A STUDY OF THE EFFECT OF SIX QUALITATIVE CHARACTER PAIRS ON YIELD AND COMPONENT CHARACTERS IN THE F_2 OF A CROSS BETWEEN TWO VARIETIES OF BARLEY[1]

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INTRODUCTION

This article reports the relationship in barley between six qualitative character pairs and the quantitative characters: weight per seed, number of heads per plant, number of seeds per head, and yield per plant in the F_2 segregating population of a cross between the Nigrillaxum (*Hordeum distichon* L.) and Brachytic chlorina (*H. vulgare* L.) varieties of barley. The six pairs of genes studied differentiated 2-row *vs.* 6-row type of spike (V,v); black *vs.* white color of glumes (B,b); covered *vs.* naked caryopsis (N,n); hooded *vs.* awned type of lemma (K,k); normal *vs.* brachytic habit of growth (Br,br); and green *vs.* chlorina type of seedling (Fc,fc). The six contrasting characters of the parents were as follows:

$$\frac{\text{Nigrillaxum}}{\text{brachytic-chlorina}} = \frac{\text{V B n K Br Fc}}{\text{v b N k br fc}}$$

The data used for the study were taken by the late Dr. F. R. Immer, on material grown at University Farm, St. Paul. The quantitative data were taken on the individual F_2 plants and their genotypes were determined by F_3 progeny trials. The study consisted primarily of comparisons of the different genotypes for a single factor pair with respect to the quantitative characters. Similar comparisons were made of the interactions between factor pairs considered two at a time.

The mode of inheritance and linkage relations of the six factor pairs used are summarized by Robertson, Wiebe and Immer (13). Each of the characters is simply inherited and all are reported to be independent except br-fc which is linked

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with about 9.8 per cent recombination. Two of the factor pairs namely 2-row vs. 6-row (11) and hooded vs. awned (10), have been reported to show a relation to yield. The recessive characters brachytic and chlorina are usually less vigorous than the normal.

Powers (11) reported the effect on quantitative characters of 3 of the 6 character pairs in a cross between *Hordeum deficiens* (Steud) and *H. vulgare* (L.). He found that the BB and bb genotypes did not differ significantly but that Bb was in general different from the two homozygotes. The vv plants yielded more than the VV and Vv; and the Vv more than the VV plants. Normal plants of the Br Br and Br br genotypes were higher in yield than the homozygous br br.

The reader may consult Smith (14) for a comprehensive review of the literature on quantitative inheritance and Hayes and Immer (6) for a review of quantitative inheritance in barley.

METHODS

The F_2 plants were grown in 1938, single seeds being planted five inches apart in rows one foot apart in a plot 18 ft. by 39 ft. in size. Three rows of each parent were planted as checks.

Notes were taken on the phenotype of each plant for the six character pairs, each plant was harvested individually and the number of heads per plant was recorded. The plants were threshed, the number of seeds counted and the yield in grams of seed determined, from which the average number of seeds per head and the average weight per seed were calculated.

Since the absence of hulls leads to a reduced weight per seed, corrections were made on the yield data for the hulles plants based on a regression between seed weight and hull weight determined from 25 seeds of each of 48 plants representing a wide range of phenotypic combinations.

The complete genotypes of the F_2 plants were determined by classifying the F_3 progeny. Of the F_2 plants, 6 of the Br Fc, 12 of the br Fc, 4 of the Br fc, and 94 of the br fc produced insufficient seed for the F_3 test (less than 0.5 grams) and were discarded leaving a total of 1044 plants.

The complete quantitative data and their squares, and the genotypes for each of the 1044 plants were punched on cards. Ordinarily the cards would then have been sorted by genotypes to obtain the data for each gene pair singly and also in combinations of two or more gene pairs at a time. In this case, since a large proportion of the F_2 plants with insufficient seed were *br, fc* or *br fc*, making the yield of these genotypes higher than they should be, it was deemed necessary to remove the effects of the Br, br and Fc, fc segregation by including their different observed genotypes with each of the genotypes for the gene pair or pairs being studied. Consequently the cards were sorted for all genotypic combinations between the gene pair or pairs being studied and Br, br, Fc, fc.

In order to study the effects of the qualitative genes on each quantitative character, the mean value for each genotype was calculated and used in the comparisons. For example, the difference Vv-vv was interpreted as the effect of substituting the first dose of the dominant gene; VV-Vv the effect of substituting the second; and VV-vv the total effect of both. In studying the interactions between two non-allelic genes, for example, V,v with B,b; the above three comparisons were made in each of the BB, Bb, and bb genotypes. Finally, the effect in one of these latter genotypes was compared with that in each of the other two. For example the Vv-vv effect in the BB genotype was compared with that in the Bb and bb genotypes.

The statistical methods for calculating the means and standard errors and for determining the significance of differences will now be described.

