

Chapter 19

Gene Recombination and Heterosis

This article will be confined primarily to the tomato (*Lycopersicon*) genetic work which has a bearing on gene recombination and heterosis. The barley (*Hordeum*) genetic research which is discussed briefly was conducted at the University of Minnesota. The tomato genetic research which constitutes the bulk of the material discussed was conducted at the United States Horticultural Field Station, Cheyenne, Wyoming.

With the present available methods of analysis it is difficult in quantitative inheritance studies to distinguish between blocks of fairly closely linked genes and individual pairs of genes. This has been shown by the work of Jones (1917), Warren (1924), Mather (1942, 1949), and Straus and Gowen (1943). Consequently, in this article where the two genetic systems are not distinguishable the term pairs of genes will be employed. Mather (1949) has used the term *effective factor* to depict such a genetic situation.

MARKER GENES AND LINKAGE IN BARLEY

Powers (1936) has shown that in a cross between B1 (*Hordeum deficiens*) and Brachytic (*Hordeum vulgare*) the F_1 , which is a two-row barley, gave a greater yield of seed per plant than either the two-row or six-row parents. Then, weight of seed per plant shows heterosis. The data on marker genes and linkage in barley presented have some bearing upon whether any of the advantages of the F_1 hybrid attributable to heterosis can be recovered in inbred lines through gene recombinations.

The *deficiens* (two-row) character was found to be differentiated from the *vulgare* (six-row) character by one pair of genes designated as *Vv*, and the brachytic character from the normal character by one pair of genes designated

as *Brbr*. Using these symbols, the genotype of the F_1 is $VvBrbr$. The Vv gene pair is carried on chromosome 1 and the *Brbr* gene pair on chromosome 7.

Table 19.1 gives the comparative effect upon four quantitative characters of genes associated in inheritance with Vv and vv and VV and vv , as deter-

TABLE 19.1

COMPARATIVE EFFECT UPON FOUR QUANTITATIVE CHARACTERS OF GENES ASSOCIATED IN INHERITANCE WITH Vv AND vv , AND VV AND vv ; F_2 GENOTYPES OF A BARLEY HYBRID

GENOTYPE	WEIGHT OF SEED*		SPIKES PER PLANT*		HEIGHT OF PLANT*		LENGTH OF AWN*	
	$Vv-vv$	$VV-vv$	$Vv-vv$	$VV-vv$	$Vv-vv$	$VV-vv$	$Vv-vv$	$VV-vv$
<i>BrBr</i>	-2.22	-3.44	1.72	0.21	1.54	0.64	16.58	7.50
<i>Brbr</i>	-2.98	-3.74	0.94	0.39	2.08	1.41	16.42	9.20
<i>brbr</i>	-1.88	-2.74	0.13	-0.94	1.03	-0.68	1.95	-6.68

* Weight of seed per plant is expressed in grams, spikes per plant in number, height of plant in inches, and length of awn in millimeters.

TABLE 19.2

COMPARATIVE EFFECT UPON FOUR QUANTITATIVE CHARACTERS OF GENES ASSOCIATED IN INHERITANCE WITH Vv AND VV , AND VV AND vv ; F_2 GENOTYPES OF A BARLEY HYBRID

GENOTYPE	WEIGHT OF SEED*		SPIKES PER PLANT*		HEIGHT OF PLANT*		LENGTH OF AWN*	
	$Vv-VV$	$VV-vv$	$Vv-VV$	$VV-vv$	$Vv-VV$	$VV-vv$	$Vv-VV$	$VV-vv$
<i>BrBr</i>	1.22	-3.44	1.51	0.21	0.90	0.64	9.08	7.50
<i>Brbr</i>	0.76	-3.74	0.55	0.39	0.67	1.41	7.22	9.20
<i>brbr</i>	0.86	-2.74	1.07	-0.94	1.71	-0.68	8.63	-6.68

* Weight of seed per plant is expressed in grams, spikes per plant in number, height of plant in inches, and length of awn in millimeters.

mined by differences between means of F_2 plants. In every case, the differences between Vv and vv are greater than the differences between VV and vv for spikes per plant, height of plant, and length of awn. With the exception of the comparison between VV and vv within the *brbr* genotype, the differences are in favor of the two-row (Vv and VV) segregates as compared with the six-row (vv) segregates. Within the *brbr* genotype, vv plants exceed the VV plants for all three characters. As regards weight of seed per plant in every case the six-row plants outyielded the two-row plants whether heterozygous deficiencies or homozygous deficiencies. However, the differences between vv and Vv were less than those between vv and VV .

The data of Table 19.2 show that for all characters the Vv plants give an

increase over the VV plants, and with the exception of the $Brbr$ genotype for height of plant and length of awn, the differences of Vv - VV are greater than the differences for VV - vv .

These facts concerning the data reveal that Vv is associated with an increase in all four quantitative characters. For spikes per plant, height of plant, and length of awn this increase results in heterosis.

Hypotheses for Difference in Vigor

If the increase noted is due solely to an interaction between V and v such as is depicted by East's physiological hypothesis, then it would not be possible to obtain homozygous lines possessing any of this increase. However, if the heterosis noted is due to a combination of favorable and unfavorable genes linked with V and v , it should be possible to obtain lines in which some of the favorable genes are recombined. These lines should show some increase in the four quantitative characters studied. In the event that linkage of genes favorable and unfavorable to an increase in the quantitative characters was found to furnish the most logical explanation, an intraallelic interaction such as depicted by East's physiological hypothesis still may be having some influence as the two systems are not mutually exclusive.

Tables 19.1 and 19.2 show that Vv results in an increase of all four characters: weight of seed per plant, number of spikes per plant, height of plant, and length of awn. This fact is most simply explained by assuming the production of a favorable growth-promoting substance which influences all of them. Then such being the case, on the basis of East's (1936) physiological hypothesis, V and v supplement each other, resulting in greater development. Next consider the development of the lateral florets which determines the number of rows of kernels per spike (two-row or six-row spikes). The Vv segregates are two-row types, whereas the vv segregates are six-row types. Hence, as regards the character number of rows of kernels per spike, the interaction between V and v is such as to prohibit the development of the lateral florets, resulting in a two-row barley spike rather than a six. Summing up, on the basis of the physiological hypothesis, in the case of four quantitative characters the interaction between V and v is such as to stimulate development. In the case of number of rows of kernels per spike the interaction is such as to prohibit development of the lateral florets. From physiological genetic considerations such a pleiotropic effect seems rather improbable.

