STUDIES ON THE NATURE OF THE INTERACTIONS OF THE GENES DIFFERENTIATING QUANTITATIVE CHARACTERS IN A CROSS BETWEEN *LYCOPERSICON ESCULENTUM* AND *L. PIMPINELLIFOLIUM*

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CONTENTS

INTRODUCTION

ALTHOUGH the genetical and statistical principles fundamental to the proper design of an experiment for studying the nature of the interactions of genes differentiating quantitative characters are the same as those essential to planning any research problem in genetics, certain difficulties arise that are of major importance in such studies. The purpose of the present paper is to report the results from an experiment designed to eliminate, in so far as possible, these difficulties and disturbing factors and to report the results from a study on the nature of the interactions of the genes differentiating number of locules and size of fruit in *Lycopersicon* hybrids.

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One of the most difficult problems is the identification of the genotypes resulting from a segregation of the genes differentiating the quantitative characters under investigation. In some studies the genotypes can be identified directly (Hayes & Harlan, 1920; Wexelsen, 1934; Powers, 1934), and thus segregates of different genotypes can be accurately classified. However, in the majority of the cases the different genotypes dependent upon segregation of the genes differentiating the quantitative character cannot be determined and then it is necessary to study the nature of the interactions of the genes by means of markers (Powers, 1936). In most cases the study is less complex if the marker genes are independently inherited. Some of the problems involved have been discussed in a previous article by Powers (1939) and need not be repeated here.

Another problem of major importance is the method of verifying genetical results. Two methods are quite commonly used by geneticists, namely, the progeny test and the backcross. Emerson (1910) in studies on the inheritance of quantitative characters points out the difficulties involved in using the progeny test. It is obvious that (with the possible exception of some asexually propagated or perennial material) the parents and progeny cannot be grown the same season and therefore the genotypic and seasonal effects are confounded. By such an experimental design the interaction between years and generations, years and genotypes, and generations and genotypes cannot be determined. All of these interactions, however, can be determined by growing F_2 and backcross generations over a period of years. In the present study the F_2 and backcross generations were grown in a randomized block experiment.

Since in such studies sections of the chromosome (Powers, 1936, 1939) are being dealt with, it is desirable to inquire as to the probable size of these sections as compared with the entire chromosome. Number of chiasmata formed in any one pair of chromosomes and their distribution have a bearing upon the size of the section. From Darlington (1937, p. 290) it can be seen that the means of 2, 3, 4 and 5 for number of chiasmata are the most common and that the range in number of chiasmata is from 1 to 14. Since one chiasma represents only 50% interchange between homologous chromatids, comparatively speaking, some, if not all of the interchanged blocks between chromatids, must be large. This can be readily comprehended by considering a bivalent chromosome having two chiasmata both of which involve the same homologous chromatids. Then the recombined chromatids would be composed of only three blocks. This means that all the genes of the two chromatids would have been recombined on the basis of only three groups; whereas the genes carried in the sister chromatids would not have undergone recombination but instead would have been passed on to their respective gametes as units. It is clear that in studying the nature of the interactions of genes affecting quantitative characters by means of marker genes the investigator may be, and probably is, dealing with more than one locus affecting the quantitative character per section of the chromosome studied.

Problems of a more statistical nature that can be studied by experimentation are those involving measurement of the quantitative character, randomness of occurrence of the genotypes dependent upon segregation of the marker genes, homogeneity of variances making up a generalized error, transformation of data and tests of significance. The purpose of this paper is to report data having a bearing on these problems together with the results obtained from a study of the nature of the interactions of genes differentiating number of locules and size of fruit in a cross between *L. esculentum* and *L. pimpinellifolium*.

DESIGN OF THE EXPERIMENT

Powers (1936) gives a method of design allowing for analysis of variance and covariance within and between genotypes. The same method of analysis was used by Currence (1938). The variation between plants within genotypes provided an estimate of error. However, this design did not provide for measuring the variability due to position in the experimental area on which the plants were grown. To allow for any possible differences due to position, the experimental area was divided into blocks and the generations and parents were replicated within blocks. The number of plots of each parent and generation was based upon genetical considerations and hence, being dependent upon the dictates of the study, should vary from experiment to experiment.

In designing the experiment, it was apparent that as many plants of the parents were not needed as of the segregating generations. Likewise, since for any one factor pair the backcross generations would be segregating in a 1 : 1 ratio and the F_2 generation would be segregating in a 1 : 2 : 1 ratio, more plants of the F_2 generation would be needed. However, it seemed desirable to have the generation resulting from backcrossing to the recessive parent occurring somewhat more frequently than was indicated by the 1 : 1 and 1 : 2 : 1 ratios because the data obtained from the progeny resulting from crossing the F_1 to the recessive parent furnish considerable information on the nature of the interactions of the genes. Also, it seemed more desirable to have the plots of the backcross to the recessive parent occurring more frequently than plots of the backcross to the dominant parent. In order to distinguish the smaller differences that would be expected between the backcrosses to the dominant parent and the dominant parent it was thought desirable to have the latter occurring somewhat more frequently than the recessive parent.

Having these points in mind the experiment was designed as follows, the numbers of each item being as indicated:

Marker gene pairs	2
Generations and parents	5
Plants within a plot	24
Plots within a block	37
Johannisfeuer	2
Red currant	3
B_1 to red currant	4
B_1 to Johannisfeuer	12
F_2 generation	16
Blocks	9

Each plot consisted of a row twenty-four plants long with the rows spaced 3½ ft. apart and the plants spaced 3½ ft. within the row. The twenty-four plant plot provides that the recessive for any one gene pair in the F_2 generation should occur on the average of six times in each row. The positions of plots, of generations and of parents were randomized within blocks by the use of Tippett's (1927) tables. This randomization existed while the plants were growing in the greenhouse as well as when they were growing in the field. Hence, any possible positional effect in the greenhouse or field would not be confounded with comparisons for which the study was designed. It will be noted that such a design allows for testing whether the genotypes occur at random; the homogeneity of variances between generations, between genotypes and between blocks; the desirability of transforming the data; and whether interactions between gene pairs exist and, if so, the nature of the interactions.

EXPERIMENTAL DATA

Inheritance of the marker characters

The genes used as markers in the present study were those differentiating depth of grooves and shape of fruit. The ratio of plants having smooth or slightly grooved fruits to those having deeply grooved fruits was 2508 : 871 for the F_2 generation and 1272 : 1229 for the progeny of the F_1 backcrossed to Johannisfeuer. All of the plants from the F_1 generation backcrossed to red currant had smooth or slightly grooved fruits. As to shape of fruit, the ratio of round fruited plants to somewhat oblate to decidedly oblate was 851 : 1651 : 877 for the F_2 generation, the ratio of somewhat oblate to decidedly oblate was 1249 : 1252 for the progeny of the F_1 backcrossed to Johannisfeuer and the ratio of round to somewhat oblate was 410 : 438 for the F_1 backcrossed to red currant. It is apparent that as to depth of grooves and shape of fruit each is differentiated by one major factor pair. Both the environment and other genes modify the expression of these two characters, but it is evident that they do not prohibit a classification based on the segregation of the major factor pairs involved. Lindstrom (1927, 1928) believes that a series of multiple alleles govern fruit shape in tomatoes. Since he found that round and oval shape of fruit segregated as expected on the basis of one factor pair, and since the segregation for round and oblate shape of fruit reported herein is that expected on the basis of one factor pair, the present study offers further support for the deductions made by Lindstrom.

The symbols used to designate the genes involved were as follows:

G, symbol used for the gene differentiating slightly grooved or smooth from deeply grooved type of fruit.

g, symbol used for the allele of **G**.

O, symbol used for the gene differentiating round from oblate shape of fruit.

$\mathbf{o^{ob}}$, symbol used for the allele of **O**.

It should be kept in mind that the homozygous dominants and the heterozygous dominants are classed together for the F_2 generation in the study that follows. The symbol B_1 which will appear both in the tables and in the text signifies that the progeny studied resulted from backcrossing the F_1 to the designated parent.