STATISTICAL METHODS

The method of removing the effects of the Br, br and Fc, fc segregation will be illustrated by the calculation for the yield of a genotype used in the study of the interaction between V,v and B,b. To obtain the corrected sum of squares of the yields for the VVBB genotype, that is, freed from the effects of segregation for Br, br and Fc, fc, an analysis of variance for individual plant yield for each of the different genotypic combinations between (Br *vs.* br) (Fc *vs.* fc) within the VVBB genotype was calculated separately and the totals combined. The formula used is as follows:

"the sum of squares" $= S(y)^2 - S(y)\bar{y}$, where: $S(y) =$ sum of the yields of all plants, $\bar{y} =$ mean yield of the plants of the given genotype and $y =$ yield of individual plants.

The results of the calculations for the VVBB genotype are given in Table 1. Since there are 69 plants in the VVBB segregation composed of 7 classes for Br, br *vs.* Fc, fc, the degrees of freedom will be 69-7 = 62. The total sum of squares, 350.75, divided by the degrees of freedom, 62, is the variance or mean square. The variance of the mean was determined from the formula: $\text{Vm} = \frac{\text{Total sum of squares.}}{\text{D.F x N}}$ This method of calculating the variance combines the differences between the genotypic combinations between Br, br and Fc, fc into a single value, this being used to calculate a generalized estimate of the error for that particular genotype of V with B.

TABLE NO. I

LLUSTRATION OF THE METHOD OF CALCULATING THE CORRECTED SUM OF SQUARES OF THE YIELDS OBTAINED WITH A GIVEN GENOTYPE (VVBB) FOR ALL COMBINATIONS OF THE QUALITATIVE CHARACTERS Br br AND Fc fc[1]

Genotype	N	$S(y^2)$	$S(y)(\overline{y})$	$S(y^2)-S(y)(\overline{y})$
VVBBBrBrFcFc	17	745.83	613.20	132.63
VVBBBrBrFcfc	5	243.24	233.93	9.31
VVBBBrBrfcfc				
VVBBBrbrFcFc	5	246.36	228.49	17.87
VVBBBrbrFcfc	31	1,265.67	1,079.11	186.56
VVBBBrbrfcfc	2	3.94	3.92	.02
VVBBbrbrFcFc				
VVBBbrbrFcfc	4	18.78	15.21	3.57
VVBBbrbrfcfc	5	5.99	5.20	.79
	69			350.75*

* Corrected sum of squares for VVBB.

[1] The method of removing the effects of Br br vs. Fc fc was suggested by W. G. Cochran in a letter to Dr. F. R. Immer.

TABLE NO. II

ILLUSTRATION OF THE METHOD OF CALCULATING THE MEAN SQUARES, AND VARIANCE OF THE MEAN USING "SUM OF SQUARES" CORRECTED BY REMOVING THE Br br VS. Fc fc EFFECTS

Genotype	N	Classes	D. F.	Mean Yield	Corrected Sum of Squares	Mean Square	Variance of mean
VVBB	69	7	62	5.343	350.75	5.6572	.081989
VVBb	122	7	115	5.163	959.01	8.3392	.068354
VVbb	79	7	72	5.589	791.72	10.9961	.139191
VvBB	144	9	135	6.356	1,217.66	9.0197	.062637
VvBb	267	7	260	5.745	2,961.78	11.3915	.042665
Vvbb	114	8	106	5.818	960.81	9.0642	.079511
vvBB	62	7	55	6.082	614.19	11.1671	.180114
vvBb	116	7	109	6.217	1,278.07	11.7254	.101081
vvbb	71	8	63	5.159	740.58	11.7552	.165567
	1,044	67	977		9,874.57		

Table 2 summarizes the calculations for the nine genotypes for the factor pairs V,v and B,b. To determine if a single generalized error could be used for the 9 genotypes insolving V,v and B,b, a homogeneity test (1) was applied to the 9 separate generalized errors. The writer found heterogeneity as Powers (11) did in his study. Since the variance were not homogeneous, and a generalized estimate of error could not be used, "t" values to determine the significance of mean differences between genotypes were calculated by the usual formula for $s_{\bar{d}}$, the standard error of a difference between two means: $s_{\bar{d}} = \sqrt{V_1 + V_2}$, where V_1 and V_2 are the respective variances of the means under comparison.

As an example, the effect of VV will be compared with that of Vv in the BB genotype, taken from Table 2. For VVBB, $V_1 = 0.081989$ and VvBB, $V_2 = 0.062637$.

