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Inheritance of Certain Economic Characters in the Squash, *Cucurbita maxima* Duch.

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Dharampal Singh[2]

INTRODUCTION

A VARIETY of squash *(Cucurbita maxima)* which possesses bush growth habit is being used in the breeding program of the Minnesota Agricultural Experiment Station at University Farm, St. Paul, Minnesota. This bush variety was found to be earlier than the commercial varieties grown in Minnesota. However, the fruits of this variety are very small and of extremely poor quality. Greengold, on the other hand, is a variety commonly grown in Minnesota and possesses high quality, desirable size fruit, vining habit of growth, and is somewhat later maturing that the bush variety of *Cucurbita maxima.*

Little has been published concerning the manner of inheritance of the economic characters of *Cucurbita maxima.* To facilitate the breeding program it was decided to study the genetics of some of the more important economic characters from crosses of the above two varieties. The results of certain of these studies are reported in this paper.

MATERIALS AND METHODS

The hybrid populations were produced from a cross between Greengold (P_1) and a *Cucurbita maxima* variety which is bush in habit and which is designated in this paper as Bush maxima (P_2). Greengold had been inbred for ten generations and Bush maxima for five. The genetic design of the experiment included P_1, P_2, F_1, B_1 to P_1, B_1 to P_2 and F_2 populations. The statistical design of the experiment was a randomized complete block with ten blocks. Each plot contained 24 plants and one plot was grown per block of the P_1, F_1, and P_2 populations. Two plots were grown per block of the B_1 to P_1, B_1 to P_2 and F_2 populations. The nine

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[2] The writer wishes to express his gratitude to Dr. A. E. Hutchins, Division of Horticulture, University of Minnesota, for suggesting this problem, for making the necessary material available, and for many helpful criticisms and suggestions, and to Dr. LeRoy Powers, Senior Geneticist, United States Department of Agriculture Research Administration, Bureau of Plant Industry, Soils and Agricultural Engineering, Cheyenne Horticultural Field Station, Cheyenne, Wyoming, for his continued guidance in the analysis of the data and in the preparation of this manuscript.

items were randomized within each block. The seeds were first sown in the greenhouse in pots and then transplanted in the field.

The inheritance of the following characters was studied:

1. Growth habit of the plant (vining *vs.* bush).
2. Number of days from seeding to the opening of the first male flower.
3. Number of days from seeding to the opening of the first female flower.
4. Difference in number of days between the opening of the first male and first female flower.
5. Color of the fruit (green *vs.* orange).
6. Weight of the fruit.
7. Cupping character caused by incomplete enclosure of the ovarian tissue.
8. Total solids.

The data on the growth habit of the plant were taken at two intervals during the growth period. The first observation was made on July 8, 1948, before flowering began, and the second observation was made on July 24, 1948, when all the plants were in full bloom.

Only one representative fruit from each vine was picked and the weight of the fruit was taken in grams. For measuring total solids, the Zeiss hand sugar refractometer was used. The degree of exposure of the ovarian tissue (cupping) was measured in centimeters with a vernier caliper.

The means and standard deviations have been calculated to study the phenotypic dominance (Powers, *13;* Powers, Locke, and Garett, *14)*. The genetic and environmental variances have been estimated according to the methods developed by Powers *(12)* to study genic dominance (Fischer, *6;* Dobzhansky, *3;* Powers, *12* and Powers, Locke, and Garett, *14)*. The methods developed by Powers, Locke, and Garett *(14)* were used to determine the number of gene pairs by which the parents are differentiated. The methods will be illustrated in connection with the analysis and the interpretation of the data in the discussion of the results obtained.

Tests of significance have been made and in interpreting the data, odds as great or greater than 19:1 have been accepted as statistically significant.

EXPERIMENTAL RESULTS

Growth Habit

The plants were grouped according to growth habit into the following classes:

The "Bush (P_2)" plants do not have any tendency to vine and the fruits are borne on a short, thick stalk. The plants have leaves with long, thick, erect petioles.

The "Bush Minus" plants are similar to the Bush plants but have a slight tendency to vine. The length of the vine may be about one foot.

The plants falling in the "Bush Tending to Vine" class are similar to the Bush or Bush Minus plants except that they have a distinct tendency to vine. The length of the vine is approximately four feet.

The "Bush Vining" plants have vines nearly as long as the vining plants. The stem, however, is thicker than that of the vining plants and the early bushy nature of the plants is evident in a larger number of leaves with thick, erect petioles at the base of the plant. These plants begin to vine about 10 days later than the vining plants.

The "Vining (P_1)" plants are vining throughout their whole growth period except for about a week after transplanting. The stem and the leaf petioles are smaller in diameter than those of any of the other groups described. The vine habit is the common type of growth habit found in all the commercial varieties.

Table 1. Frequency Distribution (expressed in percentage) for Growth Habit. Data Collected on July 8, 1948

Population	Classes					Number of individuals
	Bush	Bush minus	Bush tending to vine	Bush vining	Vining	
	per cent	*per cent*	*per cent*	*per cent*	*per cent*	
Greengold (P_1)	....	....	....	....	100.00	230
B_1 to Greengold	....	28.27	33.40	10.28	28.05	467
F_1	....	100.00	....	....	....	210
F_2	22.08	47.77	18.68	4.25	7.22	471
B_1 to Bush maxima	48.17	46.45	5.38	....	....	465
Bush maxima (P_2)	100.00	....	....	....	....	210

The observations made on July 8, 1948, (table 1) indicated that all the individuals in the F_1 population were in the Bush Minus class. A later observation made on July 24, 1948, (table 2) shows that all the F_1 individuals were in the Bush Vining class. This indicates that the type of growth habit in the heterozygous individuals is governed to some extent by the stage of growth.

NUMBER OF GENE PAIRS DIFFERENTIATING THE PARENTS

On the basis of the segregating generations, the assumption is made that the two parents are differentiated by two gene pairs. The genotypes of P_1 are symbolized as *aabb* and of P_2 as *AABB*. However, the assignment of the capital and small letters is arbitrary; there is no dominance.

According to this assumption, 25.0 per cent of the individuals *(aabb)* in the B_1 to P_1 population should be vining at any stage of development. There are 28.05 per cent of the individuals in the Vining class (table 1). This gives a good fit to the theoretical expectation, as χ^2 is 2.318 and P. lies between 0.20 and 0.10.

Twenty-five per cent of the individuals *(AaBb)* should behave like the F_1. There are 28.27 per cent of the individuals of the B_1 to P_1 population in the Bush Minus class. One hundred per cent of the F_1 individuals lie in this class. This gives an acceptable fit between the obtained and the theoretical, since χ^2 is 2.654 and P. lies between 0.10 and 0.05.

The rest of the individuals should be in the Bush Tending to Vine and Bush Vining classes and should, theoretically, make up 50.0 per cent of the population.

It will be noted that the individuals with the *AaBb* genotype fall in the Bush Minus class on July 8 (table 1), while the individuals with *Aabb* and *aaBb* genotypes, where there are three factors for vining and one for bush, have definitely begun vining.

In the B_1 to P_2 population, all but 5.38

Table 2. Frequency Distribution (expressed in percentage) for Growth Habit Data Collected on July 24, 1948

Population	Classes					Number of individuals
	Bush	Bush tending to vine	Bush vining	Vining bush	Vining	
	per cent	*per cent*	*per cent*	*per cent*	*per cent*	
Greengold (P_1)	....	....	....	....	100.00	230
B_1 to Greengold	....	....	29.98	16.70	53.32	467
F_1	....	....	100.00	....	....	210
F_2	7.66	26.60	44.89	13.62	7.23	470
B_1 to Bush maxima	31.18	40.86	27.96	....	....	465
Bush maxima (P_2)	100.00	....	....	....	....	210

per cent of the individuals fall in the Bush or Bush Minus class. This further indicates that all those genotypes which have two or more than two factors for bush are phenotypically bush or nearly so during early growth. In the B_1 to P_2 population, 25.0 per cent of the individuals should behave like the F_1. Actually there are 51.83 per cent (46.45 + 5.38) of the individuals in the Bush Minus and Bush Tending to Vine class. This could have been due to difficulty in distinguishing the Bush and Bush Minus classes, as there is very little difference between the two. It might also have been due to the fact that one of these two genotypes, *AaBB* or *AABb*, probably has the same phenotype as the F_1.

In the F_2 population, 6.25 per cent of the individuals *(aabb)* should be vining at any stage of the development and 7.22 per cent are in the Vining class. This gives a good fit to the theoretical expectation, as the χ^2 value is 0.754 and the P. value lies between 0.50 and 0.30. The F_2 individuals of the *AABB, AaBB, AABb,* and *AaBb* genotypes should be phenotypically Bush or Bush Minus. In addition, if the two genes have the same effect, the individuals with *AAbb* and *aaBB* genotypes should be phenotypically the same as the above genotypes. Thus 68.75 per cent of the individuals of the F_2 class should be in the Bush and Bush Minus classes. There are 69.85 per cent of the individuals in these two classes. The data give a good fit to the theoretical expectations; χ^2 is 0.266 and the P. value lies between 0.70 and 0.50. The remaining two genotypes *(Aabb* and *aaBb)* have to be in the Bush Tending to Vine and Bush Vining classes.

The above analysis supports the hypothesis that the growth habit is differentiated by two gene pairs.

This hypothesis is further substantiated by the analysis of the data collected on July 24, 1948, (table 2). In the B_1 to P_1 population, 25.0 per cent of the individuals should be in the Bush Vining class as are all the F_1 individuals. There are 29.98 per cent of the individuals in the Bush Vining class. This gives a χ^2 value of 6.170, and the P. value lies between 0.05 and 0.01. Though the fit is unsatisfactory, the discrepancy could have been due to the difficulty in classification.

The individuals with *Aabb* and *aaBb* genotypes which were presumably in the Bush Tending to Vine and Bush Vining classes on July 8, 1948, were in the Vining Bush and Vining classes on July 24, 1948.

In the B_1 to P_2 population, there are 27.96 per cent of the individuals in the Bush Vining class where all F_1 individuals fall. This gives a good fit to the 25.0 per cent expected (χ^2 is 2.168 and the P. value lies between 0.20 and 0.10).

