-shape locus. It was in fact suggested (Stephens (1944*b*) following Goldschmidt (1940)) that mutation at the leaf-shape locus was of two orders: (i) small quantitative changes represented by switching from one track to another (micro-mutation), (ii) major reorganization of the locus resulting in a change from, say, type 1 to type 2 (macromutation). This interpretation is now known to be erroneous since the supposed 'macromutation' has been found to be determined by the remainder of the genotype and is therefore not a function of the leaf-shape locus itself. The true interpretation was first suspected when it was found that changes of the required nature could be reproduced to some extent by transferring leaf-shape alleles from perennial (late-flowering) to annual (early-flowering) genotypes (Stephens, 1944*c*). More recently it has been found that the leaf-shape alleles  $L^A$  (type 1) and  $L^N$  (type 2)—formerly regarded

by Silow and the writer as distinct—can no longer be considered so when subjected to more critical examination. Silow (1944), making use of the linkage between lint colour and leaf shape, has been unable to separate  $L^A$  from  $L^N$  in segregating families, although his former data (1939) suggested a clear difference in lobe width. Developmental examination, by the writer has shown that the type 1 development of the  $L^A$  allele on its original *anomalum* background and also on the *arboresum* type, N 14, is converted to the type 2 development, characteristic of the Asiatic alleles, when extracted from N 14  $\times$  A 24\* crosses (Fig. 2).

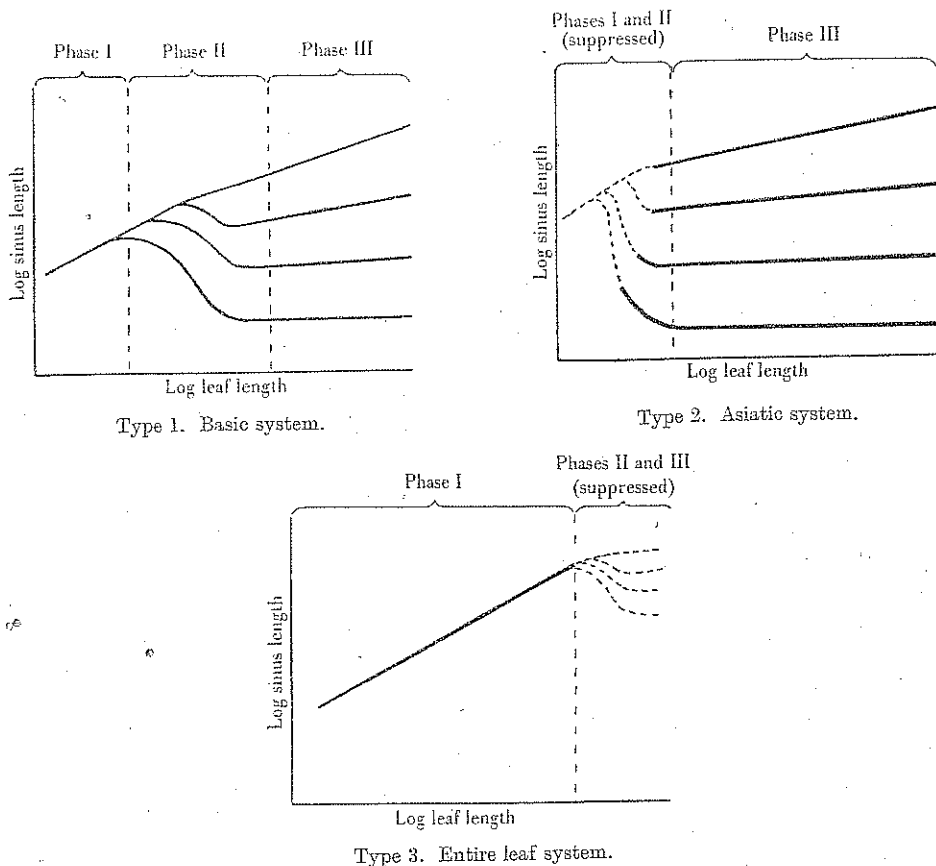


Fig. 1. The *Gossypium* leaf-shape development system and its transformations.

It seems likely that careful transferences of  $L^A$  and  $L^N$  to common backgrounds would eliminate their morphological differences. On the other hand, Silow finds some indication of difference in mutability between these two alleles so that their identity, though likely, cannot be considered proven.