Explaining the heterosis associated with Vv plants on the basis of linkage, a simple interpretation would be that the favorable linked genes and their alleles interact according to Jones's (1917) hypothesis to produce a substance favorable to growth processes, resulting in the heterosis noted; and that V is dominant to v resulting in Vv (F_1) plants having two-row barley spikes. This explanation does not require the assumption that V and v stimulate

growth in one character and inhibit it in another, and hence is more in accord with modern physiological genetic concepts.

The article by Powers (1936) furnishes additional information pertaining to gene recombination and heterosis. If genes other than *Vv* are responsible for the heterosis noted, then F_2 plants having a genotype identical to the F_1 generation should give a somewhat lower yield than the F_1 . Since the F_1 plants were not grown in a randomized experiment with the F_2 plants, the comparison must be made through the B1 parent. As compared through the B1 parent an actual reduction of one gram in yield of seed per plant was found (Powers, 1936). This reduction could be due to genes carried on chromosome 1, as are *V* and *v*, or to genes carried on other chromosomes. In either event, theoretically some of the genes favorable to increased weight

TABLE 19.3
COMPARISON BETWEEN PARENTS AND F_2 PARENTAL GENOTYPES FOR WEIGHT OF SEED PER PLANT IN A BARLEY HYBRID

TOTAL NUMBER OF PLANTS	WEIGHT OF SEED PER PLANT IN GRAMS			
	F_2	Parent	Difference	<i>t</i>
78 and 266*	3.9	1.9	2.0	28.189
64 and 63†	4.5	4.0	0.5	0.761
Interaction			1.5	5.807

* *VVBrBr*, genotype of B1 parent, two-row normal.

† *vvbrbr*, genotype of Brachytic parent, six-row Brachytic.

of seed per plant that resulted in the heterosis noted in the F_1 population must be capable of recombination.

Even though some of the genes favorable to increased growth can be recombined, the yield of the lines in which the favorable genes have been combined depends upon the nature of the interaction of the genes. The weights of seed per plant of parents and F_2 plants of the parental genotypes are given in Table 19.3. From this table it can be seen that the F_2 plants of the *VVBrBr* genotype gave an increased yield of 2.0 grams per plant over the B1 parental plants having the same genotype. However, the F_2 plants of the same genotype as the Brachytic parent gave an increase over this parent of only 0.5 grams per plant, which is not statistically significant. The interaction of 1.5 grams (Table 19.3) is statistically significant. This means that a preponderance of the genes favorable to increased weight of seed per plant must have entered the cross from the Brachytic parent. The balance of the unfavorable genes that entered the cross from the B1 parent did not cause a corresponding decrease in weight of seed per plant of the F_2 plants possessing the *vvbrbr* genotype.

In this same study (Powers, 1936) found that the greater the number of genes in the genotype tending to increase a character the greater is the effect of any given gene. It is apparent that it is not possible to definitely predict the yield of seed per plant resulting from recombining genes favorable to growth because of the interactions noted. Either a greater or smaller increase than expected may be obtained. Such interactions of genes would affect the yield of plants in which the favorable genes were recombined, and hence the feasibility of obtaining inbred lines equaling or excelling the F_1 hybrid. In some cases the probability of getting the desired results would be increased and in other cases decreased; depending on the type of interallelic and intra-allelic interactions of the genes.

GENE RECOMBINATIONS DIFFERENTIATING WEIGHT PER LOCULE WHICH EXCEED HETEROSIS OF F_1 POPULATION

The data for weight per locule of fruit for the Porter \times Ponderosa tomato hybrid and parental populations grown at Woodward, Oklahoma, in

TABLE 19.4
ARITHMETIC AND LOGARITHMIC MEANS FOR
WEIGHT PER LOCULE OF PORTER \times PONDEROSA
TOMATO HYBRID AND PARENTAL POPULATIONS*

POPULATION	MEAN	
	Arithmetic	Logarithmic
Porter.....	10.2	1.018253 \pm 0.012325
B_1 to Porter.....	11.8	1.070936 \pm 0.009939
F_1	14.4	1.168729 \pm 0.010134
F_2	13.5	1.128481 \pm 0.011879
B_1 to Ponderosa.....	13.7	1.124941 \pm 0.012651
Ponderosa.....	9.8	0.982054 \pm 0.011845

* Grown at Woodward, Oklahoma, in 1941; original data taken in grams and transformed to logarithms to obtain the means and standard errors of the logarithms.

1941 (Powers, Locke, and Garrett, 1950) will be analyzed to determine whether in F_2 and backcross populations gene recombinations are occurring which exceed the heterosis of the F_1 population.

The means for weight per locule calculated on both the arithmetic and logarithmic scales are given in Table 19.4. Weight per locule is greatest for the F_1 population, and the means of the B_1 to Porter, F_2 , and B_1 to Ponderosa populations are larger than the means of the Ponderosa and Porter parents, but smaller than the mean of the F_1 population. The only means not showing significant differences are the means of Porter and Ponderosa, and the means of the F_2 and B_1 to Ponderosa populations. Hence, in these hybrid populations weight per locule definitely shows heterosis on either scale.

The frequency distributions for weight per locule for the Porter \times Ponderosa hybrid and parental populations are given in Table 19.5. This table shows that the F_2 and B_1 to Ponderosa populations have plants falling into classes of greater value than 1.511883, the last class in which F_1 or Ponderosa plants occur. There are nine such F_2 plants and three such B_1 to Ponderosa plants. If no recombination of genes to produce plants with weight per locule greater than the F_1 plants is possible, these plants with values greater than any individual of the F_1 population must be chance deviates. Moreover, the chance deviates must be those plants in the F_2 population having the F_1

TABLE 19.5
OBTAINED FREQUENCY DISTRIBUTIONS FOR WEIGHT PER LOCULE
OF TOMATO FRUITS FOR PORTER \times PONDEROSA HY-
BRID AND PARENTAL POPULATIONS*

POPULATION	UPPER LIMIT OF CLASS IN LOGARITHMS OF GRAMS																					TOTAL PLANTS
	0.397940	0.653212	0.812913	0.929419	1.021189	1.096910	1.161368	1.217484	1.267172	1.311754	1.352182	1.389166	1.423246	1.454845	1.484300	1.511883	1.537819	1.562293	1.585461	1.607455	1.795880	
Porter.....	1	..	4	27	80	98	20	2	232
B ₁ to Porter.....	1	3	13	54	81	102	80	49	35	16	11	1	1	...	1	448
F ₁	1	6	22	35	49	37	34	23	13	4	2	3	4	233
F ₂	13	31	68	82	81	63	42	24	17	11	8	3	1	...	4	2	453
B ₁ to Ponderosa...	1	6	17	29	45	71	72	62	52	26	19	18	1	4	4	4	1	1	1	434
Ponderosa.....	..	10	21	28	25	16	18	9	4	6	2	3	1	..	1	1	145

* Grown at Woodward, Oklahoma, in 1941; original data taken in grams and transformed to logarithms to obtain the means and standard errors of the logarithms.

genotype or a very similar genotype. The probability of their being chance deviates possessing the F_1 or similar genotypes can be determined.