Measurement of the quantitative characters

One of the most important problems in such a study is an adequate measure of the quantitative characters under investigation. The two quantitative characters under consideration in this study are number of locules and size of fruit. In obtaining a measure of number of locules, it would be desirable to count the number of locules for each fruit of every plant. However, the labour involved usually prohibits such a procedure. Yeager (1937) obtained satisfactory results by counting the locule number of only ten fruits of each plant. Since, in the present study, over 7500 plants were involved it was not practical to count ten fruits per plant. Therefore, it was decided to count the number of locules of one fruit for each plant and then check the reliability of such a method by counting ten fruits from each plant of a sample of the population. Atypical fruits are frequently found within a single tomato plant. In the counts on locule number in which only one fruit per plant was counted these abnormal or fruits obviously not typical of the plant were avoided. In the case of the counts involving ten fruits per plant, the selection was entirely at random. The mean number of locules based on a count of one fruit per plant and the mean number of locules based on a count of ten fruits per plant, together with an analysis of variance of number of locules for "between and within plants", are given in Table I.

TABLE I

The mean number of locules based on a count of one fruit per plant and the mean number of locules based on a count of ten fruits per plant; and an analysis of variance of number of locules for "between and within plants", the data being based on a count of ten fruits per plant

Parent or generation	Means		Difference*	Degrees of freedom		Variances	
	1 fruit	10 fruits		Between plants	Within plants	Between plants	Within plants
Red currant	2·00	2·08	−0·08 ± 0·09	19	180	0·062	0·082
B_1 to red currant	2·41	2·19	0·22 ± 0·13	21	198	0·342†	0·176
F_2 generation	3·03	2·93	0·10 ± 0·13	69	632	13·609‡	0·611
B_1 to Johannisfeuer	4·25	4·43	−0·18 ± 0·48	23	216	30·543‡	2·742
Johannisfeuer	9·13	8·37	0·76 ± 0·67	23	216	7·362	5·363

* The standard errors of the differences are given.

† $P<0{\cdot}05$. ‡ $P<0{\cdot}01$.

The differences between means are not significant in any case if odds as great as 19 : 1 against the deviations noted as being due to the probable errors of random sampling are accepted as a criterion. Obviously, a count of one fruit per plant is satisfactory when the data are based upon means derived from a number of plants, such as is the case in the research reported herein.

From the analysis of variance listed in Table I information can be obtained concerning the suitability of number of locules for use in studies on the nature of the interactions of genes differentiating quantitative characters. It will be noted that the variances for "between plants", as regards both parents, closely approximate their respective variances for "within plants". This is not true for any of the three segregating generations, the variances for "between plants" being considerably greater than the variances for "within plants". This is particularly noticeable for the F_2 and B_1 to Johannisfeuer generations. Since differences between plants within the parents must be mainly due to the effect of position within the plot, it may be concluded that the relative importance of the variability due to the segregation of genes is considerably greater than the importance of the variability due to position of the plants in the plot. Such being the case, number of locules is a quantitative character well suited to studies for determining the nature of the interactions of the genes.

Since the sizes of the fruits of red currant (*L. pimpinellifolium*) and Johannisfeuer (*L. esculentum*) are so different, it was decided to base sizes of fruit upon observational grades of from 1 to 9 inclusive. After the grades had been recorded a sample of ten fruits per plant, including all parents and generations, was taken and the average weight in grams of each grade was determined. Such a procedure makes it possible to determine the relationship between the grades and absolute weights. Then the measurements of weights as taken provide an estimate of the weights of each grade. Such being the case, the data can be transformed to absolute weights. Tests of significance of such transformed data must be based on constants derived from the variation due to grades as well as the variation due to an estimation of the mean weights of these grades. The grades and mean weights per fruit with the standard errors are listed below:

(1) $0{\cdot}64 \pm 0{\cdot}05$
(2) $2{\cdot}69 \pm 0{\cdot}13$
(3) $4{\cdot}39 \pm 0{\cdot}20$
(4) $7{\cdot}78 \pm 0{\cdot}35$
(5) $11{\cdot}14 \pm 0{\cdot}55$
(6) $14{\cdot}95 \pm 0{\cdot}76$
(7) $20{\cdot}32 \pm 1{\cdot}25$
(8) $30{\cdot}04 \pm 2{\cdot}27$
(9) $40{\cdot}11 \pm 1{\cdot}79$

As expected, these data show that size of fruit based on grades and size of fruit based on absolute weights are closely associated. For that reason a detailed analysis of size of fruit based on a transformation of the grades to absolute weights is given only for that part of the research concerning the nature of the interactions of the genes affecting the quantitative characters.

Random distribution of genotypes

From genetic considerations alone, random distribution of genotypes as regards position within plots, distribution between plots and distribution between blocks would seem probable. However, if random assortment of genotypes was not the case, possible effects due to position would be confounded with possible genotypic effects and any conclusions regarding the nature of the interactions of the genes differentiating the quantitative characters might be misleading. The χ^2 values obtained for testing independence between genotypes and any one of twenty-four possible positions within plots, between genotypes and plots and between genotypes and blocks are given in Table II. From the data in this table it can be seen that the different genotypes are distributed at random.

TABLE II

χ^2 *values obtained for testing independence between genotypes and any of twenty-four possible positions within plots, between genotypes and plots and between genotypes and blocks*[*]

		Distribution	
Genotypes	Position within plots	Between plots	Between blocks
$\mathbf{GgOo}^{ob}$	13·230	7·632	4·731
$\mathbf{Ggo}^{ob}\mathbf{o}^{ob}$	24·355	17·835	6·160
$\mathbf{ggOo}^{ob}$	20·385	16·807	5·696
$\mathbf{ggo}^{ob}\mathbf{o}^{ob}$	13·596	5·284	2·744

[*] The χ^2 values necessary to give a P value as small as 0·05 are 35·172, 19·675 and 15·507, respectively.

Homogeneity of variances

Powers (1936) found that the variances were not homogeneous for "between genotypes", and therefore that a generalized error was not suitable for testing the significance of differences between genotypic means. From these results it seems that, in order to have information for designing an experiment on genetic studies dealing with the nature of the interactions of the genes differentiating quantitative characters and in order to have reliable methods of reducing the data from these same studies, more information concerning the variability of the variances is needed. For example, it is desirable to know whether the variances are homogeneous for "between genotypes", for "between generations", and for "between blocks"; and if such is not the case, whether some transformation of the data will overcome the difficulties involved. The experiment was designed so that the homogeneity of the variances could be tested. The data are presented in Table III.

Detailed statistical analyses are not necessary to demonstrate that the variances for number of locules are not homogeneous for "between genotypes" and for "between generations". The same was found to be true for the variances of size of fruit. However, it was not possible from an inspection of the data to determine whether the variances were heterogeneous for "between blocks". Consequently the χ^2 values for testing the heterogeneity of the variances for both number of locules and size of fruit were calculated and are shown in the last two columns of

TABLE III

Variances for number of locules together with the χ^2 values for testing the homogeneity of variances between blocks. The χ^2 values are listed for both the quantitative characters (number of locules and size of fruit)

Generations, genotypes, and parents	Blocks									χ^{2*}	
	I	II	III	IV	V	VI	VII	VIII	IX	No. of locules	Size of fruit
F_2 generation											
$GgOo^{ob}$	0·527	0·479	0·680	0·870	0·454	0·631	0·574	0·581	0·582	43·777	54·276
$Ggo^{ob}o^{ob}$	1·095	2·162	2·241	2·309	2·131	1·789	1·256	0·784	1·723	8·296	9·380
$ggOo^{ob}$	2·254	1·774	1·123	1·067	1·297	2·240	0·514	3·157	1·517	21·508	23·670
$ggo^{ob}o^{ob}$	4·121	3·700	5·093	5·852	2·684	4·372	6·460	4·617	7·584	26·872	10·649
B_1 to Johannisfeuer											
$GgOo^{ob}$	1·203	1·643	1·588	1·441	1·534	2·245	2·675	2·228	2·490	33·655	18·521
$Ggo^{ob}o^{ob}$	2·097	3·284	3·781	3·380	4·069	17·802	5·178	6·002	7·448	63·108	14·758
$ggOo^{ob}$	1·921	8·813	2·047	4·123	3·274	3·589	4·984	5·448	2·658	20·952	21·149
$ggo^{ob}o^{ob}$	5·378	5·582	9·781	8·603	7·807	8·093	7·255	8·166	12·400	29·854	13·296
B_1 to red currant											
OO	0·189	0·161	0·169	0·243	0·199	0·194	0·255	0·274	0·205	6·490	11·724
Oo^{ob}	0·250	0·255	0·276	0·206	0·247	0·377	0·399	0·289	0·291	8·736	12·042
Parents											
Red currant	0·029	0·138	0·076	0·074	0·096	0·074	0·116	0·170	0·121	46·015	—
Johannisfeuer	6·648	7·347	12·236	7·618	8·233	6·207	7·516	8·265	12·886	12·860	10·666
Average (within blocks)	1·996	2·291	2·903	2·854	2·356	2·941	2·850	2·924	3·728	110·604	14·052

* χ^2 of 15·507, $P = 0·05$.