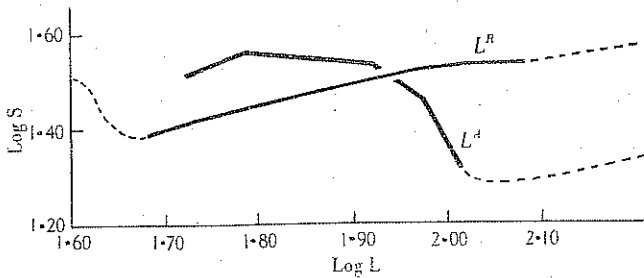
It seems, therefore, in the light of present knowledge, that leaf shape in *Gossypium* is determined by a single series of alleles whose basic system of development has become modified by changes in genotypic background during speciation. It is the purpose of this paper to attempt a more comprehensive classification of these changes and to discuss their general bearing on certain evolutionary mechanisms.

\* A 24 is the *arboresum* background upon which all the Asiatic alleles except  $L^A$  were originally compared (Stephens, 1944b).

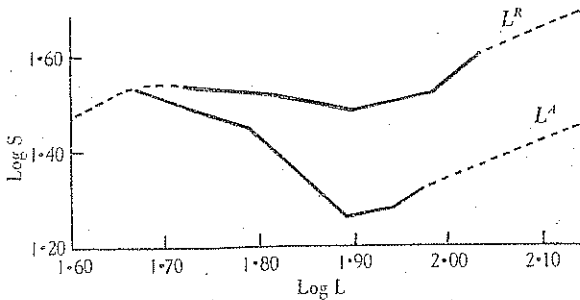
## II. CANALIZATION OF GENE ACTION

At the outset it must be borne in mind that direct tests of allelomorphism are only possible among types belonging to the same or to interfertile species. Since many interspecific hybrids in *Gossypium* are sterile, the presence of a single allelomorph system common to all species cannot be demonstrated by orthodox genetic methods. For instance, it has only been possible, so far, to analyse leaf-shape inheritance in one of the wild American diploid crosses, viz. *G. aridum* (R and S) Skovsted  $\times$  *G. thurberi* Tod. The following data were obtained:

<i>G. aridum</i>	Entire leaf
<i>G. thurberi</i>	Lacinated leaf
$F_1$	Entire or near-entire
1st backcross to <i>aridum</i>	All entire or near-entire
1st backcross to <i>thurberi</i>	4 near-entire: 6 lacinated
1st backcross selfed	12 near-entire: 35 intermediate: 9 lacinated
2nd backcross to <i>thurberi</i>	18 narrow: 24 lacinated



A



B

Fig. 2. (A) Developmental tracks of  $L^A$  on N14 background and  $L^R$  on A24 background.  $L^A$  has a type 1,  $L^R$  a type 2 development. (B) Developmental tracks of  $L^A$  and  $L^R$  on a common background (extracted from a mixed N14/A24 genotype). In both A and B the solid lines are plotted from actual measurements: the broken lines represent the supposed continuation of the tracks and are inserted to facilitate comparison. Although the tracks are clearly distinct from each other, they now have a common type of development (intermediate between type 1 and type 2 in Fig. 1).

The inheritance is probably monofactorial, although on transference to the *thurberi* background the *aridum* leaf is no longer entire. If, however, it may be assumed that a common mechanism of development implies homology of gene structure, genetic analysis can be supplemented by phenogenetic studies and consequently leaf shape throughout the genus can be examined. The writer believes this assumption to be justified, particularly

since monogenic differences of an obviously similar type are known to determine alternative leaf-shape patterns not only in all cases examined in *Gossypium* but also in the related genera *Malva* (Kristofferson, 1923), and *Hibiscus* (unpublished data of Skovsted, and of the writer). If this point of view is acceptable, the preliminary analysis illustrated in Fig. 1 may be extended to cover all leaf shapes in the genus.

In Fig. 3 the different patterns of lobed leaves are arranged in groups corresponding to their type of development (Fig. 1). Entire-leaved types are considered separately in Fig. 4. Within each group the types are listed in order of leaf laciniation. The important feature illustrated by this arrangement is that within each group there is a maximum of five alleles at definite levels of laciniation. Each allele tends to have its counterpart at a corresponding level in neighbouring groups. In other words gene action at the leaf-shape locus is canalized at five alternative levels of laciniation. An attractive possibility deserving examination is that there may be only five 'intra-genetic' (Darlington, 1939) mutations at the leaf-shape locus which are copied in different groups.