The mean of the logarithms of the F_1 population is 1.168729, and the standard error of a single determination is 0.123426. Calculations (for method see Powers, Locke, and Garrett, 1950) show that only 0.3 per cent of such a genotypic population would be expected to have a value greater than 1.511883. The following tabulation shows the theoretical number of gene pairs differentiating the parents, the theoretical percentage of the population of the F_2 or B_1 to Ponderosa populations possessing the same genotype as the F_1 , the theoretical number of plants of the F_1 genotype in a population of 453 F_2 plants and in a population of 434 B_1 to Ponderosa plants, and the theoretical number of plants of the F_1 genotype in the F_2 population and in the B_1 to Ponderosa population expected to exceed a value of 1.511883.

An examination of the data opposite one pair of genes in the tabulation below shows that only 0.68 F_2 plants would be expected to exceed a value of

1.511883, whereas 9 plants did so (see Table 19.5). The same comparison for the B_1 to Ponderosa population is 0.65 expected and 3 obtained. Also, a study of the tabulation below reveals that with an increased number of gene pairs differentiating the parents the odds become even greater against those plants which exceed 1.511883 being chance deviates.

It remains to be seen whether plants of the F_1 genotype plus plants of genotypes which might have similar effects, but do not possess recombination of favorable genes in excess of the total number of favorable genes car-

NUMBER PAIRS OF GENES	PER CENT POPULATION OF F_1 GENO- TYPE	NUMBER OF PLANTS OF F_1 GENOTYPE		NUMBER OF PLANTS EXPECTED TO EX- CEED A VALUE OF 1.511883	
		F_2	B_1	F_2	B_1
1.....	50.00	226.50	217.00	0.68	0.65
2.....	25.00	113.25	108.50	0.34	0.33
3.....	12.50	56.62	54.25	0.17	0.16
4.....	6.25	28.31	27.12	0.08	0.08
5.....	3.12	14.17	13.56	0.04	0.04

ried by the F_1 , could be responsible for the results noted. The result would be to increase the proportion of the F_2 and B_1 to Ponderosa populations fluctuating around means very similar in magnitude to that of the F_1 population. The extreme case (but highly improbable) would be to have all of these two populations made up of such plants. On this basis and on the basis that the parents are differentiated by one pair of genes, the number of plants of the F_2 population expected to exceed 1.511883 is 1.36, and for the B_1 to Ponderosa population is 1.30. The number of plants obtained (Table 19.5) is 9 for the F_2 population and 3 for the B_1 to Ponderosa population. Furthermore, the B_1 to Porter population had 1 plant in a class beyond that in which any F_1 plants occurred.

The analysis can be carried further. For the F_2 population the number of plants expected to exceed 1.562293 is 0.3223 and the number obtained is 3. Whereas the values for the B_1 to Ponderosa population are 0.3087 and 1, respectively. Also, the frequency distributions (Table 19.5) in general do not support the supposition that over one half of the plants of the F_2 and B_1 to Ponderosa populations are fluctuating around a mean as great as that of the F_1 generation. Again with an increase in number of gene pairs differentiating the parents, the odds against the plants exceeding 1.562293 being chance deviates become even greater. It is evident that the data are not in accord with the assumption that plants of the F_1 genotype have the greatest weight per locule. This is true regardless of the number of gene pairs differentiating the parents. Therefore, some of the plants falling in classes having values

greater than 1.511883 must have genotypes composed of more favorable genes than the F_1 , and therefore recombinations of genes to produce plants having a greater weight per locule than the F_1 plants have occurred.

Whether inbred lines retaining this increased weight per locule can be established is dependent upon the number of gene pairs differentiating the parents and linkage relations (Jones, 1917). Close linkage of genes favorable to increase in weight per locule would favor recombination. Whereas close linkage of genes favorable to increase in weight per locule with those not favorable would hinder recombination and hence reduce the chances of obtaining inbred lines retaining some or all of the advantages attributable to heterosis.

The data furnish evidence concerning the number of gene pairs differentiating weight per locule. From Table 19.5 it can be seen that the plants of the F_2 generation falling beyond the value 1.511883 are distributed over four different classes, and those of the B_1 to Ponderosa population falling beyond this same value occur in three different classes. The behavior of these plants cannot be explained on the basis of five or more independently inherited pairs of genes, as there are too many of these plants falling beyond the 1.511883 class. In addition, the weights per locule of those falling in these classes are greater than can be explained on the basis of chance deviation.

Further, to account for the plants of the F_2 and B_1 to Ponderosa populations falling in those classes beyond 1.511883, on the basis of five or more pairs of independently inherited genes differentiating the parents, it would be necessary to assume that 50 per cent or more of the plants were fluctuating around a mean greater than that of the F_1 generation. Since the means (Table 19.4) of the F_2 and B_1 to Ponderosa populations are less than the mean of the F_1 , these populations cannot have a greater majority of the plants fluctuating around a mean larger in magnitude than that of the F_1 plants. This deduction is confirmed by the frequency distributions of Table 19.5, as both of these populations have a greater percentage of their plants in lower classes of the frequency distributions than does the F_1 population. Powers, Locke, and Garrett (1950) have shown that the data give a good fit to frequency distributions calculated on the assumption that the parents are differentiated by three pairs of genes.

Here, proof of recombination of genes to produce plants in the F_2 and B_1 to Ponderosa populations with greater weight per locule than F_1 plants is fairly conclusive. Also, since the number of gene pairs or closely linked blocks of genes is few, it should be possible by selection to establish inbred lines retaining this advantage.