Table III. Stevens's (1936) formula for calculating the χ^2 values was used.

From these data it can be seen that in the majority of the cases the variances are not homogeneous for "between blocks". This is particularly true for number of locules. It seems the homogeneity of the variances for "between blocks" is a function of the genotype, being particularly evident in the χ^2 values listed for size of fruit. The o^{ob}o^{ob} genotype for size of fruit has a χ^2 value smaller than 15·507 for both the F_2 and B_1 generations. It can be seen from the footnote at the bottom of Table III that a χ^2 value of 15·507 gives a P of 0·05. The other χ^2 values listed for size of fruit are highly significant if odds as great as, or greater than, 19 : 1 are accepted as a criterion.

TABLE IV

Degrees of freedom and F values for testing the effect of blocks upon the means of the different genotypes and the means of the parents

			F value			
Genotype, B_1 and parents	Degrees of freedom		Number of locules		Size of fruit	
	F_2	B_1	F_2	B_1	F_2	B_1
GgOo^{ob}	2260	1026	0·840	2·489†	7·001†	3·209†
Ggo^{ob}o^{ob}	230	228	0·774	1·366	0·906	1·742
ggOo^{ob}	224	205	0·667	2·403†	1·885	2·273
ggo^{ob}o^{ob}	629	1006	1·928	2·668†	4·107†	6·603†
B_1 to red currant						
OO	401	—	0·432	—	12·534†	—
Oo^{ob}	429	—	1·168	—	12·872†	—
Red currant*	573	—	0·277	—	—	—
Johannisfeuer	394	–	5·497†	—	3·934†	—

* An F value for size of fruit of red currant could not be calculated as all fruits of the red currant plants classified in grade I.

† $P < 0·05$.

Block effect

Before finally setting up the method of reduction of the data, it is desirable to ascertain the effect of blocks upon the genotypes and parents. The degrees of freedom and F values (Snedecor, 1938) for testing the effect of blocks upon the means of the different genotypes and the means of the parents are given in Table IV. From this table it is evident that there is a block effect for both number of locules and size of fruit as regards some genotypes and the Johannisfeuer parent; showing that number of locules as well as size of fruit is influenced by environmental conditions. Also, it may be concluded that a method of reduction of the data removing the variation between blocks from an estimate of error would result in greater precision.

A comparison between the sizes of the F values listed in Table IV is interesting. In no case are the F values for the $\mathbf{Ggo^{ob}o^{ob}}$ genotype of sufficient magnitude to give a P value as low as 0·05, and in only one case are the F values for the $\mathbf{ggOo^{ob}}$ genotype of sufficient magnitude to give a P value as low as 0·05. Moreover, in only one case does the F value of the $\mathbf{Ggo^{ob}o^{ob}}$ genotype exceed that of the $\mathbf{ggOo^{ob}}$ genotype. For these two genotypes it can be seen that the degrees of freedom (Table IV), the size of the variances (Table III) and the size of the means (Table VI) are very similar. With the exception of number of locules in the F_2 generation all of the F values for the $\mathbf{GgOo^{ob}}$ and the $\mathbf{ggo^{ob}o^{ob}}$ genotypes are of sufficient magnitude to give a P value lower than 0·05; and in every case are larger than the F values for either the $\mathbf{Ggo^{ob}o^{ob}}$ or the $\mathbf{ggOo^{ob}}$ genotypes. In evaluating these findings the degrees of freedom for each genotype (Table IV), the size of the variances (Table III) and the size of the means (Table VI) should be kept in mind. From these considerations it would seem that to some extent at least the sizes of the F values are functions of the genotypes.

Estimate of error and test of significance

The analysis of the data for the variances makes it very clear that a generalized estimate of error cannot be used legitimately in evaluating differences between generations and between genotypes and for testing the statistical significance of the interactions unless some transformation of the data can be made. It is equally clear that a logical basis of transformation is dependent upon the nature of the data. Therefore, until such a basis for transformation has been established by research, it does not seem logical to use a transformation in reducing the data.

Since, as shown from a study of the variances, a generalized error is not applicable to the data, it is necessary to run an analysis of variance for each genotype within generations and for each parent. The lack of homogeneity for variances within genotypes, generations and parents shows that greater precision would be obtained by making the analysis within blocks also. However, since in this study a comparison between means of blocks is of no concern and since the added precision obtained by confining the analysis to within blocks does not warrant the extra labour required for making the calculations (in respect to these data), the analysis was not made for each block separately but instead a generalized error as regards blocks was calculated. The detailed method of analysis need be illustrated for only one genotype and generation. This is given in Table V for the $\mathbf{ggo^{ob}o^{ob}}$ genotype of the progeny obtained by backcrossing the F_1 generation to the Johannisfeuer parent. The mean square within blocks shown in the summary at the bottom of the table is used as an estimate of error. An estimate of the errors for the other genotypes was obtained in the same manner. Since the sums of squares for "within blocks" usually is obtained by subtracting the sums of squares for "between means" of blocks from the total, column 6 of this table serves as a check as to the correctness of the calculations for sums of squares. From the subheadings for rows in Table III it can be seen that this method of reducing the data involves the calculation of 12 estimates of error, one for each genotype within the three generations and one for each parent.

TABLE V

Analysis of variance for number of locules within the $ggo^{ob}o^{ob}$ *genotype of the* F_1 *generation backcrossed to Johannisfeuer*

Blocks	N'	SX	SX^2	$(SX)^2/N'$	$SX^2-(SX)^2/N'$
I	116	829	6543	5924·491	618·509
II	115	814	6398	5761·704	636·296
III	103	793	7103	6105·330	997·670
IV	119	928	8252	7236·840	1015·160
V	119	900	7728	6806·723	921·277
VI	110	813	6891	6008·809	882·191
VII	113	868	7480	6667·469	812·531
VIII	117	798	6390	5442·769	947·231
IX	103	853	8329	7064·165	1264·835
Total	1015	7596	65114	57018·301	8095·699

Correction factor = 56846·518.

Analysis summary

Variation due to	D.F.	Sums of squares	Mean square
Total	1014	8267·482	—
Between means of blocks	8	171·783	21·473
Within blocks (error)	1006	8095·699	8·047

With these estimates of error available it is possible to test for significance of differences between means of the genotypes and to test whether the interactions are statistically significant. To test significance a slight modification of the t test as given by Fisher (1934, p. 120) was used. As the variances for the different genotypes and generations were found to be non-homogeneous it is not logical to pool the sums of squares in calculating t. The formula for obtaining t used in testing the significance of the first order interactions is as follows:

$$t=\bar{x}_1+\bar{x}_4-\bar{x}_2-\bar{x}_3 \text{ divided by } \sqrt{\left(\frac{S_1^2}{n_1 n_1'}+\frac{S_2^2}{n_2 n_2'}+\frac{S_3^2}{n_3 n_3'}+\frac{S_4^2}{n_4 n_4'}\right)}.$$

In the above formula $\bar{x}_1$, $\bar{x}_2$, $\bar{x}_3$ and $\bar{x}_4$ are the means for the different genotypes within generations: S_1^2, S_2^2, S_3^2 and S_4^2 are the sums of squares for the estimation of the separate errors; n_1, n_2, n_3 and n_4 are the degrees of freedom available for an estimation of the separate errors; and n_1, n_2', n_3' and n_4' are the total number of individuals for the genotypes whose means are involved in the calculation of the interaction. This formula is easily modified for testing the significance of differences between means and for testing the significance of the higher order interactions. In fact, for testing the significance of differences between means, it is identical with the one commonly used (see Hayes & Garber, 1927, p. 38).

The effects of different regions of the chromosome and generations upon the quantitative characters, and the nature of the interactions of the genes

Fundamental considerations.

The linkage relationships of the marker genes, some matters of terminology and the theory of gene action as developed by Goldschmidt (1938) are of aid in an interpretation of the data. Therefore, they are considered before taking up the effects of the different regions of the chromosome and generations upon the quantitative characters and before going into the nature of the interactions of the genes.

The linkage relationship of the marker genes is (**GO**) (go^{ob}) with $18 \pm 0{\cdot}76\%$ of crossing-over in the F_2 generation and $15 \pm 0{\cdot}71\%$ of crossing-over among the progeny of the F_1 backcrossed to Johannisfeuer. As will be shown later, a preponderance (in effect) of the genes favourable to an increase of both the quantitative characters is linked with the g and o^{ob} marker genes and these genes tending to increase the two quantitative characters are partially recessive.

