THE EFFECT OF SELECTION ON THE MANIFOLD EXPRESSION OF THE "SUPPRESSED LATERAL" GENE IN THE TOMATO

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1. INTRODUCTION

MUTATIONS causing manifold phenotypic effects are well known and have been extensively studied (Dobzhansky, 1927; Grüneberg, 1938). They are frequently encountered in selection work on plants and animals, and, during the initial phase of selection, one seldom finds that all the character modifications that are associated with a given mutation are desirable in relation to the set objectives of selection. When apparently disconnected genetic effects can be related directly to homology of organs in development, the limits of function of a particular gene and its interaction with others are capable of more precise definition. Unfortunately this is rarely possible and in practice the finer ramifications of biochemical gene action defy recognition (Caspari, 1952). In this respect the *ls* gene in the tomato which forms the basis of the present investigation has certain advantages in that many of its manifold effects, including those which are strictly quantitative in nature, are likely to be the result of a single error in gene function which expresses itself at various stages in development. In other words the manifold effects of the mutation are probably the result of "spurious" pleiotropism (Grüneberg, 1938). Thus the conclusions from the genetic data presented later have to be considered in the light of the likelihood that most of the phenotypic modifications associated with *ls* could result from an error in a single process of growth.

The manifold effects of major gene loci can be explained either on the basis of very close linkage of genetic units with somewhat dissimilar function, or on the basis of pleiotropy. Where the linkage is very close unambiguous genetic tests to discriminate between the two possibilities are not possible in higher plants and animals and in such cases it is idle to pursue the distinction. Where correlated characters are governed by a linkage that allows a reasonable rate of recombination, the problem of eliminating undesirable associations can be solved by breaking down and reforming the linkage system. Thus it is only the region of the chromosome bearing the linkage that has to be considered and provided the homologous chromosome gives an opportunity for recombination within the region, the constitution of the rest of the genotype is of little consequence. If, on the other hand, some form of pleiotropy is involved the entire gene background becomes of primary importance in reshaping character associations. Advances under selection will then

depend on diversity throughout the whole chromosome complement and on the capacity of the gene background to modify the various character expressions independently of one another.

The independent modification by selection of the manifold effects of certain eye colour mutants in *Drosophila* was demonstrated by Dobzhansky (*loc. cit.*). As a result of outcrossing, lines were isolated having the mutant eye colours *yw* and w^i but which were wild-type in respect of spermatheca shape. The reassortment of the pleiotropic effects of the mutants was interpreted on the basis of the differential modifier effects of the gene background. Furthermore, the dominance relationships of multiple alleles at loci with manifold effects suggest that the various phenotypic expressions of a single locus may interact differently with a given gene background. This is very adequately demonstrated by the three allelomorphs W, W^v and $+$ in the mouse (Grüneberg, 1942). When the effect of all combinations of the three alleles on fur colour and on macrocytic anæmia is considered, it is found that no one serial arrangement of dominance expression will fit. For example, WW mice have white fur and severe anæmia, while $W+$ animals develop white spotting but are free from anæmia. A somewhat similar situation is shown by the mutant gene *Ri* in *Œnothera* (Weidner, 1950). The non-seriality of the dominance effects of alleles with respect to the component expressions of pleiotropic genes provides clear evidence that manifold expressions can respond independently to the influence of modifiers.

Probably the most direct line of enquiry into the problems raised here is to study the nature of the character associations that prevail at the time of origin of major mutations (Dobzhansky and Holz, 1943). Correlated characters that are based on linkage can be expected to show character expression in the direction of the preceding selective trends. If it is therefore found that the quantitative character with which a major mutation is associated at the time of its origin shows an expression in a direction opposite to the selective pressure, one must conclude either that the mutation covered a large chromosome region in the manner of a deletion or of an inversion with extended position effect, or one must accept that the associations observed are the result of the pleiotropic action of the mutation itself. In the present material the first appearance of the mutation is recent and can be dated. A study of its manifold effects might therefore provide further evidence on the relative importance of linkage and pleiotropy in determining character associations, and therefore assist in the planning of selection procedure.