In the F_2 population all heterozygous individuals should be vining or should have a tendency to vine, depending upon the number of factors for the bush and vining characters. Those individuals which are bush on July 24 should be expected to be homozygous for bush habit. Theoretically, 6.25 per cent of the individuals should be in the Bush class. Actually there are 7.66 per cent of the individuals in this class. The observed and the expected values give a good fit (χ^2 is 1.593 and the P. value lies between 0.30 and 0.20). Similarly there are 7.23 per cent of the individuals in the Vining class, and this gives a good fit as the χ^2 value is 0.776 and the P. value lies between 0.50 and 0.30.

The *AaBb, AAbb,* and *aaBB* genotypes should be phenotypically like the F_1, and the *Aabb* and *aaBb* genotypes should lie between the F_1 *(AaBb)* and the Greengold (P_1) parent. However, by July 24 it had become increasingly difficult to separate the *AaBb, AAbb,* and *aaBB* genotypic individuals from the *aaBb* and *Aabb* genotypic individuals.

These five genotypes should theoretically constitute 62.5 per cent of the F_2 population. Actually there are 58.51 per cent (44.89 + 13.62) of the individuals in the Bush Vining and the Vining Bush class. The theoretical and the expected are in close agreement with each other; the χ^2 value is 3.190 and P. lies between 0.10 and 0.05. The remaining genotypes *AABb* and *AaBB* should lie between the F_1 and P_2 parent; i.e., in the Bush Minus class.

These analyses of the preceding data support the hypothesis that the two parents are differentiated by two gene pairs.

Number of Days From Seeding to the Opening of the First Male Flower

The mean values for number of days from seeding to the opening of the first male flower (table 3) show that Greengold (P_1) has a mean of 46.10 days and Bush maxima (P^2) of 43.83. The magnitude of the difference between the two parents is 2.27 days.

DOMINANCE

The mean of Bush maxima is very close to the mean of B_1 to P_2. The mean of the F_1 is lower than the mean of Bush maxima, but the difference is barely significant. This indicates almost complete phenotypic dominance of fewer days over more days. The genetic variance of B_1 to P_2 is not significant (table 3). This indicates that probably the genetic dominance is also complete.

The frequency distribution of B_1 to P_2 and Bush maxima are very similar. Likewise the χ^2 test shows that the frequency distribution of the F_1 is not significantly different from the B_1 to P_2 and P_2 distributions, since the χ^2 value is 5.124 and the P. value lies between 0.30 and 0.20 (table 4). These data indicate almost complete phenotypic and genic dominance of the shorter period from seeding to the opening of the first male flower.

Table 4. Frequency Distribution (expressed in percentage) for the Number of Days From Seeding to the Opening of the First Male Flower

Population	Classes		
	41-43	44-45	46-48
	per cent	*per cent*	*per cent*
Greengold (P_1)	....	41.60	58.40
B_1 to Greengold (P_1)	8.00	49.61	42.39
F_1	56.89	39.91	3.20
F_2	31.48	45.04	23.48
B_1 to Bush maxima (P_2)	50.52	43.84	5.64
Bush maxima (P_2)	49.52	46.66	3.82

NUMBER OF GENE PAIRS DIFFERENTIATING THE PARENTS

The assumption is made that the two parents are differentiated by three gene pairs. The indication that three factor pairs are involved is obtained by dividing 8.00 (B_1 to P_1) by 56.89 (F_1) which gave a percentage value of 14.06 (table 4). On a three-factor-pair basis, 12.50 per cent is expected. The genotypes of

Table 3. The Means, Standard Deviations, Variances, and Number of Individuals in Each Population for the Number of Days from Seeding to the Opening of the First Male Flower

Population	Mean	Standard deviations	Total variance	Environmental variance	Genetical variance	Number of individuals
Greengold (P_1)	46.10	0.107	138.73	124.35	14.38	230
B_1 to Greengold (P_1)	45.01	0.196	575.81	93.30	482.51	438
F_1	43.37	0.087	41.56	46.58	−5.02	225
F_2	44.50	0.201	743.82	78.77	665.05	462
B_1 to Bush maxima (P_2)	43.52	0.089	57.63	50.85	6.78	432
Bush maxima (P_2)	43.63	0.087	44.63	53.98	−9.35	225

P_1 are symbolized as *aabbcc* and of P_2 as *AABBCC.*

The B_1 to P_1 and B_1 to P_2 frequency distributions are partitioned into their component genotypes (table 5). Row number 1 gives the frequency distribution of B_1 to P_1 population. In the B_1 to P_1 population, the F_1 *(AaBbCc)* and P_1 *(aabbcc)* constitute 25.0 per cent of the population. The penetrance of the F_1 and P_1 for each class is multiplied by its theoretical per cent, divided by 100, and then summed. Thus row 2 gives the frequency distribution of $F_1 + P_1$ genotypes. The difference between row 1 and row 2 gives the frequency distribution of the remaining six genotypes of the B_1 to P_1 population and the frequency distribution is tabulated in row 3. Then this frequency distribution is weighted on 100.0 per cent basis and is given in row 4. Similarly, the B_1 to P_2 population is partitioned into its component genotypes. (For this method of analyzing the frequency distribution see Powers, Locke, and Garett, *14).*

On the basis of the frequency distributions of the different genotypes of the B_1 population, a theoretical frequency distribution for the F_2 genotype is obtained (table 6). The distribution for the *AABBCC, aabbcc,* and *AaBbCc* genotypes is that of the P_2, P_1, and F_1 respectively. The distribution of the following genotypes is obtained from the indicated backcross populations and is given in table 5, rows 4 and 10, respectively.

From B_1 to P_2	*From B_1 to P_1*
AABBCc	AabbCc
AABbCC	AaBbcc
AaBBCC	Aabbcc
AABbCc	aaBbCc
AaBbCC	aabbCc
AaBBCc	aaBbcc

The following genotypes of the F_2 do not occur in either of the B_1 populations:

I.	*II.*
AaBBcc	aabbCC
AAbbCC	aaBBcc
AAbbCc	AAbbcc
AabbCC	
AABBcc	
AaBbcc	
aABBCC	
aaBbCC	
aaBBCc	

As already mentioned, there is complete genic and phenotypic dominance. If all the genes have the same effect and the gene action is additive, then all the genotypes in group I should have the same frequency distribution. Similarly the genotypes of group II will be alike in their distribution. The frequency distribution of group I genotypes can

Table 5. Partitioning the B_1 to P_1 and B_1 to P_2 Frequency Distributions into Their Component Genotypes for the Number of Days from Seeding to the Opening of the First Male Flower

Population and genotype	Row no.	Classes 41-43	44-45	46-48	Theoretical percentage
		per cent	*per cent*	*per cent*	
B_1 to P_1	1.	8.00	49.61	42.39	100.00
F_1 + P_1 (AaBbCc+aabbcc)	2.	7.11	10.19	7.70	25.00
Row 1—Row 2	3.	0.89	39.42	34.69	75.00
Row 3 (100 per cent basis)	4.	1.19	52.56	46.25	100.00
F_1 (AaBbCc)	5.	56.89	39.91	3.20	12.50
P_1 (aabbcc)	6.	....	41.60	58.40	12.50
B_1 to P_2	7.	50.52	43.84	5.64	100.00
F_1 + P_2 (AaBbCc+AABBCC)	8.	13.30	10.82	0.88	25.00
Row 7—Row 8	9.	37.22	33.02	4.76	75.00
Row 9 (100 per cent basis)	10.	49.63	44.03	6.34	100.00
F_1 (AaBbCc)	11.	56.89	39.91	3.20	12.50
P_2 (AABBCC)	12.	49.52	46.66	3.82	12.50

thus be roughly calculated by taking 66.67 per cent of the P_2 distribution and 33.33 per cent of the P_1 distribution. The frequency distribution of group II will thus lie between the frequency distributions of the group I and P_1 genotypes. Table 6 gives the theoretical frequency distributions calculated on the above assumptions.

From preceding distributions of the F_2 genotypes, the theoretical frequency distribution for F_2 population is obtained. The test for goodness of fit between theoretical and obtained numbers

Table 6. The F_2 Generation Frequency Distribution Partitioned into Its Component Genotypes on the Basis of Three-Factor-Pair Difference for the Number of Days from Seeding to the Opening of the First Male Flower

Population and genotype	Classes 41-43	44-45	46-48	Theoretical percentage
AABBCC	49.52	46.66	3.82	1.5625
AABBCc	49.63	44.03	6.34	28.1250
AABbCC				
AABbCc				
AaBBCc				
AaBbCC				
AaBBCC				
AaBbCc	56.89	39.91	3.20	12.5000
AabbCc	1.19	52.56	46.25	28.1250
AaBbcc				
Aabbcc				
aabbCc				
aaBbcc				
aaBbCc				
AaBBcc	33.02	44.97	22.01	23.4375
AAbbCC				
AAbbCc				
AABBcc				
AABbcc				
aaBBCC				
aaBBCc				
aaBbCC				
AabbCC				
aabbCC	16.51	43.29	40.20	4.6875
aaBBcc				
AAbbcc				
aabbcc	....	41.60	58.40	1.5625
F_2 population	30.69	46.10	23.21	....

Table 7. Chi-square for Testing Goodness of Fit Between the Theoretical Frequency Distribution Based on the Assumption That the Parents Are Differentiated by Three Gene Pairs and the Obtained Frequency Distribution of the F_2 Population for Number of Days from Seeding to Opening of the First Male Flower

Population	Classes 41-43	44-45	46-48	Number of individuals
	per cent	*per cent*	*per cent*	
Theoretical	30.69	46.10	23.21	462
Obtained	31.58	45.04	23.38	462
	number	*number*	*number*	
Theoretical	142	213	107	462
Obtained	146	208	108	462

$\chi^2 = 0.119$
P. lies between 0.95 and 0.90

gives a χ^2 value of 0.119, and the P value lies between 0.95 and 0.90 (table 7). The fit between the theoretical and obtained numbers supports the hypothesis that the two parents are differentiated by three gene pairs.

Number of Days From Seeding to the Opening of the First Female Flower

From the mean values listed in table 8 it can be determined that the period from seeding to the opening of the first female flower is shorter by 7.08 days in the Bush maxima parent than it is in the Greengold parent.

DOMINANCE

As is shown in table 8, the means of Bush maxima, B_1 to Bush maxima, and F_1 are not significantly different from each other. This indicates complete phenotypic dominance of fewer days over more days. The fact that the genetic variance of B_1 to Bush maxima is not significant and is very small as compared with the genetic variances of F_2 and B_1 to Greengold, indicates that genic dominance is also complete. This is further substantiated by the fact that the frequency distribution of the F_1, B_1 to Bush maxima, and Bush maxima are very similar; the χ^2 value is 3.220 and the P value lies between 0.80 and 0.70 (D.F. 6).