Then $s_{\bar{d}} = \sqrt{0.081989 + 0.062637} = .3803$

Since the ratio of the difference between means, $\bar{d}$, to its standard error, $s_{\bar{d}}$, does not follow Student's "t" distribution except in special instances (2), some other method must be used. The approximation t′ given by Cochran and Cox (2) was used. The approximation consists in calculating $t = \frac{\bar{d}}{s_{\bar{d}}}$ and finding a significance level t′ weighted in accordance with the following procedure:

$$t' = \frac{w_1 t_1 + w_2 t_2}{w_1 + w_2}^{*}$$ where t_1 and t_2 are the significance level values for n_1 and n_2 degrees of freedom and $w_1 = V_1$ and $w_2 = V_2$, the latter being the variances of the two means. In the present example for VVBB-VvBB at the 5% level:

$$t' = \frac{(.081989 \times 1.995) + (.062637 \times 1.977)}{.081989 + .062637} = 1.987.$$

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* Since $w_1 = V_1$ and $w_2 = V_2$, this formula becomes $t' = \frac{V_1 t_1 + V_2 t_2}{V_1 + V_2}$

Since t' always lies between the ordinary t values for n_1 and n_2 degrees of freedom, all cases except those on the borderline of significance can be decided without the actual calculation of t'. Since the difference in mean yields is:

VvBB — VVBB = 6.356 — 5.343 = 1.013,

$$\text{then } t = \frac{\bar{d}}{s_{\bar{d}}} = \frac{1.013}{.3803} = 2.664$$

In this example the observed "t" value of 2.664 is well above not only this t' value, but also the "t" value of 1.995 corresponding to the 5% level for 62 degrees of freedom. Therefore it would not have been necessary to calculate t' for this comparison.

For the effects of the different genotypes for each gene pair considered singly, the mean value of the corresponding quantitative character for each was calculated and the corresponding variance of the mean determined by using the corrected "sum of squares" as described above to remove the effects of the Br, br and Fc, fc segregation.

The net effects of V *vs.* v in the population classified for each of the other gene pairs considered singly were also calculated from data in which the interactions were studied. For example, for the V-v pair in the population classified for B *vs.* b the following values were calculated from the data in table 2.

Genotype	N	D. F.	Totals of yields	Corrected sum of squares	Variance of the mean
VV	270	249	16.095	2,101.48	.031258
Vv	525	501	17.919	5,140.26	.019543
vv	239	227	17.458	2,632.84	.046580

For the net effect of adding one V, we have
Vv-VV = 17.919 — 17.458 = .461 (net effect),

$$\text{and } t = \frac{.461}{\sqrt{.019543 + .046580}} = 1.794, \text{ significance being}$$

determined as before. In general these net effects should agree with the effects of each gene based on the total population. Any differences result from the fact that the net effects are based on means for genotypic combinations between two pairs of factors, the grouping being different for different cases. In determining the effects of the Br-br and Fc-fc gene pairs considered singly, mean values and their variances were calculated for each quantitative character directly in spite of the possible bias due to the elimination of a large number of the recessives. Had they been included, the differences would have been still larger.

Interactions (To determine whether a gene effect in one of the three genotypic backgrounds for a second gene pair was significantly different from its effect in either of the other two genotypic backgrounds for this gene pair).

Since an analysis of variance could not be calculated to test the significance of the interactions of one gene with a non-allele, the "t" values to determine the significance of the first order interactions were obtained by the method given by Powers (12). The formula for obtaining t as stated by him is as follows:

$$t = \frac{\bar{x}_1 + \bar{x}_4 - \bar{x}_2 - \bar{x}_3}{\sqrt{\frac{S_1^2}{n_1 n_1'} + \frac{S_2^2}{n_2 n_2'} + \frac{S_3^2}{n_3 n_3'} + \frac{S_4^2}{n_4 n_4'}}} \quad \text{or} \quad \frac{\bar{x}_1 + \bar{x}_4 - \bar{x}_2 - \bar{x}_3}{\sqrt{V_1 + V_2 + V_3 + V_4}}$$

In the above formula $\bar{x}_1$, $\bar{x}_2$, $\bar{x}_3$ and $\bar{x}_4$ are the mean of the different genotypes: S_1^2, S_2^2, S_3^2 and S_4^2 are the sum of squares for the estimation of the separate errors; n_1, n_2, n_3 and n_4 are the corresponding degrees of freedom available for an estimation of the separate errors; and n'_1, n'_2, n'_3, and n'_4 are the corresponding total numbers of individuals for the genotypes whose means are involved in the calculation of the interaction.

As an illustration of this calculation of interaction, the following data for yield from Table 2 may be used: (Vv BB — vvBB) — (Vv Bb — vv Bb) = (6.356—6.082) — (5.745—6.217). In other words the Vv-vv effect is being compared in the BB and Bb backgrounds.

$$t = \frac{6.356 + 6.217 - 6.082 - 5.745}{\sqrt{\frac{1217.66}{(135\text{x}144)} + \frac{614.19}{(55\text{x}62)} + \frac{2961.78}{(260\text{x}267)} + \frac{1278.07}{(109\text{x}116)}}}$$

$$= \frac{6.356 + 6.217 - 6.082 - 5.745}{\sqrt{0.062637 + 0.180114 + 0.042665 + 0.101081}} = \frac{.746}{.6217} = 1.200$$

For these "t" tests of significance, all values found to exceed 1.960 were considered significant at the 5% point, since the total number of degrees of freedom in each test was always very large.