2. THE MUTATION *ls* AND ITS PHENOTYPIC EXPRESSION

This mutation was first observed during 1951 growing among a crop of the pure line variety, Antimold B. The parent variety was bred at the John Innes and its history and parentage are known with

certainty. No trace of the mutation is to be found in the previous history of either the parents or grandparents of the variety, Antimold B. There can therefore be no question of selection having operated on the mutant genotype to establish character associations opposite to those present in the parent from which it arose.

The phenotypic effects of the mutation in the homozygous recessive phase comprise (*a*) suppression of branches in the axils of the leaves, (*b*) in certain genotypes suppression of apical growth at various stages of development, (*c*) suppression of corolla development: in this, its action resembles the known gene *ap* (apetalous), (*d*) deformed anthers which fail to remain united as a column around the style: this results in failure of pollination and in sterility, (*e*) reduction in flower number per inflorescence and (*f*) in certain gene backgrounds it forms partially apocarpous, parthenocarpic fruit which resemble the phenotype of the gene *gq* (grotesque). It seems clear that all these effects with the possible exception of (*d*) can be logically explained on the assumption that the locus controls the development of the primary meristem. All the expressions of the mutation show quantitative variation, and these can be intensified or reduced in segregating generations according to the genotypes of the parents. It may be noted that one of the effects associated with this mutant, namely flower number per inflorescence, is typical of characters that are used in experiments on the study of quantitative inheritance, and a detailed analysis of its genetic basis seemed therefore to be worthwhile.

3. VARIATION IN THE EFFECTS OF *ls ls* IN RELATION TO GENE BACKGROUND

(i) *Suppression of axillary branches*

Five F_2 progenies arising out of crossing *ls ls* with different pure line varieties were studied. The number of axillary branches (laterals) in the *ls ls* class of families H 56, 59 and 61 are given in fig. 1. H 59 and H 61 are derivatives of crossing *L. racemigerum* and *L. pimpinellifolium* respectively with *ls ls*, while H 56 is an intra-specific cross within *L. esculentum*. The two other intra-specific crosses resembled H 56 in lateral branch production and are therefore not given here. The plants were scored when fifteen fully developed leaves were present and the maximum number of laterals that could be recorded is therefore seventeen. It will be observed that the hybrids H 56 and H 59 behaved uniformly and very little variation in numbers of axillary branches was evident. The great majority of *ls ls* plants in these families were completely devoid of axillary branches and the maximum number of four branches recorded had a frequency of less than 0·2 per cent. By contrast, the majority of *ls ls* progeny derived from the *L. pimpinellifolium* cross had one developed lateral and the maximum number recorded in the cross was eleven. The three *esculentum* parents had been chosen because of their diversity of origin and type, but clearly

with respect to the modification of the suppressive action of *ls* on axillary meristems, the series contained little or no genetic diversity. In contrast to this, the inter-specific combination involving *pimpinellifolium* produced a wide and continuous range of modification, extending almost to normal phenotypic expression in the presence of *ls ls*.

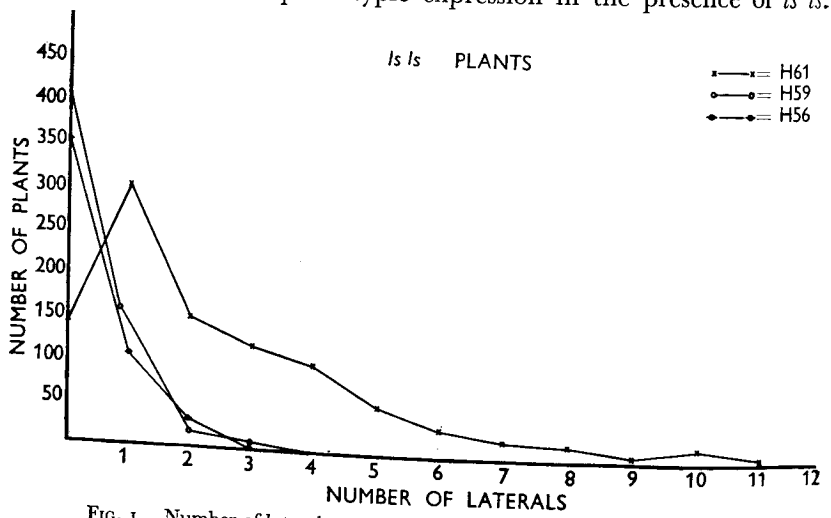

FIG. 1. Number of laterals on *ls ls* plants segregating in three F_2 families.