NUMBER OF GENE PAIRS DIFFERENTIATING THE PARENTS

The hypothesis proposed is that the two parents are differentiated by three gene pairs. The indication that three factors are involved is obtained by dividing 8.45 (41-46 class of B_1 to P_1) by 56.38 (41-46 class of F_1), (table 9) which gave a value of 14.49, whereas on a three-factor basis 12.50 per cent is expected. The genotypes of P_1 are symbolized as *aabbcc* and of the P_2 as *AABBCC*.

The B_1 to P_1 and B_1 to P_2 frequency distributions are partitioned into their component genotypes (table 10). This partitioning will give the frequency

Table 8. The Means, Standard Deviations, Variances and Number of Individuals in Each Population for the Number of Days from Seeding to the Opening of the First Female Flower

Population	Mean	Standard deviations	Total variance	Environmental variance	Genetical variance	Number of individuals
Greengold	53.44	0.801	1,338.568	1,378.914	—40.346	229
B_1 to Greengold	51.51	0.909	3,299.464	1,276.219	2,023.245	438
F_1	46.38	0.726	980.596	966.005	14.591	225
F_2	49.00	1.263	6,638.000	1,142.668	5,495.332	462
B_1 to B. maxima	46.41	0.799	1,045.832	1,004.854	40.978	432
B. maxima	46.36	0.797	1,027.942	1,002.188	25.754	225

Table 9. Frequency Distribution (expressed in percentage) for the Number of Days from Seeding to the First Female Flower

Population	Classes				Number of individuals
	41-46	47-50	51-54	55-58	
	per cent	*per cent*	*per cent*	*per cent*	
Greengold (P_1)	....	....	79.04	20.96	229
B_1 to P_1	8.45	11.64	74.20	5.71	438
F_1	56.38	35.53	7.51	0.58	225
F_2	29.44	28.36	37.88	4.32	462
B_1 to P_2	55.92	35.27	7.66	1.15	432
Bush maxima (P_2)	56.84	35.79	7.37	....	225

distribution for the different genotypes in the B_1 to P_1 and B_1 to P_2 population. On the basis of the frequency distribution of the B_1 to P_1 and B_1 to P_2 populations, a theoretical frequency distribution for the F_2 genotypes is calculated (table 11). The distribution for the *AABBCC, aabbcc,* and *AaBbCc* genotypes is taken as that of the P_2, P_1 and F_1 populations, respectively. The distribution of the following genotypes is obtained by partitioning (table 10).

Table 10. Partitioning the B_1 to P_1 and B_1 to P_2 Frequency Distributions into Their Component Genotypes

Population and genotype	Row no.	Classes				Theoretical percentage
		41-46	47-50	51-54	55-58	
B_1 to P_1	1.	8.45	11.64	74.20	5.71	100.00
F_1 + P_1 (AaBbCc + aabbcc)	2.	7.05	4.44	10.82	2.69	25.00
Row 1—Row 2	3.	1.40	7.20	63.38	3.02	75.00
Row 3 (100 per cent basis)	4.	1.87	9.60	84.50	4.03	100.00
F_1 (AaBbCc)	5.	56.38	35.53	7.51	0.58	12.50
P_1 (aabbcc)	6.	....	....	79.04	20.96	12.50
B_1 to P_2	7.	55.92	35.27	7.66	1.15	100.00
F_1 + P_2 (AaBbCc + AABBCC)	8.	14.15	8.92	1.86	0.07	25.00
Row 7—Row 8	9.	41.77	26.35	5.80	1.08	75.00
Row 9 (100 per cent basis)	10.	55.69	35.14	7.73	1.44	100.00
F_1 (AaBbCc)	11.	56.38	35.53	7.51	0.58	12.50
P_2 (AABBCC)	12.	56.84	35.79	7.37	....	12.50

Table 11. The F_2 Generation Frequency Distribution Partitioned into its Component Genotype on the Basis of Three-Factor-Pair Difference for the Number of Days from Seeding to the First Female Flower

Population and genotype	Classes				Theoretical percentage	Mean
	41-46	47-50	51-54	55-58		
AABBCC	56.84	35.79	7.37	....	1.5625	46.36
AABBCc	55.69	35.14	7.73	1.44	28.1250	46.42
AABbCC						
AABbCc						
AaBbCC						
AaBBCc						
AaBBCC						
AaBbCc	56.38	35.53	7.51	0.58	12.5000	46.38
AabbCc	1.87	9.60	84.50	4.03	28.1250	52.04
AaBbcc						
Aabbcc						
aaBbCc						
aabbCc						
aaBbcc						
AaBBcc	37.89	23.86	31.26	6.99	23.4375	48.72
AAbbCC						
AAbbCc						
AABBcc						
AABbcc						
aaBBCC						
aaBBCc						
aaBbCC						
AabbCC						
aabbCC	18.94	11.93	55.15	13.98	4.6875	51.08
aaBBcc						
AAbbcc						
aabbcc	....	....	79.04	20.96	1.5625	53.44
F_2 population	33.89	23.74	38.14	4.23	....	....

AABBCc	AabbCc
AABbCC	AaBbcc
AABbCc	Aabbcc
AaBBCC	aaBbCc
AaBbCC	aabbCc
AaBBCc	aaBbcc

The following genotypes do not occur in either of the B_1 populations.

I.	*II.*
AaBBcc	aabbCC
AAbbCC	aaBBcc
AAbbCc	AAbbcc
AabbCC	
AABBcc	
AABbcc	
aaBBCC	
aaBbCC	
aaBBCc	

As already indicated, there is complete genic and phenotypic dominance. If all the genes have the same effect and the gene action is additive, then all the genotypes in group I should have the same frequency distribution. Similarly the genotypes of group II will be alike in their distribution. The frequency distribution for the genotypes of group I can be calculated roughly by taking 66.67 per cent of the P_2 distribution and 33.33 per cent of the P_1 distribution and then summing. Naturally the distribution for genotypes in group II will be between the frequency distributions of the group I and P_1 genotypes. Table 11 gives the theoretical frequency for the F_2 genotypes calculated on the above assumption. From these distributions the theoretical frequency for the F_2 population is obtained by taking the theoretical percentage of the penetrance and summing for each class (table 12). The test for goodness of fit between the obtained and theoretical numbers (not the theoretical percentage) gives a χ^2 value of 3.369, and the P. value lies between 0.50 and 0.30. A good agreement between the obtained and theoretical values supports the hypothesis that the two parents are differentiated by three gene pairs.

The preceding analysis indicates that the gene action is probably additive or close to it. There does not appear to be any inter- or intra-allelic interaction. However, if these conclusions regarding the gene action are correct, we should be able to calculate a theoretical F_2 mean which should not be significantly different from the obtained mean of the F^2 population. The calculated means for the F_2 genotypes are shown in table 11.

The difference between the means of P_1 *(aabbcc)* and P_2 *(AABBCC)* is $(53.44 - 46.36) = 7.08$ (table 8). As already assumed, the genes have equal effect, the gene action is additive, and there is complete phenotypic and genic dominance. Hence the effect of *A*, *B*, or *C* or *AA*, *BB*, or *CC* is $7.08 \div 3 = 2.36$. Therefore the mean of the *AAbbcc*, *aaBBcc*, and *aabbCC* genotypes is $(53.44 - 2.36) = 51.08$. Similarly the

Table 12. Chi-square for Testing Goodness of Fit Between Theoretical Frequency Distribution Based on the Assumption That the Parents Are Differentiated by Three Gene Pairs and the Obtained Frequency Distribution of the F_2 Population for the Number of Days from Seeding to the Opening of the First Female Flower

Population	Class				Number
	41-46	47-50	51-54	55-58	of individuals
	per cent	*per cent*	*per cent*	*per cent*	
Theoretical	33.89	23.74	38.14	4.23	462
Obtained	29.44	28.36	37.88	4.32	462
	number	number	number	number	
Theoretical	156.5	109.6	176.4	19.5	462
Obtained	136.0	131.0	175.0	20.0	462

$\chi^2 = 3.369$
P. lies between 0.50 and 0.30.

mean of the fifth group of genotypes of table 11 is $(51.08 - 2.36) = 48.72$. The means of the *AABBCC, AaBbCc,* and *aabbcc* genotypes are taken as that of P_2 F_1 and P_1 respectively. The remaining two means are calculated from the B_1 populations by the methods given by Powers, Locke, and Garrett *(14).*

It will be noted that the calculated mean (53.04) from the B_1 to P_1 population is considerably higher than expected. The calculated mean of the fifth group of genotypes which has two dominant factors is 48.72, and of the sixth group of genotypes which has one dominant factor is 51.08. Therefore the calculated mean from the B_1 population of the fourth group of genotypes which has three genotypes with two dominant factors and three genotypes with one dominant factor should lie in between the means of the fifth and sixth groups of genotypes. The expected mean for the fourth group of genotypes is $([51.08 + 48.72] \div 2) = 49.90$. The difference between the mean obtained by partitioning the B_1 to P_1 population and the expected mean calculated immediately above is $(52.04 - 49.90) = 2.14$. Although the standard error for the 52.04 mean is not known, it may roughly be assumed that this mean has the same standard error as the P_1 mean. The standard error for the P_1 mean is 0.801. Thus the standard error of difference is $0.801 \times 2 = 1.1327$. This indicates that the difference 2.14 is not statistically significant because it is less than twice the standard error of the difference (2.26).

From the theoretical means of the F_2 genotypes, the mean of the F_2 population is calculated by multiplying the theoretical means by their respective theoretical percentages, summing, and dividing by 100. (For detailed methods see Powers, Locke, and Garett). The calculated mean of the F_2 population is 48.86 which is very close to the obtained mean, 49.00. This further supports the preceding conclusions that probably the gene action is additive and the genes are independent in their action.

The Difference in Days Between the Opening of First Male and First Female Flower

From the mean values listed in table 13 we find that in Bush maxima plants the first female flower opens 2.34 days after the opening of the first male flower. In Greengold the first female flower opens 7.30 days after the first male flower. The magnitude of the difference between the two parents is 4.96 days.

