

THE NATURE OF THE INTERACTION OF GENES
AFFECTING FOUR QUANTITATIVE CHAR-
ACTERS IN A CROSS BETWEEN
HORDEUM DEFICIENS AND
HORDEUM VULGARE

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INTRODUCTION

QUANTITATIVE characters are of extreme importance in economic plants. Because of difficulties involved in studying the inheritance of these characters less is known concerning their genetics than is the case for the qualitative characters.

SAX (1923), GRIFFEE (1925) and SIRKS (1925) were the first to study factors for quantitative characters by means of their association with factors for the production of qualitative characters. This method was used later by IMMER (1927). LINDSTROM (1926, 1928, 1929, 1931), who has studied the linkage between genes for quantitative and those for qualitative characters in the tomato, was the first to point out the possibilities of studying the inheritance of genes differentiating quantitative characters by means of their linkage with genes differentiating qualitative characters. LINDSTROM'S studies furnish rather conclusive evidence that major factors for size of fruit occur in the tomato. HAYES and HARLAN (1920) showed that there were at least three factor pairs affecting internode length in the spikes of barley. They found that these genes had different effects and were cumulative. Some long and short internode types may be differentiated by one factor pair and others by two or three. WEXELSEN (1934) studying genes influencing internode length of the barley spike substantiated these results and pointed out that the genes are not necessarily alike in their dominance relationships, since L_1 , L_2 and L_3 were found to be intermediate in a heterozygous condition, L_4 to be nearer to the short type, and L_5 nearer to the long type. RASMUSSEN (1935) in a study of quantitative characters in *Pisum* demonstrated that two main factors, both showing partial dominance towards lateness of maturity, were at work in the material investigated. He estimated that they were responsible for about half the genic variation within the F_2 populations, whereas the other half was believed to be due to modifiers. He found that these genes were not strictly additive in their combined effect and this supported his interaction hypothesis.

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This article reports a study of the effect of genes associated with color of glumes, type of spike and habit of growth upon yield of seed per plant, number of spikes per plant, height of plant, and length of awn. These include genes differentiating the qualitative characters in question as well as those which may be linked with them and which affect the quantitative characters being studied. It is apparent then that in part at least the effect of the differential genes in certain chromosomes is being measured, and it should be possible to establish the nature of the interactions of the genes located in different chromosomes.

MATERIALS

The material consists of data from F_1 , F_2 and F_3 generations of a cross of B 1 and Brachytic. The contrasted characters of the parents are as follows:

<i>Character</i>	<i>B 1</i>	<i>Brachytic</i>
Color of Glumes	Black	White
Type of spike	deficiens	vulgare
Type of growth	normal	brachytic
Yield of seed per plant in grams	$1.9 \pm .07$	$4.0 \pm .25$
Number of spikes per plant	$3.8 \pm .11$	$4.7 \pm .25$
Height of plant in inches	$25.6 \pm .24$	$16.1 \pm .15$
Length of awn in mm	141.6 ± 1.19	$71.0 \pm .71$

B 1 is a standard stock used in linkage studies at the University of Minnesota (DAANE 1931) and has been carried from individual plant selections in the crossing plots. The parent material used as checks in this study was from the progeny of plants used in making the cross. The crosses were made by Dr. F. J. STEVENSON. The Brachytic parent was obtained from Dr. L. J. STADLER, University of Missouri, and was selected by him from a population of the variety Himalaya, the seed of which originally came from the Montana Experiment Station.

METHODS

Planting, harvesting and measuring. The F_1 and F_2 were grown in the summer of 1932 and the F_3 was grown in 1934 in 6 foot rows and spaced 3 inches apart within the row. The B 1 and Brachytic parents were grown as a check in rows adjacent to the F_1 . The progeny from nine plants of the B 1 parent were grown with the 20 F_2 families, the nine B 1 families being distributed at random throughout the 20 F_2 families. As a further check the progeny from one plant of the Brachytic parent were grown at the end of the series of plantings adjacent to the progeny from one plant of the B 1 parent. Thus since the F_1 was grown some distance from the F_2 plants any comparison of the two will have to be made through the par-

ents. At the time of harvest each plant was pulled, its height measured in inches, and the spikes cut off and placed in an envelope. During the following winter the plants were classified; and the number of spikes per plant, the length of awns in millimeters, and the weight of seed in grams were recorded. In the F_3 , 32 seeds of each F_2 plant were sown and later notes on the mature plants were taken in the field. Each family was studied on the individual plant basis and classified as homozygous or segregating for each of the three qualitative characters involved.

Statistical methods. First, the data were separated into 27 different genotypes on the basis of the factor pairs differentiating the three qualitative characters. Then the sums of squares, variances and regression coefficients were obtained for each genotype. The variances used in calculating the t values were corrected on the basis of the regression coefficients, FISHER (1934, p. 257). The variances for weight of seed per plant were corrected on the basis of the regression coefficients of weight of seed on the number of spikes; those for number of spikes on the basis of the regression coefficients of number of spikes on weight of seed; those for height of plant on the basis of the regression coefficients of the height of plant on length of awn; and those for length of awn on the basis of the regression coefficients of length of awn on height of plant.

From the data analysed in this manner it was found that the variances from the homozygous black, the heterozygous black, and the homozygous white glume segregates did not differ materially. Therefore a generalized standard deviation would be applicable. Consequently the total variance for comparing plants of the genotypes BB , Bb , and bb was obtained by adding the sums of squares for each of the nine genotypes resulting from a segregation of the genes differentiating type of spike and habit of growth and dividing by the appropriate degrees of freedom. The method is illustrated in the following tabulation for weight of seed per plant:

GENOTYPE	N	D.F.	NUMBER OF SPIKES (\bar{x}) $S(X^2) - N\bar{X}^2$	$S(XY) - N\bar{X}\bar{Y}$	WEIGHT OF SEED (\bar{y}) $S(Y^2) - N\bar{Y}^2$	REGRESSION COEFFICIENTS Y on X	D.F.	REDUCED $S(Y^2) - N\bar{Y}^2$
<i>vvBrBr</i>	61	60	489.443	503.000	997.500	1.028	59	480.567
<i>vvBrbr</i>	130	129	846.531	1183.417	2488.324	1.398	128	833.954
<i>vvbrbr</i>	64	63	181.484	149.142	329.151	.822	62	206.587
<i>VvBrBr</i>	130	129	1578.992	1151.002	999.069	.729	128	160.050
<i>VvBrbr</i>	249	248	2375.406	1847.454	1864.521	.778	247	427.678
<i>Vvbrbr</i>	130	129	787.700	441.540	333.907	.561	128	86.405
<i>VVBrBr</i>	78	77	805.962	510.542	412.707	.633	76	89.300
<i>VVBrbr</i>	109	108	884.991	606.767	501.801	.686	107	85.789
<i>VVbrbr</i>	54	53	257.500	131.617	82.703	.511	52	15.430
Total							987	2385.760

The data are shown to 3 places to the right of the decimal point but in obtaining the constants used in this study the figures were carried to six places to the right of the decimal point. As can be seen from the tabulation this method of obtaining the variances took out the differences between genotypes and consequently the variance obtained was that within genotypes. For making comparisons between the nine genotypes resulting from segregation of the genes differentiating type of spike and habit of growth the variance was obtained for each by adjusting the sum of squares on the basis of their respective regression coefficients. The reduced sums of squares are shown in the last column of the above tabulation and of course the variance for each genotype is found by dividing the reduced sums of squares by the degrees of freedom left after subtracting from the original degrees of freedom the one accounted for by the regression coefficient. The *t* values to determine the significance of means and the *t* values to determine the significance of regression coefficients were obtained by use of methods given by FISHER, (1934) pp. 120 and 138 respectively. In determining whether differences between variances were statistically significant Fisher's formula (1934, p. 214) was employed. Differences giving odds as great as or greater than 19:1 against the deviations noted as being due to the errors of random sampling were considered as statistically significant.

