

ABSTRACT OF THESIS

THE INHERITANCE AND GENE INTERACTIONS OF
THREE QUANTITATIVE CHARACTERS IN A CROSS
BETWEEN HORDEUM DISTICHON NIGRINUDUM AND
MINNESOTA 84-7 BARLEY.

Submitted by
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In partial fulfillment of the requirements
for the Degree of Master of Science
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INTRODUCTION

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The inheritance of quantitative characters involves a study of size, shape, and number of parts of an organism. The increased size or vigor of an organism as manifested by its rapidity of growth, height and general robustness has been defined as "heterosis". The inheritance of quantitative characters is believed to be fundamentally the same as qualitative characters. However, due to the confounding of environmental and genetic variability, it is necessary to apply special methods to analyze the inheritance of quantitative characters.

The genetics of quantitative as well as qualitative characters is of extreme importance to the modern plant breeder. A knowledge of the inheritance of quantitative and qualitative characters is vital for workers in plant breeding desiring to improve our economic crops.

The study was designed to determine the effect of certain known qualitative characters with three quantitative characters. The qualitative characters studied were: (1) black vs. white (Bb) glume color, (2) covered vs. naked (Nn) caryopsis, (3) long vs. short haired rachilla, and (4) green vs chlorina (Ff) plant color. The quantitative characters used in relation to these qualitative characters were: (1) number of spikes per plant, (2) height of plant, and (3) weight of seed per plant.

The Problem

What is the nature of the interactions between genes differentiating quantitative and qualitative factors in cultivated barley?

Problem analysis.--1. What is the effect of the qualitative genes Bb, Nn, Ss, and Ff on the quantitative characters which are (1) number of spikes per plant, (2) height of plant, and (3) weight of seed per plant?

2. Are there correlations between the quantitative characters?

3. Are there certain qualitative genotypes favorable for the production of quantitative characters? If so, do the favorable genotypes give the same increase over the less favorable genotypes in all combinations?

Delimitations.--This study was limited to an analysis of genetic data obtained from the F₁, F₂, and F₃ generations of a cross between two varieties of cultivated barley, *i.e.*, Hordeum distichon Nigrinudum and Minnesota 84-7.

MATERIALS AND METHODS

The materials used in this study consisted of data from the F_1 , F_2 , and F_3 generations of a cross between Hordeum distichon Nigrinudum and Minnesota 84-7 barley.

Parental Description

Hordeum distichon Nigrinudum is an awned, 2-rowed, hull-less, black-grained barley with black floral bracts. The seeds are naked, the leaves are green, and the rachilla hairs are short.

Minnesota 84-7 is a two-rowed, white-hulled, awned barley. The rachilla hairs are long. This barley carries the factor for chlorina plant color. It is a pale-green chlorophyll-deficient type classified as "cosse green". The plants grow to maturity but are somewhat stunted.

Experimental Procedure

The F_1 and F_2 generations of H. distichon Nigrinudum x Minnesota 84-7 were grown in a field at the Colorado Agricultural Experiment Station in the summer of 1939. The F_3 generation was grown at the same locality during the summer of 1940. The various lines of the cross were grown in 18-foot rows, 12 inches apart, with the plants spaced 12 inches apart in the row. The parents were planted in every 10th and 11th rows within each of the lines. The plants were pulled at harvest, and the height of each

individual was measured in inches, and the number of heads for each plant was counted and placed in envelopes. Later the heads were thrashed and the weight of grain, in grams, was determined for each plant.

Seeds from each F_2 plant (F_3 generations) were planted in the field in 1940 to determine the F_2 genotypes.

Statistical Methods

The data were separated into 81 genotypes on the basis of the four factor pairs that differentiated the four qualitative characters. The sums of squares, regression coefficients, and variances were obtained for each genotype. The variances used to calculate the "t" values were corrected on the basis of the regression coefficients. The variances for weight of grain per plant was corrected on the basis of the regression coefficient of weight of grain per plant on number of heads. The number of heads per plant were corrected on the basis of regression of number of heads on height per plant. The variances for height of plant was corrected on the basis of the regression coefficient of height of plant on weight of grain per plant. The method of obtaining variances took out the differences between genotypes, and consequently, the variances obtained were those within genotypes.

Correlation coefficients were obtained between the three quantitative characters. The amount of correlation was obtained for

weight of seed and number of spikes; for height of plant and number of spikes; and for height of plant and weight of seed per plant.

The chi square test was applied to determine the linkage relations between genes differentiating the four qualitative characters.

ANALYSIS OF DATA

Correlations Between the Three Quantitative Characters

It was necessary to determine if there were correlations between the quantitative characters, i.e., number of spikes, height per plant, and weight of seed per plant, since the purpose of the study was to measure only the differences between each of the genotypes. Therefore, the effects, if any, of any one quantitative character upon the other quantitative character should be eliminated. The data indicated that there was a general correlation coefficient of (1) .805 between weight of seed and number of spikes per plant, (2) .440 between height of plant and number of spikes per plant, and (3) .510 between height of plant and weight of seed per plant. The "t" values for these correlation coefficients were 19.53, 10.67, and 12.37 respectively. A "t" value of 1.99 was sufficient to prove that these correlation coefficients associated with the given characters were not due to chance. The "r" value of .805 between weight of seed and number of spikes shows that for each additional increase in number of spikes per plant one would expect the weight of seed to increase also. Therefore, by correcting the weight of seed on the basis of the regression coefficient of weight of seed on number of spikes, the variability due to the independently inherited genes associated with, and differentiating the qualitative characters controlling weight of seed would be partially controlled.