MAIN AND COMPONENT CHARACTERS

The data from the parental and hybrid populations of tomatoes on the main and component characters provide information concerning the relations between gene recombination, dominance, and heterosis.

Weight of Fruit and Its Component Characters

The data on weight per locule, number of locules, and weight per fruit for the Porter \times Ponderosa hybrid and parental populations are given in Tables 19.4 and 19.6. On the arithmetic scale, smaller numbers of locules show partial dominance. On the logarithmic scale the means of the F_1 and F_2 populations are not significantly different from the average of the means of the Porter and Ponderosa populations. The mean of the B_1 to Porter population is not significantly different from the average of the means of the Porter and F_1 populations. The mean of the B_1 to Ponderosa population is not sig-

TABLE 19.6

THE ARITHMETIC AND LOGARITHMIC MEANS FOR NUMBER OF LOCULES AND WEIGHT PER FRUIT OF PORTER \times PONDEROSA TOMATO HYBRID AND PARENTAL POPULATIONS*

POPULATION	NUMBER OF LOCULES		WEIGHT PER FRUIT	
	Arith- metic	Logarithmic	Arith- metic	Logarithmic
Porter.....	2.1	0.307072 ± 0.002151	21.5	1.326101 ± 0.012358
B_1 to Porter.....	3.1	0.468411 ± 0.008158	36.6	1.539833 ± 0.010394
F_1	4.5	0.637265 ± 0.007663	65.0	1.806845 ± 0.009416
F_2	4.7	0.628793 ± 0.012522	63.5	1.762614 ± 0.013078
B_1 to Ponderosa..	7.1	0.829404 ± 0.007738	97.3	1.954430 ± 0.013269
Ponderosa.....	10.0	0.983292 ± 0.017094	97.7	1.965097 ± 0.008750

* Grown at Woodward, Oklahoma, in 1941; original data taken in numbers and grams and transformed to logarithms to obtain the means and standard errors of the logarithms.

nificantly different from the average of the means of the F_1 and Ponderosa populations. Hence, on the logarithmic scale there is no dominance, and the data indicate that the genetic variability follows the logarithmic scale. In other words, the effects of the genes differentiating weight per locule are multiplicative. This is true of both the intraallelic and interallelic interactions.

Thus on the logarithmic scale number of locules shows no dominance, weight per locule shows heterosis (Table 19.4) and the two combine additively to give weight per fruit. For weight per fruit the F_1 indicates partial dominance of greater weight per fruit, the B_1 to Ponderosa complete dominance, and the B_1 to Porter no dominance. On the arithmetic scale the two component characters unite multiplicatively, and the F_1 indicates partial dominance of greater weight per fruit, the B_1 to Ponderosa complete dominance, and the B_1 to Porter partial dominance of smaller weight per fruit. Then it is clear that regardless of scale, one of the component characters shows some degree of dominance, the other heterosis. They combine to produce the main character which in turn shows some degree of dominance.

Powers, Locke, and Garrett (1950) found the number of major gene pairs differentiating number of locules to be 3. Since weight per locule was found to be differentiated by 3 pairs of major genes, a comparatively few (probably 6) pairs of major genes differentiate weight per fruit. Hence, the number of major gene pairs responsible for heterosis of weight per locule is no greater than the number of major gene pairs responsible for no dominance of number of locules and partial or complete dominance of weight per fruit on the logarithmic scale. Then, in this study the number of pairs of major genes differentiating the character has no bearing on whether the hybrid populations will show no dominance, partial dominance, complete dominance, or heterosis.

From these results it follows that in this material recombination of genes to retain the advantages of heterosis is no different than recombination of genes to combine desirable characters. Furthermore, these data furnish rather convincing evidence that dominance and heterosis are different degrees of expression of the same physiological genetic phenomena, as was postulated by Powers (1941, 1944).

Main and Component Characters of 45 Hybrids Produced by Crossing 10 Inbred Lines of Tomatoes

Table 19.7 summarizes the dominance relations of the main and component characters of 45 hybrids produced by crossing 10 inbred lines of tomatoes.

The percentage values given in Table 19.7 were calculated from data presented in a previous article (Powers, 1945). The reader is referred to this article for the experimental design, a description of the material, and methods. Here, only the method of compiling the data need be given. All of the values of this table with the exception of those listed under heterosis were calculated from the formula $100[2\bar{F}_1/(\bar{P}_1 + \bar{P}_2)]$. The percentages listed under the column headings "heterosis" were calculated from the formula $100(\bar{F}_1/\bar{P}_1)$ and $100(\bar{F}_1/\bar{P}_2)$, respectively. \bar{F}_1 is the mean of the F_1 population, \bar{P}_1 the mean of the parent with the smaller value, and \bar{P}_2 the mean of the parent with the larger value. The 11 characters listed in Table 19.7 were originally expressed in the following units of measurement: Spread of plant in inches, yield per plant in grams, number of fruit that ripened per plant, height per plant in inches, weight per locule of the fruit in grams, number of days from first fruit set to first fruit ripe, number of days from first bloom to first fruit set, weight of fruit in grams, number of days from seeding to first bloom, number of locules per fruit, and number of days from seeding to first fruit ripe.

The odds against any value belonging in an adjacent classification (column) are greater than 19:1 with the exception of the two values designated with an asterisk. Even for these two values the odds against their deviating

more than one class are greater than 19:1. When interpreting the data it is necessary to have in mind that parental percentage values would have fallen into the complete dominance columns, the P_1 value into the first such column, and the P_2 into the second such column. Also, it should be kept in mind that the values listed in Table 19.7 are for the different F_1 hybrids, and with the exception of the values listed under the columns headed "heterosis" are percentages based on the means of the two respective parents. The percentages listed under the heterosis columns are based on the mean of the parent that fell into the adjacent complete dominance columns.

TABLE 19.7
PERCENTAGE RANGE IN EXPRESSION OF DOMINANCE FOR
DIFFERENT CHARACTERS OF F_1 TOMATO HYBRIDS*

CHARACTER	DOMINANCE						
	Heterosis	Complete	Partial	None	Partial	Complete	Heterosis
Spread of plant.						114	122
Yield, ripe fruit per plant.				106	117	166	171
Number, ripe fruit per plant.			78	99	142	172	155
Height of plant.			96	100	104	112	121
Weight per locule.			70	98		109	119
Period, first fruit set to first fruit ripe.		90	93	99	103		
Period, first bloom to first fruit set.	75	80				125*	
Weight per fruit.	95		53	102			
Period, seeding to first bloom.	89	95	99	100*			
Number of locules per fruit.	73	69	79	96			
Period, seeding to first fruit ripe.	95	93	96				

* As measured by percentages of averages of values of parents and percentages of parental values.