In considering the groups individually it will be convenient to begin with the wild diploids (right hand column in Fig. 3). Each leaf shape in this group is characteristic of a different species so that differences in shape are in part determined by different genotypic backgrounds and not attributable solely to changes at the leaf-shape locus. Consequently this group is more heterogeneous than the other three. Yet the five levels are clearly distinct and correspond well with their counterparts in the other groups. The intergroup relationship is confirmed by the fact that the  $L^4$  leaf shape carried by *G. anomalum* is, on transference to a common background, very similar to  $L^N$  in the Asiatic group, and also produces a copy of  $L^B$  (New World group) when it interacts with an entire-leaf gene ( $L^4 + \text{entire} = L^B$ , Stephens, 1944a). The members of the wild diploid group have other features in common besides their types of leaf-shape development. They are all shrubby perennials, none of which is cultivated or owes its distribution to man. The American species (*G. thurberi* Tod., *G. trilobum* Kearney, and *G. gossypoides* (Ulbr.) Standley), if one accepts a monophyletic origin for *Gossypium*, must have reached the New World from the Old World before the Tertiary period, whether one favours a land bridge (Harland, 1939) or a continental drift (Skovsted, 1937) hypothesis. These species must consequently be very ancient types, and since there is some evidence (Stephens, in press) that *G. anomalum* has affinities both with these and with the Asiatic cottons, it probably represents an ancient centralized type.

The Asiatic group is subdivided into a 'mutant' and 'field' series. All the types illustrated occur in *G. arboreum* Watt, and the genotypic background is thus reasonably uniform throughout the group. The mutant forms have only occurred in experimental culture—chiefly in one *arboreum* strain, A8, carrying the  $L^L$  allele. Their dominance relationships and mutability have been discussed fully elsewhere (Hutchinson, 1934; Silow, 1944) and it will suffice here to state they occur spontaneously as mutants from the  $L^L$  and  $L^N$  alleles in the sister (field) group. That the mutants are close copies of the field members is obvious from Fig. 3. In the field group, the types at the first two levels ('broad' and 'intermediate') are stable,  $L^N$  at the 'narrow' level mutates only in combination with  $L^B$ , while  $L^L$  at the lacinated level mutates spontaneously from the homozygous condition (Silow, 1944). No member has been found at the fifth level (i.e. completely divided leaf), but even if it occurred it should be unstable owing to the apparent inverse association between stability and depth of laciniation in this group.

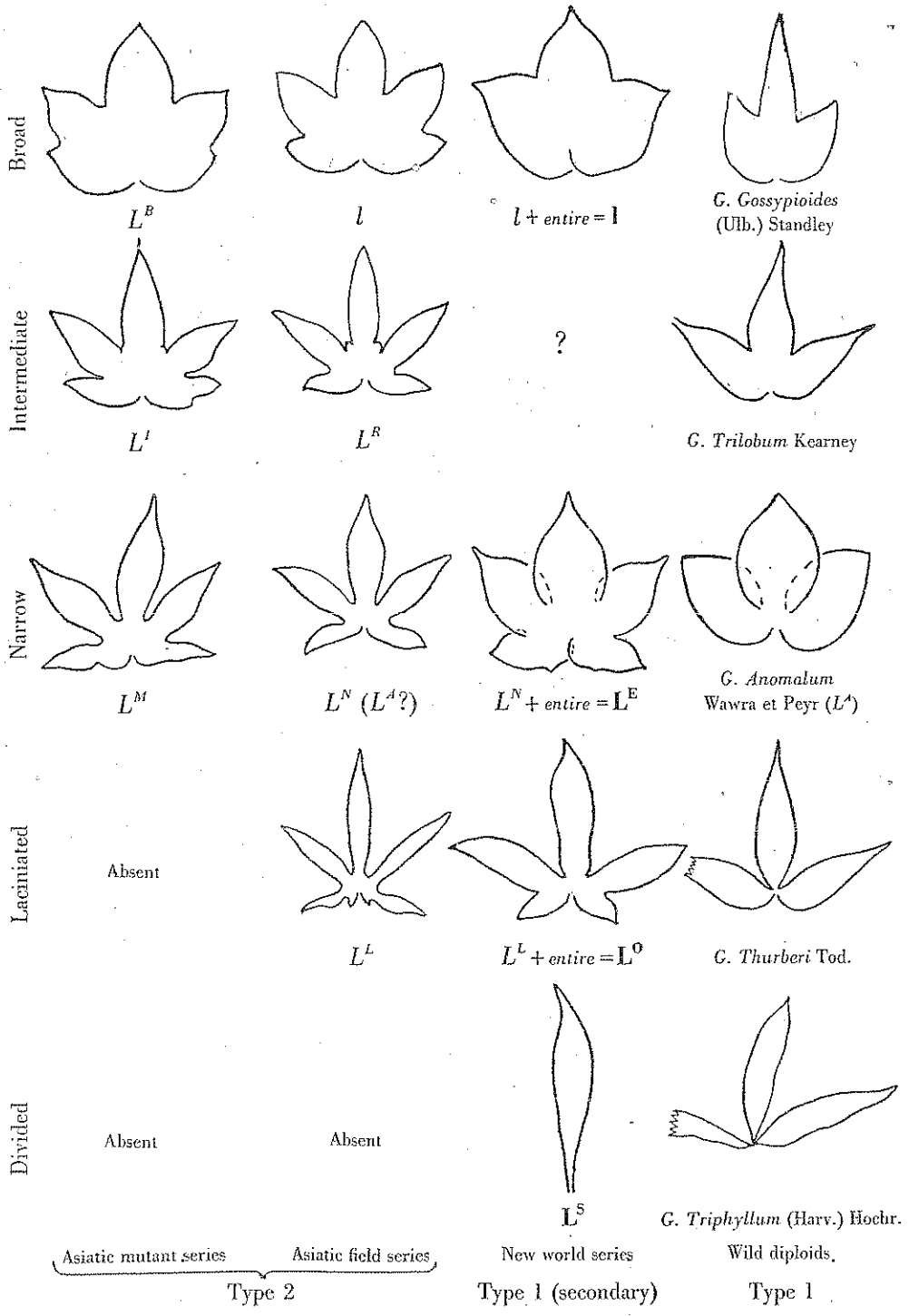
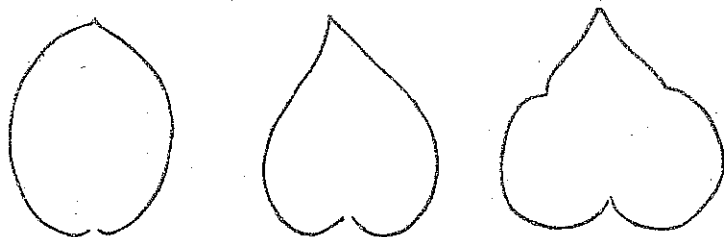


