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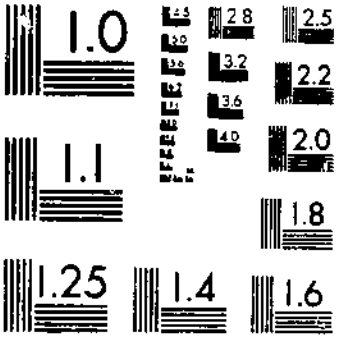

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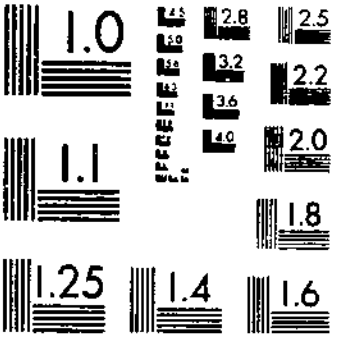

MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A

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Partitioning Method of Genetic Analysis Applied to Quantitative Characters of Tomato Crosses[1]

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INTRODUCTION

Tests by Locke[3] at the Southern Great Plains Field Station, Woodward, Okla., demonstrated that the Porter variety of tomato (*Lycopersicon esculentum* Mill.) has exceptional fruit-setting capacity. No other variety grown at Woodward approaches it in this respect. However, the fruits of this variety are entirely too small for commercial production. It was decided to attempt to combine, by hybridization, the fruit-setting capacity of Porter with desirable characteristics of commercial varieties. Developmental-genetic studies of percentage of flowers that set fruit, period from seeding to first fruit ripe, and weight per fruit are essential to intelligent and efficient execution of a breeding program with tomatoes in the Great Plains region. This

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[3] Unpublished data.

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bulletin reports findings from such studies. It presents new procedures and methods employed in experiments and in analysis of data, which should be helpful in other research projects in the same field.

MATERIALS AND GENERAL METHODS

Ponderosa (P_2) was the tomato variety used in crosses with the Porter (P_1) variety to produce the hybrid populations. Hybridizing to obtain the F_1 and backcross populations and self-pollinating to obtain the F_2 and parental populations were done at the Cheyenne Horticultural Field Station, Cheyenne, Wyo. The hybridization work was conducted in greenhouses during the winter. Both female and male parents were bagged. In all cases, the same plants crossed to produce the F_1 population were used to produce seed for the backcross populations and self-fertilized to produce the parental populations. Likewise the F_1 plants used in backcrossing were selfed to produce the F_2 population. The material was grown at the Southern Great Plains Field Station during the summer of 1941.

The symbol B_1 here signifies that the progeny indicated resulted from backcrossing the F_1 to the designated parent. The term "penetrance" as used here denotes the percentage of individuals in any given class of the frequency distributions. This use of the term broadens its meaning somewhat beyond that originally given by Timoféeff-Ressovsky (*22*).[4]

The dependent characters studied and their components are as follows:

Percentage of flowers that set fruit.	
Period from seeding to first fruit ripe	Period from seeding to first bloom.
	Period from first bloom to first fruit set.
	Period from first fruit set to first fruit ripe.
Weight per fruit	Number of locules per fruit.
	Weight per locule.

Percentage of flowers that set fruit was determined as follows: Each day from the time the first plants began to bloom, June 6, through the week of August 18, two inflorescences (whenever available) that began to bloom on that day were tagged with the date. The flowers on each of these inflorescences were counted and were examined weekly until fruit had set or abscission had taken place. Then, the total number of flowers per inflorescence and the number that set fruit were recorded. The data were taken and recorded on the basis of the individual inflorescence and were entered in the record book for the week in which the first flower of the given inflorescence bloomed. Average number of flowers examined per plant, for both parents and all generations, was 76. The data for all the component characters of period from seeding to first fruit ripe were taken on the basis of 3-day periods. Weight per fruit and number of locules were determined from two fruits taken at random from each plant. All data were taken and recorded on the basis of the individual plant.

The genetic design of the experiment employed all the different populations that could be obtained from the two parents and the F_1 by crossing and self-pollination: P_1, B_1 to P_1, F_1, F_2, B_1 to P_2, and P_2 (*14*). The statistical design was a randomized complete block. Ten

[4] Italic numbers in parentheses refer to Literature Cited, p. 55.

blocks of nine plots each were used. Each plot contained 24 plants. In each block, one plot each was grown of the P_1, F_1, and P_2 populations, and two plots each were grown of the B_1 to P_1, F_2, and B_1 to P_2 populations. The nine items were randomized within each block. The plants were spaced 5 feet within rows and 5 feet between rows. Plants that did not survive transplanting to the field were replaced, but data taken on the replants were not used in the study.

The means, variances, correlation coefficients, partial standard regression coefficients, and relative percentages of the variances of the dependent characters accounted for by regression were calculated from the individual-plant data in all cases. Detailed and condensed frequency distributions were used only in estimating the number of gene pairs differentiating the two parents as regards any given character.

The standard methods of analyzing such data, those described by Snedecor (*21*), were followed. Because of the nature of genetic data, certain modifications (*12*, *13*) of these standard methods were necessary to make them applicable. The method used to estimate the genetic and environmental variances of the segregating generations (B_1 to P_1, B_1 to P_2, and F_2) is essentially that described by the senior author in an earlier publication (*15*). The P_1, F_1, and P_2 populations were employed in estimating the environmental variances. In some cases in which both phenotypic and genic dominance were complete, the B_1 to P_1 population also was employed for this purpose. It was found that for some characters the relation between the means and the environmental variances was logarithmic rather than linear. In such instances, the means and environmental variances (total variances) of nonsegregating generations (P_1, F_1, and P_2) were transformed to logarithms in estimating the environmental variances of the segregating generations. However, the antilogarithms are given in the tables. In studying the developmental relations of the characters by means of correlation coefficients, partial standard regression coefficients, and relative percentages of the variances of the dependent characters accounted for by regression, transformation of the original data was necessary in some cases. For example, in studying the relations between number of locules, weight per locule, and weight per fruit the original individual-plant data were transformed to logarithms. The formula used for calculating the relative percentage of the variance of a dependent character accounted for by regression is $(r_{y_1} b'_{y_{1.23}})$ 100, in which r_{y_1} is the coefficient of correlation between the dependent variable and the designated independent variable and $b'_{y_{1.23}}$ is the partial standard measure regression coefficient. The interrelations of some of the characters were analyzed by determining the percentage of individuals combining any two desirable characters being studied. Details of this method have been published (*18*).

New methods and procedures used in the analyses are given and illustrated in the section entitled "Experimental Procedure and Results."

In all comparisons made when interpreting the data and drawing conclusions, tests of significance were made, usually by the standard methods (*21*). Unless otherwise stated, the odds were at least 19 to 1 against the noted differences being due to chance. In some of the analyses, significance was tested by methods developed by W. T.

Federer, of the Statistical Laboratory, Iowa State College, and now in process of publication.

EXPERIMENTAL PROCEDURE AND RESULTS

Percentage of Flowers That Set Fruit

The means and variances for percentage of flowers that set fruit are given in table 1. The standard errors of the means are not given because the data were transformed to logarithms in conducting tests of significance. In the analyses that follow, it is necessary to recognize both phenotypic and genic dominance (*7*, *16*).

MAGNITUDE OF CHARACTER DIFFERENCE

From the mean values listed in table 1, it can be determined that 51.9 percent more of the flowers of Porter tomato than of those of Ponderosa tomato set fruit.

Table 1.—*Means, variances, and numbers of individuals for different populations examined for percentage of flowers that set fruit*

Population	Mean	Variance		Individuals examined
		Environmental	Genetic	
	Percent	*Percent*	*Percent*	*Number*
Porter	53.8	53.701		232
B_1 to Porter	42.2	45.007	102.274	448
F_1	28.5	38.291		233
F_2	22.4	20.670	127.352	455
B_1 to Ponderosa	9.7	10.255	43.314	430
Ponderosa	1.9	10.959		145

DOMINANCE

If phenotypic dominance is intermediate (no dominance), the mean of the F_1 for any character equals or closely approximates the average of the means of the two parents. In this instance, the average of the means of the two parents for percentage of flowers that set fruit is 27.8, and the mean of the F_1 for this character is 28.5. The close similarity of these two values shows that phenotypic dominance was intermediate. If genic dominance was intermediate also and there were no interallelic interactions of the genes—that is, if the effects were additive—then it would be expected that the mean of the B_1 to Porter would equal the average of the means of Porter and F_1, the mean of the F_2 would equal that of the F_1, and the mean of the B_1 to Ponderosa would equal the average of the means of the F_1 and Ponderosa. The theoretical means calculated on this basis are as follows: B_1 to Porter, 41.2; F_2, 28.5; and B_1 to Ponderosa, 15.2. By comparing these figures with those in table 1, it can be seen that the magnitude of the mean of the B_1 to Porter is that expected, but the means of the F_2 and the B_1 to Ponderosa are closer than expected to the mean of Ponderosa. For this reason, and since the mean of the F_1 is intermediate between the means of the

two parents, multiple-factor inheritance must have been involved and both interallelic and intraallelic interactions must have operated to produce the results noted. In such a situation genic dominance may or may not be intermediate. The interallelic interactions were such that the effectiveness of the genes tending to produce a high set of fruit diminished as genes tending to produce a low set of fruit increased in the genotype.

If genic dominance was intermediate and there were no interallelic interactions of the genes, it would be expected that the genetic variance of the B_1 to Porter and that of the B_1 to Ponderosa would not differ materially in magnitude. On the other hand, if the effectiveness of the genes tending to produce a high set of fruit diminished as genes tending to produce a low set of fruit increased in the genotype, then the genetic variance of the B_1 to Porter would be expected to exceed that of the B_1 to Ponderosa. The variances (table 1) support the latter postulation.

NUMBER OF MAJOR GENE PAIRS DIFFERENTIATING PARENTS

In analyzing the data to ascertain the number of major gene pairs differentiating the parents, it was necessary to set up a hypothesis as to the number of gene pairs involved and to determine the phenotypes of the genotypes, the penetrances of these phenotypes, the proportion of each in the theoretical population, and, finally, the validity of the hypothesis.

An examination of the values given in table 1 shows that the mean of F_1 is not significantly different from the average of means of the two parents and that the mean of B_1 to Porter is not significantly different from the average of means of F_1 and Porter. This indicates that effects of the genes were additive both within and between gene pairs. However, the mean of B_1 to Ponderosa is less than the average of means of F_1 and Ponderosa. This indicates that effects of genes were not the same throughout all genotypes, but that genes tending to increase percentage of flowers setting fruit had a greater effect in genotypes of B_1 to Porter than in genotypes of B_1 to Ponderosa. These results tend to show that effects of the genes were additive in all genotypes having at least one dominant gene in each of the gene pairs, and that dominant genes had a greater effect in these genotypes than they did in genotypes having at least one gene pair recessive.

From table 2 it can be seen that 21.5 percent of the plants of Porter and 9.1 percent of the plants of B_1 to Porter were among those of which 60 percent or more of the flowers set fruit. Thus $(9.1 \div 21.5)100$ or 42.3 percent of the plants of the B_1 to Porter behaved like plants of Porter with respect to the 60–69 and 70-or-more classes. If equal effects of the gene pairs are assumed, this is not consistent with the assumption that effects of the genes were additive in genotypes of the B_1 to Porter. However, if one gene pair had approximately as great an effect as the other gene pairs combined, this high proportion of plants in the 60–69 and 70-or-more classes would be expected.

A study of the means and variances of table 1 shows that probably more than one or two major gene pairs differentiated the parents as regards percentage of flowers that set fruit. These means and vari-

TABLE 2.—*Theoretical and obtained frequency distributions, χ^2 values for testing goodness of fit, degrees of freedom, and values of P for percentage of flowers that set fruit*

Population	Frequency distribution by percentage of flowers that set fruit									χ^2	Degrees of freedom	*P* lies between—
	0.0	0.1–9.0	10.0–19.0	20.0–29.0	30.0–39.0	40.0–49.0	50.0–59.0	60.0–69.0	70.0 or more			
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*			
Porter:												
Obtained	0	0	0	0	4.3	24.2	50.0	18.1	3.4	10.552	4	0.05 and 0.02.
Theoretical	0	0	0	0	8.9	26.7	37.3	21.5	5.6			
B_1 to Porter:												
Obtained	0	0	3.6	13.0	25.7	29.2	19.4	9.1	0	6.688	5	0.30 and 0.20.
Theoretical	0	0	2.8	14.7	30.1	29.7	16.8	5.9	0			
F_1:												
Obtained	0	0	8.2	51.3	35.8	4.7	0	0	0	6.696	3	0.10 and 0.05.
Theoretical	0	0	14.0	43.5	35.3	7.2	0	0	0			
F_2:												
Obtained	0	15.5	32.9	25.1	14.8	8.6	3.1	0	0	10.550	5	0.10 and 0.05.
Theoretical	0	23.1	32.3	19.8	13.0	7.8	4.0	0	0			
B_1 to Ponderosa:												
Obtained	4.8	53.9	30.8	8.8	1.7	0	0	0	0	9.640	4	0.05 and 0.02.
Theoretical	9.1	47.9	33.2	7.0	2.8	0	0	0	0			
Ponderosa:												
Obtained	46.6	51.7	1.7	0	0	0	0	0	0	6.042	2	0.05 and 0.02.
Theoretical	33.0	64.1	2.9	0	0	0	0	0	0			

ances, and the frequency distributions presented in table 2, were studied to determine whether they fit the hypothesis that the parents were differentiated by four major gene pairs. In Porter, these genes are symbolized as *AABBCCDD;* in Ponderosa, as *aabbccdd.* (Since phenotypic dominance was intermediate, assignment of the capital letters to Porter was arbitrary.) The procedures and methods are new and therefore are emphasized and illustrated. The method of analysis is termed "the partitioning method," because the means, variances, and frequency distributions of the segregating generations are partitioned into their components on the basis of the genotypes of these generations.

The genetic hypothesis tested was that the parents were differentiated by four major gene pairs, the effects of the genes were additive, the effects of the genes tending to produce a higher percentage of flowers that set fruit were greater in those genotypes having at least one dominant gene in each of the four gene pairs, one of the gene pairs had as great an effect as the three others combined, and not only phenotypic but also genic dominance was intermediate.

In order to partition the backcross and F_2 populations into their components, it was necessary to have an estimate of the effect that a gene contributes. Results already stated tended to show that the dominant genes had a greater effect in the genotypes having at least one dominant gene present in each gene pair. The effects of a single gene in those genotypes were determined from the Porter and F_1 population means by the following procedure:

From table 1 it can be seen that the mean of Porter is 53.8 percent and that the mean of F_1 is 28.5 percent. These two populations differ by four dominant genes. Therefore the total effect of these four genes on the mean was 53.8—28.5 percent, or 25.3 percent. The gene contributing as much as the three other genes combined is

designated the *A* gene. Its contribution was 25.3 percent ÷ 2, or 12.65 percent. The total effect of the three other genes (*B*, *C*, and *D*) was 12.65 percent, and the effect of any one of them was 4.217 percent.

The effect of the dominant genes in those genotypes having both genes in at least one of the four gene pairs recessive was estimated from the means of the F_1, B_1 to Ponderosa, and Ponderosa populations. The procedure was as follows:

The B_1 to Ponderosa population possessed one genotype (*AaBbCcDd*) that has a dominant gene in each gene pair. This is the genotype of the F_1, and in estimating the effect of a single dominant gene its effects must be subtracted. From table 1 it can be seen that the mean of the B_1 to Ponderosa population is 9.7 percent. The least number of individuals necessary for a population having all genotypes of the backcross is 16. Since the average of such a population is 9.7 percent, the estimated total is (16) (9.7) percent, or 155.2 percent. The percentage contributed by the *AaBbCcDd* and *aabbccdd* genotypes to this total is 28.5+1.9 (mean of F_1+mean of Ponderosa). Subtracting this contribution from the total of the theoretical B_1 to Ponderosa population gives the percentage 124.8. This is the theoretical total for the remaining 14 genotypes of the theoretical B_1 to Ponderosa population, and the mean is 8.914 percent. The difference between this mean and the mean of Ponderosa is 7.014 percent. Since these 14 genotypes differ from the genotype of Ponderosa, on an average, by 2 dominant genes, the effect of four genes is twice this sum, or 14.028 percent. Since the effect of the *A* gene equals the effect of the other genes combined, it is 7.014 percent and the effect of *B*, *C*, or *D* is 2.338 percent.

The theoretical means given in table 3 were obtained by starting with 1.9 for the genotype *aabbccdd*, adding 7.014 for each *A* gene and 2.338 for each *B*, *C*, or *D* gene until the genotype whose mean was under consideration had at least one dominant gene in each of the four gene pairs, and thereafter adding 12.65 for each *A* gene and 4.217 for each *B*, *C*, or *D* gene. The means of the 81 different genotypes of the F_2 and the 16 genotypes of each of the B_1 populations form an array of 18 different values.

The first 18 stub-column entries of table 3 need some explanation. In most instances, each entry represents a group of genotypes. For example, genotype *AABBCCDd* represents a group including also *AABBCcDD* and *AABbCCDD*. Two genotypes were listed together if they represented two groups of genotypes having the same mean. For example, 18.3 is the mean for the group represented by *AABbccdd*, which includes also *AAbbCcdd* and *AAbbccDd*, and for the group represented by *AaBBCCdd*, which includes also *AaBBccDD* and *AabbCCDD*.

The grand-total variances listed in table 3 were calculated in a manner described in an earlier publication (*15*) by the senior author. The means and obtained grand-total variances for use in the formula $y=mx+b$ are given in table 4. Use of the formula $m=\left(\frac{y_1-y_2}{x_1-x_2}+\frac{y_1-y_2}{x_1-x_2}+\frac{y_2-y_3}{x_2-x_3}\right)\div 3$ yielded the value 1.646, and use of the formula $b=[(y_1-mx_1)+(y_2-mx_2)+(y_3-mx_3)]\div 3$ yielded the value 15.318.