That the regressions were obtained for each of the nine genotypes separately and adjustment of the variance for each genotype was made on the basis of its respective regression coefficient is important in that it shows what components of the variability are being controlled. By such a method the variability that is partially controlled is that due to environment and the genes independently inherited from those linked with and differentiating type of spike and habit of growth. For illustration let us consider the variances for weight of seeds per plant in which it was found that the general correlation coefficient between weight of seed and number of spikes within phenotypes was .81. This shows, as would be expected that the number of spikes per plant affects materially the yield of the plant. Now, since the purpose of this study is to measure differences between genotypes it would be desirable to have the number of spikes held constant within genotypes in so far as it affects yield. This would in no way interfere with the differences in number of spikes between genotypes, but would aid in the study of the genes differentiating the qualitative characters involved and any genes that might be linked with them. The completeness with which the effect of the linked genes is measured depends of course upon the closeness of the linkage relationship.

EXPERIMENTAL DATA

Inheritance of Color of Glumes, Type of Spikes and Habit of Growth, and their Linkage Relationships

A knowledge of the number of genes differentiating the qualitative characters and their linkage relationships is essential to a correct interpretation. The data bearing on this point are given in table 1. The proportion of homozygous black glume: heterozygous black glume: homozygous white glume segregates was 252: 504: 249; the proportion of homozygous deficient: heterozygous deficient: homozygous vulgare was 241: 509: 255; and the proportion of homozygous for normal habit of growth: those heterozygous for normal habit of growth: those homozygous for brachytic habit of growth was 269: 488: 248. These figures are based on the segrega-

TABLE 1

Linkage relationships between three qualitative characters as determined by partitioning χ^2 for goodness of fit into its components.

TYPE OF SPIKE vs. COLOR OF GLUMES		HABIT OF GROWTH vs. COLOR OF GLUMES		TYPE OF SPIKE vs. HABIT OF GROWTH		EXPECTED IF INDE- PENDENT
GENOTYPE	OBTAINED	GENOTYPE	OBTAINED	GENOTYPE	OBTAINED	
<i>VVBB</i>	56	<i>BrBrBB</i>	70	<i>VVBrBr</i>	78	62.81
<i>VVBb</i>	115	<i>BrBrBb</i>	128	<i>VVBrbr</i>	109	125.62
<i>VVbb</i>	70	<i>BrBrbb</i>	71	<i>VVbrbr</i>	54	62.81
<i>VvBB</i>	134	<i>BrbrBB</i>	118	<i>VvBrBr</i>	130	125.63
<i>VvBb</i>	256	<i>BrbrBb</i>	257	<i>VvBrbr</i>	249	251.25
<i>Vvbb</i>	119	<i>Brbrbb</i>	113	<i>Vvbrbr</i>	130	125.63
<i>vvBB</i>	62	<i>brbrBB</i>	64	<i>vvBrBr</i>	61	62.81
<i>vvBb</i>	133	<i>brbrBb</i>	119	<i>vvBrbr</i>	130	125.63
<i>vvbb</i>	60	<i>brbrbb</i>	65	<i>vvbrbr</i>	64	62.81
P between .50 and .30		P between .80 and .70		P between .30 and .20		

tion as determined by classification of the F_2 and a progeny test in the F_3 generation. The expected ratio for all three characters based on the hypothesis that the contrasted characters are differentiated by 1 factor pair is 251.25: 502.50: 251.25. The P values obtained by applying the χ^2 test were found to lie between .98 and .95, .80 and .70 and .50 and .30 for color of glume, type of spike and habit of growth, respectively. It is apparent that the three qualitative characters are differentiated by a single factor pair.

The data concerning the linkage relationships of these three qualitative characters are given in table 1 also. The P values of χ^2 for independent inheritance for type of spike and color of glume, habit of growth and color of glume and type of spike and habit of growth lie between .50 and .30, .80 and .70, and .30 and .20 respectively. It may be concluded that the

genes differentiating the characters under consideration are located in different chromosomes. That color of glumes and type of spike are independently inherited has been shown by previous workers. For a review of literature on linkage relationships see DAANE (1931). It is apparent that any effect upon yield, number of spikes, height, or length of awn that may be found to be associated with any of these pairs of alleles will be independent, as far as linkage relationships are concerned, from the effect that any different pair of alleles might be exerting.

Genes Associated With Color of Glumes

The means of weight of seed, spikes per plant, height of plant, and length of awn for the three different genotypes are given in table 2. The genotype was determined by segregation in the F_2 and a progeny test in the F_3 generation; whereas, the measurements are for the F_2 generation.

TABLE 2

The means of four quantitative characters measured in the F_2 generation of a cross between B_1 , and $Brachytic$, classified into phenotypes and genotypes according to color of glumes.

PHENOTYPES	GENOTYPES	WEIGHT OF SEEDS IN GRAMS	NUMBER OF SPIKES PER PLANT	HEIGHT OF PLANT IN INCHES	LENGTH OF AWN IN MM
White	(<i>bb</i>)	4.7	5.9	24.4	117.3
Black	(<i>Bb</i>)	5.0	6.0	24.6	119.6
Black	(<i>BB</i>)	4.7	5.8	24.2	117.8

If a t value of 1.960 which gives a P value of .05 is taken as statistically significant, the seed yield of the *Bb* segregates was significantly greater than either those of the genotype *BB* or *bb*; whereas, the weights of seed per plant for the *BB* and *bb* segregates were practically the same. The t values were 2.501, 2.491 and .148 respectively. The only other t values exceeding 1.960 were those for *Bb* and *bb* in comparing length of awn and *Bb* and *BB* in comparing height of plant. However it can be seen from table 2 that in every case the mean of the heterozygote exceeds those of the two homozygotes for the four characters. Even though the differences between the two homozygotes and the heterozygote are small, there seems to be little reason for questioning their biological significance. Since the differences between the two homozygotes are neither consistent nor have t values sufficiently large to closely approach a P of .05, it can be concluded that *bb* and *BB* do not have a differential effect upon weight of seed, spikes per plant, height of plant, nor length of awn.