It will be noted that the total variance for Bush maxima in relation to its mean is significantly higher than the total variance for Greengold in relation to its mean. Therefore the genetical variances are not calculated. The larger total variance for the Bush maxima parent is probably due to a certain degree of heterozygosity. As compared to the total variance of the

Table 13. The Means, Standard Deviations, Total Variance, and Number of Individuals in Each Population for the Difference in Days Between the Opening of First Male and First Female Flower

Population	Mean	Standard deviation	Total variance	Number of individuals
Greengold (P_1)	7.30	0.110	607.54	229
B_1 to P_1	5.61	0.162	3,507.84	438
F_1	2.38	0.124	692.48	225
F_2	4.10	0.177	4,925.50	462
B_1 to P_2	2.52	0.132	805.86	432
Bush maxima (P_2)	2.34	0.125	721.55	225

Table 14. Frequency Distribution (expressed in percentage) for the Difference in Days Between the Opening of Male and Female Flower

Population	Classes					
	−3 to −1	0	1-2	3-5	6-8	9-11
	per cent	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
Greengold (P_1)	....	....	....	11.95	64.60	23.45
B_1 to P_1	2.63	2.41	11.62	23.25	48.90	11.19
F_1	1.49	9.90	50.50	31.68	6.43	....
F_2	2.19	9.31	23.38	27.92	30.09	7.14
B_1 to P_2	2.40	15.33	38.86	33.99	9.42	....
Bush maxima (P_2)	2.46	13.79	41.87	35.96	5.91	....

B_1 to P_1 and F_2 populations the total variance for Bush maxima is small. The heterozygosity, therefore, is probably due to minor modifying factors and not to major factors.

The mean of Bush maxima (2.34) and the mean of the F_1 (2.38) are approximately the same. The mean of B_1 to P_2 population is slightly higher than Bush maxima, but is within the limits of variation expected due to errors of random sampling. These means indicate nearly complete phenotypic dominance of shorter duration between the opening of the first male and the first female flower over longer duration. The total variance for the B_1 to P_2 population is somewhat higher than the variance of Bush maxima but is not statistically significant. This indicates that genic dominance is probably also complete.

NUMBER OF GENE PAIRS DIFFERENTIATING THE PARENTS

The assumption is made that the two parents are differentiated by two gene pairs. The genotypes of the P_1 are symbolized as *aabb* and of the P_2 as *AABB.*

The frequency distributions of B_1 to P_1 and B_1 to P_2 (table 14) are partitioned into their component genotypes as in table 15. On the basis of the frequency distribution for different genotypes of the B_1 to P_1 and B_1 to P_2 populations, the theoretical frequency distributions for F_2 genotypes are obtained. The only genotypes which do not occur in either of the B_1 populations are *AAbb* and *aaBB.* In order to obtain frequency distribution for these two genotypes, the theoretical means for the different F_2 genotypes are calculated.

Table 15. Partitioning the Frequency Distribution of B_1 to P_1 and B_1 to P_2 into their Component Genotypes

Population and genotype	Row no.	Class (in number of days)						Theoretical percentage
		−3 to −1	0	1-2	3-5	6-8	9-11	
		per cent	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	
B_1 to P_1	1.	2.63	2.41	11.62	23.25	48.90	11.19	100.0
F_1 + P_1 (AaBb + aabb)	2.	0.38	2.48	12.62	10.90	17.76	5.86	50.0
Row 1 − 2	3.	2.25	−0.07	−1.00	12.35	31.14	5.33	50.0
Row 3 on positive basis	4.	....	....	....	13.53	31.14	5.33	50.0
Aabb + aaBb (100 per cent)	5.	....	....	....	27.06	62.28	10.66	100.0
F_1 (A a B b)	6.	1.49	9.90	50.50	31.68	6.43	....	25.0
P_1 (aabb)	7.	....	....	....	11.95	64.60	23.45	25.0
B_1 to P_2	8.	2.40	15.33	38.86	33.99	9.42	....	100.0
F_1 + P_2 (AaBb + AABB)	9.	0.99	5.92	23.09	16.91	3.09	....	50.0
Row 8 − Row 9	10.	1.41	9.41	15.77	17.08	6.33	....	50.0
AABb + AaBB (100 per cent)	11.	2.82	18.82	31.54	34.16	12.66	....	100.0
F_1 (AaBb)	12.	1.49	9.90	50.50	31.68	6.43	....	25.0
P_2 (AABB)	13.	2.46	13.79	41.87	35.96	5.91	....	25.0

ESTIMATION OF THE MEANS FOR THE F_2 GENOTYPES

Means of *AABB, AaBb* and *aabb* genotypes are taken from the P_2, F_1 and P_1 populations.

Means of the *AABb* and *AaBB* genotypes are estimated from the B_1 to P_2 population as follows:

Genotype	**Mean**	**Theoretical percentage**
AABB	2.34	
AABb		25.0
AaBB		25.0
AaBb	2.38	25.0

Mean of the B_1 to P_2 as obtained = 2.52.

Total sum of the B_1 to P_2 population with the minimum of 4 individuals to have all genotypes represented is $(4 \times 2.52) = 10.08$.

Hence the mean of the *AABb* and *AaBB* genotypic individuals is: $(10.08 - [2.34 + 2.38])$ or $(10.08 - 4.72) = 5.36$.

Since 5.36 is the sum of individuals of two genotypes *AaBB* and *AABb* respectively, the mean is $(5.36 \div 2) = 2.68$.

Similarly estimated from the B_1 to P_1 population, the mean of the *aaBb* and *Aabb* genotypes is:

$([5.61 \times 4] - [7.30 + 2.38]) = (22.44 - 9.68) = 12.76 \div 2 = 6.38$.

The means of the F_2 genotypes as calculated are:

AABB	2.34
AaBB	2.68
AABb	
AaBb	2.38
AAbb	6.38
aaBB	
Aabb	6.38
aaBb	
aabb	7.30

The above means of the *AABB* (2.34), *AaBB* + *AABb* (2.68), and *AaBb* (2.38) genotypes are not significantly different from each other which probably indicates complete genic dominance. However, this could have been because the *AaBb* genotype has already reached its threshold and any further addition of the *A* or *B* gene has no discernable effect.

On the basis of complete genic dominance, the mean of *AAbb* + *aaBB* genotypes should be the same as that of *Aabb* + *aaBb* genotypes (6.38). The mean of the *Aabb* + *aaBb* genotypes (6.38) is 0.92 less than 7.30, the mean of the P_1 genotype *(aabb)*. It indicates that the effect of *A* or *B* is 0.92. If genic dominance is not complete and the gene action is additive, the mean of the *AAbb* + *aaBB* genotype should be $(6.36 - 0.92)$ 5.44. Thus the mean of *AAbb* + *aaBB* genotypes, on the basis of partial genic dominance, is 5.44. The F_2 mean calculated on the basis of partial genic dominance (4.14) is somewhat closer to the obtained mean of the F_2 population (4.10) than to the mean (4.26), which assumes complete genic dominance. In no case, however, are the differences statistically significant. This indicates that the data are not discriminatory as regards genic dominance. However, in calculating the frequency distribution of the *AAbb* + *aaBB* genotypes, the frequency distribution of the *Aabb* + *aaBb* genotypes has been taken.

The theoretical frequency distributions for the F_2 genotypes is obtained by taking the theoretical percentage of the penetrances and summing for each class (table 16). The test for goodness of fit between the obtained and theoretical numbers gives a χ^2 value of 3.452, are the P. value lies between 0.70 and 0.50 (table 17). The theoretical frequency distribution furnishes convincing evidence that the two parents are differentiated by two gene pairs.

The mean of the *aabb* (P_1) genotype is 7.30. The *Aabb* + *aaBb* genotypic mean (as calculated from the B_1 to P_1 population) is 6.38. This indicates that a substitution of *A* or *B* gene in the *aabb* genotype lowers the 7.30 mean by 0.92.

Table 16. The F_2 Generation Frequency Distribution Partitioned into its Component Genotypes On the Basis of a Two-Factor-Pair Difference for the Difference in Days Between the Opening of First Male and First Female Flower

Population and genotype	Class (in number of days)						Theoretical percentage	Theoretical mean
	—3 to —1	0.0	1-2	3-5	6-8	9-11		
A A B B	2.46	13.80	41.87	35.96	5.91	...	6.25	2.34
A a B B A A B b	2.82	18.82	31.54	34.16	12.66	...	25.00	2.66
A a B B	1.49	9.90	50.50	31.68	6.43	...	25.00	2.38
A A b b a a B B	...	...	...	27.06	62.28	10.66	12.50	6.38
A a b b a a B b	...	...	...	27.06	62.28	10.66	25.00	6.38
a a b b	...	...	...	11.95	64.60	23.45	6.25	7.30
F_2 population	1.23	8.04	23.13	29.60	32.54	5.46	...	...

The obtained mean for *AaBb* (F_1) genotype is 2.38, showing a substitution of *A* in the *aaBb* genotype or of *B* in the *Aabb* genotype lowers mean value from 6.38 to 2.38; i.e., by 4.0. It is evident that this great effect should be due to interallelic interaction between *A* and *B*, because the individual effect of *A* and *B* has been calculated to be only 0.92. This shows that the complete phenotypic dominance shown by the F_1 is mostly due to interallelic interaction between *A* and *B*.

Color of the Fruit

Fruit of the Greengold (P_1) is orange with a slightly green blossom end, which is always present, even in material inbred for 10 to 12 generations. The green may vary in degree even on the same vine. No fruit free from green blossom end has been procured in segregating generations. Either gene or genes for green blossom end are closely linked with genes for orange body color of the fruit, or genes for color of the fruit have pleiotropic effect, or both parents carry genes for green blossom end. Bush maxima is solid green.

DOMINANCE

Reciprocal F_1 crosses were sown in the summer of 1947. In the Greengold x Bush maxima cross, the F_1 fruits were orange, while in the Bush maxima x Greengold cross, the F_1 fruits were green. The color inheritance appeared to be entirely maternal. In order to verify these results the experiment was repeated in the summer of 1948. This year there was no evidence of any maternal inheritance. The F_1 fruits

Table 17. Chi-square for Testing Goodness of Fit Between the Theoretical Frequency Distribution on the Assumption that the Parents are Differentiated by Two Gene Pairs and the Obtained Frequency Distribution of the F_2 Population

Population	Class						Number of individuals
	—3 to —1	0.0	1-2	3-5	6-8	9-11	
	per cent	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	
Theoretical	1.23	8.04	23.13	29.60	32.54	5.46	462
Obtained	2.16	9.31	23.38	27.92	30.09	7.14	462
	number	*number*	*number*	*number*	*number*	*number*	
Theoretical	5.68	37.15	106.86	136.75	150.33	25.23	462
Obtained	10.00	43.00	108.00	129.00	139.00	33.00	462

$\chi^2 = 3.452$

P. lies between 0.70 and 0.50

were green with orange spots in different degrees. Even on the same vine a fruit at the base of the plant might have orange color to a large extent; other fruits might be green with few orange spots; and occasionally a fruit might be entirely green.