If dominance and heterosis are different degrees of expression of the same physiological genetic phenomena, then the different genotypes, as represented by the different F_1 hybrids, might be expected to show ranges in expression of a given character from different degrees of dominance to heterosis.

Every character listed in Table 19.7 except number of days from first fruit set to first fruit ripe, in the different hybrids, ranges from some degree of dominance to heterosis. Yield in grams of ripe fruit per plant, depending upon the genotype (F_1 hybrid), varied from no dominance through all classes to heterosis for increased yield. Number of ripe fruit per plant and height of plant varied through all classes from partial dominance of a decrease in magnitude of these two characters to heterosis for an increase. Weight of fruit in grams, number of days from seeding to first bloom, and number of locules per fruit varied from no dominance to heterosis for a decrease of these characters. Considering all of the characters there is a continuous array of values

(that is values in all classes) from heterosis for decrease of a character to heterosis for increase of a character, depending upon the character and genotype (F_1 hybrid).

The most logical conclusion from these figures is that dominance and heterosis to a considerable extent are different degrees of expression of the same physiological genetic phenomena. This hypothesis is greatly strengthened by findings of Powers (1941) that whether a character shows dominance or heterosis in some cases is dependent upon the environment and in other cases upon the genotype. As pointed out previously, gene recombination in relation to heterosis is no different from combining any two desirable characters by recombination of genes. A study of the component characters of the main characters given in Table 19.7 offers further evidence in support of this contention.

Yield of ripe fruit as determined by weight of fruit in grams is dependent upon number of fruits that ripen and weight per fruit. The first of these component characters, depending upon the F_1 hybrid being considered, varies from partial dominance of fewer number of ripe fruits to heterosis for an increased number of ripe fruits. The second component character varies from no dominance to heterosis for smaller weight per fruit. They combine multiplicatively, and in many cases result in heterosis for yield of fruit (Table 19.7 and Powers, 1944). Here again, then, is a case involving combination of characters to produce heterosis. To retain some of the benefits of heterosis in inbred lines would involve recombination of the genes differentiating the two component characters.

In turn the number of fruit that ripens is dependent to a large extent at Cheyenne, Wyoming, on earliness of maturity, number of days from seeding to first fruit ripe (Powers, 1945). Earliness of maturity varies from partial dominance of fewer days from seeding to first fruit ripe to heterosis for the shorter period. The component characters of earliness of maturity are period from seeding to first bloom, period from first bloom to first fruit set, and period from first fruit set to first fruit ripe. Number of days from seeding to first bloom varies from no dominance to heterosis for the shorter period. Number of days from first bloom to first fruit set varies from complete dominance of the longer period to heterosis of the shorter period. Number of days from first fruit set to first fruit ripe varies from partial dominance of the longer period to complete dominance of the shorter period.

Weight per fruit is dependent upon weight per locule and number of locules per fruit. Weight per locule varies from partial dominance for less weight per locule to heterosis for greater weight per locule. Number of locules varies from no dominance to heterosis for fewer locules. On the arithmetic scale these two component characters combine multiplicatively so that weight per fruit varies from no dominance to heterosis for less weight per fruit.

From the above, as was found true for yield per plant, the heterosis noted for earliness of maturity results from the combination of component characters which in certain F_1 hybrids may themselves exhibit heterosis. The same is true for weight per fruit. In other words, the study of genetics of heterosis has been somewhat simplified by breaking the main characters down into their component characters. Also, as before, the study shows that gene recombination to retain some or all of the increase of the F_1 hybrid over the parents is dependent upon the same physiological genetic phenomena as are involved in attempting to combine two or more desirable characters into a single inbred line.

RECOVERING INBRED LINES RETAINING ADVANTAGES ATTRIBUTABLE TO HETEROSIS

The physiological genetic phenomena that hinder or aid, by the recombination of genes, the recovery of inbred lines retaining some or all of the advantages attributable to heterosis are the same as those emphasized by Jones (1917) and East (1936). These are the number of gene pairs differentiating the parents, linkage relations of the genes, pleiotropy, and the interaction of the genes as determined by the measurement of end products, both interallelic and intraallelic. This genetic information can be obtained only by rather detailed genetic studies. With the quantitative characters such studies are expensive and time consuming. Hence, very few such studies have been made with tomato hybrids. Powers, Locke, and Garrett (1950) and Powers (1950b) have made a gene analysis for some of the main characters and their more obvious components. Even though the gene analysis for number of days from seeding to first fruit ripe has been completed for only one of the four crosses to be considered, this character and weight per locule will be treated as component characters of yield of ripe fruit per plant in the section dealing with number of pairs of genes differentiating the parents.

Number of Gene Pairs Differentiating Parents

In considering the bearing that number of gene pairs differentiating the parents has upon gene recombination and heterosis, just two characters will be considered: weight per locule and number of days from seeding to first fruit ripe. That both of these characters have an effect upon yield of ripe fruit should be kept in mind during the analyses and discussions which follow. Also, other component characters listed in Table 19.7 could be studied. However, the additional information gained would not justify the time and space required, as the fundamental principles involved can be brought out from an analysis and discussion of the data for the two characters chosen. The number of gene pairs (effective factors; Mather, 1949) differentiating weight per locule has been determined for all the hybrid populations listed in Table 19.8. For days from seeding to first fruit ripe the number of gene

pairs (effective factors) differentiating the parents has been determined for the Porter \times Ponderosa hybrid populations only.