Linkage Relations Between Qualitative Characters

The segregating populations for each of the four qualitative characters were analyzed to determine how closely the observed numbers fitted a given theoretical expected number. The goodness of fit for each of the segregates was measured by the chi square test. This test revealed that the qualitative characters were differentiated by one factor pair except the genes governing the color of plants. The poor fit found in the factors governing color of plants was due to differential survival of the green and chlorina plants. The death of the chlorina plants reduced the expected number. Also, grasshoppers destroyed some of the late maturing chlorina plants.

Relation Between Quantitative and Qualitative Characters

The means of the number of spikes per plant, height per plant, and weight of seed per plant for each of three different genotypes of the four qualitative characters were compiled. This data showed that one could not state that the plants heterozygous for the genes studied had a greater effect upon the quantitative characters than did the plants homozygous for the genes studied. There was no evidence to prove that different favorable growth genes were contributed by each of the homologous chromosomes of a pair in the homozygous plants to produce more favorable growth effects in the plants heterozygous for qualitative genes.

Associations of the Four Qualitative Characters in All Possible Combinations Two at a Time with the Three Quantitative Characters

Tables were assembled showing the value of each of the three quantitative characters, *i.e.*, (1) number of spikes, (2) height of plant, and (3) weight of seed per plant in combination with genotypes of different qualitative characters used were: (1) black vs. white glume color (Bb), (2) long-haired vs. short-haired rachilla (Ss), (3) green vs. chlorina plant color (Ff), and (4) covered vs. naked caryopsis.

The results of this study gave evidence that the general nature of the genes affecting the quantitative characters was extremely variable. It was generally true that the genes associated with high yield in one combination were not necessarily the high-producing genes when in other combinations. Other workers present data to show that genes governing certain qualitative characters were associated with high yield of seed per plant and when these genes were combined with other genes they remained high yielding.

However, a portion of the data followed a definite trend. It was generally true that the normal green (FF) genotypes and the heterozygous green (Ff) genotypes were more favorable for the production of number of spikes per plant, height per plant, and weight of seed per plant than were the chlorina (ff) genotypes, in all combinations with the other three qualitative characters. It was also found that the heterozygous (Ff) green

plants were more efficient than either of the homozygotes (FF or ff). The chlorina (ff) genotype was classified as physiological defective as compared to the normal and heterozygous green plants. Since the heterozygote (Ff) was more efficient in the production of quantitative characters, the author interpreted such gene reactions as being due to partially dominant linked genes. It was assumed that there was a series of favorable growth genes linked with the F allele and another series of linked genes linked with the f allele, and the combination of these genes in the heterozygote (Ff) possessing the favorable growth factors contributed by each parent, therefore being more favorable than either parent. Other workers have pointed out similar gene interactions in which the heterozygous plants were more favorable than the homozygous plants. Many have followed Jones' hypothesis of partially dominant growth genes as accounting for heterosis whereas others have assumed a greater physiological stimulation occurs in the heterozygote, and as a result, greater growth.

Suggestions for Further Study

There is much information to be gathered from the study in quantitative inheritance. It will be interesting to know if there are certain gene combinations more favorable than others for the production of quantitative characters. Such characters as yield of grain, quantity of oil, increase in vigor, and others, are being studied in the present-day crops. Special methods have been developed with such crops as tomatoes and squash which are applicable to many other economic crops. Another study may be developed in barley in which the parents are used in the analysis of the quantitative characters. Since one parent was unfortunately eliminated in the material of this study, the author was unable to compare the parental genotypes with similar genotypes in the F_2 population. A back-cross program may be used in which the F_1 generation is back-crossed to both parents. This method would furnish extra data in determining the mode of quantitative inheritance.

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THESIS

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Submitted by
Ronald D. Rasmussen

In partial fulfillment of the requirements
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Agricultural and Mechanical College
Fort Collins, Colorado

May, 1949

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ENTITLED THE INHERITANCE AND GENE INTERACTIONS OF THREE QUANTI-
TATIVE CHARACTERS IN A CROSS BETWEEN HORDEUM DISTICHON
NIGRINUDUM AND MINNESOTA 84-7 BARLEY

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Chapter I

INTRODUCTION

The inheritance of quantitative characters involves a study of size, shape, and number of parts of an organism. The increased size or vigor of an organism as manifested by its rapidity of growth, height, and general robustness has been defined by Shull (24), 1948, as "heterosis". He further states that this general vigor is "positively correlated with the degree of dissimilarity in the gametes by whose union the organism was formed." The inheritance of both quantitative and qualitative characters are believed to be fundamentally the same. However, due to the confounding of environmental and genetic variability, it is necessary to apply special methods to analyze the inheritance of quantitative characters.