The great variation in color even on the same vine could be due to different degrees of maturity of the fruit. Heterozygous fruits which may be green at the time of picking become orange to a large degree during storage in the cellar. However, it is quite possible to obtain an indication of complete maternal inheritance as evidenced during the first year's results. The rind of the fruit is a maternal tissue and the color of the rind might be due to the plastid pigments. It is not known why different results were obtained in the different years. The inheritance of the color is worked out on the basis of the second year results (table 18). On this basis, green seems to be partially dominant over orange.

NUMBER OF GENE PAIRS DIFFERENTIATING THE PARENTS

On the basis of the segregating generations, the assumption is made that the parents are differentiated by two gene pairs. The genotypes of the P_1 are symbolized as *aabb* and of the P_2 as *AABB*.

In the B_1 to P_1 population, 25.0 per cent of the individuals *(aabb)* should behave like Greengold. There are 25.70 per cent of the individuals like Greengold in the orange class. The χ^2 value is 0.120 and the P. value lies between 0.80 and 0.70. Because the individuals of the three remaining genotypes *(Aabb, aaBb,* and *AaBb)* overlap each other, it is difficult to classify the above three genotypes into separate classes.

In the B_1 to P_2 population, 34.80 per cent of the individuals fall beyond the green class. Evidently the *AaBb* genotype should largely make up for the 34.80 per cent frequency beyond the green class. Because this frequency is much higher than the expected 25.0 per cent, it is clear that there is a great degree of overlapping between the *AaBb, AaBB,* and *AABb* genotypes and therefore a proper classification of the different genotypes cannot be made. However, it does indicate that most of the *AaBB* and *AABb* genotypic individuals have green color and only a very small percentage of the individuals have fruits with orange spots.

In the F_2 population 6.25 per cent of the individuals *(aabb)* should behave like Greengold. Actually there are 6.40 per cent of the individuals in the orange class. The χ^2 value is 0.017 and the P. value lies between 0.95 and 0.90. The calculated and obtained values are somewhat closer than would be expected by chance. The rest of the F_2 genotypes show a certain degree of overlapping and therefore it is difficult to classify the different genotypes into different classes.

On the basis of the foregoing analysis, it is concluded that the parents are differentiated by two gene pairs.

Table 18. Frequency Distribution (expressed in percentage) for the Color of the Fruit in F_2, B_1 to P_1 and B_1 to P_2 Populations in 1948

Population	Orange	Orange with little green	Spotted (orange-green)	Green with few orange spots	Green	Number of individuals
	per cent	*per cent*	*per cent*	*per cent*	*per cent*	
F_2	6.40	24.10	15.30	19.10	35.10	470
B_1 to P_1	25.70	25.30	25.30	21.20	2.50	467
B_1 to P_2	....	1.50	14.30	19.00	65.20	462

Table 19. The Means, Standard Deviations, Variances and Number of Individuals in each Population for the Weight of the Fruit

Population	Mean	Standard deviation	Total variance	Environmental variance	Genetical variance	Number of individuals
Greengold (P_1)	1590	17.000	15,074,768	14,800,111	214,657	230
B_1 to P_1	1574	41.652	428,587,060	14,601,025	413,986,035	466
F_1	1372	14.643	8,828,555	11,252,025	—2,423,470	203
F_2	1606	51.857	641,260,677	15,784,681	625,475,996	468
B_1 to P_2	1362	20.857	89,233,534	11,109,690	78,123,844	463
Bush maxima (P_2)	874	10.428	4,583,603	3,121,398	2,188,815	210

Weight of the Fruit

From mean values listed in table 19 we find that average weight of the fruit of P_1 is 1590 gms., and the average weight of P_2 is 874 gms. Thus there is a difference of 716 gms. between fruit weights of the two parents.

DOMINANCE

If phenotypic dominance is intermediate, then the mean of the F_1 generation should be equal to the average of the means of the two parents. The average of the means of the two parents is 1232 gms. while the mean of the F_1 generation is 1372 gms. This shows partial phenotypic dominance for larger fruit size. Partial phenotypic dominance may be due either to partial genic dominance for larger fruit size or to interactions between the genes, or both.

The mean of the F_2 population is as large as the Greengold parent itself. Whether the gene action is geometric or arithmetic cannot be determined from the means of the F_1 and F_2 populations. The frequency distribution of the F_2 population (table 20) shows a bimodal curve, though some degree of positive skewness is evident. However, skewness is only a rough measure for the kind of gene action and cannot be relied upon.

NUMBER OF GENE PAIRS DIFFERENTIATING THE PARENTS

The assumption is made that the parents are differentiated by three gene pairs. A survey of table 20 shows transgressive segregation in all the segregating generations. The following genes have been assumed for large and small fruit size.

AA dominant genes for large fruit size *vs.* *aa* recessive genes for small fruit size.

BB dominant genes for large fruit size *vs.* *bb* recessive genes for small fruit size.

CC recessive genes for large fruit size

Table 20. Frequency Distribution (expressed in percentage) for the Weight of the Fruit

Population	Class (in grams)							
	300-499	500-899	900-1299	1300-1699	1700-2099	2100-3299	3300-4299	4300-5500
	per cent	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
Greengold (P_1)	....	....	14.22	51.29	32.33	2.16	....	....
B_1 to Greengold (P_1)	6.44	29.40	13.95	11.37	10.73	22.53	5.16	0.43
F_1	....	0.49	39.91	53.69	5.91	....	....	....
F_2	4.91	25.11	26.17	13.25	7.48	14.53	5.34	3.21
B_1 to Bush maxima (P_2)	0.22	12.74	37.37	28.94	14.25	6.48	....	....
Bush maxima (P_2)	....	59.05	40.95	....	....	....	....	....

vs. CC dominant genes for small fruit size.

The P_1 parent is symbolized as *aaBBcc* and P_2 as *AAbbCC*.

The genotype of the B_1 to P_1 and B_1 to P_2 are written below:

P_1 (aaBBcc)	*F_1 (AaBbCc)*	*P_2 (AAbbCC)*
B_1 to P_1		B_1 to P_2
AaBBCc		*AABbCC*
AaBBcc		*AABbCc*
AaBbCc		*AAbbCC*
AaBbcc		*AAbbCc*
aaBBCc		*AaBbCc*
aaBBcc		*AaBbCC*
aaBbCc		*AabbCC*
aaBbcc		*AabbCc*

For determining the number of gene pairs by which the parents are differentiated, the condensed frequency distribution (table 21) has been used. There was no way to predict the penetrances for so many central classes of those genotypes not occurring in either backcross population. By grouping the central classes it was possible to predict the behavior of those genotypes.

The B_1 to P_1 and B_1 to P_2 populations are partitioned into their component genotypes as shown in table 22. The frequency distributions of the B_1 populations have been used to calculate the theoretical frequency distributions for the F_2 genotypes (table 23).

The distributions for the *aaBBcc*, *AaBbCc*, and *AAbbCC* genotypes have been taken as that of the P_1, F_1, and P_2 respectively. The distribution of the following genotypes has been taken by partitioning the B_1 populations.

AaBBCc
AaBBcc
AaBbcc
aaBBCc
aaBbCc
aaBbcc

AABbCC
AABbCc
AAbbCc
AaBbCC
AabbCC
AabbCc

Table 21. Condensed Frequency Distribution (expressed in percentage) for the Weight of the Fruit

Population	Class (in grams)			
	300-499	500-2099	2100-3299	3300-5500
	per cent	*per cent*	*per cent*	*per cent*
Greengold (P_1)	....	97.84	2.16	....
B_1 to Greengold (P_1)	6.44	65.45	22.53	5.58
F_1	....	100.00	....	....
F_2	4.91	72.01	14.53	8.55
B_1 to Bush maxima (P_2)	0.22	93.30	6.48	....
Bush maxima (P_2)	....	100.00	....	....

Table 22. Partitioning the B_1 to P_1 and B_1 to P_2 Populations into their Component Genotypes for the Weight of the Fruit

Population and genotype	Row no.	Class (in grams)				Theoretical percentage
		300-499	500-2099	2100-3299	3300-5500	
		per cent	*per cent*	*per cent*	*per cent*	
B_1 to P_1	1.	6.44	65.45	22.53	5.58	100.00
F_1 + P_1 (AaBbCc + aaBBcc)	2.	....	24.73	0.27	....	25.00
Row 1 — Row 2	3.	6.44	40.72	22.26	5.58	75.00
Row 3 (100 per cent basis)	4.	8.59	54.29	29.68	7.44	100.00
F_1 (AaBbCc)	5.	....	100.00	....	....	12.50
P_1 (aaBBcc)	6.	....	97.84	2.16	....	12.50
B_1 to P_2	7.	0.22	93.30	6.48	....	100.00
F_1 + P_2 (AaBbCc + AAbbCC)	8.	....	25.00	....	....	25.00
Row 7 — Row 8	9.	0.22	68.30	6.48	....	75.00
Row 9 (100 per cent basis)	10.	0.29	91.07	8.64	....	100.00
F_1 (AaBbCc)	11.	....	100.00	....	....	12.50
P_2 (AAbbCC)	12.	....	100.00	....	....	12.50

Table 23. The F$_2$ Generation Frequency Distribution Partitioned into their Component Genotypes on the Basis of Three-Factor-Pair Difference for the Weight of the Fruit

Population and genotype	Class				Theoretical percentage
	300-499	500-2099	2100-3299	3300-5500	
aaBBcc (P$_1$)	....	97.84	2.16	....	1.5625
AaBBcc	8.59	54.29	29.68	7.44	28.1250
AaBbcc					
AaBBCc					
aaBBCc					
aaBbcc					
aaBbCc					
AaBbCc (F$_1$)	....	100.00	....	....	12.5000
AABbCC	0.29	91.07	8.64	....	28.1250
AABbCc					
AAbbCc					
AaBbCC					
AabbCC					
AabbCc					
AABBcc	....	....	25.00	75.00	1.5625
AABbcc	....	....	50.00	50.00	3.1250
AABBCc	....	25.00	50.00	25.00	3.1250
AABBCC	....	97.84	2.16	....	3.1250
AAbbcc					
AaBBCC	....	100.00	....	....	9.3750
Aabbcc					
aaBBcc					
aabbcc					
aaBbCC	49.00	51.00	....	....	3.1250
aabbCc	62.00	38.00	....	....	3.1250
aabbCC	90.00	10.00	....	....	1.5625
AAbbCC (P$_2$)	....	100.00	....	....	1.5625
F$_2$ population	7.37	72.63	14.39	5.61	....