As in a previous paper (Powers, 1939), that part of the chromosome delimited by the marker genes is referred to as the Gg–Oo^{ob} section of the chromosome and that part of the chromosome extending for some distance on either side of the locus of a marker gene as a region of the chromosome. Hence the sections of the chromosomes have definite limits, whereas the regions do not.

The theory of gene action as developed by Goldschmidt (1938) has a direct bearing upon an interpretation of the data concerning the nature of the increase. Goldschmidt pictures the development of the individual as due to reaction velocities in tune and further that the reactions involved are catalysed by genes. That the genes control rates of reactions (Wright, 1916) and (Goldschmidt, 1917) is basic to this theory. Other biological phenomena basic to Goldschmidt's theory of gene action are thresholds, timing, interrelationships of the different reactions catalysed by the genes and the numerical systems involved. Because of the relation they have to the interpretation of the nature of the interactions of the genes as measured by end products, it is very much worth while to consider these phenomena further.

First, consider thresholds. One type of action of the gene may be visualized as that in which a substance is produced by catalytic action at a definite rate and which must be present in a certain concentration, threshold value, before any morphogenetic effect is produced. Then the velocity of the rate reaction may depend upon the concentration of the substance above this threshold until a maximum is reached above which no speeding up of the morphogenetic change takes place. It is apparent that two thresholds may exist, one at which the morphogenetic change starts and another above which no increased speed of the morphogenetic change occurs. The above conception as developed by Goldschmidt (1938) may vary greatly in detail, but the fundamental principle of rates of reaction as regulated by genes through some catalysing agency and the fundamental principle of threshold values would still be valid.

Proper timing of these different reactions is important to the fullest development of the character. It can be seen that if one substance is totally or partially dependent upon another for its reaction, or upon a certain stage or phase of development of an organ, that the time at which this substance is produced or the quantity of the substance present is of paramount importance to development. For example, suppose that a certain substance "*A*" causes a specific morphogenetic result only in the presence of a second substance "*B*" that appears and remains only during a certain period of development. Further, let us suppose that the rate of reaction is dependent upon the concentration of the two substances. Then, it is apparent that if the processes which produce the two substances synchronize and proceed along parallel lines, both reaching their maximum concentration at the same time, the greatest morphogenetic change possible would be obtained. A continuous shift in the time of production of either one or the other of these substances would result in a smaller and smaller effect depending upon the degree of asynchronization. This proper interplay of reactions is called tuning by Goldschmidt (1938).

Turning to the interrelationships of the reactions, the researches of Wright (1916, 1917, 1925 and 1927) and the studies of Lawrence & Scott-Moncrieff (1935), dealing with mammalian coat colours and flower colour in *Dahlia*, respectively, should be mentioned. Wright obtained evidence that an assumption of competition for some common substance between factors determining yellow and those determining black was basic in interpreting factor interactions in mammalian coat colours. From their studies, Lawrence & Scott-Moncrieff concluded that the limit of pigment source which can be made available in *Dahlia*, whatever factors are present, can be expressed as six units and that each factor competes for this source in terms of its potential units. Then the total pigment production depends upon the proportion and strength of interaction of all the factors. In other words, the different reactions involved in pigment production are not independent but compete for a limited substance from a common source. It can be seen readily that if the amount were not limited, and hence no competition, the nature of the interactions as measured by the end product (amount of pigment produced) for the different genotypes would be considerably different.

The numerical system remain to be considered. It is apparent that at least two numerical systems are of interest. First, there may not be any interactions between the genes affecting the quantitative character. Then the effects of these genes will be arithmetically cumulative. Secondly, the nature of the interactions of the genes affecting the quantitative character may be such that the effects of the genes are geometrically cumulative. That in certain cases the effects of the genes are arithmetically cumulative is well illustrated by the work of Mangelsdorf & Fraps (1931) on the vitamin A units in kernels of corn. They found that the vitamin A units per gram increase approximately 2·25 for each additional *Y* gene. A number of investigators have realized that the effects of the forces influencing growth are geometrically cumulative. Galton (1879) expressed the belief that the forces acting on vital phenomena tend to have constant rate effects (effects in geometric progression). East (1913) and Groth (1915) came to the conclusion that in certain cases at least the effects of genes differentiating quantitative characters are geometrically cumulative. Lindstrom (1935), from studies to determine the nature of the interactions of the genes affecting size of fruit involving crosses between species of *Lycopersicon*, clearly realizes the importance of not confounding the interactions between pairs of alleles with dominance and the probability that the nature of the interactions of the genes may be such that their effects are geometrically cumulative. Houghtaling (1935) working with the tomato fruit came to the conclusion that the effects of the growth forces regulating cell number and cell expansion should be geometrically cumulative. Sinnott (1937), MacArthur & Butler (1938) and Charles & Smith (1939), from a study of the means and frequency distribution of the parents, F_1 and F_2 generations, interpreted the results from size inheritance studies on the basis that the effects of the genes differentiating the quantitative characters are geometrically cumulative. Powers (1939) found that the nature of the interactions between the genes carried in different regions of the chromosome and the nature of the interactions between the factors represented by generations and those carried in the different regions of the chromosome were such that the effects of these genes were geometrically cumulative. It may be concluded that at least two numerical systems are important in a study of the nature of the interactions of genes differentiating quantitative characters.

It must be kept in mind that in a large number of the studies dealing with the inheritance of quantitative characters, the geneticist is analysing measurements of end products resulting from the effects of forces regulating growth processes. Then, the interplay of thresholds, timing, interrelationships and the numerical systems would provide for a large diversity of end results. In connexion with an interpretation of the data in the present study the interest lies in what effect this interplay of the above biological phenomena would have upon the nature of the interactions of the genes as determined by measurements of end products. In those studies in which the numerical system is independent of thresholds, timing and interrelationships, the nature of the interactions of the genes may be such that the effects of the genes are either arithmetically cumulative or geometrically cumulative. However, in those cases in which independence did not exist the numerical system would be modified, resulting in at least four types of interactions of the genes as determined by measurement of end products. One would be such that the effects of the genes would be less than arithmetically cumulative, another would be such that the effects of the genes would be arithmetically cumulative, still another would be such that the effects of the genes would be somewhat more than arithmetically cumulative, and the fourth would be such that the effects of the genes would be geometrically cumulative.

Methods of analysis and derivation of formulae.

With the above considerations in mind the means of the different genotypes of the F_2 and backcross generations, for the characters number of locules and size of fruit, may be analysed more logically. Size of fruit is given on the basis of grades and on the basis of grades transformed to absolute weights expressed in grams. The means and standard errors of the different genotypes and generations for number of locules and size of fruit are given in Table VI.

From this table it can be seen that there are 7 degrees of freedom for each character. The 3 degrees of freedom attributable to main effects are gg–Gg, $\mathbf{o^{ob}o^{ob}}$–$\mathbf{Oo^{ob}}$ and B_1–F_2. The first two main effects involve comparisons between alleles of the marker genes, whereas the third main effect involves comparisons between generations. Three more degrees of freedom are accounted for by the first order interactions which may be designated as $\mathbf{Gg} \times \mathbf{Oo^{ob}}$, Gg × generations and $\mathbf{Oo^{ob}}$ × generations. The remaining degree of freedom is taken up by the second order interaction and may be designated as $\mathbf{Gg} \times \mathbf{Oo^{ob}}$ × generations. Since dominance is not confounded with the interactions (Powers, 1939) and since effects attributable to regions and generations are due to genes differentiating the quantitative characters, the interactions listed above contain all of the information concerning the nature of the interactions of those genes differentiating the quantitative characters and associated with the marker genes or with the generations.

TABLE VI

Means and standard errors of the different genotypes and generations for number of locules and size of fruit

Genotypes*	Genotypic symbols	No. of locules	Size of fruit	
			Based on grades	Based on weight in grams
		F_2		
$\mathbf{GgOo^{ob}}$	*a*	2·52 ± 0·016	2·91 ± 0·013	4·45 ± 0·221
$\mathbf{Ggo^{ob}o^{ob}}$	*b*	3·51 ± 0·086	3·60 ± 0·049	5·99 ± 0·334
$\mathbf{ggOo^{ob}}$	*c*	3·52 ± 0·085	3·46 ± 0·051	6·05 ± 0·346
$\mathbf{ggo^{ob}o^{ob}}$	*d*	5·22 ± 0·088	4·26 ± 0·038	8·78 ± 0·500
		B_1 to Johannisfeuer		
$\mathbf{GgOo^{ob}}$	*a′*	3·61 ± 0·044	4·39 ± 0·024	9·15 ± 0·475
$\mathbf{Ggo^{ob}o^{ob}}$	*b′*	5·04 ± 0·153	5·08 ± 0·059	11·76 ± 0·707
$\mathbf{ggOo^{ob}}$	*c′*	5·03 ± 0·137	5·00 ± 0·060	11·42 ± 0·677
$\mathbf{ggo^{ob}o^{ob}}$	*d′*	7·48 ± 0·089	5·89 ± 0·030	15·25 ± 0·955

* The homozygous dominants and the heterozygous dominants were not separated in the F_2 generation.