These results can be explained by JONES' (1917) hypothesis to account for heterosis. If this explanation is accepted then the increases noted for the heterozygote must be due to favorable, and at least partially dominant genes, some of which must be located on the same chromosome with

B and others on the homologous chromosome with *b*. Furthermore, it must follow from the results obtained, if we are to accept JONES' hypothesis, that in the homozygous condition the genes located in the same chromosome with *B* have a similar effect upon the characters under consideration as do the genes linked with *b* when they are in a homozygous condition.

Genes Associated with Type of Spike and Habits of Growth

The data showing the reaction of the genes upon the four quantitative characters are given in tables 3 and 4. Table 3 is designed to facilitate an analysis of the differences between the *vv* and *Vv* segregates, the *vv* and *VV* segregates, and the *Vv* and *VV* segregates. These differences are shown for plants of the genotypes *BrBr*, *Brbr*, and *brbr*, making a total of nine comparisons for each of the four quantitative characters. Table 4 is the same as table 3 except that it is designed to facilitate an analysis of the differences between the *BrBr* and *Brbr* segregates, the *BrBr* and *brbr* segregates, and the *Brbr* and *brbr* segregates.

From Table 3, it can be seen that in every case the *vv* plants gave a larger yield of seed per plant than did the *Vv* or *VV* segregates and *Vv* segregates exceeded *VV* segregates. The lowest t value obtained for any of these comparisons was 5.495 which gives odds greater than 99:1 against the deviations noted being due to the errors of random sampling. *Vv* exceeded *vv* plants among the *BrBr* and *Brbr* segregates for number of spikes per plant, height of plant, and length of awn and the t values for the differences had a P value of less than .01 in all cases. Likewise, the *Vv* plants exceeded the *vv* plants among the *brbr* progeny but the t values were less than the above; that for number of spikes per plant being .658, for height of plant 3.197, and for length of awn 1.601. It will be remembered that a value of 1.960 is necessary for a P value as low as .05. For spikes per plant, height of plant, and length of awn the *VV* segregates exceeded those possessing *vv* for the *BrBr* and *Brbr* genotypes, but the t values for this comparison in the *BrBr* genotypes were only .700 and 1.632 for number of spikes per plant and height of plant, respectively, and 2.467 for length of awn. The t values in the *Brbr* progeny for spikes per plant, height of plant, and length of awn were 2.207, 5.304 and 4.898 respectively. The reverse was true for the *brbr* segregates since the *vv* progeny exceeded the *VV* progeny. The t values were 4.268, 1.968 and 4.268 which are sufficiently large to give substantial odds against the differences noted being chance deviations due to the errors of random sampling.

Table 4 shows that in respect to weight of seed per plant *Brbr* exceeded *BrBr* in two of the three comparisons, namely, in the *VV* and *vv* segregates. The odds against the difference being due to the errors of random sampling in the first case were a trifle less than 99:1 and in the second

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TABLE 3
The comparative effect upon four quantitative characters of genes differentiating and associated in inheritance with type of spike.

PHENOTYPE AND GENOTYPE	WEIGHT OF SEED PER PLANT IN GRAMS			SPIKES PER PLANT			HEIGHT OF PLANT IN INCHES			LENGTH OF AWN IN MILLIMETERS		
	WEIGHT	DIFFERENCE	NUMBER	DIFFERENCE	HEIGHT	DIFFERENCE	LENGTH	DIFFERENCE	LENGTH	DIFFERENCE		
Vulgare (<i>vv</i>) vs. deficiens (<i>Vv</i>)												
Normal (<i>BrBr</i>)	7.3	5.1	2.22	5.7	7.4	-1.72	25.9	27.4	-1.54	127.3	143.8	-16.58
Normal (<i>Brbr</i>)	8.0	5.0	2.98	5.6	6.6	-.94	25.3	27.3	-2.08	126.3	142.7	-16.42
Brachytic (<i>brbr</i>)	4.5	2.6	1.88	4.8	4.9	-.13*	17.2	18.3	-1.03	62.7	64.7	-1.95*
Vulgare (<i>vv</i>) vs. deficiens (<i>VV</i>)												
Normal (<i>BrBr</i>)	7.3	3.9	3.44	5.7	5.9	-.21*	25.9	26.5	-.64*	127.3	134.8	-7.50†
Normal (<i>Brbr</i>)	8.0	4.2	3.74	5.6	6.0	-.39*	25.3	26.7	-1.41	126.3	135.5	-9.20
Brachytic (<i>brbr</i>)	4.5	1.7	2.74	4.8	3.8	.94	17.2	16.5	.68†	62.7	56.0	6.68
Deficiens (<i>Vv</i>) vs. deficiens (<i>VV</i>)												
Normal (<i>BrBr</i>)	5.1	3.9	1.22	7.4	5.9	1.51	27.4	26.5	.90	143.8	134.8	9.08
Normal (<i>Brbr</i>)	5.0	4.2	.76	6.6	6.0	.55	27.3	26.7	.67†	142.7	135.5	7.22
Brachytic (<i>brbr</i>)	2.6	1.7	.86	4.9	3.8	1.07	18.3	16.5	1.71	64.7	56.0	8.63
Bi parent (<i>VVBrBr</i>) vs. F₂ (<i>VVBrBr</i>)	1.9	3.9	-2.00	3.7	5.9	-2.2	25.1	26.5	-1.4	137.8	134.8	3.00*
Brachytic parent (<i>vvbrbr</i>) vs. F₂ (<i>vvbrbr</i>)	4.00	4.5	-.50*	4.7	4.8	-.10*	16.1	17.2	-1.1	71.0	62.7	8.3
Bi parent (<i>VVBrBr</i>) vs. Bi parent (<i>VVBrBr</i>)	1.9	1.9	.00	3.8	3.7	.10*	25.6	25.1	.5*	141.6	137.8	3.8*

* t test gives P > .05.
† t test gives P < .05 but > .01.

TABLE 4
The comparative effect upon four quantitative characters of genes differentiating and associated in inheritance with habit of growth.

PHENOTYPE AND GENOTYPE	WEIGHT OF SEED PER PLANT IN GRAMS		SPIKES PER PLANT		HEIGHT OF PLANT IN INCHES		LENGTH OF AWN IN MILLIMETERS	
	WEIGHT	DIFFERENCE	NUMBER	DIFFERENCE	HEIGHT	DIFFERENCE	LENGTH	DIFFERENCE
Normal (<i>BrBr</i>) vs. normal (<i>Brbr</i>)								
Vulgare (<i>vv</i>)	7.3	8.0	5.7	5.6	25.9	25.3	127.3	126.3
Deficiens (<i>Vv</i>)	5.1	5.0	7.4	6.6	27.4	27.3	143.8	142.7
Deficiens (<i>VV</i>)	3.9	4.2	5.9	6.0	26.5	26.7	134.8	135.5
Normal (<i>BrBr</i>) vs. brachytic (<i>brbr</i>)								
Vulgare (<i>vv</i>)	7.3	4.5	5.7	4.8	25.9	17.2	127.3	62.7
Deficiens (<i>Vv</i>)	5.1	2.6	7.4	4.9	27.4	18.3	143.8	64.7
Deficiens (<i>VV</i>)	3.9	1.7	5.9	3.8	26.5	16.5	134.8	56.0
Normal (<i>Brbr</i>) vs. brachytic (<i>brbr</i>)								
Vulgare (<i>vv</i>)	8.0	4.5	5.6	4.8	25.3	17.2	126.3	62.7
Deficiens (<i>Vv</i>)	5.0	2.6	6.6	4.9	27.3	18.3	142.7	64.7
Deficiens (<i>VV</i>)	4.2	1.7	6.0	3.8	26.7	16.5	135.5	56.0

* t test gives $P > .05$.