Fig. 3. Lobed-leaved patterns in *Gossypium* arranged horizontally at equivalent levels of laciniation and vertically in groups corresponding with their types of development (see Fig. 1).

The New World group includes the amphidiploids found in the New World and Polynesia. The types illustrated occur on a common (*G. hirsutum* L.) background. Phenocopies of these types can be synthesized by combining the Asiatic field alleles with an entire-leaved type (Stephens, 1944*a*). So far only phenocopies of  $L^1$  and  $L^2$  have been so constructed, but inspection of Fig. 3 shows that the possibility of synthesizing  $L^0$  by combining  $L^2$  with the entire leaf is almost beyond doubt. There is no corresponding Asiatic allele at the 'divided' level so that it is not to be expected that  $L^3$  can be synthesized in parallel fashion. At the second ('intermediate') level no leaf type has yet been found which corresponds with  $L^4$  and *G. trilobum* in neighbouring groups. But the possibility that it does occur cannot be dismissed, since in practice it is not by any means easy to distinguish  $L^1$  from  $L^2$  in segregating families owing to the genetic variability of leaf shape in this amphidiploid group.

The exact relationship between lobed and entire leaves is not yet determined, and it is for this reason that the latter types have been illustrated separately in Fig. 4. It was suggested (Stephens, 1944*b*) that two at least of the entire-leaved species should be regarded as potentially lobed-leaved types which have remained in a prolonged juvenile phase (neoteny). This suggestion is confirmed by the *aridum* × *thurberi* data given earlier.



*G. Sturtii* F. Muell.    *G. Klotzschianum* Anderss.    *G. Harknessii* Brandg.

Fig. 4. Entire-leaved types in *Gossypium*.

in this paper. On transferring the *aridum* (entire) leaf to a *thurberi* background it becomes lobed. Since a completely transferred type has not yet been extracted, it is impossible to say what depth of lacination would finally be achieved, but it is clearly possible that if all the entire-leaved types could be transferred to a suitable background they would appear as lobed-leaved types which would fit into one, or possibly several, of the five levels of lacination shown in Fig. 3. The leaf outlines in Fig. 4 show that the *G. harknessii* Brandg. leaf has incipient lobes, and occasionally the older leaves of *G. aridum*, *G. klotzschianum* Anderss. (including var.  *davidsonii* Hutchinson) and *G. raimondii* Ulb. have asymmetrical lobed leaves. *G. sturtii* F. Muell., an isolated species endemic to Australia, has the only form of leaf which shows no such sign of morphologic affinity with the lobed-leaved types, and it is possible that this may be a primitive, unlobed type.