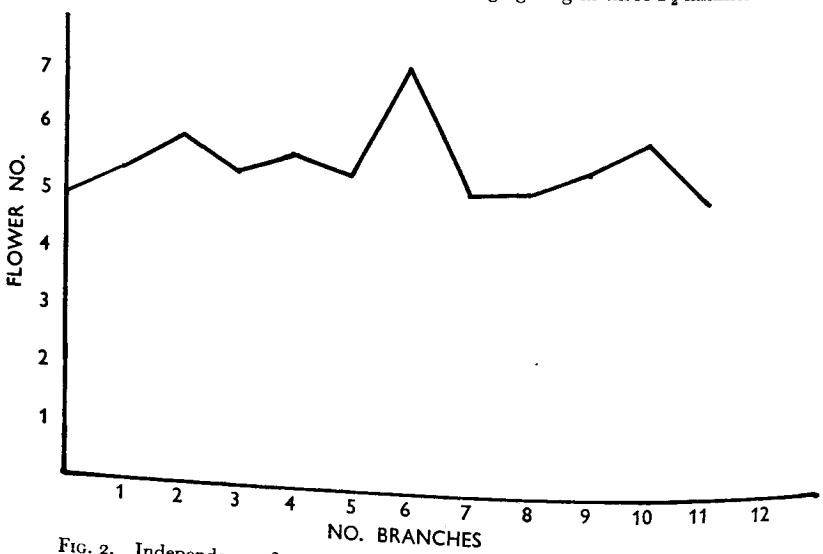

FIG. 2. Independence of number of branches and flower number in *ls ls* plants segregating in F_2.

None of the other expressions associated with the *ls* gene showed a correlated response with increased production of lateral branches, and it appears that the modifier effect of the gene background can discriminate between the several modifications. The independence of the two effects, branch number and flower number, can be seen in fig. 2.

(ii) *Suppression of apical growth*

The control of terminal growth in *ls ls* phenotypes derived from the five different F_1 hybrids can be assessed from table 1. All the " + " phenotypes among the F_2 progenies had normal indeterminate growth. Recombinants from intra-specific crosses showed considerable variability of control in respect of this character. In the cross involving

TABLE 1

Percentage of ls ls *plants segregating in* F_2 *showing cessation of apical growth at different stages of development*

Parents of F_1 and family no.	Apical growth terminated after		Normal apical growth	Total
	1st inflorescence	2-7 inflorescences		
ls ls × Wonder of Italy (H 56)	6·06	35·49	58·44	231
ls ls × Earliana (H 57) . .	28·73	28·73	42·53	268
ls ls × Market King (H 55) .	16·77	83·23	0	477
ls ls × *L. racemigerum* (H 59) .	2·61	27·16	70·22	497
ls ls × *L. pimpinellifolium* (H 61)	0·20	2·30	97·48	477

the parent " Market King ", apical growth was terminated at some stage of development in all plants of the *ls ls* class, whereas 58 per cent. of the comparable plants from " Wonder of Italy " continued growth normally. As with control of the development of lateral branches, the most successful source of genetic diversity for normalising

TABLE 2

Average number of flowers on first inflorescence in ls ls *phenotypes classified according to stage of cessation of apical growth*

Family no.	Apical growth terminated after		Normal apical growth	Total
	1st inflorescence	2-7 inflorescences		
H 55	5·68	6·58	0	477
H 56	3·71	3·78 *	7·88	231
H 57	4·81	6·86	7·88	268
H 59	3·15	4·01	4·86	497
H 61	5·00	4·00	5·46	477

* A large number of plants in family H 56 stopped growing after the second inflorescence, and thus the class resembles that in column 2 of this table.

apical growth was *L. pimpinellifolium*. *L. racemigerum* (H 59) while more effective than the *esculentum* parents was not as rich a source of modifiers as *L. pimpinellifolium*.