† t test gives $P < .05$ but $> .01$.

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case were 9:1. It seems reasonably safe to conclude that the *Brbr* segregates in the *VV* plants possessed a somewhat larger weight of seed per plant than did the *BrBr* segregates. In every case and for all four characters, the *BrBr* and *Brbr* segregates exceeded the *brbr* plants and in no comparison were the odds against the differences being due to the errors of random sampling less than 99:1.

THE NATURE OF THE INTERACTION BETWEEN THE NON-ALLELIC GENES

The nature of the interaction between the non-allelic genes is of particular interest, as it is of fundamental importance to know whether the favorable growth genes give the same increase over the less favorable growth genes in all genotypes. To facilitate the study of this problem, the data in table 5 were compiled. This table gives the interactions between the genes

TABLE 5

The interactions between those genes differentiating and associated in inheritance with type of spike and habit of growth as regards their effect upon four quantitative characters.

INTERACTION	WEIGHT OF SEED DIFFERENCE		SPIKES PER PLANT DIFFERENCE		HEIGHT OF PLANT DIFFERENCE		LENGTH OF AWN DIFFERENCE	
	GRAMS	t	NO.	t	IN.	t	MM.	t
	Vulgare (<i>vv</i>) vs. deficiens (<i>Vv</i>) and							
Normal (<i>BrBr</i>) vs. normal (<i>Brbr</i>)	.76	2.183	.78	2.693	.54	1.195	.16	.058
Normal (<i>BrBr</i>) vs. brachytic (<i>brbr</i>)	.34	.992	1.59	4.993	.51	1.039	14.63	5.442
Normal (<i>Brbr</i>) vs. brachytic (<i>brbr</i>)	1.10	3.543	.81	3.039	1.05	2.446	14.47	6.227
Vulgare (<i>vv</i>) vs. deficiens (<i>VV</i>) and								
Normal (<i>BrBr</i>) vs. normal (<i>Brbr</i>)	.30	.697	.18	.553	.77	1.624	1.70	.503
Normal (<i>BrBr</i>) vs. brachytic (<i>brbr</i>)	.70	1.627	-1.15	3.000	-1.32	2.484	-14.18	3.940
Normal (<i>Brbr</i>) vs. brachytic (<i>brbr</i>)	1.00	2.448	-1.33	4.503	-2.09	4.476	-15.88	5.486
Deficiens (<i>Vv</i>) vs. deficiens (<i>VV</i>) and								
Normal (<i>BrBr</i>) vs. normal (<i>Brbr</i>)	.46	2.143	.96	3.676	.23	.542	1.86	.697
Normal (<i>BrBr</i>) vs. brachytic (<i>brbr</i>)	.36	1.742	.44	1.524	.81	1.631	.45	.160
Normal (<i>Brbr</i>) vs. brachytic (<i>brbr</i>)	.10	.469	.52	1.966	1.04	2.317	1.41	.581

differentiating and associated by linkage with type of spike and those differentiating and associated by linkage with habit of growth. A brief statement concerning the formulation of this table will help to clarify the discussion which follows. For illustration consider the interaction *vv* vs. *Vv* and *BrBr* vs. *Brbr*. The information given is whether the difference between *vv* and *Vv* in combination with *BrBr* is the same as in combination with *Brbr*. This may be tested by comparing the two differences. Thus the difference $(vvBrBr - VvBrBr) - (vvBrbr - VvBrbr)$ for weight of seed is .76 grams, as can be seen from table 5 in which these differences between two differences are listed together with the t values for testing their significance. If the difference $(vvBrBr - VvBrBr) - (vvBrbr - VvBrbr)$ is statistically significant, then it must necessarily follow that the difference

$(vvBrBr - vvBrbr) - (VvBrBr - VvBrbr)$ must also be statistically significant, as the final figures are identical. The reason for this is apparent as in both cases we are dealing with the same interaction stated differently. The former statement emphasises the Vv genes whereas the latter places the emphasis on the $Brbr$ genes. In the discussion of the interactions in this article, for the sake of clarity emphasis will be placed on the Vv genes.

From the t values in table 5, it can be readily determined which interactions are statistically significant. The following interactions for weight of seed have t values larger than 1.960; vv vs. Vv and $BrBr$ vs. $Brbr$, vv vs. Vv and $Brbr$ vs. $brbr$, vv vs. Vv and $Brbr$ vs. $brbr$, vv vs. VV and $Brbr$ vs. $brbr$, and Vv vs. VV and $Brbr$ vs. $BrBr$. Considering spikes per plant, only two of the nine interactions have t values lower than 1.960; whereas, both height of plant and length of awn have five t values below this figure. These data are conclusive in showing that the interactions between the non-allelic genes are of such a nature that the more favorable growth factors do not give the same increase over the less favorable growth factors in all genotypes.

The nature of this interaction as determined by which genotype induces larger increases can be determined from the data in tables 3, 4, and 5. Table 3 shows that vv plants combined with a high producing genotype are favored more than are Vv or VV plants, as concerns weight of seed per plant. For example, the difference between vv and Vv plants in the $BrBr$ genotype is 2.22, in $Brbr$ is 2.98, and in $brbr$ is only 1.88. Likewise, the difference between vv and VV plants in the $BrBr$ genotype is 3.44, in $Brbr$ is 3.74, and in $brbr$ is only 2.74 grams. From the t tests of the interactions given in table 5, it can be seen that 2.98 is significantly different from 2.22 and 1.88 and that 3.74 is significantly different from 2.74. Table 3 shows that the difference between Vv and VV plants was greater in the $BrBr$ genotype than it was in $Brbr$ or $brbr$ and the t test for the interactions listed in table 5 show that this difference involving the $BrBr$ and $Brbr$ genotypes is probably statistically significant. Therefore, in this study, it is evident that the genes favorable to high plant yields when transferred from a low to a high yielding genotype are, in comparison with their alleles and in absolute values, still more favorable to plant growth. The only exceptions to this were the difference between the Vv and VV plants in the $Brbr$ genotype in comparison with the difference between the Vv plants and the VV plants in the $brbr$ genotype. The differences were obtained from means of 5.0 and 4.2 grams in comparison with 2.6 and 1.7 grams. In this case the smaller means did not give the smaller difference; that is, the Vv plants in comparison with the VV plants did not give an increased difference in the higher yielding genotypes.