TABLE 3.—*Theoretical values for genotypes of B_1 to Porter, F_2, and B_1 to Ponderosa and calculated means and frequency distributions of these 3 populations for percentage of flowers that set fruit*

Genotype or population	Mean	Grand-total variance	Grand-total standard deviation	Frequency distribution by percentage of flowers that set fruit									Proportion of—	
				0.0	0.1–9	10–19	20–29	30–39	40–49	50–59	60–69	70 or more	B_1	F_2
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
AABBCCDD [1]	53.8	103.873	10.192	0	0	0	1.0	7.9	26.7	37.3	21.5	5.6	6.25	0.390625
AABBCCDd [1]	49.6	96.960	9.847	0	0	.1	2.2	14.3	35.0	33.9	12.6	1.9	18.75	2.343750
AABBCcDd [1]	45.4	90.046	9.489	0	0	.4	4.9	23.1	40.0	25.4	5.7	.5	18.75	4.687500
AABbCcDd and *AaBBCCDD* [1]	41.2	83.133	9.118	0	0	1.0	9.9	33.9	38.6	14.6	1.9	.1	12.50	3.906250
AaBBCCDd [1]	36.9	76.055	8.721	0	.1	2.5	18.9	42.6	29.2	6.3	.4	0	18.75	4.687500
AaBBCcDd [1]	32.7	69.142	8.315	0	.3	6.0	31.1	43.7	17.0	1.8	.1	0	18.75	9.375000
AaBbCcDd [1 2]	28.5	62.229	7.889	0	.9	13.1	43.5	35.3	6.9	.3	0	0	6.25	6.250000
AABBCCdd	25.3	56.962	7.547	0	2.1	22.1	49.0	24.2	2.5	.1	0	0	--------	1.171875
AABbccDD	22.9	53.011	7.281	.1	3.7	30.7	49.1	15.5	.9	0	0	0	--------	4.687500
AABbccdd	20.6	49.226	7.016	.2	6.4	39.8	44.6	8.7	.3	0	0	0	--------	5.859375
AABbccdd and *AaBBCCdd*	18.3	45.440	6.741	.3	10.6	49.0	36.0	4.0	.1	0	0	0	--------	4.687500
AaBbccDD and *AAbbccdd*	15.9	41.489	6.441	.7	17.2	56.0	24.7	1.4	0	0	0	0	--------	10.159250
AaBbCcdd [2] and *aaBBCcDD*	13.6	37.704	6.140	1.4	26.4	57.3	14.5	.4	0	0	0	0	18.75	14.062500
AaBbccdd [2] and *aaBBCCdd*	11.3	33.918	5.824	2.7	38.6	51.9	6.7	.1	0	0	0	0	18.75	10.546875
Aabbccdd [2] and *aaBBCcdd*	8.9	29.967	5.474	5.4	52.5	40.0	2.1	0	0	0	0	0	12.50	8.593750
aaBbCcdd [2]	6.6	26.182	5.117	10.2	64.3	25.1	.4	0	0	0	0	0	18.75	5.859375
aaBbccdd [2]	4.2	22.231	4.715	19.2	69.9	10.9	0	0	0	0	0	0	18.75	2.343750
aabbccdd [2]	1.9	18.445	4.295	33.7	63.4	2.9	0	0	0	0	0	0	6.25	.390625
B_1 to Porter	41.2	--------	--------	0	.1	2.7	14.7	30.1	29.7	16.8	5.1	.8	--------	--------
F_2	21.1	--------	--------	2.2	20.9	32.3	19.8	13.0	7.8	3.2	.7	.1	--------	--------
B_1 to Ponderosa	9.7	--------	--------	9.1	47.9	33.2	7.0	2.3	.5	0	0	0	--------	--------

[1] Present in B_1 to Porter population.
[2] Present in B_1 to Ponderosa population.

Thus the grand-total variance of the second mean of table 3 is (49.6) (1.640)+15.318, or 96.960. The other variances of table 3 were calculated in a similar manner, as were the estimated grand-total variances of table 4. The fact that the obtained and the estimated grand-total variances of table 4 do not differ significantly allows one to place considerable confidence in the grand-total variances of table 3.

The standard deviations given in table 3 are each for a single determination. The theoretical frequency distributions listed in table 3 were calculated from the means and standard deviations given in this table and Sheppard's tables of the normal probability integral. (See Pearson (*10*).) In determining the percentage of the population expected in any given class, the lowest value of the following column heading of the frequency distributions was used, the reason for this procedure being that any plant having a value lower than the lowest value of the column heading was placed in the preceding class. For example, a plant having the value 19.99 would be placed in the 10–19

TABLE 4.—*Means, grand-total variances, and symbols thereof for percentage of flowers that set fruit, for Porter, F_1, and Ponderosa*

Population	Mean		Grand-total variance		
	Symbol	Value	Obtained		Estimated value
			Symbol	Value	
		Percent		*Percent*	*Percent*
Porter	x_1	53.8	y_1	102.467	103.873
F_1	x_2	28.5	y_2	65.188	62.220
Ponderosa	x_3	1.3	y_3	16.802	18.445

class. Hence, in determining the theoretical frequency for the 10–19 class and for the *AaBbCcDd* genotype of table 3, 20.0 is subtracted from the mean (28.5) of this genotype and the resulting value, 8.5, is divided by the corresponding standard deviation, 7.889, to give the value 1.08. From the tables of normal probability integral cited above it was found that for an x value of 1.08, $1/2(1+a)$ equals 0.860. Hence, 86.0 percent of the population fell beyond the 10–19 class, and 14.0 percent fell into this class or lower classes. Since only 0.9 percent fell into lower classes, the theoretical expected percentage of the population for class 10–19 is 13.1.

The theoretical percentages that plants of individual genotypes are of the two backcross populations, and the corresponding figures for the F_2 population, are listed in the last two columns of table 3. These values were multiplied by the corresponding frequency-distribution values divided by 100, and the resulting values were summed for each column to obtain the theoretical frequency distributions of the B_1 to Porter, F_2, and B_1 to Ponderosa populations given in the last three lines of table 3. For example, the theoretical percentage of the B_1 to Porter population in class 70 or more is (5.6)(0.0625) + (1.9) (0.1875) + (0.5)(0.1875)+(0.1)(0.1250), or 0.8.

The theoretical and obtained frequency distributions, χ^2 values for testing goodness of fit, degrees of freedom, and values of P are given

in table 2. The end classes have been combined with adjoining classes so that at least 10 individuals are expected in each class. In all cases the χ^2 values were calculated from the actual numbers given as totals in table 1. The number of individuals in each class is readily obtained from these totals. The values for Porter and Ponderosa are somewhat smaller than would be expected owing to chance, if odds of 19:1 are accepted as the standard of statistical significance. This would indicate in both cases that the obtained frequency distributions are not quite normal. Also the P value for the B_1 to Ponderosa population is slightly smaller than would be expected owing to chance. The fit between the theoretical and the obtained for the F_1 and F_2 populations is fair and that for the B_1 to Porter population is good. According to Snedecor (*21*), extreme (low or high) percentages do not follow the normal curve. The theoretical frequency distribution has a higher value than the obtained in the lowest class for the F_2, F_1, and B_1 to Ponderosa populations, and the reverse is true for the Ponderosa population. By combining the 0.0 and 0.1–9 classes, a good fit is obtained for the B_1 to Ponderosa and Ponderosa populations. It is evident that the differences between the obtained and the theoretical frequency distributions are due to the fact that the distribution of percentages in the former is not quite normal.

The theoretical means for the segregating populations, given as the last three values in the second column of table 3, were obtained by taking the theoretical percentage of the mean for each genotype represented in a given population and summing. For example, the theoretical mean percentage for the B_1 to Porter is (0.0625)(53.8)+ (0.1875)(49.6) + (0.1875)(45.4) + (0.1250)(41.2) + (0.1875)(36.9) + (0.1875)(32.7) + (0.0625)(28.5), or 41.2. The obtained means of table 1 are in close agreement with the theoretical means of table 3. This would have to be true of the B_1 to Ponderosa, because the obtained mean of this population was used to determine the effects of a single gene.

Then, the data substantiate the hypotheses that the parents were differentiated by four major gene pairs, the effects of the genes were additive within certain groups of genotypes, the effects of the genes tending to produce a higher percentage of flowers that set fruit were greater in those genotypes having at least one dominant gene in each of the four gene pairs, one of the gene pairs had as great an effect as the three other pairs combined, and both phenotypic and genic dominance were intermediate.

INTERACTIONS OF GENES

The interactions of the genes were such that any given gene did not have the same degree of effect in all genotypes. Those genes tending to increase the percentage of flowers that set fruit had a greater effect in genotypes having at least one such gene present in each of the four pairs. This shows that the effects of the genes were cumulative but not strictly additive throughout the range of genotypes. The effects of genes were not equal, because the AA genes had an effect as great as the combined effects of the three other pairs of genes.

Period From Seeding to First Fruit Ripe and Its Component Characters

MAGNITUDE OF CHARACTER DIFFERENCES AND DOMINANCE

For period from seeding to first fruit ripe and its three component characters, the magnitude of the character differences among populations can be derived from the values in table 5. In comparison with Ponderosa, Porter averaged 12.1 days less in period from seeding to first bloom, 30.6 days less in period from first bloom to first fruit set, and 14.4 days less in period from first fruit set to first fruit ripe, or 57.1 days less in period from seeding to first fruit ripe.

The means of table 5 provide information on phenotypic dominance. The differences between the means of the first five populations for period from seeding to first bloom are not statistically significant when considered collectively; this constitutes rather convincing evidence that phenotypic dominance of a shorter period was complete. For period from first bloom to first fruit set, the difference between the means of Porter and B_1 to Porter is 1.1 days, as compared with a 30.6-day difference between the means of Porter and Ponderosa. These figures, together with those of the same table showing that the mean of Porter and the mean of the F_1 do not differ significantly, are convincing evidence that phenotypic dominance for period from first bloom to first fruit set was at least almost complete. For period from first fruit set to first fruit ripe the means of Porter, B_1 to Porter, and the F_1 do not differ significantly. Again, phenotypic dominance was almost, if not entirely, complete. Since the component characters of period from seeding to first fruit ripe were at least almost completely dominant phenotypically, it was to be expected that this character, also, would show almost complete, if not complete, phenotypic dominance. Examination of the means of Porter, B_1 to Porter, the F_1, and Ponderosa reveal such to be the case. Although the difference of 4.3 days between the mean of Porter and that of the B_1 to Porter is statistically significant, it is small in comparison with the difference between the means of Porter and Ponderosa, 57.1 days. These values are in agreement with those reported previously (*14*, *17*, *20*) for a number of hybrids involving several varieties of tomato. Hence, phenotypic dominance of a shorter period from seeding to first fruit ripe seems to be the rule rather than the exception in tomato hybrids.

The means and variances given in table 5 provide some information on genic dominance (intraallelic interactions) (*13*). Some genes tending to produce a certain character may show interallelic and intraallelic interactions in the manner described by Jones (*9*) or show intraallelic interactions in the manner described by East (*2*); other genes tending to produce the same character may be partially recessive (*16*) or may show no dominance, partial dominance, or complete dominance; and yet all may interact to give complete, or nearly complete, phenotypic dominance and in some cases heterosis. If genic dominance were incomplete and both parents carried at least some partially recessive gene pairs, the genes involved would produce phenotypic segregates in the B_1 to Porter; and even though the magnitude of the means obtained would be due to interallelic interaction of the genes, the genetic variance of the B_1 to Porter would be significant.

TABLE 5.—*Means and their standard deviations, variances, and condensed frequency distributions (expressed in percentage of population) for period from seeding to first fruit ripe and its 3 component characters*

[Symbols: $\bar{X}$, mean; $s_{\bar{x}}$, standard deviation of the mean; V_e, environmental variance; V_g, genetic variance]

Population	Means, standard deviations, and variances											
	Period from seeding to first bloom			Period from first bloom to first fruit set			Period from first fruit set to first fruit ripe			Period from seeding to first fruit ripe		
	$\bar{X}\pm s_{\bar{x}}$	V_e	V_g	$\bar{X}\pm s_{\bar{x}}$	V_e	V_g	$\bar{X}\pm s_{\bar{x}}$	V_e	V_g	$\bar{X}\pm s_{\bar{x}}$	V_e	V_g
	Days	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*
Porter	110.6±1.041	36.543		6.9±0.277	8.348		30.2±0.521	20.624		147.7±0.998	44.439	
B_1 to Porter	113.6±1.069	60.787	−0.234	8.0± .163	19.005	0.632	30.4± .389	23.411	2.474	152.0±1.087	74.722	10.474
F_1	110.7±1.042	41.771		7.6± .521	16.573		31.3± .452	22.608		149.6±1.886	66.119[1]	
F_2	110.3±1.038	35.760	26.099	12.5± .847	57.336	26.804	32.2± .904	32.328	26.881	155.0±1.209	92.107	66.863
B_1 to Ponderosa	111.9±1.063	48.008	25.194	20.4± .700	124.628	53.593	36.5±1.353	83.311	29.214	168.8±1.576	172.077	65.039
Ponderosa	122.7±1.155	129.478		37.5±1.821	270.298		44.6±2.356	377.354		204.8±2.500	380.756	

Population	Condensed frequency distributions [1]											
	Period from seeding to first bloom			Period from first bloom to first fruit set			Period from first fruit set to first fruit ripe			Period from seeding to first fruit ripe		
	104 days	107–143 days	146–164 days	6 days	9–30 days	33–102 days	42 days	45–57 days	60–111 days	146 days	149–170 days	173–188 days	191–242 days
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Porter	2.6	97.4	0	73.0	27.0	0	100.0	0	0	70.0	30.0	0	0
B_1 to Porter	.2	99.6	.2	63.1	36.9	0	99.8	.2	0	51.1	44.0	4.9	0
F_1	0	100.0	0	67.4	32.6	0	98.3	1.7	0	68.2	27.5	4.3	0
F_2	1.3	98.0	.7	43.6	51.8	4.6	94.3	4.2	1.5	44.7	40.5	13.0	1.8
B_1 to Ponderosa	.7	97.2	2.1	19.4	58.8	21.8	81.8	13.4	4.8	11.1	44.1	35.2	9.6
Ponderosa	0	90.5	9.5	4.3	38.0	57.7	52.4	28.3	19.3	0	4.1	13.0	82.9

[1] The 3-day intervals in which the data were recorded have been condensed into the classes shown by the column subheadings.

In case of complete or nearly complete genic dominance, the genetic variance of the B_1 to Porter would fluctuate about 0, would not be statistically significant, and in most cases would be small in comparison with the genetic variances of the F_2 and the B_1 to Ponderosa. The genetic variances of the B_1 to Porter, the F_2, and the B_1 to Ponderosa for period from seeding to first bloom are those expected on the basis of complete genic dominance. For period from first bloom to first fruit set, period from first fruit set to first fruit ripe, and period from seeding to first fruit ripe the genetic variances of these three populations are those expected on the basis of complete or nearly complete genic dominance.

NUMBER OF MAJOR GENE PAIRS DIFFERENTIATING PARENTS

The finding that phenotypic dominance was complete, or nearly so, and the means, variances, and condensed frequency distributions, collectively, provide information concerning the number of major gene pairs differentiating period from seeding to first fruit ripe and its component characters. In analyzing these values, it is necessary to remember that we are dealing with those genes having major effects. This is brought out more clearly as the discussion proceeds. In case of complete or nearly complete phenotypic and genic dominance, segregation would be discernible only in the F_2 and the B_1 to Ponderosa. Only the recessive genes of the major gene pairs involved would tend to increase the means of these two populations appreciably.

PERIOD FROM SEEDING TO FIRST BLOOM

The fact that the means of the F_2 and the B_1 to Ponderosa for period from seeding to first bloom are not significantly different from those of the F_1 and Porter indicates that a number of genes were involved in differentiating this character. As shown previously, the genes tending to produce a shorter period were almost if not completely dominant; and these genes were epistatic to the nonallelic recessive affecting the same character. The data are examined to see if they fit these premises.

The theoretical means and theoretical percentages of individuals in the third category of the condensed frequency distributions (table 5) are given in table 6. On the basis of the genetic hypothesis advanced and of a one-factor-pair difference, it would be expected that 0.75 of the F_2 population would be homozygous or heterozygous dominants and 0.25 of the F_2 population would be recessives. Then, the theoretical mean for the F_2 would be calculated by use of the formula $(\overline{P}_1)(0.75) + (\overline{P}_2)\ (0.25)$, in which $\overline{P}_1$ is the mean of the dominant parent and $\overline{P}_2$ is the mean of the recessive parent. If it is kept in mind that the fractional parts of the formula vary according to the number of gene pairs involved and the generation under consideration, the formulas for calculating the other theoretical means are readily derived. When these theoretical means are compared with the corresponding obtained means (table 6), it is apparent that the best fit is obtained from calculations based on the hypothesis that the parents were differentiated by three major gene pairs.

TABLE 6.—*Theoretical values for period from seeding to first bloom of individuals in 146- to 164-day class (third category of condensed frequency distribution, table 5)*

[Calculations based on hypothesis that indicated number of gene pairs differentiate the parents and that genes for earliness are completely dominant (both phenotypically and genically) and epistatic to recessives affecting this character]

Number of gene pairs	Mean for—		Individuals in—	
	F_2	B_1 to Ponderosa	F_2	B_1 to Ponderosa
Hypothetical:	*Days*	*Days*	*Percent*	*Percent*
1	113.6	116.7	2.4	4.8
2	111.4	113.6	.6	2.4
3	110.8	112.1	.1	1.2
Actual	110.3±1.038	111.9±1.053	.7	2.1

It remains to be seen whether the condensed frequency distributions fit the values calculated on the basis of this hypothesis. Theoretical percentage of the F_2 population in the 146- to 164-day class was calculated by use of the formula percentage of the $F_2 = \left(F\frac{p}{2}\right)\left(P\frac{p}{2}\right)100$, in which $F\frac{p}{2}$ is the theoretical percentage, expressed as a decimal fraction, of the recessive genotype in the F_2 population and $P\frac{p}{2}$ is the penetrance, expressed as a decimal fraction, of the recessive genotype for the indicated class, obtained directly from the table 5 value for the recessive parent (Ponderosa). Again, the formulas for calculating the other theoretical percentages are readily derived. By comparing the theoretical and obtained means in table 6, it can be seen that the best fit is obtained from calculations based on the hypothesis that the two parents were differentiated by three major gene pairs.

This brings us to a consideration of the genetic variances. Theoretical genetic variances of the F_2 and B_1 to Ponderosa populations have been calculated according to the hypothesis that the parents, as regards period from seeding to first bloom, were differentiated by three gene pairs and that the genes contributed by Porter were completely dominant and in addition were epistatic to the nonallelic recessives affecting this character. The procedure involved calculating theoretical populations. According to the genetic hypothesis set forth, $0.984375\left(P\frac{p}{1}\right)$ of the F_2 population would have a mean of 110.6 days ($\bar{P}_1$) from seeding to first bloom, and the remaining $0.015625\left(P\frac{p}{2}\right)$ would have one of 122.7 days ($\bar{P}_2$). Since the number of individuals (n) in the F_2 was 455, the number of individuals having a theoretical mean of 110.6 days $\left(P\frac{p}{1}n\right)$ would be (0.984375) (455), which equals 448, and the number having a theoretical mean of 122.7 days $\left(P\frac{p}{2}n\right)$ would be (0.015625) (455), which equals 7. The theoretical genetic variance of the F_2 and that of the B_1 to Ponderosa population were

calculated, by applying the standard formula, as 2.223 and 16.079, respectively. These values are considerably less than those obtained (table 5). (When these theoretical genetic variances are being interpreted, it must be kept in mind that the interactions between genotypes and those between genes and environment are not included. See section entitled "Variances of Period from Seeding to First Fruit Ripe and its Component Characters, and Variances of Weight per Locule.")