There is a need for extending the study of the nature of the interactions between genes differentiating quantitative and qualitative factors. The genetics of quantitative as well as qualitative characters is of extreme importance to the modern plant breeder. A knowledge of the inheritance of qualitative and quantitative characters is vital for workers in plant breeding desiring to improve our economic crops.

The purpose of this study was to determine the mode of inheritance and effect of certain known qualitative characters with quantitative characters. The qualitative characters were:

(1) black vs. white (Bb) glumes, (2) covered vs. naked (Nn) caryopsis, (3) long vs. short-haired (Ss) rachilla, and (4) green vs. chlorina (Ff) plant color. The quantitative characters used in relation to these qualitative characters were: (1) number of spikes per plant, (2) height of plant, and (3) weight of seed per plant.

The Problem

What is the nature of the interactions between genes differentiating quantitative and qualitative factors in cultivated barley?

Problem analysis.--1. What is the effect of the qualitative genes Bb, Nn, Ss, and Ff on the quantitative characters which are: (1) number of spikes per plant, (2) height of plant, and (3) weight of seed per plant?

2. Are there correlations between the quantitative characters?

3. Are there certain qualitative genotypes favorable for the production of quantitative characters? If so, do the favorable genotypes give the same increase over the less favorable genotypes in all combinations?

Delimitation.--This study was limited to an analysis of genetic data obtained from the F_1 , F_2 , and F_3 generations of a cross between two varieties of cultivated barley, i. e., Hordeum distichon Nigrinudum and Minnesota 84-7.

Chapter II

REVIEW OF LITERATURE

The amount of literature dealing with quantitative inheritance is voluminous. Many hypotheses have been advanced to interpret the inheritance of characters that relate to the degree of measurable differences involved in segregating populations. Nearly all authorities agree that the genes differentiating quantitative characters are numerous, and many agree that there may be small, cumulative, individual effects which account for the total variations concerned.

Multiple-Factor Interpretation

The multiple-factor hypothesis assumes the inheritance of quantitative factors due to a number of genes or factors incompletely dominant or lacking dominance, which individually are small in effect and cumulative in action.

Studies by East, and later by Emerson, as cited by Hayes and Immer (7), 1942, have contributed greatly to the theories of size inheritance. The methods generally used involved the study of F_1 , F_2 , and F_3 generations from the cross of two parents that differ widely in the character studied.

Rasmusson (18), 1933, Wright (31), 1934, Student (28), 1934, and others, made calculations to determine the number of genes involved in quantitative inheritance. Their conclusions varied. Student (28), 1934, Sprague and Brimhall (27), 1949, concluded that at least 20-40 genes were involved in experiments to determine oil content in maize. Rasmusson (18) assumed that there were 100-200 genes involved in quantitative inheritance between crosses of species not too distinctly related. Wright (31) concluded that not less than 12 genes were involved in determining the corolla size between two species of Nicotiana.

Rasmusson (18) suggested that "the effects of each factor on the genotype is dependent upon all other factors present, the visible effects acting in the same direction." However, Powers (13), 1936, presented data which showed that although a great number of factors were acting in the same direction, the addition of other genes did not necessarily give equal effects.

The study by Hayes (6), 1946, of combining ability in corn emphasized that the number and the nature of the genes influencing yield were great. Each gene alone had no measurable modifying effects on yield, whereas, the complementary action of all genes produced somewhat greater influences. The complementary action of two genes in the homozygous recessive condition produced resistance to stem rust in Thatcher wheat.

The nature of gene interaction was studied by Powers (14), 1934. From a cross of two varieties of Triticum, Hybrid 128 x Velvet Node, he found the two varieties were differentiated by three factor pairs for habit of growth and earliness of maturity. AA, BB, and cc were factors for spring habit of growth. Their corresponding alleles were factors for winter habit of growth. The factor AA was found to be epistatic to bb and CC, whereas, BB was epistatic to aa and CC, and cc to aa and bb. The number and combinations of the genes present were necessary in determining early maturity. The AA genes were more efficient in causing early maturity than the BB and cc genes. Late maturity resulted from the action of the CC genes. For these reasons, Powers (14), 1934, concluded that the time of maturity in wheat, involving the above genotypes, depended upon "the interaction of the reaction processes." The environmental conditions also were found to influence the reaction processes.

It was pointed out by Powers (12), 1941, that, in tomatoes, there were interactions between genes and that these interactions depended upon the particular genes involved. There were also interactions between genes and environment. These genetic and environmental factors were necessary to correctly interpret yield of ripe fruit per plant. All genes did not have equal effects both within and between component characters.

Rast (2), 1936, proposed a theory to account for heterosis or superiority in the heterozygote which he believed was due to the cumulative action of many divergent, nondefective alleles. It was assumed that the members of an allelic series were different in that each allele performs a different physiological function. The cumulative effect of such alleles produces a hybrid more vigorous than either homozygote due to specific physiologic contributions of each parent. Thus a_1a_2 , in the hybrid, would produce more vigorous plants than either a_1a_1 or a_2a_2 .