It remains to be seen whether the same general conclusions can be drawn

for the other three quantitative characters studied. In making the comparison between *vv* and *Vv* plants for the *BrBr* and *Brbr* genotypes, it is necessary to know whether the latter two genotypes differ. The only statistically significant difference between these two genotypes, as can be seen from table 4, was for spikes per plant in the *Vv* genotype. Then, if the more favorable genes give still greater increases when in the higher tillering genotypes, it would be expected that the difference between *vv* plants and *Vv* plants would be still greater in the *BrBr* genotype than the same comparison in the *Brbr* genotype. That such actually was the case can be seen from table 3, and that the difference between the two differences of -1.72 and $-.94$ was significant can be seen from table 5. The *t* value is larger than necessary to give odds of 99:1 against the deviation of .78 being due to the errors of random sampling. Likewise, according to the hypothesis that the genes more favorable to growth give greater increases over those less favorable in combination with genes also favorable to growth, the difference between *vv* and *Vv* plants of the genotypes *BrBr* and *Brbr* should be greater than the difference between *vv* and *Vv* plants in the *brbr* genotype. Such was found to be the case for all characters (see table 3) and with the exception of the comparison between the differences involving *vv* and *Vv* in the *BrBr* and *brbr* genotypes for height of plant the differences were statistically significant.

In comparing the *vv* and *VV* plants the *BrBr* and *Brbr* genotypes may be omitted as the latter two genotypes do not differ significantly in the three quantitative characters measured. The hypothesis that the differences would be still greater in the genotypes of higher values does not fit the data as regards the comparison between *vv* and *VV* plants in the genotypes *BrBr* and *Brbr* compared with *brbr*. For example, in the *brbr* genotype *vv* plants have a greater number of spikes per plant, a greater height and a longer awn; whereas, in the *Brbr* genotype the reverse is true and in the *BrBr* genotype the only significant difference is for length of awn and it is in favor of the *VV* plants. As regards the comparison between *Vv* and *VV* plants and involving the three characters spikes per plant, height of plant, and length of awn, the only consistent difference seems to be that in every case the *Brbr* genotype gave lower differences (table 3) than did the *BrBr* and *brbr* genotypes. The differences noted for the interaction *Vv* vs. *VV* and *BrBr* vs. *Brbr* for number of spikes were statistically significant as were also the differences for the interaction *Vv* vs. *VV* and *Brbr* vs. *brbr* for number of spikes and height of plant. The differences are given in tables 3 and 4 and the interaction in table 5.

The regression coefficients of weight of seed on number of spikes give additional information concerning the nature of the interactions of the genes influencing yield of seed per plant. Table 6 shows that in every case

the addition of a spike among the *vv* segregates gave a greater increased yield than did an addition of a spike among the *Vv* or *VV* segregates. Likewise an addition of a spike per plant gave a greater increase in yield among the *Vv* segregates than did the addition of a spike per plant among the *VV* segregates. The difference between these two genotypes is statistically significant in two out of the three comparisons. Turning to the different combinations of *Br* and *br*, the *Brbr* plants gave a greater increased yield for each additional spike per plant than did the *BrBr* plants, (see table 7). In only one case however, did the odds against the differences being due to the errors of random sampling exceed 19:1. In every case an

TABLE 6

The regression coefficients of weight of seed on number of spikes compared on the basis of genes associated in inheritance with type of spikes.

PHENOTYPE AND GENOTYPE	WEIGHT OF SEED PER PLANT ON NUMBER OF SPIKES			
	REGRESSION COEFFICIENTS		DIFFERENCE	t
	grams	grams	grams	
Vulgare (<i>vv</i>) vs. deficiens (<i>Vv</i>)				
Normal (<i>BrBr</i>)	1.03	.73	.30	3.121
Normal (<i>Brbr</i>)	1.40	.78	.62	8.448
Brachytic (<i>brbr</i>)	.82	.56	.26	2.555**
Vulgare (<i>vv</i>) vs. deficiens (<i>VV</i>)				
Normal (<i>BrBr</i>)	1.03	.63	.40	3.348
Normal (<i>Brbr</i>)	1.40	.69	.71	7.490
Brachytic (<i>brbr</i>)	.82	.51	.31	2.297**
Deficiens (<i>Vv</i>) vs. deficiens (<i>VV</i>)				
Normal (<i>BrBr</i>)	.73	.63	.10	1.995**
Normal (<i>Brbr</i>)	.78	.69	.09	1.942*
Brachytic (<i>brbr</i>)	.56	.51	.05	.915*
B ₁ parent (<i>VVBrBr</i>) vs. F ₂ genotype (<i>VVBrBr</i>)	.53	.63	-.10	1.968**
Brachytic parent (<i>vvbrbr</i>) vs. F ₂ genotype (<i>vvbrbr</i>)	.70	.82	-.12	.870*
B ₁ parent (<i>VVBrBr</i>) vs. B ₁ parent (<i>VVBrBr</i>)	.54	.53	.01	.142*

* t gives $P > .05$

** t gives $P < .05$ but $> .01$.

additional spike gave a greater increase per plant in the *BrBr* segregates than was the case as regards the *brbr* segregates. Here again, only one of the differences was statistically significant but it was decidedly so. In all cases the *Brbr* segregates gave a greater increased yield per additional spike than was true for the *brbr* segregates and all the differences were statistically significant.

It is of interest to know the manner of interaction that exists among the genes affecting yield. For example, do *vv* plants give the same increase per additional spike over *Vv* plants, whether in combination with *BrBr*, *Brbr*, or *brbr*? It is evident from table 6 that the increase is greater in combination with *Brbr* than when in combination with *BrBr* or *brbr*. The same is

true for the comparison between the *vv* and *VV* plants. The *t* values for these interactions were found to exceed 1.96. It is evident that a difference in interaction of factors exists, and the only general conclusion to be drawn, and which does not hold for all cases, is that genes favorable to increased yield per additional spike give still greater absolute increased yields when in combination with other genes which also favor the development of this character.

TABLE 7

The regression coefficients of weight of seed on number of spikes compared on the basis of genes associated in inheritance with habit of growth.

PHENOTYPE AND GENOTYPE	WEIGHT OF SEED PER PLANT ON NUMBER OF SPIKES			
	REGRESSION COEFFICIENTS		DIFFERENCE	<i>t</i>
	grams	grams	grams	
Normal (<i>BrBr</i>) vs. Normal (<i>Brbr</i>)				
Vulgare (<i>vv</i>)	1.03	1.40	-.37	2.459**
Deficiens (<i>Vv</i>)	.73	.78	-.05	1.200*
Deficiens (<i>VV</i>)	.63	.69	-.06	1.260*
Normal (<i>BrBr</i>) vs. brachytic (<i>brbr</i>)				
Vulgare (<i>vv</i>)	1.03	.82	.21	.994*
Deficiens (<i>Vv</i>)	.73	.56	.17	3.934
Deficiens (<i>VV</i>)	.63	.51	.12	1.853*
Normal (<i>Brbr</i>) vs. brachytic (<i>brbr</i>)				
Vulgare (<i>vv</i>)	1.40	.82	.58	3.010
Deficiens (<i>Vv</i>)	.78	.56	.22	4.512
Deficiens (<i>VV</i>)	.69	.51	.18	3.089