The fact that the theoretical genetic variances are considerably less than the genetic variances obtained indicated that minor genes were involved in differentiating the two parents as regards period from seeding to first bloom. The genetic variances and the detailed frequency distributions furnish some information concerning these minor genes. First, as the genetic variance for the B_1 to Porter population is not statistically significant, it is evident that Porter contributed genes that prohibited the expression of these minor genes in the B_1 to Porter. The recombination and distribution of these minor genes among individuals of the F_2 and B_1 to Ponderosa populations were such as not to shift the means of those populations away from the means of Porter and the B_1 to Porter. Since these minor genes affected the variances, they would be expected to affect the frequency distributions. If our supposition is correct, the individuals would not be so closely grouped about the mean as the individuals of the Porter, B_1 to Porter, and F_1 populations. The detailed frequency distributions would have more individuals in the lower and higher valued classes. Examination of the detailed frequency distributions revealed such to be the case. The χ^2 value for testing whether the differences in the detailed frequency distributions are statistically significant is 157.696, which, when tested by the formula $\sqrt{2\chi^2}-\sqrt{2n-1}$ (Fisher (5)), was found to be highly significant.

In summary, the means, variances, and condensed frequency distributions prove that three major gene pairs differentiated the parents as regards period from seeding to first bloom.

PERIOD FROM FIRST BLOOM TO FIRST FRUIT SET

The means and their standard errors, variances, and condensed frequency distributions for period from first bloom to first fruit set are given in table 5. Examination of the means and variances revealed phenotypic dominance of a shorter period. The means contribute only supplementary evidence as to how many gene pairs differentiated the two parents in this respect.

If phenotypic dominance was complete, as indicated by the means, then the frequency distributions for the Porter, B_1 to Porter, and F_1 populations would be expected not to differ materially. When the χ^2 test for goodness of fit was applied to the numbers (not percentages), a value of 3.676 was obtained, which has 2 degrees of freedom, since there are no individuals in the third class as regards these three populations. This value does not reach significance. Hence, the data are interpreted as supporting the hypothesis that phenotypic dominance was complete, or so nearly complete as to justify considering that the Porter, B_1 to Porter, and F_1 populations have the same penetrances for all classes of the condensed frequency distributions. Examination of the fre-

quency distributions for period from first bloom to first fruit set given in table 5 shows that the percentages of the F_2, B_1 to Ponderosa, and Ponderosa populations falling into the 33- to 102-day class are 4.6, 21.8, and 57.7, respectively. These values are not in agreement with the assumption that Porter and Ponderosa, as regards this character, were differentiated by one or two pairs of factors. The theoretical genotypes based on the hypothesis that Porter and Ponderosa were differentiated by three gene pairs as regards period from first bloom to first fruit set are given in table 7.

In determining phenotypes and their penetrances, usually it is easier to start with recessives. Longer period from first bloom to first fruit set has been shown to be recessive and is the contrasted character possessed by the Ponderosa parent. The penetrance of Ponderosa for the 33- to 102-day class is 57.7 (table 5). The percentage of the B_1 to Ponderosa population falling into this class is 21.8. This is 37.8 percent of 57.7 and is the percentage of the B_1 to Ponderosa population expected to have the same average penetrances as Ponderosa. The last three genotypes of the B_1 to Ponderosa in table 7 compose 37.5 percent of the population, and with the possible exception of the *Aabbcc* genotype are the closest genetically to Ponderosa. If these three genotypes do have the same penetrance for the 33- to 102-day class as Ponderosa, the theoretical percentage of the F_2 population falling into this class can be calculated. Since both phenotypic and genic dominance were found to be complete, the genotypes of the F_2 (table 7) that would have these penetrances are *aaBBcc*, *aaBbcc*, *aabbCC*, *aabbCc*, and *aabbcc* and are given the pheno-

TABLE 7.—*Theoretical genotypes and phenotypes of different populations, based on the hypothesis that Porter and Ponderosa are differentiated by 3 major gene pairs as regards period from first bloom to first fruit set*

Porter (P_1) *AABBCC*		F_1 *AaBbCc*		Ponderosa (P_2) *aabbcc*	
B_1 to Porter		F_2		B_1 to Ponderosa	
Genotype	Phenotype	Genotype	Phenotype	Genotype	Phenotype
AaBBCC	Porter.	*AABBCC*	Porter.	*AaBbCc*	F_1.
AaBBCc	P_1 and F_1 intermediate.	*AABBCc*	P_1 and F_1 intermediate.	*AaBbcc*	F_1 and P_2 intermediate.
AABbCC	do.	*AABBcc*	F_1 and P_2 intermediate.	*AabbCc*	Do.
AaBBCC	do.	*AABbCC*	P_1 and F_1 intermediate.	*Aabbcc*[1]	Do.
AaBBCc	do.	*AABbCc*	do.	*aaBbCc*	Do.
AaBbCC	do.	*AABbcc*	F_1 and P_2 intermediate.	*aaBbcc*[1]	Ponderosa intermediate.
AaBbCc	F_1.	*AAbbCC*	do.	*aabbCc*[1]	Do.
		AAbbCc	do.	*aabbcc*	Ponderosa.
		AAbbcc[1]	do.		
		AaBBCC	P_1 and F_1 intermediate.		
		AaBBCc	do.		
		AaBBcc	F_1 and P_2 intermediate.		
		AaBbCC	P_1 and F_1 intermediate.		
		AaBbCc	F_1.		
		AaBbcc	F_1 and P_2 intermediate.		
		AabbCC	do.		
		AabbCc	do.		
		Aabbcc[1]	do.		
		aaBBCC	do.		
		aaBBCc	do.		
		aaBBcc[1]	Ponderosa intermediate.		
		aaBbCC	F_1 and P_2 intermediate.		
		aaBbCc	do.		
		aaBbcc[1]	Ponderosa intermediate.		
		aabbCC[1]	do.		
		aabbCc[1]	do.		
		aabbcc	Ponderosa.		

[1] The data are not discriminatory as regards differences in penetrance of this genotype for the condensed frequency distributions.

typic designations Ponderosa intermediate and Ponderosa. The theoretical percentage of plants of these genotypes in the F_2 population is 10.9375. Then, the theoretical percentage for the 33- to 102-day class and for the F_2 is $\frac{(10.9375)\ (57.7)}{100}$, or 6.3. Since phenotypic dominance and, as shown later, genic dominance were each complete, or nearly so, the penetrances of the Porter, B_1 to Porter, and F_1 populations would be expected to average about the same for individual classes of the condensed frequency distributions. That such is the case in respect to the data obtained has been shown. The averages are 73.0, 27.0, and 0.0, respectively. Then, the percentage of the B_1 to Ponderosa population having the penetrances 73.0, 27.0, and 0.0, respectively, for the three classes of the condensed frequency distribution is 12.5 (*xaRbCc*).

This leaves only the F_1 and P_2 intermediate phenotype of the B_1 to Ponderosa population for which the penetrances have not been determined. The penetrance of any given phenotype of any population for any desired class can be determined by use of the formula $100x=(a_1b_1+a_2b_2+a_3b_3+\ .\ .\ .+a_nb_n)$, in which x is the percentage (table 5) of the population in any given class, a_1, a_2, a_3, . . . a_n are the penetrances of the phenotype under consideration for the same class, and b_1, b_2, b_3, . . . b_n are the corresponding theoretical percentages of plants of each of these phenotypes in the population for which the determinations are being made. Since the F_1 and P_2 intermediate phenotype occurred in both the F_2 and the B_1 to Ponderosa population, these two populations were used to estimate the penetrance of this phenotype for the 6-day class of the condensed frequency distributions. The formula for determining the penetrance of plants of the F_2 population for the 6-day class is $a_y=(100x-a_1b_1-a_2b_2-a_3b_3-a_5b_5-a_6b_6)\div b_y$, in which the value a_y corresponds to a_4, because the F_1 and P_2 intermediate phenotype is the fourth phenotype listed under the F_2 population in table 8. Similarly, the formula for determining the penetrance of plants of the B_1 to Ponderosa population is $a_y=(100x-a_3b_3-a_5b_5-a_6b_6)\div b_y$, in which the symbols have the connotations just given. For obtaining an average of the two penetrances the formula is $\bar{a}_y=[(100x-a_1b_1-a_2b_2-a_3b_3-a_5b_5-a_6b_6)+(100x'-a'_3b'_3-a'_5b'_5-a'_6b'_6)]\div(b_y+b'_y)$, in which b_y is the theoretical percentage of plants of the F_1 and P_2 intermediate phenotype in the F_2 population and b'_y is the corresponding value for the B_1 to Ponderosa population. In using this formula, the penetrances for individual classes must be adjusted so that the percentages total 100. For example, since plants of the F_1 and P_2 intermediate phenotype fall into the 6-day and 9- to 30-day classes only, the Ponderosa intermediate and Ponderosa penetrances for these two classes must be adjusted to total 100. This is most easily done by expressing them as percentages of their sum. For the 6-day class this is $[4.3\div(4.3+38.0)]\ 100=10.2$. Likewise, the obtained values of the condensed frequency distributions must be adjusted so that the percentage values for these two classes total 100. Substituting the proper values from tables 5 and 8, making the necessary adjustments, and rearranging so that the plus values fall together and the minus values fall together, we have $\bar{a}_y=[(100)(45.7)+(100)(24.8)-(73.0)(1.5625)-(73.0)(28.1250)-(73.0)(12.5000)-(10.2)(9.3750)-(10.2)(1.5625)-(73.0)(12.5000)-$

TABLE 8.—*Phenotypes and their penetrances for period from first bloom to first fruit set, theoretical proportions of each phenotype in the F_2 and B_1 to Ponderosa populations, obtained and theoretical proportions of these populations in each class of the condensed frequency distributions (table 5), and χ^2 values for testing goodness of fit*

Phenotype	Penetrance in indicated class			Theoretical proportion of indicated population	
	6 days	9-30 days	33-102 days	F_2	B_1 to Ponderosa
	Percent	*Percent*	*Percent*	*Percent*	*Percent*
Porter	73.0	27.0	0	1.5625	0
P_1 and F_1 intermediate	73.0	27.0	0	28.1250	0
F_1	73.0	27.0	0	12.5000	12.5
F_1 and P_2 intermediate	26.5	73.5	0	46.8750	50.0
Ponderosa intermediate	4.3	38.0	57.7	9.3750	25.0
Ponderosa	4.3	38.0	57.7	1.5625	12.5

Population	Proportion in indicated class			χ^2	Degrees of freedom
	6 days	9-30 days	33-102 days		
	Percent	*Percent*	*Percent*		
F_2:					
Obtained	43.6	51.8	4.6	1.456	2
Theoretical	43.7	50.0	6.3		
B_1 to Ponderosa:					
Obtained	19.4	58.8	21.8	2.898	2
Theoretical	21.0	57.4	21.6		

$(10.2)(25.0000) - (10.2)(12.5000)] \div (46.8750 + 50.0000)$. Completing the calculations, we find the average penetrance of the F_1 and P_2 intermediate phenotype for the 6-day class to be 26.5. From the foregoing examples, derivation of the appropriate formula and its application are apparent for any class and phenotype of any given population. This completes the information essential to determining the phenotypes, their penetrances into the condensed frequency distributions, the theoretical percentage of each phenotype in the population, and the obtained and theoretical values for the F_2 and B_1 to Ponderosa populations with respect to number of days from first bloom to first fruit set. The values are given in table 8.

The χ^2 values for testing goodness of fit between the obtained and theoretical values of the F_2 and B_1 to Ponderosa populations are 1.456 and 2.898, respectively, and in both cases $P>0.20$ (*21, p. 190*).

One other test, involving the original data for each plant, was needed. The theoretical mean of the F_2 was calculated from the genetic hypothesis advanced and the data for the two backcross populations. Below are given the phenotypes (as shown in table 8), the symbols for their percentages in the population, and the theoretical means and their symbols.

Phenotype:	*Symbol for percentage of population*	*Mean*	
		Days	*Symbol*
Porter	x_1	6.9	$\bar{x}_1$
P_1 and F_1 intermediate	x_2	8.2	$\bar{x}_2$
F_1	x_3	7.6	$\bar{x}_3$
F_1 and P_2 intermediate	x_4	10.8	$\bar{x}_4$
Ponderosa intermediate Ponderosa	x_5	37.5	$\bar{x}_5$

The mean ($\bar{x}_2$) of P_1 and F_1 intermediate was determined as follows: As can be seen from the above tabulation and table 7, the formula for the mean ($\bar{x}_6$) of the B_1 to Porter is $100\bar{x}_6 = x_1\bar{x}_1 + x_2\bar{x}_2 + x_3\bar{x}_3$. Substituting the appropriate values from the above tabulation and tables 5 and 8 gives $(8.0)(100) = (12.5)(6.9) + 75\bar{x}_2 + (12.5)(7.6)$, or $\bar{x}_2 = 8.2$ days. The mean ($\bar{x}_4$) of the F_1 and P_2 intermediate phenotype was determined similarly. The formula for the mean ($\bar{x}_7$) of the B_1 to Ponderosa is $100\bar{x}_7 = x_3\bar{x}_3 + x_4\bar{x}_4 + x_5\bar{x}_5$. Substituting in this formula the values from the above tabulation and tables 5 and 8, we have $(20.4)(100) = (12.5)(7.6) + 50\bar{x}_4 + (37.5)(37.5)$, or $\bar{x}_4 = 10.8$ days. The formula for calculating the theoretical mean ($\bar{x}_8$) of the F_2 is $100\bar{x}_8 = x_1\bar{x}_1 + x_2\bar{x}_2 + x_3\bar{x}_3 + x_4\bar{x}_4 + x_5\bar{x}_5$. Substituting the proper values from the above tabulation and tables 5 and 8 gives $100\bar{x}_8 = (1.5625)(6.9) + (28.1250)(8.2) + (12.5)(7.6) + (46.8750)(10.8) + (10.9375)(37.5)$, or $\bar{x}_8 = 12.5$ days. This is the obtained mean of the F_2, 12.5 ± 0.847 days. Since the various analyses of the data support the hypothesis that period from first bloom to first fruit set was differentiated by three major gene pairs, it can justifiably be concluded that such was the case.

PERIOD FROM FIRST FRUIT SET TO FIRST FRUIT RIPE

The means and their standard deviations, variances, and condensed frequency distributions for period from first fruit set to first fruit ripe are given in table 5. A study of the means and variances has revealed phenotypic dominance of a shorter period.

As regards this character, 19.3 percent of the plants of Ponderosa fell into the 60- to 111-day class of the condensed frequency distributions and the percentages of the F_2 and B_1 to Ponderosa populations in this class were 1.5 and 4.8, respectively (table 5). Hence, 7.8 percent of the F_2 population and 24.9 percent of the B_1 to Ponderosa population behaved the same as the Ponderosa parent in respect to the third class of the condensed frequency distributions. This would indicate that Porter and Ponderosa were differentiated by two gene pairs as regards period from first fruit set to first fruit ripe. Theoretical genotypes based on this assumption are listed in table 9. The theoretical mean of the *A-abb* and *aaB-* genotypes of the B_1 to Ponderosa population was calculated in the same manner as the theoretical means of period from first bloom to first fruit set. The mean for the F_1 and P_2 intermediate phenotype was found to be 35 days. Since

TABLE 9.—*Theoretical genotypes and phenotypes of different populations, based on the hypothesis that Porter and Ponderosa are differentiated by 2 major gene pairs as regards period from first fruit set to first fruit ripe*

Porter (P_1) *A-bb*		F_1 *AaBb*		Ponderosa (P_2) *aaB-*	
B_1 to Porter		F_2		B_1 to Ponderosa	
Genotype	*Phenotype*	*Genotype*	*Phenotype*	*Genotype*	*Phenotype*
A-BB	Porter.	*A-BB*	Porter.	*AaBb*	F_1.
A-Bb	P_1 and F_1 intermediate.	*A-Bb*	P_1 and F_1 intermediate.	*Aabb*	F_1 and P_2 intermediate.
AaBB	Do.	*A-bb*	F_2 and P_2 intermediate.	*aaBb*	Do.
AaBb	F_1.	*AaBB*	P_1 and F_1 intermediate.	*aabb*	Ponderosa.
		AaBb	F_1.		
		Aabb	F_2 and P_2 intermediate.		
		aaBB	Do.		
		aaBb	Do.		
		aabb	Ponderosa.		

this lies between the mean of the F_1 (31.3 days) and that of Ponderosa (44.6 days), the effects of the gene pairs must have been cumulative. Since phenotypic dominance and, as shown later, genic dominance were each complete or nearly so, plants of the F_2 population possessing the genotype *AAbb* or *aaBB* were of the F_1 and P_2 intermediate phenotype. Plants of the *AABb* and *AaBB* genotypes were of the P_1 and F_1 intermediate phenotype and had the same penetrances for the different classes of the condensed frequency distributions as Porter. The penetrances of plants of the F_1 and P_2 intermediate phenotype can be calculated by the methods and formula already presented. This completes the information essential to determining the phenotypes, the penetrances of these phenotypes into the condensed frequency distributions, the theoretical percentage of each phenotype in the segregating populations, the obtained and theoretical percentages of the condensed frequency distributions, and the validity of the hypothesis as regards period from first fruit set to first fruit ripe. The results are given in table 10.

TABLE 10.—*Phenotypes and their penetrances for period from first fruit set to first fruit ripe, theoretical proportions of each phenotype in the segregating populations, obtained and theoretical proportions of these populations in each class of the condensed frequency distributions (table 5), and $^2\chi$ values for testing goodness of fit*

Phenotype	Penetrance in indicated class			Theoretical proportion of indicated population		
	42 days	45–57 days	60–111 days	B_1 to Porter	F_2	B_1 to Ponderosa
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Porter	100.0	0	0	25.0	6.25	0
P_1 and F_1 intermediate	100.0	0	0	50.0	25.00	0
F_1	98.3	1.7	0	25.0	25.00	25.0
F_1 and P_2 intermediate	92.5	7.5	0	0	37.50	50.0
Ponderosa	52.4	28.3	19.3	0	6.25	25.0

Population	Proportion in indicated class			χ^2	Degrees of freedom
	42 days	45–57 days	60–111 days		
	Percent	*Percent*	*Percent*		
B_1 to Porter:					
Obtained	99.8	0.2	0	0.334	1
Theoretical	99.6	.4	0		
F_2:					
Obtained	94.3	4.2	1.5	.718	2
Theoretical	93.8	5.0	1.2		
B_1 to Ponderosa:					
Obtained	81.8	13.4	4.8	.886	2
Theoretical	83.9	11.3	4.8		

The χ^2 values 0.334, 0.718, and 0.886 (table 10) have P values between 0.7 and 0.5, showing that the fit between the obtained and theoretical values is good. The theoretical mean of the F_2 population as calculated by substituting values from tables 5 and 10 and the F_1 and P_2 intermediate mean (35 days) in the formula $100\bar{x}_s = x_1\bar{x}_1 + x_2\bar{x}_2 + x_3\bar{x}_3 + x_4\bar{x}_4 + x_5\bar{x}_5$ is 33.2 days, which is not significantly different from the obtained mean, 32.2 ± 0.904 days. Thus the means, variances, original (nonclassified) individual-plant data, detailed frequency distributions, and condensed frequency distributions confirm the

hypothesis that as regards period from first fruit set to first fruit ripe Porter and Ponderosa are differentiated by two major gene pairs.