Robertson and Austin (21), 1936, reported a study involving the segregates of green versus white seedling colors in Hordeum vulgare. They reported plants segregating for the two factor pairs, X_cx_c and $A_c a_c$, and found statistically significant difference in favor of the heterozygous plants of the genotype $X_cx_c A_c a_c$ for the following characters: (1) average length of head, (2) total number of grains per plant, and (3) total weight of grain per plant. The authors suggested the possibility that the heterosis effect may be due to the recombining of dominant favorable growth genes linked with the lethal factors.

Dominant gene action.--The genetic interpretation by Jones (8), 1917, assumed that certain dominant relationships existed between alleles, and the interaction between these genes

have decided influence on the genetics of quantitative characters. He explained that "factors in the $1n$ condition would have more than one-half the effect of the $2n$ condition." It was assumed that dominant favorable growth factors were contributed by each parent which make up the F_1 generation. Because more favorable factors were present in the F_1 than in either parent, one would expect greater development in the F_1 . This effect was described as heterosis. Jones (8), 1917, assumed that the genes were evenly distributed on the chromosomes, that each had equal effects, and that there were no crossovers. Jones, (8), 1917, cited the work of Keeble and Pellew with peas in which the interaction of two genes, one for thick stem and one for long internode, produced a plant taller than either of the parent plants. If these genes were designated as T and L respectively, then the genotypes of the parents would be $Ttll$ and $tTlL$. If T and L were dominant over their allelomorphs, then the F_1 would be taller than either parent, because it would contain the genotype $TtLl$. This combination is the one found in thick stem and long internode plants.

Powers, (11), 1944, expanded Jones' theory of heterosis. He showed that genes may exhibit intermediate conditions when in the heterozygous condition, but when the interaction of two pairs of genes are considered, heterosis was exhibited for yield of fruit

per plant. This was shown from data taken from a cross of two inbred lines of Lycopersicon. The genotype of one inbred line was AAbb. The other inbred line was aaBB. The F_1 genotype from the cross was AaBb. In this case Powers assumed bb to be recessive for small number of fruit, and aa was recessive for small size of fruit. The F_1 was partially dominant for small number of fruit and small size of fruit, yet it produced an increased yield over the parents. Powers concluded, therefore, that the genes were not additive but multiplicative in effect.

Powers, (15), 1949, following a study of the interaction of genes affecting yield in crosses of Lycopersicon esculentum and L. pimpinellifolium, concluded that size of fruit was partially dominant, and the small number of locules per fruit was either completely or partially dominant. The number of fruits per unit length of branch also exhibited partial dominance.

Richey (19), 1946, pointed out that there was competition between alleles in corn. Each allele had individual additive effects, and one gene could not express itself because of the dominance of its allele.

According to East (1), 1935, there may be genes which are defective or nondefective in the physiological processes of an organism. He assumed that these genes may be recessive or dominant

in function. The defective genes were considered to be numerous and caused considerable effect upon the quantitative and qualitative characters.

The nature of gene interaction between four quantitative characters in a cross between Hordeum deficiens and Hordeum vulgare was reported by Powers (13), 1936. He studied the effects 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 per plant, and length of awn. The data supported East's hypothesis in which the genes were grouped into physiological defective or physiological nondefective. The "brbr" gene causing brachytic habit of growth was classified as physiological defective as was the VV gene causing deficiens type of spike. The Vv plants were more favorable than the VV plants for all the quantitative characters studied, and this was due to a number of partially dominant linked growth factors in the chromosome containing V and v genes. Small differences were reported for color of glumes, and, therefore, the genes responsible for color of glumes were classified as physiological nondefective. The interaction between genes affecting weight of seed per plant was such that they produced higher yields independent of the combination of qualitative genes with which they were associated. Powers concluded that the nature of the gene

interactions affecting quantitative characters was somewhat variable, and therefore, he was unable to develop a definite hypothesis to predict yield.

Following a review of the literature on quantitative inheritance, Smith (25), 1944, and Whaley (30), 1944, pointed out the need for further investigations on the nature of inheritance of quantitative characters.

Chapter III

METHODS AND MATERIALS

The materials used in this study consisted of data from the F_1 , F_2 , and F_3 generations of a cross between Hordeum distichon Nigrinudum and Minnesota 84-7, a genetic strain of Hordeum distichon.

Parental Description

Hordeum distichon Nigrinudum is an awned, 2-rowed, hull-less, black-grained barley with black floral bracts. The seeds are naked, the leaves are green, and the rachilla hairs are short.

Minnesota 84-7 is a two-rowed, white-hulled, awned barley. The rachilla hairs are long. This barley carries the factor for chlorina plant color (ff). It came originally from G. Hallquist but was obtained from the Minnesota Agricultural Experiment Station. According to Ridgway (20), 1912, it is a pale-green chlorophyll deficient type classified as "cosse green". The plants grow to maturity but are somewhat stunted.