The following genotypes do not occur in either of the B$_1$ populations.

I	II	III
AABBcc *AABbcc*	*aabbCC* *aabbCc*	*AABBCc*
IV	**V**	**VI**
AABBCC *AAbbcc*	*AaBBCC* *Aabbcc* *aabbcc* *aaBBcc*	*aaBbCC*

Table 22 (row 3) shows that 5.58 per cent of the individuals fall in the 3300-5500 class. This percentage evidently is due to the *AaBBcc* genotype. On the basis of 100.0 per cent penetrance of the *AaBBcc* genotype for the 3300-5500 class, 12.50 per cent of the individuals are expected. A frequency of 5.58 per cent will indicate roughly 50.0 per cent penetrance for the *AaBBcc* genotype in the 3300-5500 class. The penetrance for the *AABBcc* genotype should be close to the *AaBBcc* genotype but because the *AABBcc* genotype has *A* in the homozygous condition, it is assumed that it has 75.0 per cent penetrance in the 3300-5500 class as against 50.0 per cent penetrance of the *AaBBcc* genotype. The remaining 25.0 per cent will then be in the 3100-3299 class. Similarly the *AABbcc* genotype should have the same frequency distribution as the *AaBBcc* genotype. Therefore, the *AABbcc* genotype will have 50.0 per cent penetrance in the 3300-5500 class and the remaining 50.0 per cent in the 2100-3299 class.

The *aabbCC* genotypic individuals will have the smallest fruits. A frequency of 6.44 per cent in the 300-499 class of the B$_1$ to P$_1$ populations is probably due the *aaBbCc* and *aaBBCc* genotypic individuals. This frequency indicates 50.0 per cent penetrance of the *aaBbCc* and *aaBBCc* individuals in the 300-499 class. However, this 50.0 per cent penetrance should be due largely to the *aaBBCc* genotypic individuals. Only a small portion can be attributed to the *aaBBCc* genotypic individuals. Therefore, it is assumed that the *aaBbCc* genotype has approximately 35.0 per cent penetrance in the 300-499 class. On this basis it is assumed that the *aabbCc* genotype will probably have 90.0 per cent penetrance in the 300-499 class and the remaining 10.0 per cent in the 500-2099 class. The frequency distribution of the *aabbCc* genotype will then lie between the frequency distribution of the *aaBbCc* and *aabbCC* genotypes. Hence, it is assumed that the *aabbCc* genotypes will have 62.0 per cent penetrance in the 300-499 class and the remaining 38.0 per cent in the 500-2099 class.

The partitioning of the B_1 to P_2 population (table 22, row 3) shows that 6.48 per cent of the individuals fall in the 2100-3299 class. The frequency of 6.48 per cent should be due to the *AABbCc* genotype. This will indicate nearly 50.0 per cent penetrance of the *AABbCc genotype* in the 2100-3299 class. The frequency distribution of the *AABBCc* genotype should lie between the frequency distribution of the *AABbCc* and *AABBcc* genotypes. Hence, the *AABBCc* genotype is taken as having 25.0 per cent penetrance for the 3300-5500 class, 50.0 per cent for the 2100-3299 class, and 25.0 per cent for the 500-2099 class.

The *aaBBcc* genotype (P_1) has a penetrance of 97.84 per cent in the 300-499 class and 2.16 in the 2100-3299 class. The *AABBCC* and *AAbbcc* genotypes which have the same number of genes for large and small fruit size are taken as having the same frequency distribution as P_1.

In the frequency distribution of the fourth group of genotypes (table 23) it has already been assumed that 8.64 per cent of the population in the 2100-3299 class is due to the *AABbCc* genotypic individuals. The rest of the genotypes have 100.0 per cent penetrance in the 500-2099 class. Because the *AABbCC* genotype has 100.0 per cent penetrance in the 500-2099 class, it is evident that the following genotypes, some of which probably have as much value as *AABbCC* genotypes and others less than this, should have 100.0 per cent penetrance in the 500-2099 class.

AaBBCC
Aabbcc
aaBBCC
aabbcc

It has already been shown that the *aaBbCc* genotype has 35.0 per cent penetrance in the 300-499 class and the penetrance of the *aabbCc* genotype has been assumed to be 62.0 per cent in the 300-499 class. Hence the frequency distribution of the *aaBbCC* genotype should lie between the frequency distribution of the *aaBbCc* and *aabbCc*

Table 24. Chi-square for Testing Goodness of Fit Between Theoretical Frequency Distribution on the Assumption that the Parents are Differentiated by Three Gene Pairs and the Obtained Frequency Distribution of the F_2 Population for the Weight of the Fruit

Population	Class (in grams)				Number of individuals
	300-499	500-2099	2100-3299	3300-5500	
	per cent	*per cent*	*per cent*	*per cent*	
Theoretical	7.37	72.63	14.39	5.61	468
Obtained	4.91	72.01	14.53	8.55	468
	number	*number*	*number*	*number*	
Theoretical	34.50	339.91	67.34	26.25	468
Obtained	23.00	337.00	68.00	40.00	468

$\chi^2 = 5.332$

P. lies between 0.20 and 0.10.

genotypes. Therefore, it is assumed that the *aaBbCC* genotype has a penetrance of 49.0 per cent in the 300-499 class and 51.0 per cent in the 500-2099 class. This completes the calculation of the frequency distributions for the different F_2 genotypes.

From the frequency distributions of the F_2 genotypes (table 22) the theoretical frequency distribution of the F_2 population is obtained. The test for goodness of fit to the theoretical and obtained numbers gives a χ^2 value of 5.332, and the P. value lies between 0.20 and 0.10 (table 24). A good agreement between the theoretical and obtained frequency supports the hypothesis that the two parents are differentiated by three major gene pairs.

Cupping Caused by the Incomplete Enclosure of The Ovarian Tissue

The fruits of the Greengold variety have an average cup diameter of 1.92 cms. and the fruits of Bush maxima variety have an average cup diameter of 3.36 cms. The magnitude of difference between the two parents is 1.44 cms.

From the mean values listed in table 25 it will be seen that F_1 shows considerable heterosis. The genetic variance of the B_1 to P_1 and B_1 to P_2 indicate that both the parents carry recessive genes.

NUMBER OF GENE PAIRS DIFFERENTIATING THE PARENTS

The frequency distributions of the different segregating generations show transgressive segregation (table 26). This indicates that both parents carry recessive genes. In the B_1 to P_1 population, 29.71 per cent of the individuals fall in the 0.0 class (correction made for the frequency of P_1 in the 0.0 class). This indicates that probably two factor pairs are involved. A frequency of 23.28 per cent of the B_1 to P_2 population in the 0.0 class also suggests that probably

Table 25. The Means, Standard Deviations, Variances, and Number of Individuals in Each Population for the Cupping Character Caused by Incomplete Enclosure of Ovarian Tissue

Population	Mean	Standard deviation	Total variance	Environmental variance	Genetical variance	Number of individuals
Greengold (F_1)	1.92	0.243	127.83	127.93	—0.10	230
B_1 to P_1	2.56	0.729	2,336.34	158.93	2,177.41	466
F_1	5.32	0.414	292.12	292.59	—0.47	202
F_2	2.69	0.912	3,665.04	165.22	3,499.82	467
B_1 to P_2	3.39	0.843	3,030.04	199.12	2,830.92	462
Bush maxima (P_2)	3.36	0.324	198.25	197.67	—0.58	210

Table 26. The Frequency Distribution (expressed in percentage) for the Cupping Character Caused by Incomplete Enclosure of Ovarian Tissue

Population	Classes (in centimeters)						
	0.0	1.5	3.5	5.5	7.5	9.5	11.5
	per cent	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
Greengold (P_1)	3.92	80.87	14.78	0.43	....	....	....
B_1 to P_1	30.69	24.68	21.25	18.88	3.43	1.07	....
F_1	....	0.50	26.73	57.43	14.85	0.50	....
F_2	40.13	13.52	18.45	15.45	9.01	2.58	0.86
B_1 to P_2	23.38	20.35	24.08	19.48	9.89	2.82	....
Bush maxima (P_2)	....	19.05	70.00	10.48	0.48	....	....

the parents are differentiated by two factor pairs. However, the frequency of 40.13 per cent of the F_2 population in the 0.0 class is higher than is expected on a two-factor basis, but it is evident that such a high percentage of individuals in the 0.0 class cannot be due to a large number of factors.

The writer was not able to make a factorial analysis as the data could not be fitted to a two- or three-factor hypothesis. It appears that the parents most probably are differentiated by two or three factor pairs but some complex inter- and intra-allelic interactions make it difficult to analyze the data. To obtain very conclusive proof for the exact number of genes involved, it will be necessary to grow the progenies of the backcross and F_2.

Total Solids

The mean values for total solids (table 27) show that the fruits of the Greengold variety gave a mean value of 6.73, and the fruits of the Bush maxima 2.74. The magnitude of difference between the two parents is 3.99.

If phenotypic dominance is intermediate and gene effects are additive, the F_1 mean should equal the average of the means of the two parents. The average means of the parents is 4.74, which is slightly higher than the obtained mean of the F_1 (4.63) but not significantly so. The obtained mean is closer to the arithmetic mean (4.74) than to the geometric mean (4.29). The F_2 mean (4.60) is very close to the F_1 mean (4.63). These values are those expected if gene effects are additive and there is no genic dominance.