PERIOD FROM SEEDING TO FIRST FRUIT RIPE

The means and their standard deviations, variances, and condensed frequency distributions for period from seeding to first fruit ripe are given in table 5. Phenotypic dominance was complete or nearly so. Since the parents were found to be differentiated by at least three major gene pairs as regards period from seeding to first bloom, by three as regards period from first bloom to first fruit set, and by two as regards period from first fruit set to first fruit ripe, the number of gene pairs differentiating Porter and Ponderosa in respect to period from seeding to first fruit ripe provides some evidence as to whether total pleiotropy was involved and hence whether three gene pairs explain the results for all three component characters. Of course, if such is the case, one of the gene pairs had no effect on period from first fruit set to first fruit ripe. The data were examined to see whether they fit the hypothesis that the parents were differentiated by only three major gene pairs as regards period from seeding to first fruit ripe. To facilitate analysis of the data, the theoretical genotypes are listed in table 11.

From table 5 it can be seen that the percentages of the F_2, B_1 to Ponderosa, and Ponderosa populations in the fourth class of the con-

TABLE 11.—*Theoretical genotypes and phenotypes of different populations, based on the hypothesis that Porter and Ponderosa are differentiated by 3 major gene pairs as regards period from seeding to first fruit ripe*

Porter (P_1) *AABBCC*		F_1 *AaBbCc*		Ponderosa (P_2) *aabbcc*	
B_1 to Porter		F_2		B_1 to Ponderosa	
Genotype	Phenotype	Genotype	Phenotype	Genotype	Phenotype
AABBCC	Porter.	*AABBCC*	Porter.	*AaBbCc*	F_1.
AABBCc	P_1 and F_1 intermediate.	*AABBCc*	P_1 and F_1 intermediate.	*AaBbcc*	F_1 and P_2 intermediate.
AABbCC	do.	*AABBcc*	F_1 and P_2 intermediate.	*AabbCc*	Do.
AABbCc	do.	*AABbCC*	P_1 and F_1 intermediate.	*Aabbcc*	Do.
AaBBCC	do.	*AABbCc*	do.	*aaBbCc*	Do.
AaBBCc	do.	*AABbcc*	F_1 and P_2 intermediate.	*aaBbcc*	Do.
AaBbCC	do.	*AaBBCC*	P_1 and F_1 intermediate.	*aabbCc*	Do.
AaBbCc	F_1.	*AaBBCc*	do.	*aabbcc*	Ponderosa.
		AaBBcc	F_1 and P_2 intermediate.		
		AaBbCC	P_1 and F_1 intermediate.		
		AaBbCc	F_1.		
		AaBbcc	F_1 and P_2 intermediate.		
		AabbCC	do.		
		AabbCc	do.		
		Aabbcc	do.		
		aaBBCC	do.		
		aaBBCc	do.		
		aaBBcc	do.		
		aaBbCC	do.		
		aaBbCc	do.		
		aaBbcc	do.		
		aabbCC	do.		
		aabbCc	do.		
		aabbcc	Ponderosa.		

densed frequency distributions are 1.8, 9.6, and 82.9, respectively. On the basis of three gene pairs differentiating Porter and Ponderosa and the assumption that the plants represented by the first two of these percentages had the triple recessive genotype, the expected percentages of the F_2 and B_1 to Ponderosa populations in this class are 1.3 and 10.4. The χ^2 values for testing goodness of fit are 0.290 and 0.206, neither of which has a P value less than 0.05. So far, the data support the hypothesis of three pairs of genes differentiating the parents. From the genotypes listed under B_1 to Ponderosa, it is apparent that the *AaBbCc* genotype has the same phenotype and penetrances as the F_1. Similarly, the *aabbcc* genotype has the same phenotype and penetrances as Ponderosa. The six other genotypes of the B_1 to Ponderosa population are designated F_1 and P_2 intermediate. The penetrances of the F_1 and P_2 intermediate phenotype for the four classes of the frequency distribution, calculated by applying procedures and formulas already given to the B_1 to Ponderosa population, are presented in table 12. Turning to a consideration of the genotypes of the B_1 to Porter listed in table 11, we see that plants of the *AABBCC* genotype had the same phenotype and penetrances as plants of Porter and that plants of the *AaBbCc* genotype had the same phenotype and penetrances as the F_1 plants. The phenotypic designation given to plants having any of the six other genotypes of the B_1 to Porter population was P_1 and F_1 intermediate. The penetrances of plants of this phenotype were calculated from the B_1 to Porter data in the usual manner and are given in table 12. Since phenotypic and, as shown later, genic dominance were both complete or nearly so, the phenotypes for the F_2 population were as listed in table 11.

Next comes the test of the validity of the hypothesis. Since the B_1 to Porter population was used to estimate the penetrances of the P_1 and F_1 intermediate phenotype and the B_1 to Ponderosa population to estimate the penetrances of the F_1 and P_2 intermediate phenotype

TABLE 12.—*Phenotypes and their penetrances for period from seeding to first fruit ripe, theoretical proportion of each phenotype in the F_2 population, obtained and theoretical proportions of that population in each class of the condensed frequency distribution (table 5), and χ^2 value for testing goodness of fit*

Phenotype	Penetrance in indicated class				Theoretical proportion of F_2 population
	146 days	149–170 days	173–188 days	191–242 days	
	Percent	*Percent*	*Percent*	*Percent*	*Percent*
Porter	70.0	30.0	0	0	1.5625
P_2 and F_1 intermediate	45.1	49.0	5.9	0	28.1250
F_1	68.2	27.7	4.3	0	12.5000
F_1 and P_2 intermediate	5.0	51.5	38.5	0	56.2500
Ponderosa	0	4.1	13.0	82.9	1.5625

F_2 population	Proportion in indicated class				χ^2	Degrees of freedom
	146 days	149–170 days	173–188 days	191–242 days		
	Percent	*Percent*	*Percent*	*Percent*		
Obtained	44.7	46.5	13.0	1.8	45.258	3
Theoretical	25.1	49.5	21.1	1.3		

(whereas the averages of all three segregating generations were used previously), the testing of the validity of the hypothesis was necessarily limited to the obtained and theoretical percentages of the F_2 population. The analysis is given in table 12. The χ^2 value, 45.258, has a P value considerably less than 0.01. Calculated as previously and on the basis that the parents are differentiated by three pairs of genes, the theoretical mean of the F_2 is 160.6 days, which is considerably greater than the obtained value, 155.0 ± 1.209 days. The hypothesis that Porter and Ponderosa, as regards period from seeding to first fruit ripe, were differentiated by only three major gene pairs is not in conformity with the data. If none of the major gene pairs differentiating the component characters exhibit pleiotropy, then the parents, as regards period from seeding to first fruit ripe, must have been differentiated by at least eight major gene pairs.

INTERACTIONS OF GENES

In studying the data to determine the nature of the interactions of the genes, period from seeding to first fruit ripe and its component characters were considered together.

As has been pointed out, the evidence from a study of the genetic variances supports the hypothesis that the genes for a shorter period from seeding to first bloom, a shorter period from first bloom to first fruit set, and a shorter period from first fruit set to first fruit ripe were completely dominant, or nearly so. The hypotheses advanced and tested as to the number of gene pairs differentiating the two parents in respect to all three of these component characters involve the assumption that the genes tending to produce shorter periods were completely dominant, or nearly so. Since tests confirmed the hypotheses, genic dominance of those genes tending to produce the shorter periods must have been complete, or nearly so. Hence, the intraallelic interactions of the genes must have been such that their effects were not cumulative as measured by the end results (the characters studied). Period from seeding to first bloom was found to be as short for plants of the *Aabbcc*, *aaBbcc*, or *aabbCc* genotype as for plants of the *AABBCC* genotype. Hence, one of the dominant genes produced almost as great, if not as great, an effect as all six dominant genes together. Therefore, the interallelic interactions of the genes were such that the effects of the genes were not cumulative. Period from first bloom to first fruit set was longer for plants of the *Aabbcc*, *aaBbcc*, and *aabbCc* genotypes than for plants of the *AaBbCc* genotype. Period from first fruit set to first fruit ripe, likewise, was longer for plants of the *Aabb* and *aaBb* genotypes than for plants of the *AaBb* genotype. Thus the interallelic interactions of the genes differentiating these two component characters were such that the effects of the genes were cumulative.

The facts just stated are most simply explained on the assumption that as regards genic dominance the genes studied were responsible for the production of substances having a threshold above which no additional shortening of period, or periods, resulted. The same is true of the interallelic interactions of those genes differentiating period from seeding to first bloom. Then, as regards period from seeding to first bloom any one of the dominant genes was capable of bringing about production of the amount of such a substance necessary for

maximum reaction in a given time. This is not true of the interallelic interactions of the genes differentiating period from first bloom to first fruit set, or of those of the genes differentiating period from first fruit set to first fruit ripe, as maximum reaction was not reached until at least one dominant gene of each pair of alleles was present. For the history of the development of the hypothesis of thresholds see Goldschmidt (7).

The nature of the interactions between genes differentiating individual component characters is considered later, in connection with the analyses of the interrelations of the characters.

Weight per Fruit and Its Component Characters

Number of Locules

Magnitude of Character Differences and Dominance

Porter plants averaged 2.1 locules per fruit and Ponderosa plants 10.0, or 7.9 more (table 13). The genetic variance for the F_2 population is greater than that for either backcross, and the genetic variance for B_1 to Porter is greater than that for B_1 to Ponderosa. The mean of the F_1 lies somewhat closer to the mean of Porter than to that of Ponderosa, the mean of B_1 to Porter lies somewhat closer to that of Porter than to that of the F_1, and the mean of the B_1 to Ponderosa lies somewhat closer to that of the F_1 than to that of Ponderosa. These findings show that phenotypic dominance was partial for fewer locules and indicate that genic dominance was partial also.

Number of Major Gene Pairs Differentiating the Parents

Examination of the frequency distributions for number of locules (table 13) reveals that 62.8 percent of Ponderosa plants fell into classes having averages of 10 or more locules per fruit. Of the B_1 to Ponderosa population, 19.5 percent of the plants fell into these classes. On the basis of two partially dominant gene pairs for fewer locules per fruit and one partially dominant gene pair for more locules per fruit, approximately 15.7 percent of the plants of the B_1 to Ponderosa population would be expected to fall into classes having averages of 10 or more locules per fruit. This value is not greatly different from the one obtained. The data are analyzed to determine whether they conform to the hypothesis that the parents were differentiated by three pairs of genes of which two were partially dominant for fewer locules per fruit and one was partially dominant for more locules.

To calculate the theoretical frequency distributions it was necessary to have an estimate of (1) the effects of gene substitution and (2) the standard deviation of a single determination.

The means of the parental, F_1, and backcross populations given in table 13 were used to obtain a rough estimate of the effects of gene substitution in the genotypes of the backcross populations. The differences between means of number of locules per fruit are: Porter and F_1, 2.4; F_1 and Ponderosa, 5.5; Porter and Ponderosa, 7.9. The values 2.4 and 5.5 are 30.4 and 69.6 percent, respectively, of 7.9. With these percentage figures available, the effect of the substitution of a gene tending to produce more locules per fruit can be roughly estimated for the B_1 to Porter population. The percentage effects added

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TABLE 13.—*Means, within-plot variances, grand-total variances and standard deviations of the nonsegregating populations, and frequency distributions for number of locules*

Population	Mean	Within-plot variance [1]		Grand-total variance [2]	Grand-total standard deviation [2]	Frequency distribution by average number of locules per fruit													
		Environmental	Genetic			2	3	4	5	6	7	8	9	10	11	12	13	14	15
	Number	*Number*	*Number*	*Number*	*Number*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Porter	2.1	0.001033	----------	0.033775	0.184	96.5	3.5	0	0	0	0	0	0	0	0	0	0	0	0
B_1 to Porter	3.1	.004987	0.019036	----------	----------	36.6	32.2	18.1	10.0	2.2	.5	0	.4	0	0	0	0	0	0
F_1	4.5	.009840	----------	.995309	.998	.9	15.9	35.6	36.0	8.6	2.6	.4	0	0	0	0	0	0	0
F_2	4.7	.008211	.025992	----------	----------	12.4	20.5	19.6	20.8	8.8	8.4	4.0	2.9	1.6	.4	.2	.2	.2	0
B_1 to Ponderosa	7.1	.011407	.009389	----------	----------	.2	2.1	6.5	21.2	17.8	14.5	10.8	7.4	9.2	5.5	3.0	1.4	.2	.2
Ponderosa	10.0	.013031	----------	6.414375	2.533	0	0	1.1	2.8	7.8	5.0	10.5	10.0	20.5	12.2	15.6	6.7	2.2	5.6

[1] Original individual-plant data were transformed to logarithms.
[2] No transformation of original data.

in going from *AABBcc*, the genotype of Porter, to *AaBbCc*, the genotype of the F_1, are 30.4 (*a*)+30.4 (*b*)+69.6 (*C*), or a total of 130.4. On the basis of 100 percent, *a* or *b* adds (30.4÷130.4) 100 or 23.3 percent, and *C* adds (69.6÷130.4) 100 or 53.4 percent. Then in the genotypes of the B_1 to Porter substitution of *a* or *b* results in an increase of 0.233×2.4 or 0.56 locules per fruit and substitution of *C* results in an increase of 0.534×2.4 or 1.28 locules per fruit. In the genotypes of the B_1 to Ponderosa, substitution of *a* or *b* results in a 69.6-percent gain and substitution of *C* in a 30.4-percent gain. Therefore the difference between plants of the F_1 (*AaBbCc*) and Ponderosa (*aabbCC*) genotypes is 69.6+69.6+30.4 or 169.6 percent, *a* and *b* contribute 0.410×5.5 or 2.25 locules, and *C* contributes 0.180×5.5 or 0.99 locule.

The means of the genotypes of the backcross populations (table 14) were calculated from these estimates of effects of gene substitutions.

The formula $y=mx+b$ (*15*) was used in estimating the grand-total variances of genotypes of table 14. The means (table 13) of Porter, F_1, and Ponderosa were designated x_1, x_2, and x_3 and the grand-total variances of these populations (table 13) were designated y_1, y_2, and y_3, respectively. The value of m_1 was obtained by use of the formula $m_1=\frac{y_2-y_1}{x_2-x_1}$, and is 0.400677. The value of b_1 was obtained by use of the formula $b_1=y_1-m_1x_1$, and is −0.807647. The corresponding values of m_2 and b_2 were obtained by use of the formulas $m_2=\frac{y_3-y_2}{x_3-x_2}$ and $b_2=y_2-m_2x_2$, and are 0.985268 and −3.438306, respectively. The difference between m_1 and m_2 and the difference between b_1 and b_2 are too great to justify using averages for *m* and *b*. Consequently, the values of m_1 and b_1 were used to estimate the grand-total variances for genotypes of B_1 to Porter and the values of m_2 and b_2 were used to estimate the grand-total variances for genotypes of B_1 to Ponderosa.

The grand-total standard deviations, and hence the grand-total variances, had to be used in estimating the frequency distributions of the genotypes because the obtained frequency distributions of the populations with which the theoretical frequency distributions are compared include differences between means of blocks, differences between plants within blocks, and, finally, differences attributable to interactions, which, all together, compose grand-total variation.

The methods and procedures used in calculating the theoretical frequency distributions of table 14 are the same as those used in calculating the theoretical frequency distributions of table 3, except that average values of *m* and *b* were not used in estimating the grand-total variances. In the stub of table 14, "total" signifies all plants of the indicated population and "balance" signifies all except those of the F_1 and parental genotypes. A comparison between the theoretical frequency distributions (table 14) and the obtained frequency distributions (table 13) for the backcross populations shows that there are more individuals in some of the lower classes of the latter than can be explained by chance deviation. Also, the theoretical means for both backcross populations are higher than the comparable obtained means. However, the fits between the obtained frequency distributions and the theoretical frequency distributions for the two parental

TABLE 14.—*Theoretical means, grand-total variances and standard deviations, and frequency distributions of the B_1 to Porter and B_1 to Ponderosa populations for number of locules*

Population and genotype	Mean	Grand-total variance	Grand-total standard deviation	Frequency distribution by average number of locules per fruit													
				2	3	4	5	6	7	8	9	10	11	12	13	14	15
B_1 to Porter:	*Number*	*Number*	*Number*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
AABBcc	2.1	0.033775	0.184	98.5	1.5	0	0	0	0	0	0	0	0	0	0	0	0
AABbcc	2.7	.274181	.524	35.2	58.5	6.3	0	0	0	0	0	0	0	0	0	0	0
AaBBcc	2.7	.274181	.524	35.2	58.5	6.3	0	0	0	0	0	0	0	0	0	0	0
AaBbcc	3.2	.474519	.689	15.4	51.6	30.1	2.9	0	0	0	0	0	0	0	0	0	0
AABBCc	3.4	.554755	.745	11.3	43.9	37.9	6.7	.2	0	0	0	0	0	0	0	0	0
AABbCc	3.9	.754993	.869	5.4	26.9	43.2	21.2	3.2	.1	0	0	0	0	0	0	0	0
AaBBCc	3.9	.754993	.869	5.4	26.9	43.2	21.2	3.2	.1	0	0	0	0	0	0	0	0
AaBbCc	4.5	.995400	.998	2.3	13.6	34.1	34.1	13.6	2.2	.1	0	0	0	0	0	0	0
Total	3.3			26.1	35.2	25.1	10.8	2.5	.3	0	0	0	0	0	0	0	0
Balance [1]				18.0	44.4	27.8	8.7	1.1	0	0	0	0	0	0	0	0	0
B_1 to Ponderosa:																	
AaBbCc	4.5	.995400	.998	2.3	13.6	34.1	34.1	13.6	2.2	.1	0	0	0	0	0	0	0
AaBbCC	5.5	1.980668	1.407	1.7	6.1	16.1	26.1	26.1	16.1	6.1	1.5	.2	0	0	0	0	0
AabbCc	6.8	3.261516	1.806	.9	2.5	6.8	13.4	19.7	21.3	17.4	10.7	4.7	1.5	.5	0	0	0
aaBbCc	6.8	3.261516	1.806	.9	2.5	6.8	13.4	19.7	21.9	17.4	10.7	4.7	1.5	.5	0	0	0
AabbCC	7.8	4.246784	2.061	.5	1.3	3.7	7.6	13.3	17.6	18.3	16.1	11.1	5.9	2.5	.8	.3	0
aaBbCC	7.8	4.246784	2.061	.5	1.3	3.7	7.6	13.3	17.6	19.3	16.1	11.1	5.9	2.5	.8	.3	0
aabbCc	9.0	5.429106	2.330	.3	.6	1.8	4.0	7.5	11.9	15.6	16.6	15.6	11.9	7.5	4.0	1.8	.9
aabbCC	10.0	6.414374	2.533	.2	.3	1.0	2.3	4.6	7.7	11.7	14.3	15.8	14.3	11.7	7.7	4.6	3.8
Total	7.3			.9	3.5	9.2	13.6	14.7	14.6	13.4	10.7	7.9	5.1	3.2	1.7	.9	.6
Balance [1]				.8	2.4	6.5	12.0	16.6	17.8	15.8	12.0	7.9	4.5	2.2	.9	.4	.2

[1] Total less plants of the F_1 and parental genotypes. The theoretical proportion of each genotype in balance of population is 16.6667 percent.

genotypes and the F_1 genotype are good, as the P values of the χ^2 values for testing goodness of fit lie between 0.20 and 0.10, between 0.70 and 0.50, and between 0.70 and 0.50, respectively. (The genotypes having the same theoretical frequency distributions as the nonsegregating populations are: Porter, *AABBcc*; F_1, *AaBbCc*; Ponderosa, *aabbCC*.) These facts indicate that the poor fit for the backcross populations is probably due to overestimation of the means of the genotypes. The difficulty could be due to failure of m_1 and b_1, and m_2 and b_2 to give sufficiently accurate estimates of the grand-total variances from which grand-total standard deviations of a single determination were calculated.