* *t* gives $P > .05$

** *t* gives $P < .05$ but $> .01$.

COMPARISON BETWEEN THE F₁ GENERATION, CERTAIN F₂ GENERATION GENOTYPES AND THE PARENTS

The comparison of the F₁ generation and parents and certain genotypes of the F₂ generation and parents provides information concerning the effect upon weight of seed per plant of genes not linked with the qualitative characters analyzed in this study (table 8). It will be remembered from the discussion of methods that due to the fact that F₁ and F₂ generations were grown some distance apart, although in the same series, a comparison between them must be made by use of the parents. The difference in yield between the F₁ generation *VvBrbr* and the B₁ parent *VVBrBr* was 4.1 grams; whereas, the difference in yield between the F₂ generation plants *VvBrbr* and the B₁ parent *VVBrBr* plants was 3.1 grams (table 8). Both of these differences have a *P* value of less than .01 and therefore, are undoubtedly statistically significant. The difference between the two differences also shows $P < .01$. This means that the difference between F₁ *VvBrbr* and the B₁ parent was greater than the difference between F₂

VvBrbr and B₁ parent. The same relationship held for the comparison between F₁ *VvBrbr* and F₂ *VvBrbr* plants with the Brachytic parent plants, but the difference between the two differences was not statistically significant. These data show that there must have been a reduction in weight of seed per plant between F₁ (*VvBrbr*) and F₂ (*VvBrbr*) plants. This reduction can be accounted for by partially dominant genes affecting yield and at least not closely linked with *Vv* or *Brbr*, probably the ones having the most effect being independently inherited.

The presence of these genes may be tested further by comparing the F₂ plants of the genotypes *VVBrBr* and *vvrbr* with the parental plants of the same genotypes, respectively (see table 8). If there are no genes other

TABLE 8
Weight of seed per plant of the parents compared with weight of seed per plant of the F₁ and of certain F₂ genotypes.

COMPARISON	N	WEIGHT OF SEED PER PLANT IN GRAMS			
		WEIGHT	DIFFERENCE	t	
F ₁ (<i>VvBrbr</i>) vs. B ₁ parent (<i>VVBrBr</i>)	57 and 50	5.6	1.5	4.1	7.930
F ₁ (<i>VvBrbr</i>) vs. brachytic parent (<i>vvrbr</i>)	57 and 60	5.6	4.3	1.3	2.012**
F ₂ (<i>VvBrbr</i>) vs. B ₁ parent (<i>VVBrBr</i>)	249 and 266	5.0	1.9	3.1	34.171
F ₂ (<i>VvBrbr</i>) vs. brachytic parent (<i>vvrbr</i>)	249 and 63	5.0	4.0	1.0	3.229
F ₂ (<i>VVBrBr</i>) vs. B ₁ parent (<i>VVBrBr</i>)	78 and 266	3.9	1.9	2.0	28.189
F ₂ (<i>vvrbr</i>) vs. brachytic parent (<i>vvrbr</i>)	64 and 63	4.5	4.0	.5	.761*
F ₁ (<i>VvBrbr</i>) vs. B ₁ parent (<i>VVBrBr</i>) and F ₂ (<i>VvBrBr</i>) vs. B ₁ parent (<i>VVBrBr</i>)				1.0	4.148
F ₂ (<i>VVBrBr</i>) vs. B ₁ parent (<i>VVBrBr</i>) and F ₂ (<i>vvrbr</i>) vs. brachytic parent (<i>vvrbr</i>)				1.5	5.807

* t test gives $P > .05$.

** t gives $P < .05$ but $> .01$.

than those closely linked with *Vv* and *Brbr* which affect yield and are segregating, the differences in yield between parental and F₂ plants of the corresponding genotype should not be statistically significant. Table 8 shows that the difference between F₂ plants *VVBrBr* and the B₁ parent *VVBrBr* is statistically significant, whereas that between the F₂ *vvrbr* plants and the Brachytic parent *vvrbr* is not. Also, the difference between the two differences is statistically significant. It is evident that the genes more favorable to high yield in the F₂ plants of the genotype *VVBrBr* than in F₂ plants of the genotype *vvrbr* must have entered the cross from the Brachytic parent. There is no corresponding depressing effect on yield of grain per plant of the alleles of these genes entering the cross from the B₁ parent; if there were, the F₂ *vvrbr* segregates should yield less than the Brachytic parent *vvrbr*. Such was not the case. Again there is proof of a difference in the interaction of factors.

THE VARIANCES OF THE DIFFERENT GENOTYPES AND PARENTS

When studying quantitative characters, it has been the practice of geneticists to use homozygous material as a measure of the environmental variability. By the analysis of variance, it is possible to divide the total variability into that due to the genes isolated in the population being studied and that due to residual genetic variability plus environmental variability. In certain cases it is desirable to determine the residual genetic variability. If the parents can be used to measure the environmental variability, it can be accomplished readily by analyzing the variability into that due to genotypes and within genotypes. The variability within genotypes minus the environmental variability which has been measured by the parents would leave the residual genic variability. This method has been used by RASMUSSEN (1935).

TABLE 9
The means and non-adjusted variances for the different phenotypes and genotypes.

PHENOTYPE	GENOTYPE	WEIGHT OF SEED IN GRAMS		NUMBER OF SPIKES PER PLANT		HEIGHT OF PLANT IN IN.		LENGTH OF AWN IN MM.	
		MEAN	VARIANCE	MEAN	VARIANCE	MEAN	VARIANCE	MEAN	VARIANCE
Vulgare normal	(<i>vvBrbr</i>)	8.0	19.289	5.6	6.562	25.3	5.705	126.3	237.516
Vulgare normal	(<i>vvBrBr</i>)	7.3	16.625	5.7	8.157	25.9	6.794	127.3	384.996
Deficiens normal	(<i>VvBrBr</i>)	5.1	7.744	7.4	12.240	27.4	7.323	143.8	265.903
Deficiens normal	(<i>VvBrbr</i>)	5.0	7.518	6.6	9.578	27.3	7.067	142.7	226.634
Vulgare Brachytic	(<i>vvbrbr</i>)	4.5	5.224	4.8	2.880	17.2	3.824	62.7	73.577
Deficiens normal	(<i>VVBrbr</i>)	4.2	4.646	6.0	8.194	26.7	4.726	135.5	239.844
Deficiens normal	(<i>VVBrBr</i>)	3.9	5.359	5.9	10.467	26.5	5.837	134.8	320.472
Deficiens Brachytic	(<i>Vvbrbr</i>)	2.6	2.588	4.9	6.106	18.3	5.834	64.7	75.796
Deficiens Brachytic	(<i>VVbrbr</i>)	1.7	1.560	3.8	4.858	16.5	5.536	56.0	121.754
B 1 Parent	(<i>VVBrBr</i>)	1.9	1.668	3.7	4.553	25.1	9.224	137.8	241.487
Brachytic Parent	(<i>vvbrbr</i>)	4.0	7.693	4.7	7.426	16.1	2.027	71.0	47.822
B 1 Parent	(<i>VVBrBr</i>)	1.9	1.690	3.8	4.641	25.6	6.617	141.6	163.416

Table 9 gives the variances and means for the different genotypes and parents. It should be recalled that the variances found for the Brachytic and B 1 parents listed in the last two rows of table 9 are not directly comparable with these given for the F₂ genotypes and B 1 parent, as they were grown in rows at the end of the series, whereas the data from the nine B 1 families, distributed at random with the twenty F₂ families would be comparable with the data from the F₂. The Brachytic parental data would be comparable with the F₂ data by means of the B 1 parent.