The linkage groups and the contrasted characters of the parents for the quantitative characters studied are listed in Table 1.

Table 1.--LINKAGE GROUPS AND CONTRASTING CHARACTERS FOUND IN A CROSS OF HORDEUM DISTICHON NIGRINUDUM AND MINNESOTA 84-7 BARLEY.

Linkage group number	Character	Symbol	Nigrinudum	Minnesota 84-7
II	Black vs. white floral bracts	Bb	Black	White
III	Covered vs. naked caryopsis	Mn	Naked	Covered
V	Long vs. short-haired rachilla	Ss	Short	Long
VII	Green vs. chlorina plants	Ff	Green	Chlorina

Experimental Procedure

The F_1 and F_2 generations of H. distichon Nigrinudum x Minnesota 84-7 were grown in the field at the Colorado Agricultural Experiment Station in the summer of 1939. The F_3 generation was grown in the same locality during the summer of 1940. The H. distichon Nigrinudum and Minnesota 84-7 parents were grown in the same test with the F_1 and F_2 generations. The various lines were grown in 18-foot rows 12 inches apart with the plants spaced 12 inches apart in the row. The parents were planted in every 10th and 11th rows within each of the lines. The plants were pulled at

harvest, and the height of each individual was measured in inches, and the number of heads for each plant was counted and placed in envelopes. Later the heads were thrashed and the weight of grain, in grams, was determined for each plant.

The seeds from each F_2 plant (F_3 generation) were planted in the field in 1940 to determine the F_2 genotypes. Each of the 6 families was studied on an individual plant basis to classify the plants for homozygosity or heterozygosity for the gene pairs differentiating each of the four qualitative characters.

Statistical Methods

The statistical methods used to analyze the data were similar to those used by Powers (13), 1936. First, the data were separated into 81 different genotypes on the basis of the four factor pairs that differentiated the four qualitative characters. The sums of squares, regression coefficients, and variances were obtained for each genotype. The variances used to calculate the "t" values were corrected on the basis of the regression coefficients. The variances for weight of grain per plant were corrected on the basis of the regression coefficient of weight of grain per plant on number of heads. The number of heads per plant were corrected on the basis of regression of number of heads on height per plant. The variance for height of plant was corrected on the basis of the

regression coefficient of height of plant on weight of grain per plant. This method of obtaining variances took out the differences between genotypes and consequently, the variances obtained were those within genotypes. The "t" values to determine the significance of the differences between the means were obtained by the use of methods described by Snedecor (26), 1946. Correlation coefficients were obtained between the three quantitative characters by the methods described by Leonard and Clark (9), 1939. Correlation coefficients were obtained between weight of seed and number of spikes; between height of plant and number of spikes per plant; and between height of plant and weight of seed per plant. The chi square test was applied to determine the linkage relations between genes differentiating the four qualitative characters. The knowledge of the number of genes differentiating the qualitative characters and their linkage relations is essential to a correct interpretation. The data showing the linkage relations of the qualitative characters are presented in the following chapter.

Location of Original Data

The original data from which this thesis was written are on file in the vault at the Agronomy Experiment Station in Fort Collins, Colorado.

Chapter IV

ANALYSIS OF DATA

Linkage Relations Between Qualitative Characters

The study consisted of measuring the differences between genotypes of the four qualitative characters, i. e., color of glumes, color of plants, adherence of glumes to caryopsis, and length of rachilla hairs. It was important to know the linkage relations and the number of genes involved in differentiating the qualitative characters. The data to determine the linkage relations were based upon the F_2 genotypes as determined from a progeny test in the F_3 generation.

The segregating populations for each of the four qualitative characters were analyzed to determine how closely the observed numbers fitted a given theoretical expected number. The goodness of fit for each of the segregates was measured by the chi square test and the results presented in Table 2. The chi square test revealed that the qualitative characters were differentiated by one factor pair except for the genes governing color of plants. It was apparent that the deviation from the calculated 1:2:1 ratio was due to differential survival of the green and chlorina plants.

Table 2.--THE SEGREGATION OF THE FOUR QUALITATIVE CHARACTERS FOUND IN THE F₂ GENERATION FROM A CROSS OF NIGRINUDUM AND MINNESOTA 84-7.

Phenotype	Genotype	Observed	Calculated	X ²	P-value
Black	BB	319	342.50		
Black	Bb	694	685.00		
White	bb	357	342.50	2.33	.50-.30
Covered	NN	359	342.50		
Covered	Nn	714	685.00		
Naked	nn	295	342.50	8.89	.02-.01
Long-Haired Rachilla	SS	317	342.50		
Long-Haired Rachilla	Ss	714	685.00		
Short-Haired Rachilla	ss	339	342.50	3.27	.20-.10
Normal Green	FF	409	342.50		
Normal Green	Ff	729	685.00		
Chlorina	ff	232	342.50		
				51.49	less than .001

The death of many of these chlorina plants reduced the expected number. Another difficulty arose in classifying the green and chlorina plants due to a severe epizootic of grasshoppers which destroyed the late-maturing chlorina plants. However, the number of these missing plants was not great enough to have an appreciable effect upon the total average mean differences.