A method is needed whereby the frequency distributions obtained for the segregating populations can be used to estimate the frequency distributions of the genotypes. Such a method is developed, and the procedures are illustrated, in connection with the analysis that follows.

In this study the B_1 to Porter and B_1 to Ponderosa populations were used to estimate the frequency distributions and means of the genotypes. All three segregating populations can be so used if this is necessary or desirable. Again, the partitioning method was used. Frequency distributions obtained for Porter, F_1, and Ponderosa were accepted as those of the genotypes *AABBcc*, *AaBbCc*, and *aabbCC*. Hence, the frequency distribution given (table 14) for the balance of each of the backcross populations does not include plants of these three genotypes. The frequency distribution of the balance of B_1 to Porter (table 14) was obtained by multiplying each class percentage of each genotype from *AABbcc* to *AaBBCc*, inclusive, by 0.166667 and summing the results for each class. The corresponding values for the balance of B_1 to Ponderosa were obtained similarly from the percentages of the genotypes *AaBbCC* to *aabbCc*, inclusive. In order to estimate these frequency distributions, it was necessary to have obtained frequency distributions for the balance of B_1 to Porter and the balance of B_1 to Ponderosa. These were obtained by deducting the frequency distributions of the parental and F_1 genotypes from the obtained distributions of the backcross populations. The method of procedure and results for the B_1 to Porter are given in table 15. With the exception that the P_2, not the P_1, frequency distribution was used, the procedure followed in calculating the obtained frequency distribution of the B_1 to Ponderosa was the same.

The theoretical proportions of the *AABBcc* (P_1) and *AaBbCc* (F_1) genotypes of the B_1 to Porter population were taken for each class of the frequency distributions (last two lines of table 15). The sums of the values thus obtained were entered as the second line of table 15, opposite the entry "*AABBcc*+*AaBbCc*." These values were subtracted from the values of line 1, and the remainders (with the minus value for the "8 locules" class eliminated by combination with a plus value) were entered as line 3. Line 4 was obtained by expressing the values of line 3 on the basis of 100 percent.

To determine the proportions that the obtained frequency-distribution values are of the theoretical ones, each value in line 4 of table 15 was divided by the corresponding value of the theoretical frequency distribution of the balance of B_1 to Porter (table 14). For example, $32.5 \div 18.0 = 1.805556$, the value for class 2. Then the corresponding

TABLE 15.—*Deduction of the frequency distributions of the P_1 and F_1 genotypes from the B_1 to Porter frequency distribution for number of locules*

Genotype or genotypes of B_1 to Porter population	Frequency distribution by average number of locules per fruit								Theoretical proportion [1]
	2	3	4	5	6	7	8	9	
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
All genotypes	36.6	32.2	18.1	10.0	2.2	0.5	0	0.4	100.0
AABbcc+*AaBbCc*	12.2	2.4	4.4	4.5	1.1	.3	.1	0	25.0
Balance: [2]									
As a part of B_1 to Porter	24.4	29.8	13.7	5.5	1.1	.2	0	.3	75.0
As a unit	32.5	39.7	18.3	7.3	1.5	.3	0	.4	100.0
AABBcc (P_1)	96.5	3.5	0	0	0	0	0	0	12.5
AaBbCc (F_1)	.9	15.9	35.6	36.0	8.0	2.6	.4	0	12.5

[1] Base is B_1 to Porter except in line 4, in which it is balance of B_1 to Porter.
[2] Line 3 was obtained by subtracting line 2 from line 1 and adjusting the resulting values in the "8 locules" and "9 locules" columns to eliminate a minus quantity. Line 4 is values of line 3 expressed on basis of 100 percent.

figures of the theoretical frequency distributions of the genotypes from *AABbcc* to *AaBBCc* of the B_1 to Porter (table 14) were multiplied by the appropriate class proportions to obtain the frequency distributions listed in table 16 opposite the portion of the stub headed "First operation." For example, $(35.2)(1.805556)=63.6$.

The second operation involved placing the figures for each frequency distribution given under the first operation on the basis of 100 percent. This was done by dividing each figure by the appropriate total percentage given in the last column of table 16 and multiplying by 100. For example, $63.6 \div 120.0 = 53.0$, the figure listed under the second operation for genotype *AABbcc* and class 2. The new theoretical frequency distribution for the balance of the B_1 to Porter population, given in the next-to-last line of table 16, was obtained by multiplying the class values by 0.166667 and summing for each class. The ratio of the percentage value for each of the classes 2 to 6 of the obtained frequency

TABLE 16.—*Calculation of theoretical frequency distributions of the genotypes of the balance of the B_1 to Porter for number of locules*

Item	Frequency distribution by average number of locules per fruit					Total
	2	3	4	5	6	
First operation:	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
AABbcc	63.6	52.3	4.1	0	0	120.0
AaBBcc	63.6	52.3	4.1	0	0	120.0
AaBbcc	27.8	46.1	19.8	2.4	0	96.1
AABBCc	20.4	39.3	24.9	5.6	.4	90.6
AABbCc	9.8	24.1	28.4	17.8	6.6	86.7
AaBBCc	9.8	24.1	28.4	17.8	6.6	86.7
Second operation:						
AABbcc	53.0	43.6	3.4	0	0	100.0
AaBBcc	53.0	43.6	3.4	0	0	100.0
AaBbcc	28.9	48.0	20.6	2.5	0	100.0
AABBCc	22.5	43.4	27.5	6.2	.4	100.0
AABbCc	11.3	27.8	32.8	20.5	7.6	100.0
AaBBCc	11.3	27.8	32.8	20.5	7.6	100.0
Balance of population	30.0	30.0	20.1	8.3	2.6	100.0
Ratio of obtained to theoretical [1]	1.083333	1.017940	.910448	.870518	.846154	

[1] Ratio of value given in line 4 of table 15 to value given for same class of frequency distribution of balance of B_1 to Porter in table 16.

distribution (line 4, table 15) to that in this new theoretical frequency distribution was calculated and appears in the last line of table 16. For example, 32.5÷30.0=1.083333, the first figure in that line.

The two operations given in table 16 were repeated twice. Usually two repetitions are sufficient to give a very good fit between the obtained and the theoretical frequency distributions. The theoretical frequency distributions for the genotypes of the balance of the B_1 to Porter are given in table 17 together with those for the balance of the B_1 to Ponderosa and the parental and F_1 genotypes. That a good fit was obtained by two repetitions can be seen by comparing the obtained and theoretical frequency distributions of these two backcross populations (table 18). Any degree of accuracy desired can be had by varying the number of repetitions when doing the calculations partitioning the backcrosses into their component genotypes.

The means of the genotypes of table 17 other than *AAbbCc* and the parental and F_1 genotypes were estimated from the frequency distributions by the standard methods. The 27 genotypes of the F_2 population have only 12 different means and in this respect are represented by the 12 genotypes given in table 17. The 8 genotypes of the B_1 to Porter have 6 different means, and the same is true of the 8 genotypes of the B_1 to Ponderosa. The two backcross populations have only 1 mean in common, that of the F_1 genotype.

To illustrate the method of determining what genotypes have the same means, the group represented by *AaBbCc* is discussed. The other genotypes of this group are *AABbCC*, *AaBBCC*, *Aabbcc*, and *aaBbcc*. Under the hypothesis advanced, the genes tending to produce more locules per fruit have equal effects; *A* and *B* are partially dominant for fewer locules per fruit; and *C* is partially dominant for more locules per fruit. Then, *a* substituted in *AA* to give *Aa*, *b* substituted in *BB* to give *Bb*, and *C* substituted in *Cc* to give *CC* all have equal effects. Likewise, *a* substituted in *Aa* to give *aa*, *b* substituted in *Bb* to give *bb*, and *C* substituted in *cc* to give *Cc* have equal effects. It follows that *aa*, *bb*, and *CC* have equal effects in increasing number of locules or, to put it another way, that *AA*, *BB*, and *cc* have equal effects in decreasing number of locules. *AaBbCc* and *AABbCC* have the same means, because *C* added to *Cc* has the same effect as *a* added to *AA*, and *A* added to *Aa* has the same effect in decreasing number of locules as *c* added to *CC*. Substitution of *A* for *c* and *C* for *a* gives *AaBbCc*, the F_1 genotype, which of course has the same mean as the F_1 population, 4.5 locules per fruit. Identical reasoning shows that *AaBBCC*, also, has a mean of 4.5 locules. *Aabbcc* and *AABbCC* have the same mean, because the effects of *Aa* and *Bb* are the same—as are the effects of *bb* and *CC*, and those of *cc* and *AA*. Substitution in the *Aabbcc* genotype of those gene pairs having the same effects gives *AABbCC*. Identical reasoning shows that the *aaBbcc* and *AABbCC* genotypes have the same mean. The 11 other groups of genotypes having the same means were determined in the same manner and likewise are represented by only 1 genotype in table 17.

The only genotypes whose frequency distributions and, hence, means were not determined by partitioning the frequency distributions of the B_1 populations into those of the component genotypes are *AAbbCc* and *aaBBCc*. The means of these genotypes, which are identical,

TABLE 17.—*Estimated theoretical means and frequency distributions of the genotypes of the balance of B_1 to Porter, the F_2, and the balance of B_1 to Ponderosa for number of locules and proportions of B_1 and F_2 populations that are of individual genotypes*

Genotype or population	Mean	Frequency distribution by average number of locules per fruit													Proportion of—	
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	B_1	F_2
	Number	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
AABBcc [1]	2.10	96.5	3.5	0	0	0	0	0	0	0	0	0	0	0	0	12.5	1.5625
AABbcc [1]	2.48	55.2	41.9	2.9	0	0	0	0	0	0	0	0	0	0	0	25.0	6.2500
AaBbcc [1]	2.91	31.5	48.4	18.0	2.1	0	0	0	0	0	0	0	0	0	0	12.5	6.2500
AABBCc [1]	3.11	25.1	44.8	24.5	5.3	.3	0	0	0	0	0	0	0	0	0	12.5	3.1250
AABbCc [1]	3.74	13.4	30.5	31.1	18.5	6.5	0	0	0	0	0	0	0	0	0	25.0	17.1875
AaBbCc [1 2]	4.50	.9	15.0	35.6	36.0	8.6	2.6	.4	0	0	0	0	0	0	0	12.5	25.0000
AAbbCc [2]	5.46	1.7	6.2	16.6	26.7	26.1	15.5	5.7	1.3	.2	0	0	0	0	0	-------	6.2500
AaBbCC [2]	5.69	.2	.3	5.9	43.6	30.1	14.6	4.2	.9	.2	0	0	0	0	0	12.5	6.2500
AabbCc [2]	6.67	.1	.1	2.7	24.3	24.6	21.4	13.1	6.9	4.9	1.7	.2	0	0	0	25.0	17.1875
AabbCC [2]	7.56	.1	.1	1.6	14.8	17.8	18.5	15.6	11.2	12.3	6.8	.8	.3	.1	0	25.0	6.2500
aabbCc [2]	8.55	0	0	.8	8.5	11.1	13.8	13.9	12.8	19.0	15.1	2.6	1.4	.7	.3	12.5	3.1250
aabbCC [2]	10.00	0	0	1.1	2.8	7.8	5.0	10.5	10.0	20.5	12.2	15.6	6.7	2.2	5.6	12.5	1.5625
B_1 to Porter	3.13	36.4	32.2	18.3	10.0	2.7	.3	.1	0	0	0	0	0	0	0	-------	-------
F_2	4.97	10.4	16.7	18.3	22.3	12.6	7.9	4.5	2.6	2.5	1.4	.4	.2	.1	.1	-------	-------
B_1 to Ponderosa	7.15	.2	2.1	6.5	21.1	17.8	14.5	10.8	7.5	9.3	5.5	2.5	1.1	.4	.7	-------	-------

[1] Present in B_1 to Porter population.
[2] Present in B_1 to Ponderosa population.
[3] The theoretical frequency distribution for this genotype was calculated in the same manner as those of table 3. The standard deviation for this genotype is 1.393.

TABLE 18.—*Theoretical and obtained frequency distributions, χ^2 values for testing goodness of fit, degrees of freedom, and values of P for number of locules*

Population	Frequency distribution by average number of locules per fruit														χ^2 [1]	Degrees of freedom	*P* lies between—
	2	3	4	5	6	7	8	9	10	11	12	13	14	15			
	Per-cent	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*			
Porter:																	
Obtained	96.5	3.5	0	0	0	0	0	0	0	0	0	0	0	0	2.327	1	0.20 and 0.10
Theoretical	98.5	1.5	0	0	0	0	0	0	0	0	0	0	0	0			
Balance of B_1 to Porter: [1]																	
Obtained	32.5	39.7	18.3	7.3	2.2	0	0	0	0	0	0	0	0	0			
Theoretical	32.3	39.7	18.4	7.4	2.2	0	0	0	0	0	0	0	0	0			
F_1:																	
Obtained	0	16.8	35.6	36.0	8.6	3.0	0	0	0	0	0	0	0	0	3.352	4	0.70 and 0.50.
Theoretical	0	15.9	34.1	34.1	13.6	2.3	0	0	0	0	0	0	0	0			
F_2:																	
Obtained	12.4	20.5	19.6	20.8	8.8	8.4	4.0	2.9	2.6	0	0	0	0	0	8.888	8	0.50 and 0.30.
Theoretical	10.4	16.7	18.3	22.3	12.6	7.9	4.5	2.6	4.7	0	0	0	0	0			
Balance of B_1 to Ponderosa: [2]																	
Obtained	0	0	2.8	21.9	21.1	18.0	12.5	8.3	8.8	6.6	0	0	0	0			
Theoretical	0	0	2.8	21.7	21.0	18.0	12.6	8.3	8.9	6.7	0	0	0	0			
Ponderosa:																	
Obtained	0	0	0	3.9	7.8	5.0	10.5	10.0	20.5	12.2	15.6	6.7	2.2	5.6	7.789	10	0.70 and 0.50
Theoretical	0	0	0	3.8	4.6	7.7	11.7	14.3	15.8	14.3	11.7	7.7	4.6	3.8			

[1] Total population less plants of the P_1 and F_1 genotypes.
[2] Total population less plants of the P_2 and F_1 genotypes.

were estimated as follows: In certain combinations *aa*—*Aa* equals *bb*—*Bb* equals *Cc*—*cc*. These combinations and differences are:

aa—*Aa*	*bb*—*Bb*	*Cc*—*cc*	*Difference*
BBcc	*AAcc*	*AABb*	1.26
Bbcc	*Aacc*	*AaBb*	1.59
bbCc	*aaCc*	*aabb*	1.88
bbcc	*aacc*	*aaBb*	2.17

The difference *AAbbCc*—*AABbCc* approximates the average of the above differences, which is 1.72. The estimated mean of *AAbbCc* is 1.72+3.74 (mean of *AABbCc*), or 5.46. The frequency distribution of the *AAbbCc* and *aaBBCc* genotypes was calculated from this mean and the standard deviation of a single determination given in footnote 3, table 17, in the same manner as the frequency distributions of the genotypes given in table 3.

This completes the estimation of the theoretical frequency distributions and means of all genotypes of the segregating populations. The values are given in table 17. The theoretical means and frequency distributions of the three segregating populations were calculated in the same manner as those in table 3. A comparison of the means of the segregating populations given in tables 13 and 17 reveals that the obtained and theoretical means are in close agreement. The tests to determine whether the obtained frequency distributions are in agreement with the hypothesis advanced are given in table 18.

A study of the obtained and theoretical frequency distributions and the *P* values reveals that the obtained frequency distributions are in close agreement with the hypothesis that Porter and Ponderosa are differentiated by three pairs of major genes as regards number of locules per fruit. Two of these pairs of genes are partially dominant for fewer locules, and one is partially dominant for more locules per fruit.

WEIGHT PER LOCULE

MAGNITUDE OF CHARACTER DIFFERENCES AND DOMINANCE

The means for weight per locule are given in table 19. Weights per locule for the two parents were not materially different, averaging 10.2 gm. for Porter and 9.8 gm. for Ponderosa. The mean for the F_1 is greater than the mean for either parent. The same is true of the means for the B_1 to Porter, the F_2, and the B_1 to Ponderosa; but the means for these populations are smaller than that for the F_1. Clearly, the F_1 showed heterosis for weight per locule.

The genetic variances for weight per locule and weight per fruit could not be calculated, for reasons given later (in the section on the variances).