The mean, variance, variance of the mean and the standard errors of the yields and its components were calculated for the six character pairs singly and in all combinations of two each. Differences giving probabilities as low or lower than 0.05 that the deviations as great as those noted might arise because of errors of random sampling were considered to be statistically significant; although some caution must be exercised since with such a large number of comparisons, certain of them are undoubtedly chance variations.

EXPERIMENTAL RESULTS

Each factor pair except Fc-fc in F_2 and all of them in F_3 gave good agreement with a monogenic ratio as expected from previous studies (13). For the Fc *vs.* fc pair there was a deficiency of chlorina plants in F_2 due possibly to low germination or poor survival.

The X^2 values for the linkage components indicated no association except between Br,br and Fc,fc factor pairs and between N,n and K,k. All other combinations of two factor pairs showed a good fit to dihybrid segregations. The F_2 data on which these are based are in table 3.

TABLE NO. III

F_2 SEGREGATIONS FOR CHARACTERS SHOWING LINKAGE, F_2 DATA

Segregation	AB	Ab	aB	ab	Total	Linkage Component		Per Cent Recombination Product Method	Weighted p value F_2 and F_3 Data
						X^2	P		
N-K......	575	200	210	59	1,044	1.63	.30—.20	47.0±2.40	46.1±1.71
Br-Fc.....	860	21	32	131	1,044	376.10	.0001	6.3± .78	7.6± .58

The loose but significant linkage btween N and K suggests a chromosome abnormality, possibly a translocation, but was not found in time for a cytological study. The interpretations of the results may be affected since two closely linked qualitative factors might be expected to show similar associations with linked quantitative factors.

MAIN EFFECTS—DIFFERENCES BETWEEN GENOTYPES FOR EACH GENE PAIR CONSIDERED SINGLY

The average values for yield and its components for the homozygous and the heterozygous genotypes are in table 4 and the comparisons for each gene pair are in table 5. Any observed difference may be interpreted either as due to the effect of the gene itself or to the effect of one or more linked quantitative factors. If the latter, the observed degree of effect will depend on the closeness of the linkage, i.e. the closer the linkage the more nearly will the observed difference represent the actual effect of the quantitative gene itself. For ease of discussion the difference will be described as due to the effect of the qualitative factor itself throughout the presentation of the results, although in reality it may be due to an association with a quantitative factor.

The comparisons between genotypes for a given gene pair, for example Vv-vv, VV-Vv, and VV-vv, are interpreted as being the effect of substituting the first dominant, the second dominant, and both respectively for either or both recessive alleles. The effect of the second dominant is the effect of adding another one to a genotype which already has one. The VV-vv difference is the algebraic sum of the other two.

TABLE NO. IV

A SUMMARY OF QUANTITATIVE CHARACTER MEANS FOR THE DIFFERENT GENOTYPES CONSIDERED SINGLY

Genotype	N	Mean yield in grams of seeds per plant	Mean number of heads per plant	Mean number of seeds per head	Mean weight of seed in grams per seed
VV	270	5.334	9.211	154.65	.032384
Vv	525	5.929	9.265	223.46	.025778
vv	249	5.882	7.924	261.59	.021481
BB	275	6.040	9.516	225.12	.026812
Bb	505	5.713	8.824	213.51	.026514
bb	264	5.572	8.527	206.34	.025997
NN	276	5.832	8.887	222.70	.026170
Nn	499	5.674	8.894	211.25	.026344
nn	269	5.859	9.045	213.15	.026979
KK	264	5.153	9.015	197.11	.025725
Kk	521	5.729	9.142	214.13	.026678
kk	259	6.455	8.420	234.00	.026776
BrBr	360	6.639	10.006	253.81	.026681
Brbr	521	6.602	9.994	236.73	.028603
brbr	163	1.148	3.160	58.26	.019154
FcFc	333	6.585	10.048	248.92	.026952
Fcfc	559	6.601	9.968	240.46	.028110
fcfc	152	.885	2.671	45.39	.019354

TABLE NO. V

DIFFERENCES IN QUANTITATIVE CHARACTER MEANS BETWEEN GENOTYPES FOR INDIVIDUAL CHARACTER PAIRS CONSIDERED SINGLY

Genotype	Difference between mean yields	Difference between mean number of heads	Difference between mean number of seeds	Difference between mean weight of seed
Vv-vv	.047	1.341**	—38.13**	.004297**
VV-Vv	—.595*	—.054	—68.81**	.006605**
VV-vv	—.548*	1.287**	—106.95**	.010903**
Bb-bb	.141	.297	7.17	.000517
BB-Bb	.327	.692*	11.61	.000298
BB-bb	.468	.989**	18.78	.000815
Nn-nn	—.185	—.151	—1.90	—.000635
NN-Nn	.158	—.007	11.45	—.000174
NN-nn	—.027	—.158	9.55	—.000809
Kk-kk	—.726**	.722*	—19.87*	—.000098
KK-Kk	—.576**	—.127	—17.02*	—.000953*
KK-kk	—1.302**	.595	—36.89**	—.001051*
Brbr-brbr	5.454**	6.834**	178.47**	.009450**
BrBr-Brbr	.037	.012	17.08	—.001920**
BrBr-brbr	5.491**	6.846**	195.55**	.007530**
Fcfc-fcfc	5.716**	7.297**	195.07**	.008760**
FcFc-Fcfc	—.016	.080	8.46	—.001160*
FcFc-fcfc	5.700**	7.377**	203.53**	.007600**

* Significant at the 5% probability level.
** Significant at the 1% probability level.