Each of the characters was analyzed to determine if linkage was present. The genotypes, color of glume (Bb), adherence of glume (Mn), and length of rachilla hairs (Ss) were analyzed using a calculated 1:2:2:4:1:2:1:2:1 ratio for independence. The genotype responsible for color of seedling was analyzed by using a 1:2:2:4, 1:2 and 1:2 ratio. This was necessary because a poor fit was obtained for the chlorina plants when a genotypic segregation of a single factor pair in the F_2 generation was assumed. This poor fit was probably due to the loss of chlorina plants in the F_2 and F_3 segregating families. Since all necessary data were collected from the genotype consisting of homozygous chlorina plants, it was not necessary to include these in determining independent inheritance. The P-values for independent inheritance are shown in Table 3. It was apparent that the genes governing the inheritance of the four qualitative characters were independent of each other as far as linkage relations were concerned. The summary of linkage

Table 3.--LINKAGE RELATIONS BETWEEN THE COMBINATIONS OF FOUR QUALITATIVE CHARACTERS AS DETERMINED BY THE χ^2 TEST FOR GOODNESS OF FIT.

Color of glumes vs: adherence of glumes		Color of glumes vs: length of rachilla hairs		Adherence of glumes vs: length of rachilla hairs		Adherence of glumes vs: color of plants		Length of rachilla hairs vs: color of plants		Color of glumes vs: color of plants	
Geno- types	Ob- tained	Geno- types	Ob- tained	Geno- types	Ob- tained	Geno- types	Ob- tained	Geno- types	Ob- tained	Geno- types	Ob- tained
BBNN	76	BBSS	74	NNSS	93	NNFF	115	SSFF	98	BBFF	102
BbNN	179	BbSS	171	NnSS	166	NnFF	209	SsFF	210	BbFF	209
BBNn	156	BBSe	162	NNSe	168	NNFf	187	SSFf	167	BBFf	175
BbNn	373	BbSe	352	NnSe	390	NnFf	369	SsFf	383	BbFf	364
bbNN	104	bbSS	72	nnSS	58	nnFF	85	ssFF	101	bbFF	98
bbNn	185	bbSe	200	nnSe	156	nnFf	173	ssFf	179	bbFf	190
BBnn	87	BBse	83	NNse	98	NNff	57	SSff	52	BBff	42
Bbnn	142	Bbse	171	Nnse	158	Nnff	136	Ssff	121	Bbff	121
bbnn	68	bbse	85	nnse	83						
P between .02 and .01		P between .30 and .20		P between .02 and .01		P between .30 and .20		P between .30 and .20		P between .20 and .10	

studies by Robertson, Wiebe, and Shands (22), 1947, also showed that the genes differentiating these qualitative characters were independent.

Correlations Between the Three Quantitative Characters

The paragraph of statistical methods pointed out that variances were obtained for each genotype and these variances were corrected on the basis of the regression coefficients. By such a method the variability due to environment was partially eliminated. It was necessary to determine if there were correlations between the quantitative characters, i. e., number of spikes, height per plant, and weight of seed per plant, since the purpose of the study was to measure only the differences between each of the genotypes. Therefore, the effect, if any, of any one quantitative character upon the other quantitative character should be eliminated. The correlation coefficients were calculated from the original data on file with the Agronomy Department at Colorado A & M College. The results obtained indicated the general correlation coefficient of

- (1) .805 between weight of seed and number of spikes per plant,
- (2) .440 between height of plant and number of spikes per plant, and
- (3) .510 between height of plant and weight of seed per plant. The "t" values for these correlation coefficients were 19.53, 10.67, and

12.37 respectively. A "t" value of 1.99 was sufficient to prove that these correlation coefficients associated with the given characters were not due to chance.

With an "r" value of .805 for weight of seed and number of spikes, it would be expected that the weight of seed would increase for each additional increase in number of spikes per plant. Therefore, by correcting the weight of seed on the basis of the regression coefficient of weight of seed on number of spikes, the variability due to the independently inherited genes associated with, and differentiating, the qualitative characters controlling weight of seed would be partially controlled.

Relation Between Quantitative and Qualitative Characters

The means of the number of spikes per plant, height per plant, and weight of seed per plant for the three different genotypes of the four qualitative characters studied are shown in Table 4. These are the measurements obtained from the F_2 plants. The genotypes of the F_2 plants were determined from a progeny test in the F_3 generation.

The genes associated with color of glumes, adherence of glume, and length of rachilla hairs were independent of each other, and an analysis made from Table 4 indicated that there was no significant difference in the quantitative characters within the

Table 4.--MEANS OF THREE QUANTITATIVE CHARACTERS MEASURED IN THE F₂ GENERATION OF A CROSS BETWEEN NIGRINUDUM AND MINNESOTA 84-7, CLASSIFIED INTO GENOTYPES AND PHENOTYPES ACCORDING TO COLOR OF GLUMES, ADHERENCE OF GLUME TO SEED, LENGTH OF RACHILLA HAIRS, AND COLOR OF SEEDLING.