NUMBER OF MAJOR GENE PAIRS DIFFERENTIATING THE PARENTS

Examination of the condensed frequency distributions for weight per locule (table 19) reveals that the F_2 and B_1 to Ponderosa populations are the only ones having any individuals falling into the 33.5- to 61.5-gm.-per-locule class. This suggests that comparatively few major gene pairs may have been responsible for the heterosis noted for weight per locule. The fact that only 1.9 percent of the F_2 plants fall into the 33.5- to 61.5-gm. class indicates that three major gene

TABLE 19.—*Means and condensed frequency distributions for weight per locule and weight per fruit*

Population	Mean weight per locule	Mean weight per fruit
	Gm.	*Gm.*
Porter	10.2	21.5
B_1 to Porter	11.8	36.6
F_1	14.4	65.0
F_2	13.5	63.5
B_1 to Ponderosa	13.7	97.3
Ponderosa	9.8	97.7

Population	Condensed frequency distribution by—					
	Weight per locule in grams			Weight per fruit in grams		
	1.5–15.5	17.5–31.5	33.5–61.5	12.5–32.5	37.5–92.5	97.5–232.5
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Porter	99.6	0.4	0	99.6	0.4	0
B_1 to Porter	85.5	14.5	0	54.2	45.8	0
F_1	64.3	35.7	0	0	100.0	0
F_2	74.6	23.5	1.9	11.5	76.0	12.5
B_1 to Ponderosa	69.9	29.5	.6	3.1	50.7	46.2
Ponderosa	90.0	10.0	0	4.0	50.5	45.5

pairs differentiated weight per locule in this cross. The fact that 0.6 percent of the plants of the B_1 to Ponderosa population fall into that class indicates the same thing and suggests that two of the gene pairs tending to increase weight per locule entered the cross from the Ponderosa parent. The genotypes given in table 20 are those expected on the hypothesis that, as regards weight per locule, Porter and Ponderosa were differentiated by three major gene pairs, and that two of these gene pairs tending to increase weight per locule were carried by Ponderosa.

In the B_1 to Ponderosa population the Ponderosa$_1$ minus phenotype might be expected to have the same penetrances for the different classes of the condensed frequency distributions as plants of Ponderosa. Plants of the F_1 genotype would be expected to have the same penetrances as plants of the F_1 population. This leaves undetermined, as regards the B_1 to Ponderosa population, only the penetrances of the F_1 plus phenotype. To estimate these penetrances, the B_1 to Ponderosa population was used and the same formulas and methods given previously were applied.

Examination of table 19 reveals that 0.6 percent of the plants of the B_1 to Ponderosa population fall into the 33.5- to 61.5-gm.-per-locule class, whereas none of the plants of the B_1 to Porter population do so. It is logical to assume that the plants of the B_1 to Ponderosa population falling into this class are of the *AaBBCC*, *AaBBCc*, and *AaBbCC* genotypes. In the B_1 to Porter population of 448 plants, however, if the plants of the *AABbCc* genotype (B_1 to Porter) had the same penetrance for the 33.5- to 61.5-gm. class as plants of the above-mentioned genotypes in the B_1 to Ponderosa population, theoretically only 1 plant [(0.006)(0.125)(448)] would fall into this class. Hence, it would be expected that, by chance, a large percentage of B_1 to Porter populations would have no plants falling into the 33.5- to

TABLE 20.—*Theoretical genotypes and phenotypes of different populations, based on the hypothesis that Porter and Ponderosa are differentiated by 3 major gene pairs as regards weight per locule*

Porter (P_1) *AAbbcc*		F_1 *AaBbCc*		Ponderosa (P_2) *aaBBCC*	
B_1 to Porter		F_2		B_1 to Ponderosa	
Genotype	Phenotype	Genotype	Phenotype	Genotype	Phenotype
AABbCc	F_1 plus.	*AABBCC*	F_1 plus.	*AaBBCC*	F_1 plus.
AABbcc	F_1 and P_1 intermediate.	*AABBCc*	Do.	*AaBBCc*	Do.
AAbbCc	Do.	*AABBcc*	F_1 and P_1 intermediate.	*AaBbCC*	Do.
AAbbcc	Porter.	*AABbCC*	F_1 plus.	*AaBbCc*	F_1.
AaBbCc	F_1.	*AABbCc*	Do.	*aaBBCC*	Ponderosa.
AaBbcc	F_1 and P_1 intermediate.	*AABbcc*	F_1 and P_1 intermediate.	*aaBBCc*	$Ponderosa_1$ (minus).
AabbCc	Do.	*AAbbCC*	Do.	*aaBbCC*	Do.
Aabbcc	$Porter_1$ (minus).	*AAbbCc*	Do.	*aaBbCc*	Do.
		AAbbcc	Porter.		
		AaBBCC	F_1 plus.		
		AaBBCc	Do.		
		AaBBcc	F_1 and P_1 intermediate.		
		AaBbCC	F_1 plus.		
		AaBbCc	F_1.		
		AaBbcc	F_1 and P_1 intermediate.		
		AabbCC	Do.		
		AabbCc	Do.		
		Aabbcc	$Porter_1$ (minus).		
		aaBBCC	Ponderosa.		
		aaBBCc	$Ponderosa_1$ (minus).		
		aaBBcc	Do.		
		aaBbCC	Do.		
		aaBbCc	Do.		
		aaBbcc	$Ponderosa_2$ (minus).		
		aabbCC	$Ponderosa_2$ (minus).		
		aabbCc	$Ponderosa_2$ (minus).		
		aabbcc	Do.		

61.5-gm. class. *AABbCc* genotype plants were therefore considered as having a penetrance of 0.6 percent for this class, also. Since 99.6 percent of the Porter phenotype plants of the B_1 to Porter population fall into the 1.5- to 15.5-gm. class, all the $Porter_1$ minus phenotype plants might be expected to fall into this class. Examination of table 20 reveals that plants of the $Ponderosa_2$ minus genotypes would be expected to fall into the same class of the condensed frequency distributions as plants of the *Aabbcc* genotype. This was assumed to be the case. By using the B_1 to Porter population for purposes of estimation, the penetrances of the F_1 and P_1 intermediate phenotype were determined. The formulas and methods of procedure were the same as for the analysis of number of major gene pairs differentiating period from first bloom to first fruit set. In using these formulas, the penetrances of the plants of the phenotype being estimated were adjusted so that the percentages totaled 100, if they did not do so already. The penetrances, theoretical frequencies of the different genotypes, and theoretical percentages of the condensed frequency distributions were calculated with the results given in table 21.

Since the χ^2 value of table 21 has a P value greater than 0.05, the fit between the obtained and theoretical values is good. To calculate the theoretical mean of the F_2, it was necessary to estimate the means of all the phenotypes of table 21. The means of the F_1, Porter, and Ponderosa populations are given in table 19. The mean of plants of the $Ponderosa_1$ minus phenotype would be expected to approximate that of the Ponderosa parent. Since all the plants of the $Porter_1$

minus and Ponderosa$_2$ minus phenotypes fall into the 1.5- to 15.5-gm.-per-locule class, the average of this class would be expected to approximate the means for these two phenotypes. It is [(1.5+15.5)÷2], or 8.5 gm. With these constants available, the mean of plants of the F_1 plus phenotype was estimated from the B_1 to Ponderosa population by applying methods and formulas already given. It is 18.7 gm. The mean of plants of the F_1 and P_1 intermediate phenotype was estimated from the data of the B_1 to Porter population, and is 10.7 gm. The theoretical mean of the F_2 population as estimated by methods and formulas already given is 13.1 gm., which is very close to the obtained mean, 13.5 gm. On the whole, the data convincingly support the hypothesis that Porter and Ponderosa were differentiated by three major gene pairs as regards weight per locule.

TABLE 21.—*Phenotypes and their penetrances for weight per locule, theoretical proportion of each phenotype in the F_2 population, obtained and theoretical proportions of that population in each class of the condensed frequency distribution (table 19) and χ^2 values for testing goodness of fit*

Phenotype	Penetrance in indicated class			Theoretical proportion of F_2 population
	1.5–15.5 gm.	17.5–31.5 gm.	33.5–61.5 gm.	
	Percent	*Percent*	*Percent*	*Percent*
F_1 plus	45.0	53.4	1.6	20.6875
F_1	64.3	35.7	0	12.5000
F_1 and P_1 intermediate	93.6	6.4	0	28.1250
Porter	99.6	.4	0	1.5625
Porter$_2$ (minus)	100.0	0	0	3.1250
Ponderosa	90.0	10.0	0	1.5625
Ponderosa$_1$ (minus)	90.0	10.0	0	14.0625
Ponderosa$_2$ (minus)	100.0	0	0	9.3750

F_2 population	Proportion in indicated class			χ^2	Degrees of freedom
	1.5–15.5 gm.	17.5–31.5 gm.	33.5–61.5 gm.		
	Percent	*Percent*	*Percent*		
Obtained	74.6	23.5	1.9	4.510	2
Theoretical	75.5	23.7	.5		

WEIGHT PER FRUIT

MAGNITUDE OF CHARACTER DIFFERENCES AND DOMINANCE

The means for weight per fruit are given in table 19. The difference between the means of the two parents is 76.2 gm. The means of the parents average 59.6 gm., and the mean of the F_1 is 65.0 gm. The mean of F_2 does not differ significantly from that of F_1, the mean of B_1 to Porter is closer to the mean of Porter than to that of F_1, and the mean of B_1 to Ponderosa does not differ significantly from the mean of Ponderosa. It is evident that these values do not fit any simple interpretation of intraallelic and interallelic interactions of the genes. However, the F_1 showed phenotypic dominance of greater weight per fruit. It is interesting to note that fewer locules showed partial dominance, greater weight per locule showed heterosis, and these two component characters combined multiplicatively to produce partial phenotypic dominance of greater weight per fruit.

NUMBER OF MAJOR GENE PAIRS DIFFERENTIATING THE PARENTS

Since number of locules and weight per locule were each differentiated by three major gene pairs, weight per fruit was differentiated by six major gene pairs if pleiotropy was not involved. The means and condensed frequency distributions for weight per fruit, given in table 19, were examined to determine whether as few as three major gene pairs differentiated Porter and Ponderosa as regards this character. It can be seen that 99.6 percent of the plants of the Porter population fall into the 12.5- to 32.5-gm.-per-fruit class of the condensed frequency distributions, and that 54.2 percent of the B_1 to Porter plants and none of the F_1 plants do so. This would indicate that one major gene pair differentiated the two parents. On the basis of an assumption that this was the case, it would be expected that 25 percent of the F_2 population would fall into the first class of the condensed frequency distributions. Instead, only 11.5 percent do so. Moreover, within the limits of the probable errors of random sampling the percentage of the B_1 to Ponderosa population in any given class of the condensed frequency distributions does not differ materially from the percentage of the Ponderosa population in that class. The means and condensed frequency distributions cannot be explained on the basis that as few as three pairs of genes differentiated the parents. Hence, the values in table 19 do not provide any evidence of pleiotropy.

INTERACTIONS OF GENES

Information concerning the nature of the interactions of the three major pairs of genes differentiating number of locules per fruit is provided by table 17. The means of this table show that in general the genes tending to increase number of locules per fruit have a greater effect in combination with genes tending to produce more locules than they do in combination with the alleles of these genes. The *Aa* and *Bb* gene pairs showed partial dominance for fewer locules per fruit and the *Cc* gene pair partial dominance for more locules per fruit. Both the interallelic and intraallelic interactions were found to be cumulative; and there is considerable evidence that these types of interactions are not independent, because the differences between the homozygous dominant and heterozygous individuals with respect to any given gene pair tend to increase as number of genes tending to produce more locules increases.

With respect to weight per locule, genic dominance is not complete, since a higher percentage of the plants of the *AABBCC* genotype than of those of the *AaBbCc* genotype falls into the 33.5- to 61.5-gm.-per-locule class of the condensed frequency distributions. Since a higher percentage of the plants of the *AABBCC* genotype falls into this class than of the plants of any other genotype, both the interallelic and intraallelic interactions of the genes must be such that the effects of the genes are cumulative. Also, the fact that the mean (table 19) for the *AAbbcc* genotype (Porter population) is as large as that for the *aaBBCC* genotype (Ponderosa population) shows that the *AA* gene pair is as effective in increasing weight per locule as the *BB* and *CC* gene pairs combined.

INTERRELATIONS OF CHARACTERS

PERIOD FROM SEEDING TO FIRST FRUIT RIPE AND ITS COMPONENT CHARACTERS

To obtain information on relations between the three components of period from seeding to first fruit ripe and the relative importance of each in causing the variability of the dependent character, the correlation coefficients and the relative percentages of the variances accounted for by regression were calculated. The correlation coefficients for period from seeding to first bloom (X_1), period from first bloom to first fruit set (X_2), and period from first fruit set to first fruit ripe (X_3), together with the relative percentages of the variance of period from seeding to first fruit ripe (Y) accounted for by regression, are given in table 22.

TABLE 22.—*Correlation coefficients for period from seeding to first bloom* (X_1), *period from first bloom to first fruit set* (X_2), *and period from first fruit set to first fruit ripe* (X_3), *together with the relative percentages of the variance of period from seeding to first fruit ripe* (Y) *accounted for by regression*

Population	Correlation coefficients			Relative percentage of variance accounted for by regression		
	r_{12}	r_{13}	r_{23}	$r_{y1}{}^2{}_{y(23)}$	$r_{y2}{}^2{}_{y(13)}$	$r_{y3}{}^2{}_{y(12)}$
				Percent	*Percent*	*Percent*
Porter	0.1720	−0.2656	−0.4792	72.9	11.3	15.8
B_1 to Porter	−.0006	−.0219	−.3952	70.3	13.1	16.6
F_1	.1010	−.0856	−.4166	61.9	17.3	18.7
F_2	−.0706	−.0078	−.2196	35.5	38.6	25.9
B_1 to Ponderosa	−.1581	−.0053	−.2580	19.2	51.5	29.3
Ponderosa	−.1814	−.0740	−.4631	20.8	23.2	56.0

The correlation coefficients (r_{12}) for period from seeding to first bloom and period from first bloom to first fruit set are small. This is true also of the correlation coefficients (r_{13}) for period from seeding to first bloom and period from first fruit set to first fruit ripe. For all practical purposes, period from seeding to first bloom and the other component characters are essentially independent. Then, as regards the interrelations of these characters there is no evidence of pleiotropy or genetic linkage. There is evidence, however, of a slight negative interaction involving the component characters and the environment. That this relation is physiological is shown by the fact that it is exhibited by both the nonsegregating and the segregating populations. Because the correlation coefficients are small, this relation has little practical significance. In other words linkage, pleiotropy, or the interactions involving the component characters and the environment offer little hindrance to combining shorter period from seeding to first bloom with shorter period from first bloom to first fruit set and shorter period from first fruit set to first fruit ripe.

The correlation coefficients (r_{23}) for period from first bloom to first fruit set and period from first fruit set to first fruit ripe are larger. All those for the nonsegregating populations (Porter, B_1 to Porter, F_1, and Ponderosa) are larger than those for the segregating populations, and are negative. (Here B_1 to Porter is considered a nonsegregating

population because both the characters mentioned exhibited almost complete, if not complete, phenotypic dominance of the genes contributed by Porter.) Since a shorter period from first bloom to first fruit set and a shorter period from first fruit set to first fruit ripe were combined in the Porter parent, the fact that the correlation coefficients for the segregating populations are smaller than those for the nonsegregating populations constitutes fairly dependable evidence that some of the genes tending to produce a shorter period from first bloom to first fruit set were linked with some of the genes tending to produce a shorter period from first fruit set to first fruit ripe, or that some of the genes exhibited pleiotropy. The negative correlation for the nonsegregating populations shows that the physiological reactions were such that on an average less length of one of these two periods was accompanied by greater length of the other. The genetic linkage or pleiotropy, as the case may be, facilitates combining the two desirable characters, whereas the physiological reactions involving the component characters and the environment that lead to negative correlation coefficients hinder combination of such characters. That the physiological reactions noted did not prohibit combination of the two desirable characters is shown by the fact that the two were combined in the Porter parent.

The relative percentages (table 22) of the variance of period from seeding to first fruit ripe accounted for by the regression of this character on its component characters indicate the relative contributions of the latter to the variance of the dependent character. In interpreting these data, it is necessary to keep in mind that the percentages were obtained by multiplying the simple correlation coefficients (ry) by their respective standard partial regression coefficients ($b'y$) and then by 100. By this procedure, the proportionate contribution of each component character to the variance of the dependent character is evaluated in its relation to that of the other component characters. Study of the values listed under "Relative percentage of variance accounted for by regression" in table 22 reveals that for the Porter, B_1 to Porter, and F_1 populations the greater part of the variance was contributed by period from seeding to first bloom ($ry_1b'y_{1.23}$); for the F_2 and B_1 to Ponderosa populations, by period from first bloom to first fruit set ($ry_2b'y_{2.13}$); and for the Ponderosa population, by period from first fruit set to first fruit ripe. This shows that, of the three component characters, period from first bloom to first fruit set has the lowest relative percentage values for the nonsegregating populations and has the highest for the segregating populations. Since dominance was almost, if not entirely, complete for all three component characters of period from seeding to first fruit ripe, segregation of the genes differentiating these characters is phenotypically discernible only in the F_2 and B_1 to Ponderosa populations. Since the regression of period from seeding to first fruit ripe on period from first bloom to first fruit set accounts for a greater relative percentage of the variance of this main character in the segregating populations than do its regressions on the two other component characters, it is evident that this situation is due to segregation of the genes differentiating period from first bloom to first fruit set. This is confirmed by the differences between the means of Porter and Ponderosa for the three components of period from seeding to first fruit ripe. These differ-

ences (table 5) are 12.1, 30.6, and 14.4 days, respectively. Hence, the interrelations of the characters were such as to indicate that, other things being equal, the greatest strides toward combining earliness of maturity with other desirable characters in tomatoes can be made by emphasizing, in selection, shortness of period from first bloom to first fruit set.

The values listed under "Relative percentage of variance accounted for by regression" in table 22 provide some evidence as to whether the proportionate part of the environmental variance of the dependent character contributed by each of the component characters, as determined by regression, was inherited. As regards the earliness-of-maturity characters in the nonsegregating populations, examination of the table reveals that the relative percentage values for the regressions involving period from seeding to first bloom form a continuously decreasing series from Porter to Ponderosa, and those for the regressions involving period from first bloom to first fruit set and period from first fruit set to first fruit ripe form continuously increasing series from Porter to Ponderosa. Since the populations are listed in table 22 in accordance with the closeness of their genetic relations, the seriation just noted constitutes convincing evidence that the relative proportionate parts of the environmental variance of the main character contributed by each of the component characters, as determined by regression, were inherited. The tendency for the regression involving period from seeding to first bloom to account for the greater part of the environmental variance of period from seeding to first fruit ripe was partially dominant, and the degree of partial dominance was of a rather high order. Here again, since one of the greatest difficulties in applied genetics is to select plants that are superior because of their genotype rather than because of the environment, the interrelations of the characters were such that selection of tomatoes for a shorter period from first bloom to first fruit set rather than on the basis of either of the other component characters offers the greatest promise.

With this information available concerning the interrelations of the component characters for period from seeding to first fruit ripe, some conclusions can be drawn about the number of major gene pairs differentiating this character and also the nature of the interactions of these genes. At this point it is appropriate to remark that in this study, as in most such studies, the research worker is not dealing directly with the interactions of genes but instead is dealing with the interactions of substances and characters differentiated by genes. For a discussion of this point, see Goldschmidt (7).