An analysis of flower number in the various growth classes among the *ls ls* genotypes showed that a severe reduction in flower number accompanied early cessation of apical development. The figures set out in table 2 indicate that the mean flower number in *ls ls* plants

showing cessation of apical development after the formation of the first inflorescence, is consistently lower than in *ls ls* plants in which apical growth was normal throughout the period of observation. Plants in which the apex failed after 2-7 inflorescences had developed, had intermediate flower numbers. None of the other effects normally expressed by *ls ls* genotypes showed detectable modifications which could be correlated with the stage at which apical development failed.

(iii) *Control of flower number*

The effect of the *ls* gene on flower number in several different gene backgrounds can be seen in table 3. The average number of

TABLE 3

Degree of expression of the manifold effects of ls *in* F_2 *and backcross families*

Parents * and family no.	No. of flowers on 1st inflorescence		No. of axillary branches	No. of petals per flower
	ls ls phenotypes	+ phenotypes	*ls ls* phenotypes	*ls ls* phenotypes
H 55 . . .	6·42±0·137	10·48	0·10	0·0
H 56 . . .	6·15±0·158	17·00	0·27	0·0
H 57 . . .	6·76±0·234	12·22	0·23	0·0
H 59 . . .	4·58±0·112	13·32	0·20	0·04
H 61 † . . .	5·42±0·160	15·14	2·59	0·85
H 69 (*ls ls*×P)†§ .	6·24±0·103	13·14	1·51	0·45
H 60 (P ‡×*ls ls*) .	6·22±0·171	13·38	1·11	0·41
[H 68 (*ls ls*×P ‡)] .	6·53±0·152	14·13	1·31	0·67
[(*ls ls*×P)×P] .	6·87±0·148	14·74	1·96	2·84
[(*ls ls*×P)×E §] .	6·59±0·179	10·86	1·72	1·15
[(*ls ls*×P)×P]×P .	6·42±0·112	17·44	1·21	3·34
[(*ls ls*×P)×P]×E .	5·98±0·104	9·76	1·37	1·70

* The parents of H 55-H 61 are as in table 1.
† Red fruited form of *pimpinellifolium*.
‡ Yellow fruited form of *pimpinellifolium*.
§ In the table P = *Lycopersicum pimpinellifolium* and E = *L. esculentum*.

axillary branches and average petal number per plant are also presented. The reduction in flower number was very marked in each family and the figures obtained for the *ls* class were on average over 50 per cent. less than in normal plants segregating in the same family. The range of the variation in the mutant and wild-type classes can be assessed from fig. 3. Apart from the progenies derived from *L. racemigerum* where the reduction was most severe, the means for flower number in table 3 are homogeneous. No correlation exists between the means for flower number, number of laterals and petal number in the *ls ls* class within the different families listed in table 3. Although the mean flower number in *ls ls* plants was similar in all families the mean petal number in progenies derived from *L. pimpinellifolium* was

significantly higher than in the other crosses. Thus the modifiers which affect petal number also behave differentially with respect to the manifold effects of the major gene mutation.

The backcross data given in table 3 indicate clearly that intensification of the *pimpinellifolium* background brings about a rapid advance towards normality of the corolla. In the backcrosses, maximum expression of corolla formation alone was selected, hence the other