The genetic significance of the interactions can be understood most easily by examining the means of one of the characters partitioned into the 7 degrees of freedom. The main effects and their interactions for number of locules are given in the first row of figures under each row heading of Table VII. In every case the main effects and interactions represent differences. Any main effect is the difference between two means (column 3 of Table VI), any first order interaction is the difference between two main effects and any second order interaction is the difference between two first order interactions. The differences listed under main effects provide information as to whether the regions of the chromosome and the generations possess genes differentiating number of locules. The differences listed under interactions furnish information as to whether there is an interaction between pairs of alleles as represented by regions and generations, and if so, the nature of the interaction. If there is no interaction between the genes carried in one region of the chromosome and those carried in another region of the chromosome, then the differences listed under the first order interactions (in our example **Gg** × **Oo**^{ob}) should not be statistically significant. Likewise, if there is no interaction between the genes carried in different regions of the chromosome and the genes differentiating generations, the first order interactions (in our example **Gg** × generations and **Oo**^{ob} × generations) should not be statistically significant. Then, if there is no interaction of the genes, the effects of the genes as represented by regions and generations must be arithmetically cumulative. On the other hand, if the first order interactions are statistically significant, it may be that the nature of the interactions of the genes is such that their effects are geometrically cumulative.

This brings up the problem of testing whether the data obtained meet the specifications required by the hypothesis that the nature of the interactions of the genes is such that the effects of the genes are geometrically cumulative. The formulae necessary for making such a test need to be developed. The definition for a geometric progression given by Wilczynski & Slaught (1916, p. 86) may be used as a basis for deriving such formulae. Their definition is as follows. "Let us divide each term of a sequence (excepting the first) by the term which immediately precedes it. If all of the quotients obtained in this way have the same value r, the sequence is called a geometric progression, and r is called the common ratio of the progression." In order to expedite the derivation of the formulae for testing whether the effects of the genes are geometrically cumulative, consider the mean values for number of locules given under column heading 3 of Table VI. Further, let us limit the consideration to the means of the F_2 generation. It is apparent that all 4 of these means are involved in the first order interaction **Gg** × **Oo**^{ob}; because by using the symbols a, b, c and d for the different genotypic means this interaction may be written either $(b-a)-(d-c)$ or $(c-a)-(d-b)$. Since b and c do not necessarily need to be equal, the means involved in the interaction do not form a sequence from which any logical conclusions can be drawn, concerning the nature of the interactions, by dividing each term by the term which immediately precedes it. However, if b and c were always equal, as would be the case if **Gg** and $\mathbf{Oo^{ob}}$ were duplicate regions of the chromosome, b/a should equal d/b if a geometric progression were involved. It is apparent that the test cannot be for a geometric progression, but the data can be tested to determine whether a common ratio is involved. For example, b/a should equal d/c, within the limits expected due to the probable errors of random sampling, if the nature of the interactions of the genes for the interaction $\mathbf{Gg} \times \mathbf{Oo^{ob}}$ is such that the effects of these genes are geometrically cumulative. Then, the ratio $(b \div a) \div (d \div c)$ which tests the interaction $\mathbf{Gg} \times \mathbf{Oo^{ob}}$ should not differ significantly from unity. By use of the same arguments the following formulae for obtaining the ratios of the main effects and the interactions were developed.

Main effects

Regions	F_2 generation		B_1 generation	
	$\mathbf{Oo^{ob}}$	$\mathbf{o^{ob}o^{ob}}$	$\mathbf{Oo^{ob}}$	$\mathbf{o^{ob}o^{ob}}$
gg–Gg	$c \div a$	$d \div b$	$c' \div a'$	$d' \div b'$
	Gg	**gg**	**Gg**	**gg**
$\mathbf{o^{ob}o^{ob}}$–$\mathbf{Oo^{ob}}$	$b \div a$	$d \div c$	$b' \div a'$	$d' \div c'$
Generations				
	$\mathbf{GgOo^{ob}}$	$\mathbf{Ggo^{ob}o^{ob}}$	$\mathbf{ggOo^{ob}}$	$\mathbf{ggo^{ob}o^{ob}}$
B_1–F_2	$a' \div a$	$b' \div b$	$c' \div c$	$d' \div d$

Interactions

	F_2 generation	B_1 generation
$\mathbf{Gg} \times \mathbf{Oo^{ob}}$	$(d \div b) \div (c \div a)$	$(d' \div b') \div (c' \div a')$
	$\mathbf{Oo^{ob}}$	$\mathbf{o^{ob}o^{ob}}$
Gg × generations	$(c' \div a') \div (c \div a)$	$(d' \div b') \div (d \div b)$
	Gg	**gg**
$\mathbf{Oo^{ob}}$ × generations	$(b' \div a') \div (b \div a)$	$(d' \div c') \div (d \div c)$
$\mathbf{Gg} \times \mathbf{Oo^{ob}}$ × generations	$[(d' \div b') \div (c' \div a')] \div [(d \div b) \div (c \div a)]$	

Data partitioned into genotypes and generations.

The effects of the different regions of the chromosome and generations upon number of locules together with the interactions are shown in Table VII. The data in Table VII show that the different regions of the chromosomes as represented by alleles have an effect upon number of locules. Also, more than one gene pair is necessary to account for the differences noted between regions for the two generations and the differences between generations show that a gene pair or pairs other than those located in the **Gg** and $\mathbf{Oo^{ob}}$ regions of the chromosome have an influence upon number of locules. Finally, since all of the first order interactions are statistically significant, at least three gene pairs affecting number of locules must be segregating during gametogenesis of the F_1 hybrid. In every case the nature of the interactions of the genes was such that those favourable to an increase in number of locules gave greater differences over their contrasted alleles when in combination with genes also tending to increase number of locules than when in combination with genes not so favourable to an increase in this character.

TABLE VII

*The effects and the interactions of the genes differentiating number of locules**

Contrasted regions, generations and interactions		Differences expressed in numbers and the ratios for "within the various generations and genotypes"			
		Main effects			
Regions					
		F_2 generation		B_1 generation	
		Oo^{ob}	$o^{ob}o^{ob}$	Oo^{ob}	$o^{ob}o^{ob}$
gg–Gg	No.	1·00	1·71	1·42	2·44
	Ratio	1·397	1·487	1·393	1·484
		Gg	gg	Gg	gg
$o^{ob}o^{ob}$–Oo^{ob}	No.	0·99	1·70	1·43	2·45
	Ratio	1·393	1·483	1·396	1·487
Generations					
		$GgOo^{ob}$	$Ggo^{ob}o^{ob}$	$ggOo^{ob}$	$ggo^{ob}o^{ob}$
B_1–F_2	No.	1·09	1·53	1·51	2·26
	Ratio	1·433	1·436	1·429	1·433
		Interactions			
		F_2	B_1		
Gg × Oo^{ob}	No.	0·71	1·02		
	Ratio	1·064‡	1·065‡		
		Oo^{ob}	$o^{ob}o^{ob}$		
Gg × generations	No.	0·42	0·73		
	Ratio	0·997‡	0·998‡		
		Gg	gg		
Oo^{ob} × generations	No.	0·44†	0·75†		
	Ratio	1·002‡	1·003‡		
Gg × Oo^{ob} × generations	No.	0·31‡			
	Ratio	1·001‡			

* The t test gives a value of $P < 0{\cdot}01$ for all values unless stated otherwise.

† $P > 0{\cdot}01$ but $< 0{\cdot}02$.

‡ $P > 0{\cdot}05$.

This fact indicates that the nature of the interactions of the genes might be such that the effects of the genes are geometrically cumulative. For the reasons previously given the ratios provide a test whether the results obtained are those expected on the basis of such a hypothesis. The fact that none of the ratios (Table VII) listed under the interactions are significantly different from unity shows that the data do fit the hypothesis, that the nature of the interactions of the genes is such that their effects are geometrically cumulative.