Period from seeding to first bloom was found to be differentiated by three major gene pairs. None of these genes were carried in the same chromosomes as the genes differentiating the two other component characters. Pleiotropy played no part, and the negative relation between period from seeding to first bloom and period from first fruit set to first fruit ripe was so small as to be of little practical significance. Such being the case, the three gene pairs differentiating period from seeding to first bloom were not the same as those differentiating either of the other component characters. Period from first bloom to first fruit set was found to be differentiated by three major

gene pairs, and period from first fruit set to first fruit ripe by two. This signifies involvement of genetic linkage or pleiotropy or both. If pleiotropy was involved, it was shown by only one pair, as individuals combining the two characters were obtained in both segregating generations. This proves that period from seeding to first fruit ripe was differentiated by at least seven major gene pairs and that if (as seems probable) genetic linkage alone was involved, rather than pleiotropy or both, this character was differentiated by eight major gene pairs.

Since the genes differentiating period from seeding to first bloom were independent of those differentiating the two other component characters as regards linkage, pleiotropy, and—essentially—the interactions involving the component characters and the environment, it is apparent that the effects of the genes differentiating the first-mentioned character and the effects of those differentiating the two other characters were additive. However, the effects of the genes differentiating period from first bloom to first fruit set and those differentiating period from first fruit set to first fruit ripe were less than additive, because the interactions involving these two characters and the environment produced a negative relation, that is, a shorter period from first bloom to first fruit set tended to be accompanied by a longer period from first fruit set to first fruit ripe.

Findings on interactions of the genes are summarized as follows: In all cases pertaining to the maturity characters, the intraallelic interactions of the genes were such that the effects were not cumulative, as both phenotypic and genic dominance were complete, or nearly so. Likewise the interallelic interactions of the genes differentiating period from seeding to first bloom were such that the effects were not cumulative. However, the opposite was true of the interallelic interactions of the genes differentiating period from first bloom to first fruit set and those of the genes differentiating period from first fruit set to first fruit ripe. The effect of interallelic interactions within a component character were cumulative. The interactions between the genes differentiating period from seeding to first bloom and those differentiating the two other component maturity characters were such that the effects were cumulative and additive. The interactions between the genes differentiating period from first bloom to first fruit set and those differentiating period from first fruit set to first fruit ripe were such that the effects were cumulative but less than additive.

The data do not furnish evidence whether the genes differentiating period from seeding to first bloom had equal effects. It has been shown that the genes differentiating the two other component maturity characters, respectively, did not. In respect to the dependent character, period from seeding to first fruit ripe, on an average the genes differentiating period from first bloom to first fruit set had a greater effect than those differentiating period from first fruit set to first fruit ripe; and, in turn, on an average the latter had greater effects than the genes differentiating period from seeding to first bloom. This shows that the seven or eight major gene pairs differentiating period from seeding to first fruit ripe did not have equal effects.

WEIGHT PER FRUIT AND ITS COMPONENT CHARACTERS

The correlation coefficients for number of locules per fruit (X_1) and weight per locule (X_2) are given in table 23. The correlation coefficient of the two independent characters is largest for the F_1, smallest for Ponderosa, and next smallest for Porter. Among the segregating populations, the correlation coefficient for the B_1 to Porter is the largest and those for the F_2 and B_1 to Ponderosa do not differ materially. These results are those expected on the assumption that the covariance of number of locules and weight per locule, as depicted by the correlation coefficients, is differentiated by genes and that the degree of covariance exhibits decided heterosis. Since the highest and lowest degrees of covariance were found in nonsegregating populations, it is evident that pleiotropy and linkage of genes played little if any part in producing the results noted. It follows that the relations found must have been due to interactions between the populations and the environment.

TABLE 23.—*Correlation coefficients for number of locules per fruit* (X_1) *and weight per locule* (X_2), *together with relative percentages of variance of weight per fruit* (Y) *accounted for by regression*

Population	Correlation coefficient r_{12}	Relative percentage [1] of variance accounted for by regression	
		$ry_1b'y_{1.2}$	$ry_2b'y_{2.1}$
		Percent	*Percent*
Porter	−0.4015	2.0	94.3
B_1 to Porter	−.5317	58.7	37.6
F_1	−.8126	1.7	95.0
F_2	−.4225	67.9	31.0
B_1 to Ponderosa	−.4329	34.1	65.7
Ponderosa	−.2866	11.9	85.0

[1] The failure of the relative percentages for any given population to add up to 100 is due to the fact that in calculating average number of locules per fruit and average weight per locule the values were expressed in whole numbers.

The relative percentages of the variance of weight per fruit (Y) accounted for by the regression of weight per fruit on number of locules per fruit ($ry_1b'y_{1.2}$) and its regression on weight per locule ($ry_2b'y_{2.1}$) are given in table 23. In all the nonsegregating populations weight per locule had the preponderant influence on this variance. The relative percentage of the variance accounted for by the regression on weight per locule is less for the Ponderosa population than it is for the Porter or the F_1 population. This supports the conclusion, already drawn regarding period from seeding to first fruit ripe and its component characters, that in some cases, at least, the relative proportionate part of the variance of the dependent character accounted for by the regression of this character on any given component character was genetically controlled to some extent. Among the segregating generations the relative proportionate part of the variance of weight per fruit accounted for by the regression of this character on number of locules per fruit was considerably greater. This is due to the segregation of the genes differentiating the two component characters. Such being the case, since for the B_1 to Porter and F_2 populations the relative percentage values are larger for number of locules, it is

evident that in these generations the genes differentiating that character had a preponderant influence. The practical interpretation is that in breeding for large size of fruit the most rapid strides can be made by selecting for large number of locules in the F_2 population.

Since number of locules and weight per locule were each differentiated by three major gene pairs and were found not to exhibit either genetic linkage or pleiotropy, it is apparent that weight per fruit is differentiated by six major gene pairs.

As regards the genes differentiating number of locules, both the intraallelic and the interallelic interactions of the *Aa*, *Bb*, and *Cc* gene pairs were such that the effects were cumulative. Both the intraallelic and the interallelic interactions of the genes differentiating weight per fruit were found to be cumulative. The interactions between the genes differentiating the two component characters, also, were such that the effects were cumulative. It has been shown that the interactions between the populations and the environment were such that greater number of locules tended to be accompanied by lesser weight per locule, or vice versa. The end results of these reactions cumulated geometrically, as number of locules per fruit times weight per locule gives weight per fruit.

Since the *Aa* gene pair for weight per locule had a preponderant effect and number of locules had greater influence than weight per locule in determining weight per fruit, it is apparent that all the genes differentiating these two component characters did not have equal effects.

PERCENTAGE OF FLOWERS THAT SET FRUIT, PERIOD FROM SEEDING TO FIRST FRUIT RIPE, AND WEIGHT PER FRUIT

The analysis to determine interrelations of percentage of flowers that set fruit, period from seeding to first fruit ripe, and weight per fruit dealt with the component characters rather than the dependent characters. The reason for this is that any interrelation of component characters influenced the dependent character unless the effect of one component character exactly offset that of another. (The latter is unlikely. If it did occur, this could be ascertained by studying the component characters.) Table 24 presents the data on interrelations of percentage of flowers that set fruit, period from seeding to first fruit ripe, and weight per fruit as determined by comparing percentage of population expected in the most desirable class on the basis of independent inheritance and percentage obtained in this class. The characters considered desirable are greater percentage of flowers that set fruit; shorter period from seeding to first bloom, from first bloom to first fruit set, and from first fruit set to first fruit ripe; more locules per fruit; and greater weight per locule. Details of the method used in analyzing the data are given in an earlier publication (*18, p. 113*). With reference to table 24, it should be pointed out that pleiotropy of one of a few gene pairs cannot be distinguished from genetic linkage in cases involving multiple gene inheritance. For convenience, and because it seems that in most cases genetic linkage is involved rather than pleiotropy or both phenomena, the term "genetic linkage" is used in interpreting the data. It must be kept in mind that, unless otherwise stated, pleiotropy or both phenomena could be involved.

TABLE 24.—*Interrelations of components of period from seeding to first fruit ripe, components of weight per fruit, and percentage of flowers that set fruit, as determined by comparison of percentage of population expected in the most desirable class on the basis of independent inheritance and corresponding obtained percentage*

Character and population	Proportion of population in most desirable class [1] both as to character in stub and as to—									
	Period from seedling to first bloom		Period from first bloom to first fruit set		Period from first fruit set to first fruit ripe		Number of locules		Weight per locule	
	Expected	Obtained	Expected	Obtained	Expected	Obtained	Expected	Obtained	Expected	Obtained
Percentage of flowers that set fruit:	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Porter	4.44	5.60	15.73	15.00	1.40	8.19	0	0	2.14	1.29
B_1 to Porter	3.55	2.90	18.03	21.87	.07	7.37	3.71	.00	4.14	2.90
F_1	1.24	1.72	3.19	4.72	.27	1.29	2.26	2.15	1.69	1.72
F_2	7.75	4.83	11.37	18.08	1.83	5.50	7.08	.22	6.72	5.50
B_1 to Ponderosa	8.06	7.44	7.09	13.40	1.33	8.98	15.57	5.35	12.44	13.40
Ponderosa	3.22	2.70	4.42	6.00	.52	2.70	6.00	4.14	5.56	7.59
Number of locules:										
Porter	0	0	0	0	0	0				
B_1 to Porter	1.61	2.46	8.19	6.70	.44	3.67				
F_1	12.47	11.59	32.10	32.10	2.68	10.73				
F_2	7.81	7.69	11.60	6.37	1.84	6.15				
B_1 to Ponderosa	7.40	8.84	7.33	2.56	1.22	5.58				
Ponderosa	4.83	6.21	6.63	3.45	.93	6.90				
Weight per locule:										
Porter	2.04	2.58	7.23	8.19	.64	3.02				
B_1 to Porter	1.80	1.70	9.15	8.48	.49	3.70				
F_1	9.33	9.44	24.01	21.80	2.00	8.58				
F_2	7.42	7.47	11.08	10.55	1.75	5.71				
B_1 to Ponderosa	5.91	6.51	5.85	6.05	.97	4.65				
Ponderosa	4.48	4.14	6.14	7.59	.86	6.90				

[1] Desirable characters: Higher percentage of flowers that set fruit, fewer days from seeding to first bloom, fewer days from first bloom to first fruit set, fewer days from first fruit set to first fruit ripe, higher number of locules, and greater weight per locule.

For all practical purposes, percentage of flowers that set fruit was independent of period from seeding to first bloom and weight per locule. Interdependence of these characters was slight or nonexistent. However, percentage of flowers that set fruit was not independent of period from first bloom to first fruit set, period from first fruit set to first fruit ripe, or number of locules. For period from first bloom to first fruit set and percentage of flowers that set fruit (table 24), the differences between the expected and obtained percentages for the Porter, F_1, and Ponderosa populations are no greater than would occur by chance. However, for the segregating populations the obtained values are greater than those expected on the basis of independent inheritance. Since the two desirable characters entered the cross from the Porter parent, these are the results expected in the event of genetic linkage. As regards number of locules and percentage of flowers that set fruit, the obtained values are less than those expected. Again, since genes differentiating the two desirable characters entered the cross from different parents, the results are those expected in the event of genetic linkage. Pleiotropy could be responsible for the results noted, but genetic linkage is the more probable cause.

Very little, if any, interdependence appears between number of locules per fruit and period from seeding to first bloom (table 24). For number of locules and period from first bloom to first fruit set the

obtained percentages of the segregating populations are less than those expected on the basis of independent inheritance. Since the genes tending to produce more locules per fruit and those tending to produce shorter period from first bloom to first fruit set entered the cross from different parents and since the obtained and expected values are percentages of plants combining these two desirable characters, the results are those expected on the basis of genetic linkage. Genetic linkage was to be expected, since percentage of flowers that set fruit was found to be linked with period from first bloom to first fruit set and number of locules per fruit. As regards number of locules and period from first fruit set to first fruit ripe, in every instance the obtained percentages are greater than the expected. Since the magnitude of the discrepancies does not differ significantly between the segregating and the nonsegregating populations, the relation is not due to genetic linkage or pleiotropy. This relation facilitates rather than hinders the breeding program. It means that the environmental conditions conducive to increase in number of locules per fruit are also conducive to shortening of the period from first fruit set to first fruit ripe.

The conclusions to be drawn regarding weight per locule are these: Weight per locule is essentially independent of period from seeding to first bloom and period from first bloom to first fruit set. However, weight per locule and period from first fruit set to first fruit ripe show a rather strong relation, due to interactions involving the two characters and the environment. The interactions are such that environmental conditions tending to increase weight per locule also tend to shorten the period from first fruit set to first fruit ripe.

Variances of Period From Seeding to First Fruit Ripe and Its Component Characters, and Variances of Weight per Locule

The variances of period from seeding to first fruit ripe and its component characters and the variances of weight per locule provide a means of testing the validity of the method employed to estimate the environmental and genetic variances and determining whether the genetic variances as estimated include the interactions. The total, environmental, and genetic variances of period from seeding to first fruit ripe and its component characters are given in table 25.

For all maturity characters the total variances for all three nonsegregating populations approximate the corresponding environmental variances within the limits of the deviations expected owing to probable errors of random sampling. Consequently, the validity of the method employed to estimate the environmental variances, and hence the genetic variances also, is substantiated for period from seeding to first fruit ripe and its component characters. If there had been no interactions, the sums of the variances of the component characters would approximate the respective variances of period from seeding to first fruit ripe, within the limits of the deviations expected owing to probable errors of random sampling. The theoretical variances (sums of variances of component characters) and the obtained variances are given in table 26. In every case the theoretical variances are larger than the obtained. This proves that there were interactions. To determine whether the data for the segregating generations

TABLE 25.—*Total, environmental, and genetic variances for period from seeding to first fruit ripe and its component characters*

Character and population	Variance		
	Total	Environmental	Genetic
Period from seeding to first bloom:	*Days*	*Days*	*Days*
Porter	36.543	38.056	
B_1 to Porter	60.787	61.021	
F_1	41.771	38.822	
F_2	61.859	35.760	26.099
B_1 to Ponderosa	73.202	48.108	25.194
Ponderosa	129.478	130.680	
Period from first bloom to first fruit set:			
Porter	8.348	9.635	
B_1 to Porter	19.637	19.005	
F_1	16.873	15.508	
F_2	84.140	57.336	26.084
B_1 to Ponderosa	178.221	124.628	53.593
Ponderosa	270.298	270.286	
Period from first fruit set to first fruit ripe:			
Porter	20.624	10.918	
B_1 to Porter	21.411	20.937	
F_1	22.009	26.097	
F_2	50.209	32.328	20.881
B_1 to Ponderosa	112.525	83.311	29.214
Ponderosa	377.354	378.501	
Period from seeding to first fruit ripe:			
Porter	44.439	49.804	
B_1 to Porter	85.196	74.722	10.474
F_1	66.119	60.814	
F_2	158.970	92.107	66.863
B_1 to Ponderosa	237.116	172.077	65.039
Ponderosa	380.756	380.606	

and those for the nonsegregating generations differ, the percentages that the obtained variances are of the theoretical variances were calculated. They are presented in the last column of table 26. In every case, the percentages for the B_1 to Porter, F_1, and F_2 populations are higher than that for either parent and those for the B_1 to Ponderosa population are higher than that for Ponderosa. Clearly, the relations between the different populations are those expected on the basis of heterosis. Considered as a whole, the differences due to heterosis are statistically significant. Thus there is no indication of a difference in response between the segregating and nonsegregating populations. Such being the case, and since there is no consistent difference among the total, environmental, and genetic percentages for the F_2 population or among those for the B_1 to Ponderosa population, the heterosis noted for the percentages that the obtained variances are of the respective theoretical variances is due to interactions between the populations and the environment. One other interaction pertaining to the maturity characters has been demonstrated (see section entitled "Interrelations of Characters"), that involving two of the component characters and the environment. It has been shown that a shorter period from bloom to first fruit set tended to be accompanied by a longer period from first fruit set to first fruit ripe. Such a relation between these characters in respect to environmental variability would tend to cause a decrease in the variance of the dependent character such as was noted for all the populations. (See table 26.) Then, it is apparent that the interactions are included in the genetic variances as well as in the total and environmental variances. However, in this study the nature and effects of the interactions were such that the

variances of the dependent character were less than those expected on the basis of no interactions. Such being the situation, and since the component characters are undoubtedly the end result of the interactions of substances and other component characters differentiated by the genes and the environment, the variances of period from seeding to first fruit ripe and its component characters are of little value in estimating number of gene pairs, unless the nature and effects of all the interactions are known and formulas are developed and employed that take into account the effects of these interactions.

TABLE 26.—*Obtained and theoretical variances for period from seeding to first fruit ripe*

Population	Kind of variance	Variance		
		Theoretical, in days	Obtained	
			Days	In terms of theoretical
		Number	*Number*	*Percent*
Porter	Total	65.515	44.439	67.8
B_1 to Porter	do	103.835	85.196	82.0
F_1	do	81.253	66.119	81.4
F_2	Total	205.308	158.970	77.5
	Environmental	125.424	92.107	73.4
	Genetic	79.784	66.863	83.8
B_1 to Ponderosa	Total	363.048	237.116	65.2
	Environmental	255.947	172.077	67.2
	Genetic	108.001	65.039	60.2
Ponderosa	Total	777.130	380.756	49.0

The means and total variances of weight per locule, obtained from the original individual-plant data transformed to logarithms, are given in table 27. The mean of the logarithms for Porter is 1.018253 and that for Ponderosa is 0.954593; the respective variances are 0.005147 and 0.036949. Total variance is larger for the Ponderosa population than for the F_2 or the B_1 to Ponderosa population. Also, the total variance for the B_1 to Ponderosa population is larger than that for the F_2, which constitutes rather convincing evidence that the high variability of the Ponderosa population was inherited. Clearly, there is no readily detectable consistent relation between the means and variances such as was noted for all the other characters. From these results it is evident that the genetic variances for weight per locule cannot be estimated by use of the procedures and formulas employed previously. It follows that the genetic variances for weight per fruit cannot be estimated.

TABLE 27.—*Means and total variances of weight per locule, obtained from original individual-plant data transformed to logarithms*

Population	Mean	Total variance
Porter	1.018253	0.005147
B_1 to Porter	1.070936	.020171
F_1	1.168729	.014822
F_2	1.128481	.025018
B_1 to Ponderosa	1.124941	.029745
Ponderosa	.954593	.036949

DISCUSSION

Matters calling for discussion include the genetic and statistical design of the experiment and the procedures and methods developed and employed in analyzing and interpreting the data, the number of major gene pairs differentiating the parents as regards the characters studied, the comparative effects of these gene pairs, and the interactions involving the genes and the environment.