As regards weight of seed per plant, it is apparent that all genotypes are not equally variable. The genotypes with the larger means also have the larger variances. This is equally true for the parents. The relationship is not so close for the number of spikes per plant, height, and length of awn, but it does exist.

The comparison between the parents and F_1 plants furnishes additional evidence. In this study the mean weight per plant of the B 1 parent was 1.5 grams and the variance 1.379, for the Brachytic parent was 4.3 grams and the variance 6.219 and for the F_1 the mean was 5.6 grams and the variance 10.526.

It seems advisable to determine whether genotypes having means of similar magnitude have variances of different magnitudes. The means of the *Brbr* segregates for all four quantitative characters are similar to the means of the *BrBr* segregates. To ascertain whether differences in variability existed, the variances were obtained for all of the *Brbr* and *BrBr* segregates. FISHER'S Z test (1934, p. 216) was applied. It was found that the variance for the *BrBr* plants was larger than the variance for the *Brbr* segregates for number of spikes and length of awn. The values obtained by dividing Z by its standard error were 2.260 and 2.624 respectively. It appears that all genotypes do not have the same variance even though their means may be of similar magnitude.

These results make it apparent that in studies such as this, erroneous conclusions are likely to be drawn in estimating the residual genic variability, by use of parental data as an absolute measure of environmental variation, as the amount of variation due to the environment is not the same for all genotypes.

THE NATURE OF THE INTERACTION BETWEEN THE GENES AFFECTING WEIGHT OF SEED PER PLANT AND THE ENVIRONMENT

It was found that in general the genes more favorable to higher yields of seed per plant gave still higher absolute yields in comparison with their alleles when in combination with high yielding genotypes than when in combination with low yielding genotypes. This raises the question as to whether the same relationship might not exist in a comparison involving different environments.

To obtain evidence the population for each of the nine genotypes was divided into three levels of yield by the use of the normal curve. The levels thus established within reasonable limits gave the same number of individuals in each class. This method of division does not eliminate the residual genic variability as genes not closely linked and those inherited independently of those identified in this study would have an effect as well as environmental conditions. Thus some of the plants falling in the upper $1/3$ may be in that range partially because of favorable genes. An estimate of the importance of the effect of the residual genic variability can be obtained by a comparison of the weight of seed per plant for the parents and the F_2 segregates of the same genotype. The comparison is given in table 3. The B 1 parent (*VVBrBr*) yielded 2 grams less than the F_2 plants

of the genotype *VVBrBr* and the Brachytic parent (*vvbrbr*) yielded .5 of a gram less than the F_2 plants of the genotype *vvbrbr*. From table 10, it can be seen that the range in yields of any one genotype for the different levels is considerably greater than the above. Therefore, from these data it appears that the environment played the most important part in determining into which level of yield a plant of a given genotype would fall.

The three levels of weight of seed per plant are listed in table 10. The difference between combinations of *Vv* and the differences between the combinations of *Brbr* are listed in table 11. As in all the previous studies these comparisons include the effect upon weight of seed per plant of the genes linked with *Vv* and *Brbr* as well as the effect of these genes themselves. The completeness with which the effect of the linked genes is meas-

TABLE 10
Weight of seed per plant of the different genotypes for three levels of yield.

PHENOTYPE	GENOTYPE	LEVEL OF YIELD		
		UPPER	MIDDLE	LOWER
Vulgare normal	(<i>vvBrBr</i>)	12.1	7.2	3.2
Vulgare normal	(<i>vvBrbr</i>)	13.5	7.9	4.1
Vulgare brachytic	(<i>vvbrbr</i>)	6.9	4.4	2.1
Deficiens normal	(<i>VvBrBr</i>)	8.7	5.2	2.3
Deficiens normal	(<i>VvBrbr</i>)	8.1	4.9	2.3
Deficiens brachytic	(<i>Vvbrbr</i>)	4.5	2.4	1.1
Deficiens normal	(<i>VVBrBr</i>)	6.9	3.9	1.4
Deficiens normal	(<i>VVBrbr</i>)	6.8	4.1	2.2
Deficiens brachytic	(<i>VVbrbr</i>)	3.3	1.6	.7

ured depends of course upon the closeness of the linkage relationship. It is apparent from table 11 that, with the possible exception of *BrBr* compared with *Brbr* in combination with *VV*, the more favorable the environmental conditions the greater in absolute values the spread between the genes more favorable to yield and those less favorable to yield. Also, as noted from the previous data, the differences are greater for the higher yielding genotypes.

DISCUSSION AND CONCLUSIONS

Recently geneticists have become interested in the nature of the interaction of factors governing the inheritance of quantitative characters. Of interest in this respect is RASMUSSEN'S (1935) interaction hypothesis which assumes "that the effect of each factor on the genotype is dependent upon all the other factors present, the visible effect of a certain factor being smaller the greater the number of factors acting in the same direction."

RASMUSSEN found support for his hypothesis in a study on the interaction of factors governing early and late maturity in *Pisum*. POWERS (1934) in studying the inheritance of habit of growth in *Triticum* obtained results which would support this hypothesis also. However, the nature of the interaction of the factors affecting weight of seed per plant, number of spikes per plant, height of plant and length of awn was, generally speaking, quite the reverse of that expected on the above hypothesis in that the effect of certain factors was not smaller the greater the number acting in a certain direction.

TABLE II
Differences in weight of seed per plant for three levels of yield.

GENOTYPE	LEVELS OF YIELD		
	UPPER	MIDDLE	LOWER
<i>vv</i> vs. <i>Vv</i> (<i>BrBr</i>)	3.4	2.0	.9
<i>vv</i> vs. <i>VV</i> (<i>BrBr</i>)	5.2	3.3	1.8
<i>Vv</i> vs. <i>VV</i> (<i>BrBr</i>)	1.8	1.3	.9
<i>vv</i> vs. <i>Vv</i> (<i>Brbr</i>)	5.4	3.0	1.8
<i>vv</i> vs. <i>VV</i> (<i>Brbr</i>)	6.7	3.8	1.9
<i>Vv</i> vs. <i>VV</i> (<i>Brbr</i>)	1.3	.8	.1
<i>vv</i> vs. <i>Vv</i> (<i>brbr</i>)	2.4	2.0	1.0
<i>vv</i> vs. <i>VV</i> (<i>brbr</i>)	3.6	2.8	1.4
<i>Vv</i> vs. <i>VV</i> (<i>brbr</i>)	1.2	.8	.4
<i>BrBr</i> vs. <i>Brbr</i> (<i>vv</i>)	-1.4	-.7	-.9
<i>BrBr</i> vs. <i>brbr</i> (<i>vv</i>)	5.2	2.8	1.1
<i>Brbr</i> vs. <i>brbr</i> (<i>vv</i>)	6.6	3.5	2.0
<i>BrBr</i> vs. <i>Brbr</i> (<i>Vv</i>)	.6	.3	.0
<i>BrBr</i> vs. <i>brbr</i> (<i>Vv</i>)	4.2	2.8	1.2
<i>Brbr</i> vs. <i>brbr</i> (<i>Vv</i>)	3.6	2.5	1.2
<i>BrBr</i> vs. <i>Brbr</i> (<i>VV</i>)	.1	-.2	-.8
<i>BrBr</i> vs. <i>brbr</i> (<i>VV</i>)	3.6	2.3	.7
<i>Brbr</i> vs. <i>brbr</i> (<i>VV</i>)	3.5	2.5	1.5