Effect of 2-row versus 6 row (V vs. v). There was no effect on yield due to the substitution of the first dominant as measured by the Vv-vv comparison. The substitution of the second V as measured by the VV-Vv comparison significantly decreased yield. The total effect of substituting both V's as measured by the VV-vv comparison was a significant decrease in yield.

The substitution of the first V significantly increased the number of heads per plants, the second V had no effect, while the total effect of both was to significantly increase the number of heads.

For number of seeds per head the first V produced a decrease, the second V reduced it still further, and the total effect of both was necessarily a significant decrease.

As to average weight per seed the first V increased it significantly, the second V increased it still further and again the effect of both was, as expected, a significant increase.

The effect of the first V to increase number of heads and weight per seed was counterbalanced by a decrease in number of seeds, the net result being no effect on yield. The substitution of the second V had no further effect on number of heads, but decreased the number of seeds and increased the weight per seed. The decrease in number of seeds per head accounts for the net decrease in yield as a result of substitution of the second V. These comparisons thus represent the change from 6- to 2-row.

Effect of black versus white color of glumes (*B vs. b*). There was no effect on yield, number of seeds per head nor weight per seed due to the substitution of the first or the second B or of both.

For number of heads per plant the substitution of the first B had no effect. However, the second B significantly increased the number of heads per plant, and the total effect of both B's was a significant increase. In spite of this, there was no significant net effect on yield.

Effect of covered versus naked caryopsis (*N vs. n*). No one of the quantitative characters was affected by substituting either the first or second N or both.

Effect of hooded versus awned lemma (*K vs. k*). The substitution of the first K significantly decreased the yield, the second K decreased it still further, while the effect of both K's was necessarily a significant decrease.

There was an increase in number of heads per plant due to the substitution of the first K.

As to number of seeds per head the first K decreased it significantly, the second K decreased it still further, while the total effect of both K's was a significant decrease.

For weight per seed the first K had no effect, while the substitution of the second K and of both K's significantly decreased it.

The significant decrease in yield due to the substitution of the first K appears to have been brought about mainly by a decrease in seed number, since the number of heads was actually increased. The decrease in yield attributed to the second K seems to have been the result of a decrease in weight of seeds as well as in number of seeds.

Effect of normal versus brachytic habit of growth (*Br vs. br*). The substitution of the first Br produced a significant increase in the yield, number of heads, number of seeds and weight per seed. The second Br had no effect, except to decrease the weight per seed. The total effect of both was a significant increase in yield, number of heads, number of seeds and weight per seed. As to weight per seed the heterozygous Br br seeds were heavier than either of the homozygotes, an indication of heterosis or of Hull's superdominance (7).

Effect of normal versus chlorina seedlings (Fc vs. fc). The substitution of the first Fc produced a significant increase in the yield, number of heads per plant, number of seeds, and weight per seed. The second Fc had no effect except to decrease weight per seed. The total effect of both F'cs was a significant increase in yield, number of heads, number of seeds, and weight per seed. The heterozygous (Fcfc) seeds were heavier than the homozygous ones, again an indication of heterosis.

Interactions of each gene pair with a non-allelic pair. Two questions will be considered here: first, in which genetic backgrounds is a given gene effect significant; and second, are there effects which are significantly different in the different genotypes for a given non-allelic gene pair. For brevity, only the data on the interactions of the V-v pair with non-alleles are presented, information on the first question being in table 6. Information on the second question is in table 7. It is helpful in interpreting the latter tables to refer to the corresponding tables 6 and 7 to determine the magnitude and direction of the differences being compared. For example, the significant interaction (VVBb-vvBb)—(VVbb-vvbb) = —1.484 (table 7) is a comparison between (VVBb-vvBb) = —1.054 and the (VVbb-vvbb) = .430 given in table 6. Interactions of the other gene pairs will be discussed without presenting the data.