Phenotypes	Genotypes	N	Number of spikes	Height per plant	Weight of seed
			per plant		per plant
			<u>Number</u>	<u>Inches</u>	<u>Grams</u>
Black	BB	957	27.26	31.10	23.53
Black	Bb	2082	26.40	32.65	23.16
White	bb	1071	27.64	31.05	23.46
Covered	NN	1078	26.70	31.50	23.79
Covered	Nn	2142	26.81	30.09	24.28
Naked	nn	891	27.46	32.21	22.05
Long-hair rachilla	SS	951	25.51	29.42	21.15
Long-hair rachilla	Ss	2142	25.42	30.32	22.60
Short-hair rachilla	ss	1025	25.01	30.49	22.69
Normal green plants	FF	1220	28.27	31.11	24.66
Normal green plants	Ff	2187	30.15	31.11	26.76
Chlorina plants	ff	696	13.24	26.44	11.23

different qualitative genotypes. A "t" value of 1.960 which gives a P-value of .05 was taken as statistically significant. There was no significance between normal green (FF) seedlings and normal green (Ff) seedlings for the three quantitative characters studied. However, significance was evident between FF and Ff segregates associated with the chlorina (ff) plants. The normal green (FF) plants, as shown in Table 4, produced a greater number of spikes per plant, greater height per plant, and a greater yield than did the ff plants. The "t" values between the homozygous (FF) green plants and the homozygous (ff) chlorina plants were 4.449 for the average number of spikes per plant, 3.316 for the average height per plant, and 3.895 for the average weight per plant. These measurements were, of course, in favor of the homozygous (FF) green plants. The plants heterozygous for green (Ff) were also more favorable than the homozygous chlorina (ff) plants. The "t" value for this difference was 4.904, 3.456, and 3.883, for the number of spikes, height of plant, and weight of seed per plant respectively.

The results in Table 4 show that one cannot conclude that plants heterozygous for the genes studied had a greater effect upon the quantitative characters than did the plants homozygous for the genes studied.

There was no evidence to prove that different favorable growth genes were contributed by each of the homozygous plants to

produce more favorable growth effects in the heterozygous plants. According to Jones' hypothesis the heterozygote possessed more favorable, and at least partially dominant, growth factors from the parents from which it came.

The following tables and discussions report a study of the value of each of the three quantitative characters, *i. e.*, (1) number of spikes per plant, (2) height per plant, and (3) weight of seed per plant when in combination with genotypes of different qualitative characters in all possible combinations two at a time. The qualitative characters are (1) black vs. white glume color (Bb), (2) long-haired vs. short-haired rachilla (Ss), (3) green vs. chlorina plant color (Ff), and (4) covered vs. naked seeds (Nn).

Genes Associated with Color of Glume and Adherence of Glume to Caryopsis.

Tables 5 and 6 show the reactions of genes concerned with the three quantitative characters. An analysis of the BB and bb genotypes, the BB and Bb genotypes, and the Bb and bb genotypes is shown in Table 5. The analysis shows the comparison of nine genotypes for each of the three quantitative characters. These differences are for the BB, Bb, and bb genotypes within the NN, Nn, and nn genotypes. Table 6 is the reverse of Table 5, *i. e.*, the differences are for the NN, Nn, and nn genotypes within the BB, Bb, and bb genotypes.

Table 5.—THE EFFECT UPON THREE QUANTITATIVE CHARACTERS OF GENES DIFFERENTIATING AND ASSOCIATED IN INHERITANCE WITH COLOR OF GLUME.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Black (BB)												
vs:												
White (bb)												
Covered (NN)	27.80	27.50	.30	.330	29.99	29.51	.48	1.440	24.54	24.14	.40	.40
Covered (Nn)	26.12	28.08	-1.96	2.254*	30.94	31.44	-.50	1.800	22.69	26.77	-4.08	5.720*
Naked (nn)	27.85	27.34	.51	.560	32.38	32.20	.18	.522	23.45	19.48	3.97	3.652*
Black (Bb)												
vs:												
White (bb)												
Covered (NN)	25.79	27.50	-1.71	1.966*	35.00	29.51	5.05	11.615*	22.78	24.14	-1.36	1.632
Covered (Nn)	26.24	28.08	-1.84	2.760*	30.91	31.44	-.53	2.491*	23.48	26.77	-3.29	5.264*
Naked (nn)	27.19	27.34	-.15	.145	32.04	32.20	-.16	.521	23.31	19.48	3.83	3.562*
Black (BB)												
vs:												
Black (Bb)												
Covered (NN)	27.80	25.79	2.01	1.172	29.99	35.00	-5.01	10.200*	24.54	22.78	1.76	1.760
Covered (Nn)	26.12	26.24	-.12	.168	30.94	30.91	.03	.144	22.69	23.48	-.79	1.224
Naked (nn)	27.85	27.19	.66	.759	32.38	32.04	.34	1.156	23.45	23.31	.14	.160
Parent BBNN												
vs:												
F ₂ BBNN	24.32	27.80	-3.48	1.253	31.72	29.99	1.73	.201	17.60	24.54	-6.94	1.986*