The logical conclusion to be drawn from these data is that the nature of the interaction of the genes affecting the quantitative characters is sufficiently variable to render any hypothesis of doubtful value as a means of prediction. From our more extensive knowledge of the interaction of factors governing the inheritance of quantitative characters it is not surprising that this is the case. In fact, BRINK (1934) found that the interaction of factors governing anthocyanin plant colors in maize was such that plants of the genotypes *AbPl* and *ABpl* averaged higher in dry weight of ears per plant than did plants of the genotypes *ABPl* and *Abpl*. It seems from these

results and others reported here that the nature of the interaction of factors affecting quantitative characters is sufficiently variable to require extensive genetic studies involving a large variety of characters and organisms before a hypothesis of much value for prediction purposes can be formulated and then it may be expected to be rather limited in application.

EAST (1935) develops a concept concerning genes that is useful in the interpretation of any studies on quantitative inheritance. He divides gene mutations into two broad classes: physiological defectives and physiological non-defectives. These are discussed in connection with the bearing that they have upon evolution. Physiological defective gene mutations comprise the great bulk of those found in the genetic laboratory, usually are recessive to the wild type and cause restrictions in the physiological processes in which they are involved. This would mean that they may have both quantitative and qualitative effects and are easily detectable. Because of the comparative ease with which they are detected the effect must be pronounced. The non-defective gene mutations are frequent in nature but are difficult to detect individually and may show either an approach to dominance or to recessiveness. The effect of any one gene resulting as a non-defective mutation must be small.

The importance of this conception of the two broad types of gene mutations for a better understanding of the genes differentiating quantitative characters is obvious. It can be expected that the characters depending upon physiological defective genes for their expression will be differentiated from their alleles by comparatively few factor pairs; whereas, larger differences involving non-defective genes would be expected to be differentiated by a large number of gene pairs, because as is pointed out by EAST (1935) the effect of any one pair of non-defective genes is small.

The results from the present study offer some evidence for the conception that genes having an effect upon quantitative characters may be grouped into the classes noted above. The *brbr* genes which cause brachytic habit of growth would certainly be classed as physiological defective, as would the *VV* genes which produce *deficiens* type of spike. Plants possessing *VV* genes do not have kernels developed in the rudimentary lateral florets. The heterozygote *Vv* approaches the *deficiens* parent in that no lateral grains are produced, but it is distinguishable from the *VV* homozygote in that the lateral florets although rudimentary are noticeably developed. Undoubtedly the effects of the *Brbr* and *Vv* genes are both quantitative and qualitative. The genes affecting the four quantitative characters and associated with color of glume are of the non-defective type. In heterosis at least two factor pairs are necessary to account for the increases noted in the heterozygote, since the differences between the two homozygotes are not statistically significant (table 2). It seems highly probable

that even larger numbers of factor pairs than these are operating to produce the results obtained. For all four characters the Vv plants exceeded the VV plants. Again the most probable explanation seems to be that a number of partially dominant linked factors are responsible for the differences between the two genotypes. As regards the genes associated with color of glumes, the effect of any one factor pair must necessarily be small, and as EAST (1935) has pointed out such small differences are difficult to detect.

ROBERTSON AND AUSTIN (1936) studied homozygous and heterozygous green plants of *Hordeum vulgare* from families segregating for the single factor pairs $X_c x_c$ and $A_c a_c$ and found statistically significant differences in favor of the heterozygous plants for the following characters: average length of head, total number of grains per plant, and total weight of grain per plant. Again the differences were small and may be due to a number of physiologically non-defective genes. The residual genic variability noted in the study reported in this article is due probably to factors of the same nature (non-defective) as the writer failed to find any qualitative expression of them. That these genes did not react alike in all genotypes was shown by the fact that greater increases in weight of seed per plant were obtained when combined in plants of the genotype $VVBrBr$ than when combined in plants of the genotype $vvbrbr$. These results show that both groups of genes—physiological defective and non-defective—do not necessarily react alike in all genotypes.

It should be pointed out that the terms physiological defective and non-defective are used by EAST in reference to gene mutations, but it is apparent that his theorems are important in a study of the inheritance of quantitative characters. Undoubtedly these two classes grade into each other and exceptions exist, but this does not vitiate the value of such a classification. It is apparent that the above conception is very useful to the workers in the field of applied genetics. Rapid strides can be made by the breeder when dealing with the physiological defective genes, whereas, when non-defective genes are involved, the advantage gained by recombining several desirable factor pairs may be expected to be small and the progeny possessing them difficult to select because of the limited number in large populations. This does not mean that the non-defective genes are not important in a breeding program, but only that they are more difficult to work with.

SUMMARY

1. A method involving the analysis of variance and co-variance was used in reducing the data.
2. The nature of the interactions of genes was such that no general rule could be drawn. However, with one exception, which was not well estab-

lished statistically, the genes favorable to high weight of seed per plant gave as great or greater differences over their alleles in combination with genes for higher yield than they did in combination with genes for lower yield. The same general behavior was noted for the genes affecting number of spikes per plant, height of plant, and length of awn, but cases were found in which plants of a given genotype surpassed plants possessing their alleles in some combinations and were surpassed by plants possessing identical alleles in other combinations.

3. The genic variability not associated with any of the three chromosome groups identified by genes having qualitative effects was found to give a greater increased weight of seed per plant when in combination with *VVBrBr* than when in combination with *vvbrbr*. Here, again, is proof of a difference in the interaction of factors.

4. It was found that genotypes affecting the same character may have different variances even though their means may be of similar magnitude.

5. It was found that the more favorable the environmental conditions the greater in absolute values would be the spread between the genes more favorable to yield and those less favorable to yield.

6. The nature of the interaction of the factors affecting weight of seed per plant, number of spikes per plant, height of plant, and length of awn was generally speaking quite the reverse of RASMUSSEN'S interaction-hypothesis which assumes that the visible effect of a certain factor is smaller the greater the number of factors acting in the same direction.

7. The genes affecting the four quantitative characters are grouped into physiological defective and non-defective according to EAST'S (1935) terminology and the data offer some evidence in favor of his conception as to the nature of the effects of these genes. Both classes of genes showed that they necessarily did not give the same type of interaction in all genotypes.

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