In discussing the bearing the number of gene pairs differentiating the two parents has upon gene recombination and heterosis, information concerning phenotypic dominance of the characters for the hybrid populations is necessary and will be derived by studying the means of the parental and hybrid

TABLE 19.8

MEANS FOR WEIGHT PER LOCULE AND NUMBER OF DAYS FROM SEEDING TO FIRST FRUIT RIPE WITH TYPE AND NUMBER OF GENE PAIRS DIFFERENTIATING THE PARENTS FOR WEIGHT PER LOCULE*

POPULATION	DANMARK \times RED CURRANT		DANMARK \times JOHANNISFEUER		JOHANNISFEUER \times RED CURRANT		PORTER \times PONDEROSA	
	Weight per Locule (Gm.)	No. of Days From Seeding to Fruit Ripe	Weight per Locule (Gm.)	No. of Days From Seeding to Fruit Ripe	Weight per Locule (Gm.)	No. of Days From Seeding to Fruit Ripe	Weight per Locule (Gm.)	No. of Days From Seeding to Fruit Ripe
P ₁ †.....	0.45	156.9	4.61	164.9	0.44	126.0	10.2	147.7
B ₁ to P ₁	0.97	155.0	6.72	165.0	1.04	123.1	11.8	152.0
F ₁	2.33	153.8	7.96	165.6	2.70	118.9	14.4	149.6
F ₂	2.12	156.6	8.35	166.4	2.12	125.5	13.5	155.0
B ₁ to P ₂	4.82	159.7	8.32	167.6	4.48	124.7	13.7	168.8
P ₂ ‡.....	10.36	169.8	9.92	170.0	6.20	136.1	9.8	204.8
Type and number of pairs of genes.....	Minor 40+	Major 2 or 3	Minor 40+ Major 2 or 3	Major 3	Major 8

* For the hybrid populations of Danmark \times Red Currant, Danmark \times Johannisfeuer, Johannisfeuer \times Red Currant, and Porter \times Ponderosa.

† P₁ is Red Currant, Johannisfeuer, Red Currant, and Porter, respectively.

‡ P₂ is Danmark, Danmark, Johannisfeuer, and Ponderosa, respectively.

populations given in Table 19.8: The means for weight per locule of tomato fruits and number of days from seeding to first fruit ripe together with the type and number of gene pairs differentiating the parents for weight per locule for the hybrid populations of Danmark \times Red Currant, Danmark \times Johannisfeuer, Johannisfeuer \times Red Currant, and Porter \times Ponderosa are given in Table 19.8.

The first two hybrid populations were grown at Cheyenne, Wyoming, in 1938, the third hybrid population at the same location in 1939, and the last hybrid whose means are listed in the extreme right hand column of Table 19.8 was grown at Woodward, Oklahoma, in 1941. The means of this table

were taken from the following publications: Powers and Lyon (1941), Powers, Locke, and Garrett (1950), and Powers (1950a). The data will be analyzed to obtain information concerning the recombination of the genes differentiating weight per locule and number of days from seeding to first fruit ripe. Also, the data will be studied to ascertain the probable bearing this information has upon the production of inbred lines, by gene recombination, that retain some or all of the advantages attributable to heterosis of yield of ripe fruit per plant which the hybrid populations would be expected to exhibit.

On the arithmetic scale the Danmark \times Red Currant populations show partial phenotypic dominance for smaller weight per locule. The parents of the Danmark \times Red Currant hybrid were found to be differentiated by a large number of gene pairs (probably more than 40) which individually had minor effects. From these results it is evident that, if somewhere near one-half of the genes for smaller weight per locule in the Danmark \times Red Currant hybrid populations had entered the cross from one parent and the balance from the other parent, smaller weight per locule would have shown heterosis. Some of the genes must be linked because the parents have a haploid chromosome number of 12. In fact, since 40 or more pairs of genes are differentiating the parents, it seems highly probable that a system of linked polygenes is involved. With 40 pairs of genes differentiating the parents in the F_2 , to recover an individual possessing all of the genes for increased weight per locule (without linkage) would require a population of 10^{24} individuals. The size of such a population can be appreciated by considering the fact that 10^{11} is 100 billion. The bearing this has upon the feasibility of recovering from segregating populations inbred lines retaining much of the advantage that might be exhibited by F_1 hybrids is apparent.

The Red Currant parent which possesses small weight per locule also possesses earliness of maturity. Hence, some of the genes tending to increase weight per locule are almost certain to be located on the same chromosomes with a non-beneficial gene or genes tending to increase the time required for maturity. However, due solely to the large number of gene pairs differentiating weight per locule, with no close linkage, pleiotropy, or unfavorable interallelic and intraallelic interactions of the genes, only a comparatively small amount of the increased weight per locule of the Danmark parent could be combined with the earliness of maturity of the Red Currant parent by selection in the F_2 or backcross populations.

Weight per locule and earliness of maturity have a material influence on yield of ripe fruit per plant (Powers, 1945). In some crosses (see Tables 19.7 and 19.8) greater weight per locule is at least partially dominant. Since the shorter period for days from seeding to first fruit ripe for the Danmark \times Red Currant cross shows heterosis (Table 19.8) the hybrid populations would be expected to show heterosis for yield of ripe fruit per plant in crosses hav-

ing such a polygenic system conditioning weight per locule, provided greater weight per locule was at least partially dominant, and provided the genes for increased weight per locule and shorter period from seeding to first fruit ripe were divided between the two parents. The analyses and discussions in the immediately preceding paragraphs show that in such an event it would be almost impossible to obtain inbred lines which through gene recombination would retain any appreciable amount of the yield of the F_1 hybrid.

On the arithmetic scale the *Johannisfeuer* \times Red Currant populations show partial phenotypic dominance of smaller weight per locule with the exception of the B_1 to P_2 which indicates no dominance. The parents of the *Johannisfeuer* \times Red Currant hybrid populations were found to be differentiated by a large number of gene pairs (probably more than 40) each of which individually had minor effects and in addition by a few gene pairs (probably 2 or 3) having major effects. In these hybrid populations the total effect of the minor genes was greater than the total effect of the major genes. Again the shorter period from seeding to first fruit ripe showed heterosis.

With the number and type of gene pairs conditioning weight per locule found for the *Johannisfeuer* \times Red Currant hybrid, and provided the genes differentiating weight per locule exhibited at least partial dominance, as is indicated for the *Danmark* \times *Johannisfeuer* populations, certain parental combinations of the genes would result in the hybrid populations showing heterosis for increased yield of fruit per plant. Since comparatively few major gene pairs differentiate weight per locule, it should be possible by recombination of genes through selection in F_2 and backcross populations of such a cross to combine into inbred lines some of the increased yield attributable to heterosis.

The *Danmark* \times *Johannisfeuer* hybrid populations show partial phenotypic dominance for greater weight per locule, and complete dominance for shorter period from seeding to first fruit ripe. Two or three major gene pairs were found to be differentiating weight per locule. For weight per locule and number of days from seeding to first fruit ripe, dominance is such that had the genes tending to increase each of these two characters been divided between the two parents, the hybrid populations would have shown heterosis for both component characters. Likewise, if the above conditions had been fulfilled, yield of ripe fruit per plant would have shown heterosis in the hybrid populations.