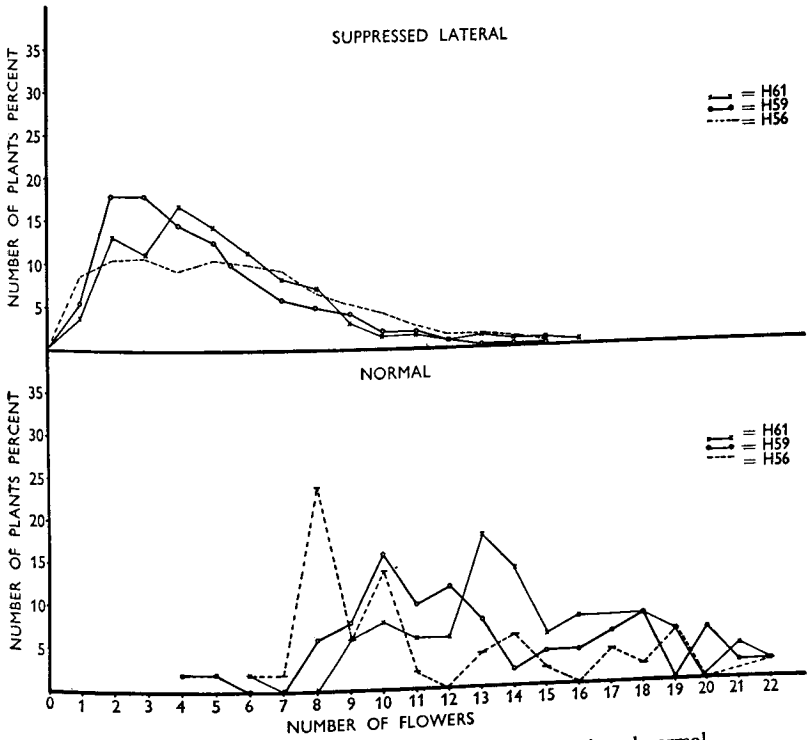

FIG. 3. Frequency distribution of flower number in *ls ls* and normal segregates in F_2 families.

phenotypic expressions remained virtually unchanged by backcrossing. The progressive advance under backcrossing shown here is consistent with the effects of a background of modifiers, and the extent of the variability released in the inter-specific, as opposed to intra-specific crosses, indicates that genetic elements of a kind that characterise large specific differences are involved.

Furthermore, although modification of each of the various effects of the mutant occurred in one or other of the families, the variation was continuous and no phenotype resembling a cross-over where one or more of the expressions had been restored to normal was observed. In all, segregating progenies amounting to over 57,000 individuals were recorded and the observations are summarised below. The class,

" Cross-over 1 ", refers to recombination between absence of laterals and one of the other phenotypic expressions, and the class, " Cross-over 2 " is the reciprocal recombinant.

Wild-type	" Cross-over 1 "	" Cross-over 2 "	*ls ls*	Total
43,994	0	0	13,274	57,268

The failure to recover cross-over types between absence of laterals and petal development in these large segregating populations is particularly significant, since there is no possibility that a full recombinant involving these two expressions would have remained undetected. The absence of cross-over phenotypes must also be considered in relation to the observations regarding the differential effects of the modifiers on the separate expressions of the mutant. If cross-over types had been detected, such differential effects of the modifiers could be explained on the basis of specific interactions with linked blocks of polygenes. Although the numbers observed cannot be considered adequate to preclude all possibility of very close linkage (Pontecorvo, 1959), the absence of a single recombinant between the component parts of the syndrome make this interpretation less probable, particularly since all the other evidence tends to emphasise the influence of the gene milieu on the various effects of the *ls* mutation.

4. INTERACTIONS BETWEEN *ls* AND OTHER CHROMOSOME REGIONS

The effect of the *ls* region on flower number provided a sensitive test for studying interactions between it and other marked regions of the chromosome complement. In all, thirteen marked regions, spread over seven different chromosomes, were studied. Unfortunately it was not possible at the time to study interactions with whole chromosomes adequately marked by suitable genes. Three marker stocks were crossed with homozygous *ls ls* parents carrying homozygous wild-type alleles at the marked loci. The single and double recessive classes involving the markers were recovered in F_2, and the flower number of each class scored. The results are set out in tables 4 and 5. The genetic constitution of the marker stocks can be gathered from the tables.