It may be concluded that all the evidence available suggests that mutations at the leaf-shape locus form a closed system, i.e. mutation occurs in 'steps' and not completely at random. Five and only five mutations appear to be possible in so far as the developmental mechanism of the leaf is affected, but the phenotypic expressions may be modified according to the genotypic background on which the leaf-shape alleles are working. Differences in genotypic background have accompanied speciation in the genus, so that as regards phenotypic expression the five basic levels of lacination are copied imperfectly

in different taxonomic groups. It is probable that the chief differences in background which affect leaf-shape expression are the genes which control flowering habit. Thus, transferring  $L^A$  from a perennial late-flowering background (*G. anomalum*) to an annual early-flowering background (*G. arboreum*) results in a change from a type 1 to a type 2 development, since genes accelerating flowering also accelerate leaf-shape development (Stephens, 1945). Similarly, the entire-leaved species are all semi-arboreal extremely late-flowering types, and transferring the leaf shape of one of them (*G. aridum*) to the shrubby, earlier flowering *G. thurberi* results in a change from a type 3 to a type 1 development.

The relationship between the Asiatic mutants and the other series falls into a different category. The mutant alleles occur spontaneously from the 'sister' field members, and they must therefore be the result of true intragenic changes, or of intergenic rearrangements within the cross-over unit, i.e. of such small magnitude that they are not detectable as cytologic irregularities or by change in relative cross-over positions (Silow, 1944). To some extent the situation is similar to that of the unstable alleles 'reddish-a' and certain 'miniatures' in *Drosophila virilis* (Demerec, 1941). Here also mutation occurs to a dominant,\* stable allele and the period of instability varies. Reddish-a (like  $L^N$  in the *Gossypium* leaf-shape series) is unstable only in the heterozygous condition with the dominant type, while miniature-a (like  $L^L$ ) is unstable both in somatic and germinal tissues. Since Demerec finds that the unstable alleles in *D. virilis* are not associated with any detectable aberrations in the salivary gland chromosomes it must be accepted provisionally that the changes involved are intragenic. If this is also the case in the *Gossypium* leaf-shape mutants, some type of molecular rearrangement which scarcely affects the developmental mechanism or ultimate phenotypic expression of leaf shape is implied. The nearest analogy would seem to be the phenomenon of isomerism in organic compounds.

### III. THE BEARING OF CANALIZATION ON CERTAIN EVOLUTIONARY MECHANISMS

Canalization of gene action is important from two aspects. In the first place the number of distinct mutations is limited, and secondly the capacity of each mutant to become modified in expression by changes either in environment or in the rest of the genotype becomes restricted. It is the purpose of this paper to consider these limitations with regard to their bearing on (a) dominance phenomena, (b) non-adaptive trends.

#### (a) Dominance

Three different mechanisms for the evolution of dominance of the wild-type allele over its mutants have been suggested by Fisher (1928, 1931), Haldane (1930) and Wright (1934) respectively. According to Fisher's theory, dominance at any particular locus is conditioned by interaction of the genes at that locus with the remainder of the genotype. If the wild-type allele possesses a selective advantage over its mutant, the genotypic background will be altered by selection in such a way that the heterozygote will approach the wild type in phenotypic expression. In its original form the theory postulates that initially the heterozygote is intermediate, but does not consider the possibility of threshold effects. It is clear that if the wild type is already at a saturation level of expression, changes in genotypic background intensifying gene effects at the main locus will push the

\* In the case of *D. virilis* this is the wild type, in the case of *Gossypium* the dominant stable allele ( $L^B$ ) is only found in culture.

heterozygote over the saturation threshold without in the first instance altering the relative expressions of heterozygote and mutant homozygote. There is good reason for supposing that such threshold effects do occur as the result of a non-linear relation between gene dosage and phenotypic expression (Goldschmidt, 1938). Haldane suggests that dominance results from threshold effects brought about by a different mechanism. In this case wild-type alleles which are, in a sense, supersaturated and hence capable of attaining saturation level in the heterozygous phase, are supposed to have a selective advantage. Wright regards dominance as a special physiological property (greater activity) of the wild-type allele, which is not necessarily influenced by natural selection. Examination of a canalized system such as the *Gossypium* leaf-shape alleles suggests that two of these three mechanisms may be regarded as variants of a common underlying threshold phenomenon, rather than independent mechanisms.

The operational field of the leaf-shape alleles is bounded by two mechanical thresholds or limits: (i) the dosage large enough to produce a sinus in the unbroken contour of an entire leaf, (ii) the minimum dosage required to divide a lobed leaf completely into independent leaflets. These two limits are approached by (i) the *harknessii* leaf (Fig. 4) and

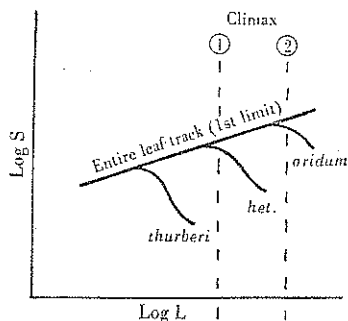


Fig. 5. Diagram illustrating 'modification' of dominance by 'Fisher effect'. At climax 1, *aridum* leaf shape is almost completely dominant to that of *thurberi*: at climax 2 *aridum* and *thurberi* have an intermediate heterozygote.