Next consider size of fruit as based on grades. The effects and the interactions of different regions of the chromosome and generations upon size of fruit are listed in Table VIII. Before proceeding with the interpretation of the data, it is advantageous to determine the dominance relationship of the genes affecting size of fruit. All of the red currant parent plants were classified in grade 1, the F_1 generation had a mean grade value of 3·2 ± 0·20 and the Johannisfeuer parent had a mean grade value of 7·98 ± 0·337. Data were collected again in 1938 in which five fruits of each plant were weighed and expressed in grams. The weight of the red currant parent was 0·93 ± 0·040 g. per fruit, that of the F_1

TABLE VIII

*The effects and the interactions of the genes differentiating size of fruit based on grades**

Contrasted regions, generations and interactions	Differences expressed in grades and the ratios for "within the various generations and genotypes"				
		Main effects			
Regions					
		F_2 generation		B_1 generation	
		Oo^{ob}	$o^{ob}o^{ob}$	Oo^{ob}	$o^{ob}o^{ob}$
gg–Gg	Grade	0·55	0·66	0·61	0·81
	Ratio	1·189	1·183	1·139	1·159
		Gg	gg	Gg	gg
$o^{ob}o^{ob}$–Oo^{ob}	Grade	0·69	0·80	0·69	0·89
	Ratio	1·237	1·231	1·157	1·178
Generations					
		$GgOo^{ob}$	$Ggo^{ob}o^{ob}$	$ggOo^{ob}$	$ggo^{ob}o^{ob}$
B_1–F_2	Grade	1·48	1·48	1·54	1·63
	Ratio	1·509	1·411	1·445	1·383
		Interactions			
		F_2	B_1		
Gg × Oo^{ob}	Grade	0·11*	0·20*		
	Ratio	0·995*	1·018*		
		Oo^{ob}	$o^{ob}o^{ob}$		
Gg × generations	Grade	0·06*	0·15*		
	Ratio	0·958*	0·980*		
		Gg	gg		
Oo^{ob} × generations	Grade	0·00*	0·09*		
	Ratio	0·935*	0·957*		
Gg × Oo^{ob} × generations	Grade	0·09*			
	Ratio	1·023*			

* The t test gives a value of $P < 0{\cdot}01$ for all values not marked with an asterisk, and a value of $P > 0{\cdot}05$ for all values marked with an asterisk.

generation was 4·53 ± 0·152 g. per fruit and that of the Johannisfeuer parent was 38·29 ± 1·611 g. per fruit. Clearly, small size of fruit is partially dominant if the phenotypic expression of the character in the F_1 as compared with the parents is taken as a criterion. In an interpretation of the data listed in Table VIII; it is essential to know what effect partial dominance of small size of fruit would have upon the differences.

Powers (1939) has published tables to aid in determining the effects of different degrees of dominance together with a consideration of other problems that arise in reaching a correct interpretation of such data as presented in Table VIII. From this work it is evident that certain facts must be kept clearly in mind. The values listed in Table VIII for comparisons between regions are not so large as they would have been if dominance were complete. However, any interactions noted are true interactions since neither dominance nor crossing-over is confounded with possible interactions. With these facts as a guide a logical interpretation of the data may be made.

From Table VIII it can be seen that both regions of the chromosome have an effect upon size of fruit based on grades. The effect of the **Oo^{ob}** region is consistently greater than that of the **Gg** region. Likewise, there is an effect due to generations, which shows that genes other than those located in the **Gg** and **Oo^{ob}** regions of the chromosomes are affecting size of fruit. Any one interaction considered alone is not statistically significant if odds of 19 : 1 against the deviation noted being due to chance are accepted as significant. However, taken as a whole, it is evident that these deviations cannot be explained as due to the probable errors of random sampling. Here, as shown by previous work (Powers, 1936), the nature of the interactions is such that genes favourable to an increase in the quantitative character give greater increases over their alleles when in combination with genes also favourable to an increase than when in combination with the alleles that are not so favourable to an increase in the character being studied. Since the same was found to be true for number of locules the question arises as to the nature of the increase. None of the ratios given in Table VIII and listed under the interactions are statistically significant, which shows that the data obtained are those expected based on the hypothesis that the nature of the interactions of the genes is such that their effects are geometrically cumulative.

Since the grades were determined by observation, it seemed desirable to transform the grades to absolute weights and thus determine the effects and the interactions of the genes differentiating size of fruit. The data are presented in Table IX. All of the main effects are statistically significant if odds of 19 : 1 against the deviations noted being due to the probable errors of random sampling are accepted as a criterion. Again, the values for the interactions, expressed in grams, are all positive, which shows that the effects of the genes are more than arithmetically cumulative. Since none of the ratios are significantly different from unity it may be concluded that the data are in accord with the hypothesis, that the nature of the interactions of the genes is such that the effects of the genes are geometrically cumulative.

TABLE IX

*The effects and the interactions of the genes differentiating size of fruit based on the grades transformed to absolute weights**

Contrasted regions, generations and interactions		Differences expressed in grams and the ratios for "within the various generations and genotypes"			
		Main effects			
Regions					
		F_2 generation		B_1 generation	
		Oo^{ob}	$o^{ob}o^{ob}$	Oo^{ob}	$o^{ob}o^{ob}$
gg–Gg	Grams	1·60	2·79	2·27	3·49
	Ratio	1·360	1·466	1·248	1·297
		Gg	gg	Gg	gg
$o^{ob}o^{ob}$–Oo^{ob}	Grams	1·54	2·73	2·61	3·83
	Ratio	1·346	1·451	1·285	1·335
Generations					
		$GgOo^{ob}$	$Ggo^{ob}o^{ob}$	$ggOo^{ob}$	$ggo^{ob}o^{ob}$
B_1–F_2	Grams	4·70	5·77	5·37	6·47
	Ratio	2·056	1·963	1·888	1·737
		Interactions			
		F_2	B_1		
Gg × Oo^{ob}	Grams	1·19*	1·22*		
	Ratio	1·078*	1·039*		
		Oo^{ob}	$o^{ob}o^{ob}$		
Gg × generations	Grams	0·67*	0·70*		
	Ratio	0·918*	0·885*		
		Gg	gg		
Oo^{ob} × generations	Grams	1·07*	1·10*		
	Ratio	0·955*	0·920*		
Gg × Oo^{ob} × generations	Grams	0·03*			
	Ratio	0·964*			

* The t test gives a value of $P < 0·01$ for all values not marked with an asterisk, and a value of $P > 0·05$ for all values marked with an asterisk.

Data partitioned on the basis of parents and generations.

Charles & Smith (1939) present formulae for use in testing whether the data taken on the parents and on the F_1, F_2 and backcross generations are in accord with the geometric gene effect hypothesis. They state: "Since no 'genic' dominance is ordinarily assumed in the geometric scheme $a'_i a'_i$ is as many times larger than $a'_i a_i$ as $a'_i a_i$ is than $a_i a_i$, namely by a factor which is here represented as $(1+k_i)$." It is apparent that their formulae do not take into account "genic" dominance.

Dominance or recessiveness is generally accepted as the phenotypic result of the action and interactions of genes and usually is determined in the F_1 generation. Then, it is evident that two types of interactions are involved, those between the two members of any one allelic pair and those between pairs of alleles. The nature of the interactions of the genes determining dominance differs from that involving comparisons between genes within generations in that the interactions between alleles within pairs is additional. Wright (1934) and Goldschmidt (1938) believe that the phenomenon of dominance or recessiveness is based on the velocities of reaction controlled by the main gene or genes. Goldschmidt (1938) also points out the importance of threshold values, the type of effect and the numerical system of the independently determined process that is involved. In other words, the phenomenon of dominance or recessiveness is based upon genic actions of the same nature as those involved in the differentiation of any character. Such being the case, it is clear that a study of dominance should lead to a better understanding of the nature of the action of the gene.