The *Porter* \times *Ponderosa* hybrid populations showed at least partial genic dominance for weight per locule (Powers, Locke, and Garrett, 1950). The parents were found to be differentiated by three pairs of genes and the genes tending to increase weight per locule were distributed between the two parents. As was to be expected, the hybrid populations showed heterosis for increased weight per locule. Period from seeding to first fruit ripe showed almost if not complete dominance for the shorter period from seeding to first

fruit ripe. The number of major gene pairs found to be differentiating the parents was eight. Due to the magnitude of the work involved it was not possible to measure yield of fruit, but in all probability the hybrid populations of this cross would have shown heterosis for yield of ripe fruit per plant. In such an event it seems highly probable that some and perhaps a considerable amount of the increase in yield attributable to heterosis could be obtained in inbred lines through recombination of genes.

Considering the data for all the crosses listed in Table 19.8 the information may be summarized as follows: In the Danmark \times Red Currant cross a large number of gene pairs differentiates the parents and individually the genes have minor effects. The same is true of the Johannisfeuer \times Red Currant cross with the exception that two or three pairs of genes have major effects. In both the Danmark \times Johannisfeuer and the Porter \times Ponderosa crosses weight per locule is differentiated by a comparatively few pairs of genes having major effects. It is apparent that in the Porter \times Ponderosa cross it should be possible by selection in the segregating populations to obtain by recombination of genes inbred lines equaling if not excelling the F_1 fruits in weight per locule.

The discussions treating weight per locule and number of days from seeding to first fruit ripe as component characters of yield of ripe fruit per plant reveal that the recombination of genes to retain some or all of the advantages of the F_1 hybrid is analogous to recombination of genes for the purpose of combining desirable characters.

Linkage Relations

Linkage may be an aid or a hindrance to gene recombination. The data in Table 19.9 were computed to facilitate a consideration of the manner in which different linkage relations may affect recombination of genes.

Certain assumptions were essential to a calculation of the data. First, it was assumed that the coefficient of coincidence is 1. Since in most cases there is interference, to assume a coefficient of coincidence of 1 is to err on the conservative side. For example, all the values given in the second row heading (with the exception of the first and last) would increase as the coefficient of coincidence became smaller. The reverse is true of the figures in the third and fourth columns. The frequencies listed in the second, third, and fourth columns of Table 19.9 are the theoretical number of individuals in the F_2 population carrying the 12 plus genes in the homozygous condition. The cross-over values expressed as decimal fractions are assumed to be equal for the different sections of the chromosomes delimited by any two adjacent genes.

The conclusions to be drawn from the theoretical data of Table 19.9 are not invalidated by these assumptions. They merely serve the purpose of allowing the calculation of theoretical values for illustrative purposes. Other assumptions such as different values of crossing over for the various sections of the

chromosomes and different numbers of genes, combinations of genes in the parents, and number of linkage groups would not alter the conclusions to be drawn. In the illustration chosen only two linkage groups are shown and each has three pairs of genes. Also, the top row of genes represents the gamete from one parent and the lower row of genes the gamete from the other parent. In all three assumed cases, 3 plus and 3 minus genes entered the cross from each parent.

It is evident that innumerable plausible cases could be assumed, but the fundamental principles derived from a consideration of the theoretical values given in the table would not be altered. One further assumption should be

TABLE 19.9
THEORETICAL NUMBER OF INDIVIDUALS IN THE F_2 POPULATION THAT CARRY 12 PLUS (+) GENES WHEN THE PARENTS ARE DIFFERENTIATED BY 6 PAIRS OF GENES, EACH OF 2 CHROMOSOME PAIRS CARRYING 3 PAIRS OF GENES*

CROSS- OVER VALUE	LINKAGE RELATIONS IN F_1 (NUMBER PER MILLION)		
	$\begin{pmatrix} + + + \\ - - - \end{pmatrix} \begin{pmatrix} - - - \\ + + + \end{pmatrix}$	$\begin{pmatrix} + + - \\ - - + \end{pmatrix} \begin{pmatrix} - - + \\ + + - \end{pmatrix}$	$\begin{pmatrix} + - + \\ - + - \end{pmatrix} \begin{pmatrix} - + - \\ + - + \end{pmatrix}$
0.000...	62,500	0.000	0.000000
0.075...	33,498	1.448	0.000063
0.225...	8,134	57.787	0.410526
0.375...	1,455	188.596	24.441630
0.450...	523	234.520	105.094534
0.500...	244	244.141	244.140625

* The crossover values for each section of the chromosome being equal and of the magnitude shown.

mentioned. In every case the plus genes are assumed to give an increase in some desirable quantitative character and, comparatively, the minus genes a decrease. Finally, in the table two extreme situations are shown, namely that in which there is no crossing over and that in which the two sections of the chromosome between adjacent genes show 50 per cent of crossing over.

The data in the second column apply to that situation in which all of the plus genes occur in one member of the homologous chromosomes in each of the two pairs of chromosomes depicted. In the case of 50 per cent of crossing over or independent inheritance, only 244 individuals in a million of the F_2 population possess all twelve plus genes. The number of such individuals among a million F_2 individuals increases with a decrease in the percentage of crossing over until with no crossing over 62,500 individuals in a million possess all six pairs of the plus genes in the homozygous condition.

The data in the third column apply to that situation in which two plus genes are linked with one minus gene in one member of a chromosome pair and two minus genes with one plus gene in the other member of the same

chromosome pair. In this column the situation is reversed as compared to column two. Again 50 per cent of crossing over gives 244 individuals among a million in the F_2 possessing all twelve plus genes. This decreases with a decrease in the percentage of crossing over until with no crossing over no individuals in the infinite F_2 population contain more than eight plus genes. However, since two of the plus genes are carried on the same chromosome in each of the two linkage groups, an increase in the linkage intensity results in an increased number of individuals in the F_2 population possessing all eight plus genes in the homozygous condition.

Here, then, is a case in which close linkage facilitates recombination of desired genes up to a certain number, and from a practical standpoint further advances by selection in that generation are impossible. Also, it would be difficult to make further advances by continued selection in later generations. In the F_2 population with a crossover value of 0.075 the frequency of the $\begin{pmatrix} + & + & - \\ + & + & - \end{pmatrix}$ genotype expressed as a decimal fraction is 0.183024 and of the $\begin{pmatrix} + & + & - \\ + & + & + \end{pmatrix}$ genotype is 0.014840.