(ii) the *triphylllum* leaf (Fig. 3). Outside these limits, changes in dosage can produce no measurable effect on the climax leaf. As discussed earlier, and as illustrated in Fig. 1, five possible levels (or dosages) occur, and in each case the ultimate phenotypic expression (i.e. the shape of the climax leaf) is not fixed but is determined by the rate of leaf-shape development (cf. types 1, 2 and 3 in Fig. 1). Dominance judged by comparisons of the ultimate phenotypic expressions of the alleles is determined, therefore, by the adjustment of two variables: (i) dosage-controlled by the allele, (ii) the rate of leaf-shape development—controlled by the genotypic background. For example, the *aridum* entire leaf is almost completely dominant to the *thurberi* lacinated leaf, as judged by the shape of the  $F_1$  leaf. Transference to the *thurberi* background shifts the climax (alters the leaf development from type 2 to type 1) and dominance disappears. This is illustrated diagrammatically in Fig. 5. Dominance conditioned by genotypic background in this fashion clearly follows the Fisher mechanism.

A similar threshold effect with accompanying dominance phenomena is seen in compounds of the Superokra allele ( $L^S$ ) which completely divides the leaf into its component leaflets. As soon as this stage of development is attained, no further change in shape can be illustrated metrically. Nevertheless, there is good evidence that at this stage the



allele has not attained its maximum potential (i.e. genotypic) expression. At first, three completely separated leaflets are carried by the petiole but at later nodes the laterals disappear. Still later, the lamina recedes from its normal point of junction with the petiole, and the nectary borne on the midrib eventually lies between the petiole and the base of the lamina (Fig. 6). In other words  $L^S$  is 'supersaturated' with regard to its effect on laciniation, and, as a consequence, exhibits varying degrees of dominance over its sister alleles,  $L^O$ ,  $L^E$  and  $I$  (Fig. 7) in accordance with Haldane's interpretation. Usually  $L^S$  is completely dominant to  $L^O$  and incompletely dominant to  $L^E$  and  $I$ , but on certain backgrounds leaf development is accelerated slightly so that the  $L^S L^E$  leaf becomes completely divided (i.e.  $L^S$  becomes dominant to  $L^E$  by operation of the Fisher effect).

The dominance mechanism so far considered results from interaction between the two variables, dosage and rate of leaf-shape development, but it is important to note that it only occurs at the limits of the operational field, i.e. in cases where either (i) the entire

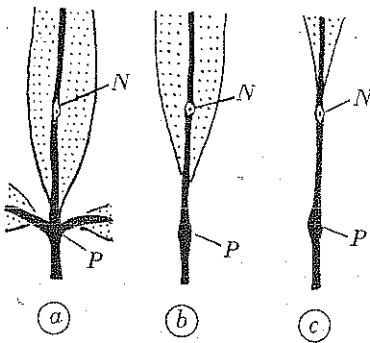


Fig. 6.

Fig. 6. The sinus region of the Superokra ( $L^S$ ) leaf at three successive stages of development: (a) lateral lobes still present, (b) lateral lobes eliminated, lamina of median lobe receding from original point of insertion, (c) lamina receded sufficiently to expose nectary. ( $P$  = point of lamina insertion,  $N$  = nectary.)

Fig. 7. Diagram illustrating dominance attained by (1) 'Haldane', (2) 'Fisher effect'.  $L^S L^E$  is supersaturated, i.e. its effect on leaf laciniation is more than the minimum necessary to reduce sinus length ( $\log S$ ) to 0. At climax 1,  $L^S$  is therefore incompletely dominant to  $L^E$ . At climax 2,  $L^S L^E$  also reduces  $\log S$  to 0, i.e.  $L^S$  becomes completely dominant to  $L^E$ .