The effect of the *ls* gene on flower number (table 4) is not so marked in these families as in those described previously, and in family 71 although the *ls ls* genotype possessed the lowest average number of flowers, the difference between it and the wild-type is not significant. With the exception of the region marked by the gene *f* whose known effect is to increase floral parts (compartments of the ovary, stamens and corolla), no significant direct effect on flower number can be ascribed to any of the regions when present singly. When the marked regions are combined with *ls* (table 5) their effect on flower number in some cases becomes very striking. The combination *ls e* in family 72, *ls a* in families 70 and 72, and *ls dm* in family 71 clearly alter the

flower number as compared with *ls* +. It is almost certain, in spite of the lack of significance in family 71 as a whole, that the effect of *ls dm* in this progeny is real. Several other combinations, *ls y* in

TABLE 4

Flower numbers of F_2 plants homozygous for marker genes

Family 72			Family 71			Family 70		
Genotype	No.	Flower no.	Genotype	No.	Flower no.	Genotype	No.	Flower no.
e e	20	8·5	*dm dm*	21	8·1	*c c*	23	7·6
a a	20	8·6	*wt wt*	20	9·2	*a a*	20	7·1
t t	8	8·5	*f f*	20	13·5	*d d*	21	6·9
wf wf	20	9·1	*al al*	20	8·3	*l l*	20	8·1
y y	20	8·5	*ls ls*	43	6·8	*ls ls*	24	6·0
u u	12	8·4	+ +	20	7·2	+ +	73	7·4
ls ls	20	5·8						
+ +	20	9·2						
5 per cent. L.S.D. = 1·69			5 per cent. L.S.D. = 2·20			5 per cent. L.S.D. = 1·16		

family 72, *ls d* and *ls l* in family 70, and *ls wt* in family 71 would probably show significant effects on more extensive testing.

The behaviour of *ls a* is noteworthy since in family 70 it behaves in a negative direction, while in family 72 it increases flower number above the level of *ls* +. The variable interactions of *a*, if they are to be

TABLE 5

Flower numbers of F_2 plants homozygous for combinations of marker genes and ls

Family H 70			Family H 72			Family H 71		
Genotype	No.	Flower no.	Genotype	No.	Flower no.	Genotype	No.	Flower no.
+ +	40	7·35	+ +	20	9·15	+ +	20	7·20
ls +	73	6·02	*ls* +	20	5·85	*ls* +	43	6·77
ls c	24	5·71	*ls e*	18	4·11	*ls al*	14	6·90
ls a	37	5·14	*ls a*	18	7·88	*ls H*	19	6·10
ls d	28	5·39	*ls t*	14	5·78	*ls dm*	29	4·33
ls l	35	5·40	*ls y*	12	7·20	*ls wt*	10	7·55
			ls u	12	5·91	*ls f*	14	7·10
5 per cent. L.S.D. = 0·92			5 per cent. L.S.D. = 1·52			Not sign.		

explained on the basis of linkage, demand that the action of the linked units is reversible and that they function only in the presence of *ls*. Similarly, *dm* and *e* proved entirely neutral when present alone; their negative effect became evident only in combination with *ls*, while the combination *ls f* completely neutralised the positive effect due to *f* seen in table 4.

5. DISCUSSION

The point was made earlier that no conscious selection could have operated on this mutation since its first appearance in 1951. The variety Antimold B in which the mutant arose, as well as the parents of that variety, are all cultivated varieties in which high flower number is an expression of prime importance. Antimold B has an average flower number of 16·7 per inflorescence which is above average for forms of *esculentum*. The direction of selection in all the parental lines has therefore consistently been for high flower number, and one would expect an accumulation of positive genetic units controlling this expression to have occurred. The fact that on first appearance, the mutant gene affected flower number in a negative direction seems to rule out the possibility that quantitative factors accumulated under selection are operating. There is no evidence from meiosis or pollen viability that the mutation is a sizable deletion or inversion which could account for a large region comprising segments with separate functions being affected.