NUMBER OF GENE PAIRS DIFFERENTIATING THE PARENTS

The hypothesis to be tested is that the two parents are differentiated by two gene pairs. The indication that two factor pairs are involved is obtained by dividing 16.16 (7-9 class of B_1 to P_1) by 54.78 (7-9 class of Greengold), and 3.23 (1-2 class of F_2) by 33.81 (1-2 class of Bush maxima), which gave values of 29.45 and 9.55 respectively. On the basis that the parents are differentiated by two factor pairs, the expected values

Table 27. The Means, Standard Deviations, Variances, and Number of Individuals in Each Population for Total Solids

Population	Mean	Standard deviation	Total variance	Environmental variance	Genetical variance	Number of individuals
Greengold (P_1)	6.73	0.350	219.856	239.184	—19.328	230
B_1 to P_1	5.34	0.412	710.295	182.611	527.684	464
F_1	4.63	0.327	188.726	153.714	35.012	198
F_2	4.60	0.455	795.184	152.493	642.691	464
B_1 to P_2	3.47	0.328	441.349	106.502	334.847	459
Bush maxima (P_2)	2.74	0.195	61.105	77.198	—16.093	210

Table 28. Frequency Distribution Expressed in Percentage for Total Solids

Population	Classes				Number of individuals
	1-2	3-4	5-6	7-9	
	per cent	*per cent*	*per cent*	*per cent*	
Greengold	....	....	45.22	54.78	230
B_1 to Greengold	....	25.65	58.19	16.16	464
F_1	....	46.97	53.03	....	198
F_2	3.23	45.04	45.91	5.82	464
B_1 to P_2	12.20	70.80	16.99	....	459
Bush maxima	33.81	66.19	....	....	210

Table 29. Partitioning the Frequency Distribution of B_1 to P_1 and B_1 to P_2 Population into their Component Genotypes

Population and genotype	Row no.	Frequency distribution in per cent				Theoretical percentage
		1-2	3-4	5-6	7-9	
		per cent	*per cent*	*per cent*	*per cent*	
B_1 to P_1	1.	....	25.65	58.19	16.16	100.00
F_1 + P_1 (AaBb + aabb)	2.	....	11.75	24.56	13.69	50.00
Row 1 — Row 2	3.	....	13.90	33.63	2.47	50.00
Aabb + aaBb (100 per cent)	4.	....	27.80	67.26	4.94	....
F_1 (AaBb)	5.	....	46.97	53.03	....	25.00
P_1 (aabb)	6.	....	....	45.22	54.78	25.00
B_1 to P_2	7.	12.20	70.80	16.99	....	100.00
F_1 + P_2 (AAaBb + AABB)	8.	8.45	28.29	13.26	....	50.00
Row 7 — Row 8	9.	3.75	42.51	3.73	....	50.00
AABb + AaBB (100 per cent)	10.	7.50	85.02	7.46	....	100.00
F_1 (AaBb)	11.	....	46.97	53.03	....	25.00
P_2 AABB	12.	33.81	66.19	....	....	25.00

Table 30. The F_2 Generation Frequency Distribution Partitioned into its Component Genotypes on the Basis of a Two-Factor-Pair Difference

Population and genotype	Frequency distribution in per cent				Theoretical percentage	Calculated mean
	1-2	3-4	5-6	7-9		
A A B B	33.81	66.19	....	....	6.25	2.74
A A B b	7.50	85.02	7.46	....	25.00	3.25
A a B B						
A a B b	....	46.97	53.03	....	25.00	4.63
A A b b	....	46.97	53.03	....	12.50	4.63
a a B B						
A a b b	....	27.80	67.26	4.94	25.00	5.00
a a B b						
a a b b	....	....	45.22	54.78	6.25	6.73
F_2 population	3.98	49.95	41.43	4.66	....	....

are 25.00 and 6.25 (table 28).

The genotypes of the P_1 are symbolized as *aabb* and of the P_2 as *AABB*. It has already been shown that the P_1, P_2, F_1, and F_2 mean values indicate that the gene action is additive and there is no dominance.

Table 29 shows the B_1 to P_1 and B_1 to P_2 frequency distributions partitioned into their component genotypes on the basis of the above findings. On the basis of the frequency distributions of the B_1 population, the theoretical frequency distribution of the F_2 genotypes are obtained (table 30). The frequency distribution of the *AAbb* and *aaBB* genotypes does not occur in either of the B_1 populations. It has been shown that probably the gene action is additive and that there is no dominance. Further it has been assumed that the genes have equal effect. Hence, the frequency distribution of the *AAbb* and *aaBB* genotypes will be the same as that of the *AaBb* genotype.

From the frequency distributions of the F_2 genotypes (table 30) the theoretical frequency distribution of the F_2 population is obtained. The test for goodness of fit to the theoretical and obtained numbers gives a χ^2 value of 3.258, and the P. value lies between 0.50 and 0.30 (table 31). This supports the hypothesis that the two parents are differentiated by two gene pairs.

The preceding analysis indicated that

Table 31. Chi-square for Testing Goodness of Fit Between Theoretical Frequency Distribution on the Assumption that the Parents are Differentiated by Two Gene Pairs and the Obtained Frequency Distribution of the F_2 Population

Population	Frequency distribution in per cent				Number of individuals
	1-2	3-4	5-6	7-9	
	per cent	*per cent*	*per cent*	*per cent*	
Theoretical	3.98	49.95	41.43	4.66	464
Obtained	3.23	45.04	45.91	5.82	464
	number	*number*	*number*	*number*	
Theoretical	18	232	193	21	464
Obtained	15	209	213	27	464

$\chi^2 = 3.258$

P. lies between 0.50 and 0.30.

the effects of the genes are additive and that they have equal effects. However, if these assumptions regarding the gene action are correct, then we should be able to calculate the theoretical mean of the F_2 population which should not be significantly different from the obtained mean. The calculated mean of the F_2 genotypes are given in table 30. The means of the *AABB, AaBb,* and *aabb* genotypes are taken as that of the P_2, F_1, and P_1 respectively. The means of the *AABb, AaBB, Aabb,* and *aaBb* genotypes are calculated from the mean of the B_1 populations. If the gene action is additive and the genes have equal effect, the means of the *AAbb* and *aaBB* genotypes should be the same as that of F_1 *(AaBb)*. The mean of the F_2 population is calculated by taking the theoretical percentage of the class values and summing. The calculated mean of the F_2 population is 4.39, which is not significantly different from the obtained mean (4.60). This further supports the conclusions that probably the gene action is additive and the genes have nearly equal effect.

DISCUSSION AND CONCLUSIONS

Goldschmidt *(7)* postulated that "the quantity of the thing that is called a gene is important for the result of gene action and that gene and effect are linked by the simple relation of a proportion between the quantity of the gene and the velocity of the chain of reactions." According to Dobzhansky and Holz *(4)*, "The velocity of the chain of reactions controlled by the gene and the velocity or the amount of substance produced by the gene in a given individual depend on the interactions with the physiological states induced by all other genes of the organism along with the environmental processes at a given stage of the developmental process."

The type of gene action as stated in the hypothesis above seems to be operating in the growth habit of the material in this study. The amount of substance produced by a particular gene may vary at different stages of the growth of the plant. Whether a plant is bush or vining will be determined by a balance of the substances produced by the respective genes for bush and vining habit.

In the early stages of growth before flowering where there are two genes for bush habit and two for vining *(AaBb, AAbb, aaBB)*, the genes for bush habit *(AB)* probably produce some bush habit substance in a greater quantity than do the genes for vining *(ab)* and hence the plant remains bush in growth habit at the early stage of growth.

At a later stage of development the genes for vining *(ab)* begin to produce that vining habit substance with a greater velocity. Thus the individuals with *AaBb, AAbb,* and *aaBB* genotypes become vining in habit at the later stage. Naturally the individuals with three dosages of genes for vining and one for bush *(Aabb, aaBb)* must be vining. The individuals with *AABb* and *AaBB* genotypes are bush in habit in the early growth period. At a later stage when the velocity of the chain of reactions for the vining genes is faster, the individuals with *AaBB* and *AABb* genotypes show a tendency to vine, but at no stage of the development are they vining in habit.

This indicates that the amount of substance produced by one dosage of the vining factor is not sufficient to overcome completely the effect of the substance produced by three dosages of genes for the bush factor. Thus the growth of the plant seems to be determined by the quantity of the substance produced by the respective genes. The quantity of the substance produced is controlled by the stage of the development of the plant and the dosage of the factors. It is perhaps this kind of change in the growth habit during the growth period that has been termed "developmental reversal of dominance" by Shifriss *(16)*.

In studying the phenomenon of dominance, it is necessary to recognize both phenotypic and genic dominance. Phenotypic dominance can be determined by comparing the means of the two parents and the mean of the F_1 generation. Genic dominance is determined from a study of the means, variances, and phenotypes of the different genotypes. It must also be realized that genic dominance is dependent upon the genotypic milieu (Fisher, *6*, Dobzhansky, *3)*. "Genes affecting a character may be partially recessive, show no dominance, partial dominance or complete dominance, yet all may interact to give complete or nearly complete, phenotypic dominance and in some cases heterosis." (Powers, *13)*.

Fewer days from seeding to opening of the first male and of the first female flower show complete phenotypic dominance over more days. The genetic variances also indicate complete genic dominance. The difference in days between the opening of the first male and first female flower indicates complete phenotypic and genic dominance for shorter duration. Complete phenotypic and genic dominance for fewer days has also been reported in tomatoes (Power, *11)*.

The F_1 mean for the weight of the fruit is significantly higher than the average mean of the two parents. This indicates partial phenotypic dominance for the larger fruit size. As both the parents carry recessive genes and show transgressive segregation in the backcross populations, genic dominance cannot be determined from the genetic variances. However, it is quite evident from the F_1 mean that the genic dominance is not complete.

For total solids there is no phenotypic or genic dominance.

The cupping character caused by incomplete enclosure of the ovarian tissue exhibits a great degree of heterosis. As both the parents carry recessive genes, no indication of genic dominance can be obtained from the genetic variances of the B_1 populations. The frequency distribution of the segregation generation shows a higher percentage of individuals in the 9.5 class (table 26) than does the F_1. This indicates that the genic dominance is not complete but it cannot be determined whether there is any partial genic dominance.

The nature of gene interactions will be considered next. For the number of days from seeding to the opening of the first male and first female flower, the nature of the gene action has been found to be nearly additive. Similarly, for total solids the calculated F_2 mean indicated a probably additive gene action.