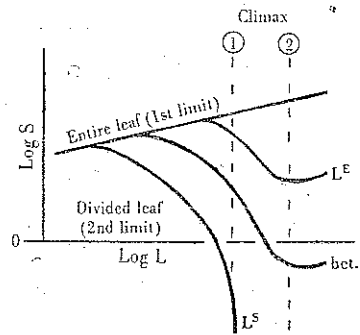


Fig. 7.

leaf or (ii) the completely divided leaf is involved. There is, in addition, a general dominance mechanism which is an inherent property of the growth mechanism of the leaf; and which affects the relations of *all* the leaf-shape alleles. Silow (1939), in examining the Asiatic alleles, showed that dominance, as measured by leaf-index\* comparisons, increases with increasing laciniation. In the present writer's opinion there can be no doubt that magnitude of difference in index measurement accurately portrays the magnitude of difference in shape which is appreciable visually, i.e. *the dominance is real*. Nevertheless, it can be shown that the dominance may not be due to any greater activity or potency of the more 'dominant' alleles as Wright (1934) has suggested, *but to an unavoidable consequence of the mechanism of leaf growth*. It is implicit in this mechanism that rates of cell division are logarithmic functions of the final dimension of the leaf. Since the alleles determine leaf shape indirectly by controlling rates of cell division (Hammond, 1941), it is evident that the logarithmic scale measures their actions more appropriately than the normal scale. Adopting this form of measurement, the actions of the alleles may be ex-

\* Index  $C$  = sinus length ( $S$ )/leaf length ( $L$ ), Index  $D$  = lobe width ( $W$ )/leaf length ( $L$ ).

pressed allometrically as developmental tracks. Unfortunately, no suitable data are available for comparing critically the developmental tracks of heterozygotes with those of homozygotes, but the general impression gained from both Asiatic and New World material is that the developmental track of the heterozygote follows a strictly intermediate course between those of the homozygotes. Indirectly, this supposition may be tested by the method illustrated in the following table:

*Climax leaf dimensions in the Asiatic allelomorph series*

Genotype	Log $L^*$	Log $S^*$	Index $C = S/L$	
			(1) Calculated	(2) Silow (1939)
$L^L L^L$	2.0969	1.0414	0.09	0.08
$L^L l$	(2.0632)	(1.3425)	(0.19)	0.13
$L^N L^N$	2.1038	1.2788	0.15	0.12
$L^N l$	(2.0666)	(1.4612)	(0.25)	0.21
$L^R L^R$	2.1072	1.4624	0.23	0.26
$L^R l$	(2.0683)	(1.5530)	(0.31)	0.29
$ll$	2.0294	1.6435	0.41	0.36
Mean differences between Index $C$ estimates:				
Homozygotes		0.015 $\pm$ 0.017		
Heterozygotes		0.040 $\pm$ 0.012		

The logarithmic values for climax leaf dimensions of the Asiatic homozygotes are shown in the second and third columns. From these, *Index C* values are calculated (column 4) which agree reasonably well with those calculated independently by Silow (1939, p. 261) and reproduced in column 5. Now if the developmental tracks of the heterozygotes follow strictly intermediate courses, the logarithmic dimensions of their climax leaves will be equal to the arithmetic means of the logarithmic dimensions of the corresponding homozygotes. These calculated values and their corresponding *Index C* values are shown as bracketed figures in the table. Comparing columns 4 and 5, it can be seen that the calculated indices for the heterozygotes also agree with Silow's actual figures, and it may be inferred that the degree of dominance found by him is no more than might arise as an unavoidable consequence of strict intermediacy of each heterozygote in its course of development. The data therefore support Wright's thesis that dominance may be a physiological property of the alleles themselves, but suggest that this property may be resident in the general mechanism of development controlled by the allelomorph system and not necessarily conditioned by differential activity of the individual alleles.

(b) *Non-adaptive trends ('orthogenesis')*

Huxley (1942) has summarized evidence showing that the apparent 'orthogenesis' of adaptive characters can be regarded as the progressive fitting of an organism to a specialized mode of life, which the generally accepted principles of natural selection are sufficient to explain. Non-adaptive trends furnish a more difficult problem. A wealth of apparently non-adaptive trends is provided by palaeontological data, of which the excessive 'armaments' of the dinosaurs (e.g. *Stegosaurus*; *Triceratops*) and of certain mammals (e.g. Titanotheres) and the apparently aimless coiling of Ammonite and *Gryphaea* shells furnish well-known examples. It is clear that such trends offer a two-fold problem: (1) the nature of the genetic mechanism which could (theoretically) produce trends, (2) the types of environment which would favour, or at least allow, the resulting products to survive.

(i) The first part of the problem has already been clarified by the application of the principle of allometry to palaeontological interpretation (Huxley, 1932; Hersh, 1934;

\* Taken from data published elsewhere (Stephens, 1944b).