Design of Experiment, and Procedures and Methods Used in Analyzing Data

The genetic design of the experiment involved determining the populations to be grown and the component characters to be studied (*14*, *17*). The three nonsegregating populations, the P_1, F_1, and P_2, were essential to the genetic design because all were needed in evaluating phenotypic and genic dominance, in estimating penetrances, in estimating environmental variances and hence genetic variances, and in detecting the interactions involving genotypes and the environment and determining their nature. All three segregating populations, the B_1 to P_1, F_2, and B_1 to P_2, were essential in determining the entire genetic hypothesis. In other words, the data for these six populations were necessary to development of the formulas and methods of procedure used in analyzing and interpreting the data in this bulletin. Dividing the dependent characters into their respective component characters was of equal importance to the genetic design of the experiment. Neither the number of major gene pairs differentiating period from seeding to first fruit ripe nor the nature of the interactions of these genes could have been determined without study of the components of this character.

The statistical design of the experiment was a randomized complete block (*6*, *8*, *21*) adapted to use in genetic studies (*12*, *13*, *15*). The variances, correlation coefficients, and regression coefficients were calculated from the data within blocks and within replications. That the 10 blocks of plots used were sufficient to provide adequate randomization is shown by the consistency of the results obtained. Since each block included two 24-plant plots of each of the segregating populations and one of each of the nonsegregating populations, sufficient plants of all generations were grown to make the conclusions drawn from the study reliable. The portion of the genetic variances confounded with variances attributable to differences between means of blocks (*15*) amounts to less than 3 percent. Hence, the randomized complete block was well adapted to the genetic investigations made.

In determining the magnitude of the character differences and in testing significance, the only deviation from standard procedure (*21*) was calculating within the respective populations the standard errors for testing the significance of differences (*12*, *13*). This was necessary because variances were not homogeneous.

In studying the phenomenon of dominance the means, the variances, and a comparison of the phenotypes of the different genotypes were used. Phenotypic dominance was determined by comparing

the means of the two parents and the mean of the F_1. Genic dominance was determined from a study of the means, variances, and phenotypes of the different genotypes. Of the three, a comparison between phenotypes of the different genotypes provides the most information and hence is the most reliable. The information obtained from a comparative study of the phenotypes and genotypes needed supplementing because of the rather broad grouping of the original data into condensed frequency distributions. Such broad grouping is likely to obscure some of the smaller differences, and as a result what appears as complete dominance may in reality be only partial genic dominance. Conclusions drawn from any such study can and should be checked by a study of the original data, the means of the different populations, and the variances. If this is done, the data can be interpreted correctly as to genic dominance.

For determining the number of gene pairs differentiating the two parents, it was found necessary to study the original individual-plant data, the condensed frequency distributions, and the means, and to calculate the F_2 mean from the genotypes and phenotypes of the two backcross generations. Study of the detailed and the condensed frequency distributions held the most promise.

The partitioning method was developed for making genetic analyses of the data. This method was applied, and is illustrated in this bulletin, for both detailed and condensed frequency distributions. With respect to percentage of flowers that set fruit, the theoretical frequency distributions were based on the parental and F_1 data and the means of the two backcross populations; with respect to number of locules, the frequency distributions of the two backcrosses and the data from the parents and F_1 were used to calculate the theoretical frequency distribution of the F_2. The validity of the hypotheses was determined by χ^2 for testing goodness of fit between the theoretical and obtained frequency distributions. In the application of this method to *percentage of flowers that set fruit*, theoretical frequency distributions were calculated for all three segregating generations. In the *number-of-locules* application, if the genetic hypothesis had not been substantiated by the χ^2 test for goodness of fit between the theoretical and obtained frequency distributions of the F_2, the obtained frequency distributions of the F_2 could have been used together with those of the backcrosses, parents, and F_1 to calculate theoretical frequency distributions for all three segregating generations. In that case the validity of the hypothesis would have been determined by testing goodness of fit between the theoretical and obtained frequency distributions of the segregating generations. Detailed frequency distributions afford a sounder basis for genetic analyses than condensed frequency distributions. However, both kinds have a place in genetic analyses.

In condensing the frequency distributions, maximum differentiation of the six populations was sought. One procedure that aided in attaining this objective was to make the groupings such (when possible) that for each of the nonsegregating populations all plants fell into classes containing no plants of any other such population. Whenever this cannot be done, the condensing should be such that a minimum of overlapping occurs. Once a particular grouping is

decided upon, of course, it must be applied uniformly to all six of the populations. The purpose of grouping is to discern major differences that are obscured by minor variations in the detailed frequency distributions and to provide a method of analysis for those cases in which the detailed theoretical frequency distributions cannot be determined for genotypes that have different but somewhat similar frequency distributions. Inevitably, the grouping obscures much of the variation attributable to minor causes. In analyzing and interpreting condensed frequency distributions, these facts must be kept in mind and the detailed frequency distributions must be studied also. All constants (means, variances, coefficients, etc.) should be calculated from the individual-plant data.

It should be noted that the means of the different populations provide the most information as to the number of gene pairs differentiating the parents when phenotypic and genic dominance and epistasis are complete—that is, when one dominant gene produces as great, or almost as great, an effect as all the dominant genes together. Such was the case in respect to the genes differentiating the parents as regards period from seeding to first bloom.

Comparisons were made involving the phenotypes and respective genotypes of the different populations; variances, correlation and regression coefficients, and relative percentages of the variance accounted for by regression were calculated; and the frequency of occurrence of individuals in the more desirable class as regards two characters was determined. Details of the methods used in this determination appeared in an earlier publication (*18*). These statistical constants and methods of analysis were applied to a study of the populations and of the dependent and component characters. Again, the comparisons involving the phenotypes and genotypes of the respective populations provided the most information. However, the constants calculated and other methods of procedure contributed much to the analysis and aided materially in the final interpretation of the data. Here it should be pointed out that relative percentages of the variance of the dependent character accounted for by regression sometimes are negative in sign.

The methods and procedures outlined do not provide for a progeny test. For progeny tests of selections made at random or otherwise, the methods and procedures involving penetrances were developed and illustrated by the senior author previously (*11*). Progenies obtained by self-fertilizing plants of the segregating populations should be included. Progenies obtained by self-fertilizing plants of the F_2 and the two backcross generations could be grown either in an inclusive study with all the generations used in this study or in an experiment the following year with the P_1, F_1, and P_2 generations. In either event the partitioning method of genetic analysis should be used.

Thus far in this bulletin, gene pairs have been designated by symbols that differentiate the genes within characters but not between characters. This procedure simplified the analyses; but it is inappropriate for general use, owing to the confusion that might result. Therefore, different symbols are now assigned to those genes found to have differentiated the parents. The new symbols, in which the subnumerals

1, 2, 3, and 4 stand for *A*, *B*, *C*, and *D*, respectively, of the former designations, follow:

Character:	Gene symbols
Percentage of flowers that set fruit	$F_1f_1F_2f_2F_3f_3F_4f_4$.
Period from seeding to first bloom	$B_1b_1B_2b_2B_3b_3$.
Period from first bloom to first fruit set	$S_1s_1S_2s_2S_3s_3$.
Period from first fruit set to first fruit ripe	$R_1r_1R_2r_2$.
Number of locules	$Lc_1lc_1Lc_2lc_2Lc_3lc_3$.
Weight per locule	$W_1w_1W_2w_2W_3w_3$.

Number of Major Gene Pairs Differentiating Characters

Period from seeding to first fruit ripe is differentiated by eight major gene pairs. It seems highly probable that linkage instead of pleiotropy produced the relations noted between the four series of genes *Ff*, *Ss*, *Rr*, and *Lclc* with the exception of the *Ff* and *Ss* relation, because all the associations noted are those expected on the basis of linkage. If pleiotropy were involved, such relations would be coincidental, which for all these gene series is highly improbable. However, as pointed out before, some of the genes of the *Ff* and *Ss* series must be identical, as percentage of flowers that set fruit has an effect on period from first bloom to first fruit set. The *Lclc* and *Ww* series of genes, differentiating number of locules and weight per locule, respectively, were independent as regards linkage and pleiotropy. Thus, since all 6 of the characters affect yield of ripe fruit per plant, at least 15 major gene pairs played a part in the differentiation of this character. That only 15 and not 18 have been definitely identified is attributed to the fact that the *Ff* and *Ss* series have some gene pairs in common.

Interactions

The information on dominance for the dependent and independent characters is summarized in table 28. All the eight characters listed in the table affect yield of ripe fruit per plant; therefore, any of the genes listed in the table were instrumental in differentiating yield of ripe fruit per plant. With these facts in mind, it is interesting to consider the dominance relations. For percentage of flowers that set fruit phenotypic and genic dominance were intermediate. Both phenotypic and genic dominance were complete for period from seeding to first fruit ripe and its component characters. Both were partial for fewer locules per fruit. Weight per locule showed heterosis, and

Table 28.—*Summary of information on dominance for dependent and independent characters*

Character	F_1 genotype	Dominance	
		Phenotypic	Genic
Percentage of flowers that set fruit	$F_1f_1F_2f_2F_3f_3F_4f_4$	Intermediate	Intermediate.
Period from seeding to first fruit ripe		Complete	Complete.
Seeding to first bloom	$B_1b_1B_2b_2B_3b_3$	do	Do.
First bloom to first fruit set	$S_1s_1S_2s_2S_3s_3$	do	Do.
First fruit set to first fruit ripe	$R_1r_1R_2r_2$	do	Do.
Weight per fruit		Partial	Intermediate or partial.
Number of locules	$Lc_1lc_1Lc_2lc_2Lc_3lc_3$	do	Partial.
Weight per locule	$W_1w_1W_2w_2W_3w_3$	Heterosis	Intermediate or partial.

genic dominance for this character was intermediate or partial. The genes *Lelc* and *Ww* combined to produce partial phenotypic dominance for weight per fruit; hence the genes differentiating weight per fruit showed partial dominance and probably in some instances intermediate dominance. Then the component characters of yield of ripe fruit per plant showed the following degrees of phenotypic dominance: Complete dominance of the lesser contrasted character, partial dominance of the lesser contrasted character, intermediate dominance, partial dominance of the greater contrasted character, and heterosis of the greater contrasted character. The different genes affecting yield of ripe fruit per plant showed the following degrees of genic dominance: Complete dominance of the genes tending to produce the smaller values, partial dominance of the genes tending to produce the smaller values, intermediate dominance, and, perhaps, partial dominance of the genes tending to produce the larger values. Clearly, there was a wide range in the expression of both phenotypic and genic dominance as regards yield of ripe fruit per plant.

The terminology used and the concept of the phenomenon of dominance expressed in this bulletin were set forth in an earlier publication by the senior author (*10*), and the literature dealing with heterosis was reviewed by Whaley (*23*). That genic dominance is dependent upon the genotypic milieu was pointed out by Fisher (*4*) and many others (*1*). This would indicate that the interallelic and intraallelic interactions are not separable, strictly speaking. The data presented offer some evidence in support of this contention.

The interrelations of the characters as regards linkage, pleiotropy, and environment are summarized in table 29. Linkages are shown for some of the genes differentiating percentage of flowers that set fruit, period from first bloom to first fruit set, period from first fruit set to first fruit ripe, and number of locules per fruit. The association between percentage of flowers that set fruit and period from first bloom to first fruit set is that expected on the basis of pleiotropy. However, there is some question whether this should be considered

TABLE 29.—*Summary of interrelations of characters as regards linkage, pleiotropy, and environment*

Character[1]	Interrelations[2]														
	Linkage					Pleiotropy					Environment				
	Bb	*Ss*	*Rr*	*Lelc*	*Ww*	*Bb*	*Ss*	*Rr*	*Lelc*	*Ww*	*Bb*	*Ss*	*Rr*	*Lelc*	*Ww*
Percentage of flowers that set fruit (*Ff*)	0	?	0	—	0	0	?	0	0	0	0	0	+	0	0
Period from seedling to first bloom (*Bb*)		0	0	0	0		0	0	0	0		0	—	0	0
Period from first bloom to first fruit set (*Ss*)			+	—	0			0	0	0			—	0	0
Period from first fruit set to first fruit ripe (*Rr*)				0	0				0	0				+	+
Number of locules (*Lelc*)					0					0					—
Weight per locule (*Ww*)															

[1] Desirable characters: Higher percentage of flowers that set fruit, fewer days from seedling to first bloom, fewer days from first bloom to first fruit set, fewer days from first fruit set to first fruit ripe, higher number of locules, and greater weight per locule.

[2] 0, No association of the characters; ?, association indicated but not well-established; +, association of the 2 desirable characters; —, association of an undesirable and a desirable character.

an actual case of pleiotropy. The environmental effects were such that a decrease in period from first fruit set to first fruit ripe tended to be accompanied by an increase in each of the other maturity characters. Also, decrease in number of locules tended to be accompanied by increase in weight per locule.

Next linkage, pleiotropy, and the environmental relations noted are considered in regard to the interactions. Linkage is a mechanical interaction, as the relations and associations obtained are due to the fact that the genes involved are located in the same chromosome. Pleiotropy is an interaction dependent upon physiological genetic reactions, in that the genes are responsible for the production of substances that influence the development of more than one character. Environmental interactions involve the genes as well as the environment. For example, take interactions between percentage of flowers that set fruit (*Ff*) and period from first fruit set to first fruit ripe (*Rr*). As measured by the end products, this is a second-order interaction, *Ff* gene series × *Rr* gene series × environment. It follows that from the standpoint of quantitative inheritance the interactions are a statistical-genetic concept. Interactions obtained by partitioning χ^2 into its components were used by Fisher (*3*) and by Powers and Hines (*19*) to test for linkage, and statistics were used by Powers (*18*) to determine the nature of the interactions of genes carried in different regions of the chromosomes that affected number of locules and size of fruit.

Any of the interactions of genes noted as affecting any of the component characters dealt with in this study were interactions of genes differentiating yield of ripe fruit per plant. With this fact in mind, it is interesting to note the interactions of the genes differentiating the component characters. The intraallelic and interallelic interactions of the *Ff* gene series were such that genic dominance was intermediate. The intraallelic and interallelic interactions of the *Bb* series of genes were such that one of the six dominant genes shortened the period from seeding to first bloom as much as all six, which shows that both dominance and epistasis were complete. For the *Ss* series and *Rr* series of genes, genic dominance was complete. Also, the effects of the gene pairs were cumulative. Genic dominance was partial for the genes (Lc_1Lc_2) tending to produce fewer locules per fruit and for the gene (Lc_3) tending to produce more locules per fruit. The interallelic interactions of these genes were such that the effects of the gene pairs were cumulative. Finally, for the *Ww* series of genes genic dominance was at least close to intermediate but was probably partial, and the effects of the gene pairs were cumulative.

Next the interallelic interactions of the genes as demonstrated by the interrelations of the component characters are considered. The effects of the *Bb* series of genes, the *Ss* series, and the *Rr* series, respectively, were found to be cumulative. On an average the *S* genes would be expected to shorten the period from first bloom to first fruit set less in the presence of the *R* genes than in the presence of the *r* genes, if the physiological reactions affecting these two component characters that were instigated by the environment were the same as those instigated by the *Ss* and *Rr* gene series. That such was the case seems probable from the results of Goldschmidt's work (*7*) with phenocopies. In fact it seems almost axiomatic that this was the

case, because the second-order interaction (*Ss* gene series × *Rr* gene series × environment) was such that, on an average, when the *Ss* series responded to a given environment by shortening the period from first bloom to first fruit set the *Rr* series in the same plant tended to produce a longer period from first fruit set to first fruit ripe. Then the effects of these two series of genes were less than additive as regards the dependent character period from seeding to first fruit ripe. About the same situation existed in respect to the *Lclc* series and the *Ww* series of genes, in that greater number of locules, on an average, was accompanied by less weight per locule. Since number of locules times weight per locule gives weight per fruit, the effects from such a second-order interaction are multiplicative as regards the dependent character.

From this discussion of the interactions of the genes, it is clear that the nature of these interactions varied according to which genes were involved. This is equally true of the interactions between the genes and the environment. Study of interactions of genes and of genes and environment occurring in respect to differentiation of yield of ripe fruit per plant revealed that the effects of the genes and environment were less than additive, additive, or somewhat less than multiplicative. In all studies involving such interactions, it should be kept in mind that in all probability the interactions are between substances and between characters produced by the genes and the environments.

SUMMARY

In crosses between the Porter and Ponderosa varieties of tomato (*Lycopersicon esculentum* Mill.), each of the following characters was found to be differentiated by three major gene pairs: Period from seeding to first bloom, period from first bloom to first fruit set, number of locules per fruit, and weight per locule. Percentage of flowers that set fruit was differentiated by four major gene pairs; period from first fruit set to first fruit ripe, by two; period from seeding to first fruit ripe, by eight; and weight per fruit, by six. Altogether, major gene pairs definitely identified as affecting yield of ripe fruit per plant numbered 15.

For percentage of flowers that set fruit both phenotypic and genic dominance were intermediate.

For the period from seeding to first bloom, both phenotypic and genic dominance were complete. With such intraallelic and interallelic interactions, the effects of the genes for this character were not cumulative.

Both phenotypic and genic dominance were complete for period from first bloom to first fruit set and for period from first fruit set to first fruit ripe. However, epistasis was not complete for the genes differentiating either of these characters; consequently the interallelic interactions of these genes were such that the effects of the gene pairs were algebraically cumulative, whereas the intraallelic interactions were such that the effects of the genes within any given pair of alleles were not cumulative.

Both phenotypic and genic dominance were partial for the genes differentiating number of locules per fruit. The intraallelic and interallelic interactions of these genes were such that the effects of the

genes were algebraically cumulative within and between pairs of alleles. Genic dominance was partial for the genes (Lc_1Lc_2) tending to produce fewer locules per fruit and for the gene (Lc_3) tending to produce more locules per fruit.

The contrasted character greater weight per locule showed heterosis. The data are not discriminatory as to whether genic dominance was intermediate or whether the genes tending to produce greater weight per locule exhibited a small degree of partial dominance. The intra-allelic and interallelic interactions of the genes were such that the effects of the genes were algebraically cumulative. The data show conclusively that dominance and heterosis depend upon the same physiological-genetic phenomena.

The nature of the interactions between the genes differentiating the component characters of weight per fruit was studied. All these genes played a part in differentiating the yield of ripe fruit per plant. The nature of the interactions varied according to the particular genes involved. This is equally true of the interactions between these genes and the environment. Study of interactions of genes and of genes and environment in respect to differentiation of yield of ripe fruit per plant revealed that the effects of the interactions varied, being less than additive, additive, or somewhat less than multiplicative according to the component characters and the genes differentiating them. Not all the genes had equal effects, either within or between component characters.

The genetic variances as estimated included the interactions. In all cases, the genetic variances for period from seeding to first fruit ripe were less than would be expected on the basis of the assumption that the interactions between genes and between genes and environment were such that the variances of the component characters were additive.

The term "relative percentage" is applied to the relative proportionate part of the variance of a dependent character accounted for by the variance of any given individual component character.

Research procedures and methods, including genetic and statistical experimental design, are developed and illustrated that should materially facilitate physiological-genetic and developmental-genetic studies. The method of genetic analysis developed has been termed the "partitioning method."

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