The formulae given by Charles & Smith (1939) have been applied with the results reported in Table X. The standard errors are given for the obtained means. From Table X, it can be seen that the data are not in accord with the arithmetic gene effect hypothesis, nor are the obtained means in close agreement with the means calculated on the basis of formulae given by Charles & Smith (1939). The data for number of locules show small number of locules to be partially dominant on either the arithmetic or geometric scale. The same is true for the data on size of fruit taken in 1938. Wright (personal correspondence) points out that accepting partial dominance and applying the multiple factor hypothesis, the formula for obtaining the logarithm of the theoretical mean for the F_2 generation becomes

$$\frac{\dfrac{\log P_1 + \log P_2}{2} + \log F_1}{2},$$

in which P_1 and P_2 are the means of the two parents, and F_1 is the mean of the F_1 generation. Then the antilogarithm may be obtained to give the calculated mean. The means calculated thus, for the F_2 generation in 1937, are 3·31, 3·01 and 4·71 for number of locules, size of fruit based on grades and size of fruit based on weights, respectively. For 1938 the means of the F_2 generation calculated in the same manner are 3·23 and 5·20 for number of locules and size of fruit, respectively. In every case, the means for the F_2 generation calculated on the basis of partial dominance and the multiple factor hypothesis give a better fit in comparison with the obtained means than do the calculated means listed in Table X. However, as can be seen from an inspection of the standard errors, the differences between the obtained means and those calculated on the basis of partial dominance and the multiple factor hypothesis are too great to be accounted for by the probable errors of random sampling.

TABLE X

Obtained and calculated means for number of locules and size of fruit based on grades and based on grades transformed to weights. The calculated means are based on formulae given by Charles & Smith (1939)

Generations and parents	Number of locules		Size of fruit based on grades		Size of fruit based on weights	
	Obtained	Calc.	Obtained	Calc.	Obtained	Calc.
1937						
Red currant	2·04 ± 0·013	—	1·00	—	0·64 ± 0·050	—
B_1 to red currant	2·29 ± 0·017	2·54	1·92 ± 0·007	1·80	2·49 ± 0·132	1·87
F_1 generation	2·40 ± 0·245	4·58	3·20 ± 0·200	2·82	5·07 ± 0·328	4·38
F_2 generation	3·17 ± 0·022	4·58 +	3·24 ± 0·013	2·82 +	5·49 ± 0·302	4·38 +
B_1 to Johannisfeuer	5·44 ± 0·044	5·71	5·12 ± 0·017	5·08	12·07 ± 0·703	12·82
Johannisfeuer	10·27 ± 0·144	—	7·98 ± 0·337	—	29·96 ± 1·982	—
1938						
Red currant	2·03 ± 0·025	—	—	—	0·93 ± 0·040	—
F_1 generation	2·48 ± 0·087	4·21	—	—	4·53 ± 0·152	5·97
F_2 generation	2·95 ± 0·062	4·21 +	—	—	4·72 ± 0·136	5·97 +
Johannisfeuer	8·75 ± 0·269	—	—	—	38·29 ± 1·611	—

DISCUSSION AND CONCLUSIONS

The lack of homogeneity of the variances for generations and genotypes invalidates the use of a generalized error to test the significance of differences between means of generations and for testing the significance of the interactions unless some transformation of the data can be made. The fact that the variances for generations and genotypes, to a considerable extent, are a function of the means shows that the difficulties involved due to lack of homogeneity of variances might be overcome by transforming the plant measurements for number of locules and size of fruit to logarithms. However, by so doing information concerning some of the interactions is sacrificed. For example, all of the interactions for number of locules have insignificant *F* values when the data are transformed to logarithms and subjected to the analysis of variance. Since the interactions constitute that part of the data giving the most information concerning the nature of the interactions of the genes differentiating the quantitative characters, it does not seem logical to use a transformation that theoretically is based upon the assumption that an interaction exists. Also, transformation of the data to logarithms requires that one must think in terms of logarithms in interpreting the data, which adds to the complexity of the problem. At least until more information concerning the nature of the progression of such data is available, the method of estimating the error for within homogeneous groups whose means are involved in the comparisons appears to be the simplest and most efficient method of obtaining from the data all the available information. If some transformation is used in reducing the data the fundamental principles basic to such a transformation must be kept in mind when interpreting the results.

There should be some biological explanation for the nature of the interactions of the genes, differentiating number of locules and size of fruit, being such that the effects of these genes are geometrically cumulative. The morphogenetic studies conducted by Houghtaling (1935) and MacArthur & Butler (1938) furnish a basis for interpreting the results obtained. The basic principles established by their work are that the fruits of the many loculed varieties or strains start from a broader meristematic platform; that fruit size at maturity is related to cell number and to cell size; that up to flowering the potential differences in size are due to differences in cell number; and that after flowering increase in size is primarily due to cell expansion. These facts lead to the deduction that since the many-loculed fruits have a broader meristematic platform than the fewer-loculed fruits, the pattern for number of locules is laid down very early during flower development, and therefore that cell multiplication due to physiological genetic processes tending to increase number of locules is distinct from the type of cell division which follows and ceases at the time of flowering. Then chronologically cell number is superimposed upon locule pattern and cell expansion upon both number of locules and cell number.

To determine what effect such a system of morphological development would have upon the measurement of the end product, in this case size of fruit, a simple algebraic formula may be developed. Let

x = ultimate size of fruit; a = number of cells constituting the meristematic platform just after locule number pattern formation; b = cell multiplication as determined by the ratio—final number of cells $\div a$; and c = average size of the cells after expansion ceased. Then it is obvious, as regards these three variables, that $x = abc$. This formula shows that these three developmental stages would combine geometrically. It is interesting to note that "a" in this formula crorresponds to the original size of Sinnott (1921) and Reed (1927) and to Ashby's (1932) initial capital. It is undoubtedly a stage of development and probably results from locule number pattern formation within the promeristem.

Since these three developmental stages are geometrically cumulative, it seems probable that the effects of the genes differentiating number of locules, the effects of the genes differentiating cell multiplication and the effects of the genes differentiating size of cells would be geometrically cumulative. Again, the simplest method of determining what would be expected theoretically is through the development of a simple algebraic formula. Moreover, let us limit the consideration to a single pair of alleles for each of the developmental stages. Let Aa = the gene pair whose segregation results in a certain amount of differentiation in number of locules; let Bb = the gene pair whose segregation results in a certain amount of differentiation in cell multiplication; and let Cc = the gene pair whose segregation results in a certain amount of differentiation in cell expansion (cell size). Among the twenty-seven resulting genotypes let the interaction $(AABBCC - AABBCc) - (AaBBCC - AaBBCc)$ represent any possible interaction of factors. Then, on the supposition that the genic effects are geometrically cumulative, $AA.BB.CC \div AA.BB.Cc$ should equal $Aa.BB.CC \div Aa.BB.Cc$. By rearranging the equation in the form

$$\frac{AA.BB.CC}{AA.BB.Cc} = \frac{Aa.BB.CC}{Aa.BB.Cc},$$

it becomes apparent that the above statement is true as a solution of the equation shows that the two members are identities. Theoretically, the nature of the interactions between the factors differentiating number of locules and those differentiating cell multiplication and those differentiating cell expansion would be such that the effects of the genes would be geometrically cumulative. This is what may be termed an interstage type of interaction of the genes. In addition to this interaction between genes of different stages of development there would be an interaction of genes within any one particular stage. Genes differentiating number of locules were studied and the nature of the interactions was such that the effects were geometrically cumulative. Then a combination of the interactions between and within stages would be expected to be of such a nature as to result in the effects of the genes being geometrically cumulative. Such was found to be the case from the data obtained, both as regards between means of genotypes and between means of generations. Then the character size of fruit is an end product dependent for its expression upon the action and interaction of genes differentiating stages of development, three of which have been considered here.

Since the nature of the interactions of the genes affecting number of locules and size of fruit has been shown to be such that the effects the interactions produce are geometrically cumulative, it seems reasonable that the nature of the action and interactions of the genes regulating the phenomenon of dominance would be such that the mean of the F_1 generation should equal the geometric mean of the two parents. It will be remembered from a previous discussion of the experimental data that such was not the case. This finding raises a problem of biological importance, the solution of which involves a consideration of the types of interactions of genes tending to regulate the phenomenon of dominance compared with the type of interactions between non-allelic genes differentiating number of locules and size of fruit. In the expression of dominance both interactions between members of a pair of alleles (for example, between alleles such as **G** and **g**) and interactions between pairs of alleles (for example, between non-alleles such as **Gg** and **Oo^{ob}**) are involved, whereas, in studies, such as reported herein, on the nature of the interactions of genes differentiating quantitative characters by use of marker genes, only interactions between pairs of alleles are involved. Then, it may be concluded that since the experimental data have shown that the nature of the interactions regulating the expression of dominance is not such as to result in the F_1 generation mean equalling the geometric mean of the two parents, whereas, the nature of the interactions between the genes carried in different regions of the chromosome and the nature of the interactions between the genes represented by generations and those carried in different regions of the chromosome were such that their effects were geometrically cumulative; it necessarily follows that the interactions between members of a pair of alleles and the interactions between pairs of alleles are independent of each other, in the sense that both need not be the same.