Robb, 1935) and by considerations of the effect of alterations in timing and rate of gene action (Haldane, 1932; Goldschmidt, 1938; de Beer, 1940). The total evidence as weighed and presented by Huxley (1942) shows that many structural trends\* may be regarded as mechanical consequences of long-term changes in absolute body size or in rate of development. Now the probable importance of allometric and timing mechanisms in *large-scale* evolutionary processes gains particular force if they can be shown to be typical components of a common canalized system such as Waddington (1930) has deduced from *small-scale* (single gene) reactions in studies of animal development. In the *Gossypium* leaf-shape system which furnishes a particularly simple example, this is certainly the case. As has been seen, its branching track system is based on the allometric relations between the leaf dimensions, and phenotypic expression can be considerably modified by alteration in timing of the actions of the alleles. Furthermore, changes in absolute size of leaf or in rate of general plant development condition changes which follow definite trends and which can be expressed quantitatively. It is unlikely that this system is of restricted occurrence—similar types of change from juvenile to adult leaf shape are a commonplace both in flowering plants and cryptogams, and analogous changes in proportion during animal development almost certainly have a similar basis (e.g. the aristopedia system in *Drosophila*—Waddington, 1940). In general, it is probably justifiable to suppose that wherever character expression is dependent on differential rates of cell division, there also some basic canalized system of development will be involved, and from their nature it is clear that palaeontological records must fall into this category.

(ii) Although canalized systems provide a satisfactory genetic basis for the expression of trends, the latter will never be fulfilled unless the environment, and hence the intensity of selection, offers a favourable medium. In the particular case of a character which has little positive or negative adaptive value it may be supposed that the genetic mechanism controlling it will be allowed free rein. A possible example is provided by the *Gossypium* leaf-shape system itself. Here it is found that the wild semi-arboreal diploid cottons have entire leaves as a result of what is apparently a neotenic trend (see § II). Since the retardation of general plant development which is associated with the arboreal habit also retards the rate of leaf-shape development, it is possible that an entire leaf becomes a mechanical necessity when plant development is slowed down to a certain minimum rate.† In all other cases the intensity and type of selection will be of prime importance. Elton (1927) stressed the fact that in animals living at the present day, population numbers are subject to violent fluctuations which occur in cycles. The general picture of natural selection obtained is not of a steadily moulding operation, but of periods of relaxed selection alternating with periods of intense intraspecific competition. Elton suggested that the period of relaxed selection with its accompanying rapid increase in numbers would favour the appearance of many new non-adaptive characters. More recently, Fenton (1935) has argued generally that the non-adaptive trends so frequent in palaeontological records occur in the absence of, and not as a consequence of, natural selection. The bizarre forms of deep-sea fishes (Lull, 1917) offer contributory evidence. Haldane (cited Huxley, 1942) has suggested, on the other hand, that non-adaptive trends may be favoured during periods of intense intraspecific competition—in the case of a vertebrate

\* The mathematical significance of such trends had been foreseen many years previously by D'Arcy Thompson (1917), and though he never related it to genetic principles, modern interpretations owe much to his pioneer work.

† Though it cannot be definitely assumed that the shape of the leaf in *Gossypium* has no adaptive value on its own account, there is no critical evidence in favour of it.

leading to increased bulk and heavy armament which would be of advantage against its own species but not necessarily against members of others. It is clear that the development of trends under relaxed selection and under conditions of intraspecific competition are not mutually exclusive, since the former might allow initiation of a trend while the latter might accelerate its rate of development.

It may be concluded that canalized genetic systems operating under selective agencies similar to those now in operation, would provide possible means of expression for non-adaptive trends although the manner in which such trends have led to extinction in the past is by no means clear. It seems likely that studies in animal ecology may eventually throw light on the problem. For instance, Elton has shown that the normal results of rapidly increasing numbers followed by intraspecific competition, are starvation or epidemic outbreaks which often annihilate the whole stock. Presumably this 'end-point' would be delayed or avoided altogether by lowered reproductive capacity, and the latter seems to be the actual situation among types at the head of 'food-chains' whose numbers are not kept in check by predators. But lowered reproductive capacity would in the long run lower effective mutation pressure and place the type at a potential disadvantage for further evolutionary progress.

#### IV. SUMMARY

A phenogenetic analysis of leaf-shape expression in the genus *Gossypium* as a whole suggests that the alleles controlling the various forms are members of a single canalized system. The system appears to be composed of five alternative developmental tracks, the *courses* of which are but slightly affected by changes either in environment or in the rest of the genotype. The *final phenotypic expression* attained, however, may be considerably modified by such changes. The chief modifying mechanism appears to be retardation or acceleration of the actions of the leaf-shape alleles in relation to development of the plant as a whole. Every such alteration in 'timing' is capable of changing the shape of the climax leaf.

Characters dependent on a canalized system of development may be expected to show a restricted capacity for modification, though the number of phenotypic variants possible may still be considerable. The effects of such restriction are considered in relation to two evolutionary phenomena: (a) the expression of dominance, (b) the occurrence of non-adaptive trends. It is shown that both phenomena would be expected as a result of natural selection acting on characters controlled by canalized systems.

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