For the difference in days between the opening of male and female flower, the theoretical means of the F_2 genotypes are:

AABB	2.34
AaBB	2.68
AABb	
AaBb	2.38
AAbb	6.38
aaBB	
Aabb	6.38
aaBb	
aabb	7.30

The above means indicate that a substitution of *A* or *B* in the *aabb* genotype lowers the mean from 7.30 to 6.38; i.e., by 0.92. A substitution of *A* in the *aaBb* genotype and a substitution of *B* in the *Aabb* genotype lowers the mean from 6.38 to 2.38; i.e., by 4.00. This indicates that this sudden great effect when *A* and *B* are present together should be due to the inter-allelic interaction between the *A* and *B* genes. The example of complementary action affecting flower color in sweet pea *(Lathyrus odoratus)* is well known *(18)*. Beadle and Coonradt *(1)* found that two mutant strains of *Neurospora crassa, (pantothenicless* and *Lysineless)* show no measurable growth on minimal medium. When like-sexed strains of the two mutants are grown together on the same medium, however, the growth rate is as high as that of the wild type. The sort of interaction between *A* and *B* gene as reported in this thesis is not complementary because *A* and *B* genes individually have an effect of lowering the mean value 0.92. An action like this is what may be termed partially complementary. A similar type of gene action has been reported in tomatoes by Powers, Locke, and Garett *(14)*.

The cupping character caused by incomplete enclosure of the ovarian tissue shows considerable heterosis in F_1. It has also been concluded that the genic dominance is not complete. How many factors are involved in this character has not been conclusively determined, but it seems quite probable that the two parents are differentiated by two or three factor pairs. As genic dominance is not complete, it is evident that certain kinds of gene interactions are involved. Physiological effects (East, *5)*, multiplicative effects (Powers, *13)*, complementary effects (Beadle and Coonradt, *1)*, and partial complementary effects as found in this study may be involved to produce the results noted. On the other hand, only a few of these interactions may be involved.

In studying the nature of gene action, the F_1 mean approaching the geometric mean between the parents has been interpreted to indicate a probable geometric gene action (Charles and Smith, *2;* MacArthur and Butler, *9* MacArthur, *8;* Powers, *10, 11* and Smith, *19)*. As was mentioned in the discussion of experimental results, the F_1 mean for the weight of the fruit is significantly higher than the geometric or arithmetic mean between the parents, and the F_2 mean is very close to the mean of the higher parent. The kind of gene action cannot be determined from the F_1 and F_2 means. A positively skewed frequency distribution has also been interpreted to indicate a probably geometric gene action (Charles and Smith, *2;* MacArthur, *8;* MacArthur and Butler, *9;* Sinnot, *17;* and Smith, *19)*. The frequency distribution of the F_2 population shows a bimodal curve though a certain degree of positive skewness is evident. However, skewness is only a rough measure for determining the kind of gene action and cannot be relied on. "Positive skewness may be caused by a predominance of dominant genes, an approach to physiological limit of phenotypic expression, interactions of such a nature that each gene acting to reduce size has progressively less effect the more they are acting in the same direction or by geometric action of the genes; negative skewness may be caused by a preponderance of dominant genes for increasing size, an approach to a physiological limit of phenotypic expression or by interaction of such nature that each gene acting to increase size has progressively less effect the more they are acting in the same direction." (Rasmusson, *15*).

Fruits ranging from 400.00 grams to 5500.0 grams have been obtained in the F_2 generation. In a cross of Greengold (1590 gms.) and Bush maxima (874 gms.) when the parents are differentiated by three gene pairs, it is evident that fruits with such a large variation cannot be expected on a strictly arithmetic or geometric gene action basis. This indictes complex inter- and intra-allelic interactions. The gene action should probably be multiplicative in order to get fruits as large as 5500.0 grams, though the F_1 mean can be explained on the basis that the gene action is close to additive. It seems probable that gene action is close to additive up to a certain threshold, while beyond or below that threshold the gene action becomes multiplicative.

The foregoing discussion of the interaction of the genes shows that the nature of these interactions is varied. A particular gene may have a certain kind of interaction up to a certain threshhold, while beyond that threshhold the gene action may be different. Whether a gene action is arithmetic or geometric cannot strictly apply for all genes in one organism or for all organisms. Under such conditions of gene interactions, no mathematical formulae can be universally applicable in determining the gene effect.

The preceding findings regarding the inheritance of certain economic characters should prove of great importance not only in squash breeding but possibly in the breeding of all cucurbita species. Earliness is an important factor in any breeding project. There is complete phenotypic and genic dominance for fewer days from seeding to the opening of the first female flower. A squash breeder who is engaged in hybrid seed production should bear in mind that one of his inbred lines to be used in the hybrid seed production should meet the requirements of his standard of earliness.

The experimental results show that the earliness of Bush maxima is due largely to a shorter duration between the opening of male and female flowers. The duration between the opening of male and female flower is governed by two factor pairs, while the number of days from seeding to the opening of the first female flower is determined by three factor pairs. The gene interactions indicate that probably these two characters are independently inherited. This finding should be of considerable importance to a cucurbit breeder who is breeding for earliness. Even in the early varieties the shorter period between the opening of male and female flower can be transferred, and thus we should be able to breed for extra earliness.

No rapid method of estimating the quality of squash fruit has been known to squash breeders. The inheritance of total solids was studied in order to have such a measure for the quality of the fruit. The quality of the fruit seems to be dependent mostly on the density of the flesh and on the amount of total solids. Because of lack of time, the author was not able to study the inheritance of the density of the fruit. A measure of total solids, along with the density of the fruit, will probably furnish a method of determining the quality of the fruit. As the inheritance of total solids is governed by two gene pairs and the gene action is additive, a squash breeder should be able to combine easily the high quality of the fruit with other desired characters.

The results regarding the inheritance of the cupping character show that the incomplete enclosure of the ovarian tissue is dominant. Since fruits with cupping character have been found to be of poor keeping quality, the squash breeder engaged in hybrid seed production should eliminate the cupping character from his inbred lines.

In a breeding project involving Bush maxima and Greengold, it would not be difficult to isolate lines which will be free from incomplete enclosure of the ovarian tissue. Approximately 25.0 per cent of the individuals in the B_1 population and 40.0 per cent of the individuals in the F_2 population had fruits with no cups.

SUMMARY

Greengold and a variety of *Cucurbita maxima* which is bush in habit were used to produce the hybrid populations. The methods used in calculating the genetic variances and in determining the number of gene pairs are those developed by Powers *(12)* and Powers, Locke, and Garett *(14)*.

The number of days from seeding to the opening of the first male flower, the number of days from seeding to the opening of the first female flower, and the weight of the fruit are differentiated by three major gene pairs.

Each of the following characters is differentiated by two major gene pairs: 1. Growth habit of the plant. 2. Color of the fruit. 3. The difference in days between the opening of the first male and first female flower. 4. Total solids.

The number of factor pairs involved in the incomplete enclosure of the ovarian tissue have not been conclusively determined, but it seems probable that the two parents are differentiated by two or three factor pairs.

There is complete phenotypic and genic dominance for the number of days from seeding to the opening of the first male flower, for the number of days from seeding to the opening of the first female flower, and for the difference in number of days between the opening of the first male and first female flower. There is partial phenotypic dominance for the weight of the fruit. There is no phenotypic or genic dominance for total solids. The cupping character shows a great degree of heterosis in F_1.

For color of fruit, green is partially dominant over orange. There is no dominance for growth habit, as growth habit is determined by the stage of growth and number of factors present for each character.

The gene action has been found to be nearly additive for the number of days to the first male flower, for the number of days to the first female flower, and for total solids.

The inter-allelic interaction for the difference in days between the opening of the first male and first female flower is what may be termed as partially complementary. There are highly complex inter- and intra-allelic interactions for the weight of the fruit and for the incomplete enclosure of the ovarian tissue.

This report has included discussion of practical application of the foregoing findings in breeding of squash as well as in breeding all cucurbits.

LITERATURE CITED

1. Beadle, G. W., and Coonradt, Verna L. Heterocaryosis in *Neurospora crassa.* Genetics **29:** 291-308. 1944.
2. Charles, D. R., and Smith, H. H. Distinguishing between two types of gene action in quantitative inheritance. Genetics **24:** 34-48. 1939.
3. Dobzhansky, Theodosius. Genetics and the origin of species. Ed. 2, Columbia University press, New York. 1941.
4. Dobzhansky, Theodosius and Holz, A. M. A re-examination of the problem of manifold effects of genes in *Drosophila melanogaster.* Genetics **28:** 295-303. 1943
5. East, Edward M. Heterosis. Genetics **21:**375-397. 1936.
6. Fisher, R. A. The evolution of dominance. Biol. Reviews **6:**345-368. 1931.
7. Goldschmidt, Richard. Physiological genetics. 123 pp. McGraw-Hill Book Company, Inc., New York and London. 1938.
8. MacArthur, John W. Size inheritance in tomato fruits. Jour. Hered. **32:**291-295. 1941.
9. MacArthur, John W., and Butler, Leonard. Size inheritance and geometric growth processes in the tomato fruit. Genetics **23:**253-268. 1938.
10. Powers, LeRoy. Studies on the nature of the interactions of the genes differentiating quantitative characters in a cross between *Lycopersicon esculentum* and *Lycopersicon pimpinellifolium.* Jour. Genet. **39:**139-170. 1939.
11. Powers, LeRoy. Inheritance of quantitative characters in crosses involving two species of *Lycopersicon.* Jour. Agr. Res. **63:**149-174. 1941.
12. Powers, LeRoy. The nature of the series of environmental variances and the estimation of the genetic variances and the geometric means in crosses involving species of *Lycopersicon.* Genetics **27:**561-575. 1942.
13. Powers, LeRoy. An expansion of Jones's theory for the explanation of heterosis. Amer. Nat. **78:**275-280. 1944.
14. Powers, LeRoy, Locke, L. F., and Garett, J. G. Developmental genetic studies of per cent of flowers that set fruit, number of days from seeding to the first ripe fruit, and weight per fruit in crosses between two varieties of *Lycopersicon esculentum Mill.* (Unpublished).
15. Rasmusson, J. A contribution to the theory of quantitative character inheritance. Hereditas **18:**245-261. 1933.
16. Shifriss, Oved. Developmental reversal of dominance in *Cucurbita pepo.* Am. Soc. Hort. Sci. Proc. **50:**330-346. 1947.
17. Sinnott, Edmund W. The relation of gene to character in quantitative inheritance. Natl. Acad. Sci. Proc. **23:**224-227. 1937.
18. Sinnott, Edmund W. and Dunn, L. C. Principles of genetics. Ed. 3, McGraw-Hill Book Company, Inc., New York and London. 1939.
19. Smith, Harold H. Inheritance of corolla color in the cross *Nicotiana Langsdorffi* by *N. Sanderae.* Genetics **22:**347-360. 1937.
20. Smith, Harold H. The relation between genes affecting size and color in certain species of *Nicotiana.* Genetics **22:**361-375. 1937.