To obtain some F_3 families derived from F_2 plants of the latter genotype would require growing at least 300 selections in the F_3 generation. To separate the F_3 families derived from the F_2 plants of the former genotype from those derived from the latter genotype would require an adequately replicated, well designed experiment. Anyone who has worked with the quantitative characters either in genetics or plant breeding realizes the difficulties besetting such a task. After such F_3 families had been determined, only 25 per cent of the individuals would be of the $\begin{pmatrix} + & + & + \\ + & + & + \end{pmatrix}$ genotype. These would have to be tested in the F_4 to separate them from F_4 families derived from F_3 plants of the $\begin{pmatrix} + & + & - \\ + & + & + \end{pmatrix}$ and the $\begin{pmatrix} + & + & - \\ + & + & - \end{pmatrix}$ genotypes. Even with the small number of genes assumed in the above example, it would not be a simple matter to make progress by continued selection in later generations. The addition of a few more genes having the plus and minus genes alternating on the same chromosome would make further progress by continued selection in generations later than the F_2 practically impossible. From the above it is apparent that any series of plus genes being adjacent without minus genes intervening would facilitate recombination of desirable genes in the F_2 generation. It seems that in actual genetic and plant breeding materials many such combinations do exist.

The figures in the fourth column of Table 19.9 are the theoretical frequency distributions for that situation in which the plus and minus genes alternate on the chromosome. Again the number of individuals expected in the F_2 generations possessing all twelve plus genes decreases rather rapidly with a decrease in the percentage of crossing over. Even in the case of 50 per

cent of crossing over it is doubtful whether it is possible for the plant breeder or geneticist to isolate individuals from the F_2 population carrying twelve plus genes.

The data in Table 19.9 emphasize that even with the probably oversimplified genetic situation depicted it is not possible to recover in a single individual all of the genes favorable to the production of a desirable character for which the F_2 population is segregating, unless the favorable genes are located on the same chromosome and immediately adjacent to each other without unfavorable genes intervening. If any of the favorable genes are adjacent to each other without unfavorable genes intervening, then decided advances can be made by selection in the F_2 populations up to a certain point. Beyond that point further selection in the F_2 will have no effect, and selection in advanced generations does not offer much promise. The most difficult situation is that in which the linkage relation is such that the favorable and unfavorable genes alternate on the chromosome and the number of such linkage groups is at a minimum for the number of gene pairs involved.

For the sake of clarity of illustration only three linkage relations were shown. However, it is apparent that undoubtedly in the material available to plant breeders and geneticists, the possible different kinds of linkage relations are almost innumerable. Some will aid the investigator in obtaining the desired recombination of genes and others will be a decided hindrance. In the cases of undesirable linkage relations it will be almost impossible for the breeder to obtain individuals possessing recombinations of genes making that individual equal to or superior to the F_1 for the character exhibiting heterosis. On the other hand, desirable linkage relations may make it possible to obtain the recombination of genes sought even though a large number of gene pairs differentiates the parents used in hybridization.

Pleiotropy, and Interallelic and Intraallelic Interactions

Powers, Locke, and Garrett (1950) have made a rather detailed genetic study of eight quantitative characters in hybrid and parental populations involving the Porter and Ponderosa varieties of *Lycopersicon esculentum* Mill. The characters studied and the indicated number of major gene pairs differentiating the parents are as listed immediately below.

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

With most quantitative characters it is difficult to distinguish between pleiotropy and linkage. It seems highly probable that linkage instead of plei-

otropy produced the relations noted by the above authors between the four series of genes *Ff*, *Ss*, *Rr*, and *Lcl* 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 by Powers, Locke, and Garrett (1950) 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 *Lcl* and *Ww* series of genes, differentiating number of locules and weight per locule, respectively, were independent as regards linkage and pleiotropy. In these studies pleiotropy was not of major importance.

Phenotypic and genic dominance furnish some information concerning the interallelic and intraallelic interactions of the genes. That genic dominance is dependent upon the genotypic milieu was pointed out by Fisher (1931) and many others (Dobzhansky, 1941). Hence both interallelic and intraallelic interactions as measured by end products are second order interactions, genes \times genes \times the environment.

Any of the interactions of genes noted as affecting any of the component characters dealt with in the study by Powers, Locke, and Garrett (1950) 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.

Had the dominant genes of the *Ss* series entered the cross from one parent and the dominant genes from the *Rr* series entered the cross from the other parent, the F_1 hybrid would have shown heterosis for earliness of maturity. Porter would then represent an inbred line which by recombination of genes retained the earliness of maturity of the F_1 hybrid. Genic dominance was partial for genes (Lc_1Lc_2) tending to produce fewer locules per fruit and for the (Lc_3) tending to produce more locules per fruit. A series of genes such as Lc_1 and Lc_2 , some entering the cross from one parent and some from the other, would produce an F_1 hybrid showing heterosis for fewer locules per fruit. On the other hand a series of genes such as (Lc_3), some entering the cross from one parent and some from the other, would produce heterosis for more locules per fruit.

Finally, for the *Ww* series of genes, genic dominance was partial for increased weight per locule and the effects of the gene pairs were cumulative. As regards this character, both parents did contribute genes for increased

weight per locule, and the F_1 hybrid did show heterosis for increased weight. Also, as has been shown in the F_2 and B_1 and P_2 populations some individuals were obtained having greater weight per locule than the F_1 plants and this greater weight per locule proved to be due to recombination of favorable genes.

Also, the interallelic interactions of the genes as determined by the interrelations of the component characters are of interest because of the information they provide concerning recombination of genes and heterosis. 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 (1938) with phenocopies. In fact it seems almost axiomatic that this was the case, because the second order interaction (*Ss* gene series \times *Rr* gene series \times 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 *Lcl* series and the *Ww* series of genes in that greater number of locules, on an average, was accompanied by less weight per locule. This type of interallelic interaction would tend to decrease the possibility of obtaining inbred lines combining desirable characters. This would be particularly true of the interallelic interaction between the *Ss* and *Rr* gene series, because 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.

The data do not furnish any evidence concerning that type of intraallelic interaction postulated by East's (1936) physiological hypothesis, other than to say that no cases of overdominance were found. This would indicate that probably overdominance does not play a predominant part in the production of heterosis in the tomato hybrids studied.