TABLE NO. VI

QUANTITATIVE CHARACTER DIFFERENCES BETWEEN GENOTYPES FOR THE V vs. v CHARACTER PAIR WITHIN DIFFERENT GENOTYPES FOR A NON-ALLELIC PAIR

	Yield				Number of heads		
	B vs. b	N vs. n	K vs. k		B vs. b	N vs. n	K vs. k
AA	.274	—.073	—.098	Vv-vv	2.032*	.967	1.500**
Aa	—.472	.136	.361		.541	1.550**	1.355**
aa	.659	.044	—.291		1.919*	1.395**	1.085
AA	—1.013*	—1.570**	—.220	VV-Vv	—.488	—.482	—.122
Aa	—.582	—.555	—.430		—.137	—.205	—.119
aa	—.229	.149	—1.308*		.553	.550	.252
AA	—.739	—1.643**	—.318	VV-vv	1.544*	.485	1.378*
Aa	—1.054*	—.419	—.069		.404	1.345**	1.236**
aa	.430	.193	—1.599*		2.472*	1.945**	1.337

	Number of seeds				Weight per seed		
	B vs. b	N vs. n	K vs. k		B vs. b	N vs. n	K vs. k
AA	—22.65	—49.90*	—41.69*	Vv-vv	.003331**	.005938**	.004788**
Aa	—65.91**	—31.06*	—32.74**		.004573**	.003443**	.004395**
aa	—6.44	—37.09	—40.83		.004364**	.003924**	.003570**
AA	—83.78**	—88.50**	—53.62**	VV-Vv	.007229**	.003814**	.005941**
Aa	—64.73**	—71.80**	—61.98**		.006254**	.007516**	.007060**
aa	—62.68**	—46.59**	—98.50**		.006845**	.007458**	.006635**
AA	—106.43**	—138.40**	—95.31**	VV-vv	.010560**	.009752**	.010729**
Aa	—130.64**	—102.36**	—94.72**		.010827**	.010959**	.011455**
aa	—69.12**	—83.68**	—139.33**		.011209**	.011382**	.010205**

TABLE NO. VII

SIGNIFICANT INTERACTIONS OBTAINED BETWEEN A GIVEN EFFECT OF V vs. v AND DIFFERENT GENOTYPES FOR A NON-ALLELIC PAIR

Interactions	Difference
YIELD PER PLANT:	
(VVNN-VvNN)—(VVnn-Vvnn)	—1.719**
(VVNN-VvNN)—(VVNn-VvNn)	—1.015*
(VVNN-vvNN)—(VVnn-vvnn)	—1.836*
(VVBb-vvBb)—(VVbb-vvbb)	—1.484*
AVERAGE NUMBER OF HEADS PER PLANT:	
(VvBB-vvBB)—(VvBb-vvBb)	1.491*
(VvBb-vvBb)—(Vvbb-vvbb)	—1.378*
(VVBb-vvBb)—(VVbb-vvbb)	—2.068*
AVERAGE NUMBER OF SEEDS PER HEAD:	
(VvBb-vvBb)—(Vvbb-vvbb)	—59.47*
(VVNN-VvNN)—(VVnn-Vvnn)	—41.91*
(VVKK-VvKK)—(VVkk-Vvkk)	44.88*
(VVBb-vvBb)—(VVbb-vvbb)	—61.52**
AVERAGE WEIGHT PER SEED:	
(VvNN-vvNN)—(VvNn-vvNn)	.002495**
(VVNN-VvNN)—(VVNn-VvNn)	—.003702**
(VVNN-VvNN)—(VVnn-Vvnn)	—.003644**

Interactions of V-v. For average yield per plant, table 6 shows that the substitution of the first V had no significant effect in any of the genotypes of B-b, N-n, and K-k. The second V significantly decreased the yield only in the BB, NN and kk genotypes. The effect of both V's was significant only in the Bb, NN, and kk genotypes. Table 7 shows that the effect on yield of the second V, as measured by VV-Vv, was significantly different in the NN as compared with either the Nn or nn genotypes. The effect of both V's was significantly different in the NN *vs.* nn; and also in the Bb *vs.* bb genotypes. All other effects on yield were not significantly different in the three genotypes for any given non-allelic pair.

. For average number of heads per plant, (table 6), the substitution of the second V was in no case significant in any of the non-allelic backgrounds. Substitution of the first V resulted in a significant increase in all cases except in the Bb, NN and kk genotypes. The effect of both V's was also significant in all cases except in these same genotypes. The effect of the V *vs.* v for number of heads is only significantly greater, (table 7), in the BB and bb genotypes than in Bb. The effect of both V's in bb was greater than in Bb.

In the study of average number of seeds per head, the first V produced a significant decrease, (table 6), in the Bb, NN, Nn, KK and Kk genotypes. The second V produced much greater reductions which were highly significant in all genotypes. The addition of both V's was also significant in all genotypes. The decrease due to the first V was greater, (table 7), in the Bb than in the bb genotype. The further decrease due to the second V was greater, in the NN than in the nn genotype and in the kk than in the KK genotype. The decrease due to both V's was greater in the Bb than in the bb genotype.

For average weight per seed, the first V brought about a highly significant incresae in all cases (table 6). The second V still further increased the seed weight by a highly significant amount in all cases. The increase due to the first V was greater, (table 7), in the NN than in the Nn genotypes. The increase due to the second V were greater in the NN than either the Nn or the nn genotypes.

The chief component to account for the decreased yield in certain genotypes was the decrease in average number of seeds per head, since seed weight was increased in all genotypes.