Several associations of the kind described here have been reported in the tomato (Currence, 1938; and Fogle and Currence, 1950). They have without exception been interpreted on the basis of close linkage between specific units having separate effects on the associated characters. On analysing these associations critically one finds that in every instance the quantitative character is shifted in the same direction irrespective of the marker gene or chromosome involved, and the direction is generally opposite to the direction of selection pressures acting on the wild-type. Currence (1938) reported on the four recessive markers *d p o* and *s*, and showed that the homozygous recessive genotypes of three of these was associated with lateness. These four genes are located on the same chromosome but the distance between *d* and *s* is 42 units indicating that along practically the whole length of the marked chromosome, only blocks of genes with negative effect can be detected. Again Fogle and Currence (1950) studied a further six markers distributed in four linkage groups, and with one reliable exception, the results followed those for *d p* and *s* as regards the unidirectional nature of the associations. These results are all the more significant since the direction of the expression in the continuous character remained constant in segregating recessives irrespective of the direction of expression of the character in the genotype from which the class was originally derived. For example, the markers *d* and *y* were found to be associated with lateness in segregating progenies of the two types of crosses, early *dd* × late *yy* and late *dd* × early *yy*. It is difficult to see how these results can be reconciled with the interpretation of linkage given by the authors.

One of the constant features of the modifier pattern found in the present material was that, in a given segregate, only one of the multiple expressions associated with the *ls* locus was affected. Apart from apical

growth and flower number, no correlated modifications appeared in *ls ls* plants even though some possessed an almost normal phenotype in respect of one of the quantitative effects. One interpretation of this effect would be to assume that the gene background interacts differentially with specific units of a linked system of quantitative genes. The remainder of the evidence, however, is firmly set against this explanation, and the basis of the unilateral behaviour of the gene background is probably due to interactions involving the direct and indirect effects of a single, basic error at the *ls* locus. That character modifications can occur singly in a multiple system based on one inheritance unit is clearly of the utmost importance in ensuring the survival of the advantageous components of a complex character.

It is highly significant that the most spectacular modifier influence was evident in F_2 progenies from inter-specific crosses: the release of variability from crosses within *L. esculentum* being in most cases quite negligible. If the modifications observed were the result of small quantitative effects at other loci, one might have expected intra-specific crosses to have been equally successful since, presumably, the stabilisation of characters like corolla development, apical growth and fertility must be considered advantageous to all species. The fact that only *L. pimpinellifolium* possessed the genetic constitution necessary for increasing the variation patterns of the several effects of the *ls* locus, suggests that the modifications are the result of inter-action between elements of the gene system which have attained a greater measure of diversification than is characteristic of intra-specific differences.

The studies on quantitative variation in *Prunus avium* and *Prunus persica* (Williams and Brown, 1956*a* and *b*) support the general conclusions reached here and underline what is already known concerning the positive role of major gene loci in controlling continuous variation. In most examples of this kind the limits of function of the major genes are not known and therefore the connection between the known action of the locus and the quantitative characters is not as obvious as in the case of the *ls* mutation, where most of the manifold effects, including flower number, can logically be related to the control of meristematic activity. Since the relation between gene and quantitative function is in general so complex, the part played by pleiotropy in determining character associations cannot be lightly dismissed when designing selection procedures.

6. SUMMARY

1. The manifold effects of the *ls* gene in the tomato, and the influence of diversity of genetic background on the various manifestations of the gene are described.

2. It is shown that effects of modifiers on one expression is not accompanied by a correlated response in the other. Thus the gene milieu can discriminate between the components of a complex series

of reactions resulting from one gene mutation and bring about modification of the manifold effects one at a time. This results in flexibility under selection, and enables the fixation of only those parts of the variability complex which have survival value.

3. No cross-over phenotype was detected in segregating progenies amounting to 57,268 plants.

4. The effects of interactions between *ls* and other marker genes on flower number, a typically metric trait, are described. It is suggested that the results are compatible only with an interpretation based on some form of pleiotropic action of the major gene mutation which responds to the influence of certain gene backgrounds.

5. The unidirectional nature of quantitative characters when associated with major gene mutations is discussed and is given as evidence supporting the hypothesis that indirect, direct or " spurious " pleiotropic action of major genes, can account for much of the quantitative variation that has hitherto been ascribed to linkage.

6. It is concluded that, where the aim is to resolve highly associated characters, wide-crossing can be expected in many instances to provide a better opportunity for selection than procedures designed to break linkages.

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