Then, it is clear that the experimental design and methods of analysing the data involving studies of the nature of the interactions of genes affecting quantitative characters should not have the interactions between members of a pair of alleles and the interactions between pairs of alleles confounded. As shown previously by Powers (1939), the experimental design and method of analysis used in these studies are such that the nature of the interactions of the genes is not confounded with possible effects due to dominance. This is brought out further by the equation

$$\frac{AA.BB.CC}{AA.BB.Cc}=\frac{Aa.BB.CC}{Aa.BB.Cc},$$

as a solution of this equation shows that the two members are identities regardless of the value assigned to Cc. For the derivation of this equation the reader is referred to a previous paragraph of this discussion.

SUMMARY

1. The data were collected from a cross between *Lycopersicon esculentum* and *L. pimpinellifolium*.
2. The genotypes resulting from a segregation of the marker genes were found to be distributed at random as regards position within plots and as regards plot and block frequencies.
3. As regards both number of locules and size of fruits, the variances were heterogeneous for "between genotypes" and for "between generations". Also, in some of the genotypes the variances were heterogeneous for "between blocks".
4. At least to a certain extent the variability of the variances is a function of the genotype.
5. Both the **Gg** and $\mathbf{Oo^{ob}}$ regions of the chromosome were found to have an effect upon number of locules and size of fruit.
6. At least three gene pairs (probably many more are involved) affecting number of locules and size of fruit were segregating during gametogenesis of the F_1 generation.
7. The effects of the genes differentiating number of locules were geometrically cumulative. Also, this was true of the effects of the genes differentiating size of fruit.
8. It was shown from morphogenetic considerations that, theoretically, the nature of the interactions between stages of development in respect to the genes differentiating number of locules, cell multiplication and cell expansion should be such as to result in their effects being geometrically cumulative.
9. The character size of fruit is an end product dependent for its expression upon the action and interactions of genes differentiating

stages of development. Two of these stages, cell multiplication and cell expansion, were studied by Houghtaling (1935) and MacArthur & Butler (1938). Their studies pertained to the interactions between stages. A third stage, number of locules, was studied by Powers (1939, and in the present paper). Both the interactions of the genes for "between" and for "within stages" were considered in the latter study.

10. In a study of the phenomenon of dominance, or recessiveness, neither the F_1 generation mean nor the F_2 generation mean equalled the geometric mean of the two parents.

11. The interactions within pairs of alleles and between pairs of alleles were found to be independent, in the sense that they were not the same. Hence, it is important in such studies that the experimental design and methods of analysing the data be such that the interactions between members of a pair of alleles and the interactions between pairs of alleles are not confounded.

REFERENCES

ASHBY, E. (1932). "Studies on the inheritance of physiological characters. II. Further experiments on the basis of hybrid vigour and upon the inheritance of the efficiency index and respiration rate in maize." *Ann. Bot., Lond.*, **46**, 457–67.

CHARLES, DONALD R. & SMITH, HAROLD H. (1939). "Distinguishing between two types of gene action in quantitative inheritance." *Genetics*, **24**, 34–48.

CURRENCE, T. M. (1938). "The relation of the first chromosome pair to date of fruit ripening in the tomato (*Lycopersicum esculentum*)." *Genetics*, **23**, 1–11.

DARLINGTON, C. D. (1937). *Recent Advances in Cytology*, 671 pp. Philadelphia, Pa.: P. Blakiston's Son and Co., Inc.

EAST, E. M. (1913). "Inheritance of flower size in crosses between species of *Nicotiana*." *Bot. Gaz.* **55**, 177–88.

EMERSON, R. A. (1910). "The inheritance of size and shape in plants." *Amer. Nat.* **44**, 739–46.

FISHER, R. A. (1934). *Statistical Methods for Research Workers*, 319 pp. London: Oliver and Boyd.

—— (1937). *The Design of Experiments*, 260 pp. London: Oliver and Boyd.

GALTON, FRANCIS (1879). "The geometric mean in vital and social statistics." *Proc. roy. Soc.* **29**, 365–7.

GOLDSCHMIDT, RICHARD (1917). "A further contribution to the theory of sex." *J. exp. Zool.* **22**, 593–611.

—— (1938). *Physiological Genetics*, 375 pp. N.Y.: McGraw-Hill Book Co.

GROTH, B. H. A. (1915). "Some results in size inheritance." *Bull. N.J. agric. Exp. Sta.* no. 278.

HAYES, H. K. & GARBER, R. J. (1927). *Breeding Crop Plants*, 438 pp. N.Y.: McGraw-Hill Book Co.

HAYES, H. K. & HARLAN, H. V. (1920). "The inheritance of the length of the internode of the rachis of the barley spike." *Bull. U.S. Dep. Agric.* no. 869, 1–26.

HOUGHTALING, HELEN B. (1935). "A developmental analysis of size and shape in tomato fruits." *Bull. Torrey Bot. Cl.* **62**, 243–52.

LAWRENCE, W. J. C. & SCOTT-MONCRIEFF, ROSE (1935). "The genetics and chemistry of flower colour in *Dahlia*: a new theory of specific pigmentation." *J. Genet.* **30**, 155–226.

LINDSTROM, E. W. (1927). "The inheritance of ovate and related shapes of tomato fruits." *J. agric. Res.* **34**, 961–85.

—— (1928). "Linkage of size, shape and colour genes in *Lycopersicum*." *Z. indukt. Abstamm.-u. VererbLehre*, **46**, 61–2.

—— (1935). "Segregation of quantitative genes in tetraploid tomato hybrids as evidence for dominance relations of size characters." *Genetics*, **20**, 1–11.

MACARTHUR, JOHN W. & BUTLER, LEONARD (1938). "Size inheritance and geometric growth processes in the tomato fruit." *Genetics*, **23**, 253–68.

MANGELSDORF, P. C. & FRAPS, G. S. (1931). "A direct quantitative relationship between vitamin A in corn and the number of genes for yellow pigmentation." *Science*, **73**, 241–2.

POWERS, LE ROY (1934). "The nature and interaction of genes differentiating habit of growth in a cross between varieties of *Triticum vulgare*." *J. agric. Res.* **49**, 573–605.

—— (1936). "The nature of the interaction of genes affecting four quantitative characters in a cross between *Hordeum deficiens* and *vulgare*." *Genetics*, **21**, 398–420.

—— (1939). "The theoretical effect of double crossing-over and dominance upon the differences between means of the genotypes involved in studies on the inheritances of quantitative characters and the application of this information to an interpretation of data collected from a *Lycopersicon* hybrid."

REED, H. S. (1927). "Growth and differentiation in plants." *Quart. Rev. Biol.* **2**, 79–101.

SINNOTT, E. W. (1921). "The relations between body size and organ size in plants." *Amer. Nat.* **55**, 385–403.

—— (1937). "The relation of the gene to character in quantitative inheritance." *Proc. nat. Acad. Sci., Wash.*, **23**, 224–7.

SNEDECOR, GEORGE W. (1938). *Statistical Methods*, 388 pp. Ames, Iowa: Collegiate Press, Inc.

STEVENS, W. S. (1936). "Heterogeneity of a set of variances." *J. Genet.* **33**, 398–9.

TIPPETT, L. H. C. (1927). *Tracts for Computers. Random sampling numbers*, 25 pp. London: Camb. Univ. Press.

WEXELSEN, H. (1934). "Quantitative inheritance and linkage in barley." *Hereditas, Lund*, **18**, 307–48.

WILCZYNSKI, E. J. & SLAUGHT, H. E. (1916). *College Algebra with Applications*, 507 pp. Chicago: Allyn and Bacon.

WRIGHT, SEWALL (1916). "An intensive study of the inheritance of colour and other coat characters in guinea-pigs, with especial reference to graded variations." *Publ. Carneg. Instn*, pp. 59–160.

—— (1917). "Colour inheritance in mammals." *J. Hered.* **8**, 224–35.

WRIGHT, SEWALL (1925). "The factors of the albino-series of guinea-pigs and their effects on black and yellow pigmentation." *Genetics*, **10**, 223–60.

—— (1927). "The effects in combination of the major colour-factors of the guinea-pig." *Genetics*, **12**, 530–69.

—— (1934). "Physiological and evolutionary theories of dominance." *Amer. Nat.* **68**, 24–53.

YEAGER, A. F. (1937). "Studies on the inheritance and development of fruit size and shape in the tomato." *J. agric. Res.* **55**, 141–52.