Interactions of K vs. k. For average yield per plant, the effect of the first K was to significantly decrease yield in the Vv, vv, Bb, Nn and nn genotypes (all P* except in nn, P**). Addition of the second K decreased the yield only in the Vv, Bb and nn genotypes. The total effect of both K's was to decrease the yield in the Vv, vv, Bb, Nn and nn genotypes (P** for all but vv and Nn for which P*). The effect in yield of the first K was significantly different in the NN *vs.* nn genotypes (P**). The effect of the second K was different in the Bb and BB genotypes (P*) and in the Nn and nn genotypes (P**). The total effect of both K's was significantly different in BB and Bb (P*), NN *vs.* Nn and nn genotypes (P**).

For number of heads per plant, the effect of the first K, the second K and of both was not significant in any genotype. The total effect of both K's was different in the Nn and nn genotypes (P*).

For number of seeds per head, the effect of the first K was negative and significant (P*) in the Vv, and nn genotypes. The effect of the second K was significant in the Bb and nn genotypes. The effect of both was significant (P**) in the Vv, Bb and nn genotypes. The total effect of both K's was different in VV and Vv and in NN and nn (P*) genotypes.

For weight per seed the first K had no significant effect. The second K decreased the weight (P*) in the VV and vv genotypes. The total effect of both was a decrease in weight in the vv, Bb and nn genotypes. The effect of the first K was different in the NN and nn genotypes (P*). The effect of both K's was different in NN and nn genotypes (P*).

Interactions of B vs. b. For average yield per plant there was a significant increase in yield of BB over bb (P*) in the NN genotype, and in the vv genotype for the Bb-bb (P*) comparisons. In the BB-Bb comparisons there were significant differences in the KK (P**) genotype. There appeared to be a trend in favor of higher yield of the BB genotype, although this may be due to chance, since the net difference was not significant. The effect on yield of the first B was greater (P*) in the vv than in the VV genotype. The second B effect was greater (P*) in the KK than in either the Kk or kk genotypes.

For average number of heads per plant, significant differences in favor of BB over Bb plants were found in the Vv, Nn

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P* means that the difference so qualified was significant at the 5% point.
P** means that the difference so qualified was significant at the 1% point.

and KK genotypes. In the BB-bb comparisons, there were significant differences in favor of the BB genotype in Vv, NN and Nn. The effect of the first B was greater (P*) in the vv than in either the Vv or the VV genotypes. The effect of the second B was greater in the Vv than in the vv genotype (P*).

For number of seeds per head, the effect of the first B was a significant increase (P*) in the vv genotype. The effect of adding the second B was an increase only in the Vv, and KK genotypes, (P*). The total effect of both was significant only in the NN genotype (P*). The effect of the first B was greater in the vv than in either the VV or the Vv genotype.

For average weight per seed, the increase due to the first B was significant only in the NN genotype (P*). The effect of the second B was significant in no case. Only in the vv genotype was the total effect of both B's significant (P*) while the individual effects in this vv genotype were not. The effect of the first B was greater (P*) in the NN than in the nn genotype.

N vs. n interactions. For average yield per plant, the addition of the first N produced no significant effects. The same was true for the addition of the second N. The total effect of both was significant and negative in the VV (P**) genotype, positive in the KK (P*) and negative again in the kk genotype. In other words, the total effect of both was to depress the yield in the presence of kk; and to increase it in the presence of KK. The effect on yield of the first N was to increase the yield in the KK genotype and decrease it in the Kk and kk genotypes. The effect of the second N was to increase the yield VV and to decrease it in the Vv. The effect of both N's was different in the VV than in the Vv and vv (P*) and in the kk from that in either the KK (P**) or the Kk (P*) genotype.

For number of heads per plant, in no case was there any specific interaction with a non-allelic genotype. The effect of the first N was different in the kk genotype where there was a decrease in number of heads while in the KK there was an increase in number of heads.

For number of seeds per head, in the VV genotype the total effect of both N's was to significantly decrease the number of seeds per head (P*). The effect of the first N was different in the KK from that in the kk genotype (P*). The effect of both N's was significantly different in the VV from that in the Vv genotype (P*) and in the KK from that in the kk genotype (P*).

For average weight per seed, addition of the first N significantly (P*) decreased weight per seed in the bb genotype. Addition of the second N affected seed weight in the VV (P*) and Vv (P**) genotypes. In the former the weight was decreased, in the latter it was increased. The total effect of both N's was significant and negative in the VV (P**), bb (P*), and kk (P**) genotypes. The effect of the second N was different in the Vv from that in either the VV or vv genotypes (P**). The effect of both N's was different in the VV from that in the Vv genotype (P**); in the bb from the Bb genotype (P*) and in the kk from that in either the KK or Kk genotypes (P*).

DISCUSSION OF RESULTS

Before attempting to interpret the differences found to be statistically significant, it is necessary to point out that in such a large number of comparisons as was made in this study, a few of them are actually only chance differences. Which ones they are, cannot be recognized. To be safe, those which do not appear to be consistent are regarded with suspicion. In a study of sampling using Student's distribution, Treloar and Wilder (15) studied this problem to which the reader is referred if interested.

Certain of the qualitative characters were consistently associated with differences in the quantitative ones, and will be discussed here. Many of the associations can be interpreted as results expected from the known morphological or physiological differences brought about by the qualitative characters.

The higher yield of awned lemma (kk) over hooded (KK) is probably due to the favorable physiological effect of the presence of the awn which has been reported by many workers (review in Hayes and Garber (5)). The higher yield of the 6-rowed (vv) over the 2-rowed (VV) plants may be accounted for by a greater number of seeds per head since the laterals of the 2-row plants (VV) are infertile.

A higher number of seeds per head, one of the major components of yield, was found associated not only with the vulgare type of spike (vv) but also with awned lemma (kk). The latter does not naturally follow except possibly from a physiological effect of the awn. The higher weight per seed associated with 2-row type of spike (VV) and awned lemma (kk) may have similar explanations. The seed of the 2-row types is expected to weight more since the central row seeds usually are larger than those in the laterals (8). Also the reduced seed number per head, in 2-row as compared with 6-row may result in increased seed size. The higher weight per seed of awned lemma (kk) over hooded (KK) may de due to the favorable physiological effect of the awn.

Higher number of heads per plant was associated with 2-row type of spike (VV) and with black color of glumes (BB). The latter may be due to an association of the BB character pair with quantitative factors which in their total effect produced more heads per plant.

The results obtained in this study of the cross between *Hordeum distichon* and *H. vulgare* are similar to those obtained by Powers (11) for the V,v and Br, br factors pairs. Powers found that Bb plants yielded more than either of the two homozygotes. In the present study there was no such evidence of heterosis in the B *vs.* b pair. Perhaps this latter result would lead to the conclusion that the B *vs.* b factors themselves were not the cause of the greater vigor observed by Powers.

In the present study manifestations of heterosis were found for weight per seed in the heterozygotes, Br br and Fc fc, when compared with their respective homozygous types. Similarly these results may not have been caused by the factors themselves since Powers did not obtain this. Since there is no manifestation of heterosis for yield or the other components, this one effect does not appear very conclusive. The brachytic (br br) and chlorina (fc fc) character mutations may be classified as physiological defectives according to East's (3) terminology. The brachytic and chlorina genes produce weak plants, but are not lethal. Gustafsson (4) presents a hypothesis according to which mutations in plants, many of which are lethal in homozygous condition, increase vigor when they occur in a single dose. Isogenic stocks would furnish better material for the study of the effects of the qualitative genes themselves, although even then closely-linked quantitative factors may still be present to affect the results.

In the study of quantitative inheritance there are possibilities of errors due to metrical bias. This bias is due to the inherent relation between the scale of measurements and the phenotypic expression. This may or may not have genetical significance and can be removed by an appropriate transformation of scales (9), but by so doing information on certain of the interactions is sacrificed.

Since in the present study the aim was to study the effects of the different genes and their interactions no transformation of scales to account for metrical bias was made.

SUMMARY

1. Certain statistical methods that have been used for studies of quantitative inheritance are presented together with illustrations of their application.

2. The effect of *the substitution of the first dominant,* second dominant and the effect of both were calculated as the following differences between genotypes: Aa-aa, AA-Aa and AA-aa respectively, the latter being the algebraic sum of the other two.

3. Significant associations between certain qualitative and quantitative characters were found. Of the significant effects, there were several in which the first dominant produced the full effect, several in which the second produced the full effect, while in a few each produced an effect.

4. The vv (6-row) genotype was higher in yield than VV (2-row) while kk (awned) was higher in yield than either Kk or KK (hooded). Higher number of seeds per head and lower weight per seed were found in vv than in either Vv or VV. The kk genotype had a higher weight per seed than KK and a higher number of seeds per head than either Kk or KK.

5. For the most part, the above associations are explainable as expected from the known morphological or physiological effects caused by the factor pairs.

6. The *Br* and *Fc* factors were associated with higher yields and were higher in all components than the homozygous recessives.

7. The N *vs.* n gene pair showed no differential effects, indicating that a high-yielding naked barley is a definite possibility.

8. When the effects of a given gene pair are considered in the different non-allelic genotypes it was found that the V *vs.* v and K *vs.* k as a general rule were very consistent in their effects in all genotypes.

9. For the other gene pairs, certain genotypes showed specific interactions with certain non-allelic genotypes. For example, the addition of the second N decreased the weight per seed in the VV while it increased it in the Vv genotype. Also the effect of N on yield was an increase in KK plants and a decrease in kk plants.

10. The nature of these interactions was such as to permit no general conclusions. While several of them may have been due to chance, it seems clear from the number obtained that such specific interactions are a part of the general picture as to the action of quantitative factors.

11. An unexpected linkage was found between K and N of 46.1 ± 1.71. A cytological study was not made to determine the cause of this unexpected result although a translocation is suspected.

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