* t test gives $P > .05$

Table 5 shows that the BB genotypes produced a larger yield per plant than did the Bb and bb genotypes, except when the BB and bb genotypes were compared with the heterozygous (Nn) covered plants. The bb genotypes had higher yielding plants than did the Bb genotypes except when the comparison was within the naked (nn) genotypes. If one accepts odds as great as, or greater than, 19:1 against the deviations noted, not being due to errors of random sampling, then one can say that the BB genotypes produced significantly greater yields within the nn genotypes than did the bb genotypes within the nn genotypes. However, the bb genotypes produced greater yields when in combination with the Nn genotypes. No significance was shown between the yields of the BB and Bb genotypes in any of the three contrasting genotypes. The bb genotypes yielded significantly better than the Bb genotypes in combination with the NN and Nn genotypes as shown by comparisons made in Table 5. A similar comparison was drawn from number of spikes per plant, except that the bb genotypes did not show a significant difference in number of spikes over the BB genotypes when in combination with the nn genotype. The BB genotypes showed greater height than the bb genotypes except when the bb genotypes were combined with the Nn genotypes. The "t" values indicated that the small differences could be due to errors of random sampling. The

BB genotypes tended to produce taller plants than did the Bb genotypes except when associated with the NN genotypes. The Bb genotypes showed a trend of producing taller plants than did the bb genotypes when in combination with the double dominant covered (NN) genotype. The differences showed "t" values of 10.200 and 11.615, respectively. A "t" value of 2.491 indicated that there was a significant difference in height of plants possessing bbNn genotypes as compared to the BbNn combination.

Table 6 shows the effect of the covered and naked genes in combinations with the genes BB, Bb, bb for color of glumes. The NN genotypes showed greater weight of seed per plant in comparison with the nn genotypes when in combination with BB and bb genotypes, but the difference was significant only in the white plants (bb). The plants of the NN genotype showed increased yield per plant over the heterozygous Nn genotype when in combination with the BB genotype, but the heterozygous Nn covered plants showed an increased yield when in combination with the Bb or bb genotypes. The difference is statistically significant in the latter comparison. Since the NN genotypes within the bb genotypes showed significantly greater yield over the nbb combination, and the Nbb combination showed significantly greater yield per plant over the NNbb combination--then one would expect the Nbb combination to be significantly

Table 6.--THE EFFECT UPON THREE QUANTITATIVE CHARACTERS OF GENES DIFFERENTIATING AND ASSOCIATED IN INHERITANCE WITH ADHERENCE OF GLUME.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Covered (NN)												
vs:												
Naked (nn)												
Black (BB)	27.80	27.85	-.05	.050	29.99	32.38	-2.39	2.294*	24.54	23.45	1.09	1.046
Black (Bb)	25.79	27.19	-1.40	1.820	35.00	32.04	2.96	9.827*	22.78	23.31	-.53	.663
White (bb)	27.50	27.34	.16	.240	29.51	32.20	-2.69	8.070*	24.14	19.48	4.66	6.660*
Covered (Nn)												
vs:												
Naked (nn)												
Black (BB)	26.12	27.85	-1.73	1.609	30.94	32.38	-1.44	4.896*	22.69	23.45	-.76	.912
Black (Bb)	26.24	27.19	-.95	1.187	30.91	32.04	-1.13	5.311*	23.48	23.31	.17	.255
White (bb)	28.08	27.34	.74	.755	31.44	32.20	-.76	2.052*	26.77	19.48	7.29	7.436*
Covered (NF)												
vs:												
Covered (Nn)												
Black (BB)	27.80	26.12	1.68	1.572	29.99	30.94	-.95	3.135*	24.54	22.69	+1.85	1.998*
Black (Bb)	25.79	26.24	-.45	.720	35.00	30.91	+4.90	15.542*	22.78	23.48	-.70	.840
White (bb)	27.50	28.08	-.58	.696	29.51	31.44	-1.93	6.060*	24.14	26.77	-2.63	3.419*

* t test gives $P > .05$

greater than the $nnbb$ combination. This, of course, was to be expected from comparing the "t" values for the weight per plant column of Table 6. One would expect to find those combinations that have a significant difference between weight of seed per plant to also have a corresponding difference in increased number of spikes per plant, because the number of spikes per plant has direct effect on increasing the weight of seed per plant. This fact is true, as can be seen from a comparison of the columns headed 'spikes per plant' and 'weight of seed per plant' in Table 6. In every case where the nn genotypes were greater than NN in weight of seed per plant, there was also found an increase in number of spikes per plant except within the BB genotype. The same comparison was true with the Nn and nn genotype within the Bb segregates. However, as can be noted, these differences in spikes per plant showed no significance if a "t" value of 1.960 is to be assumed statistically significant.

As was shown in Tables 5 and 6, there were certain gene combinations more favorable for growth than other gene combinations. Table 7 was compiled to determine if these favorable growth genes give the same increase over the less favorable growth genes in all genotypes. Table 7 places emphasis on the interactions of the Nn genes. For example, we want to know if the difference between NN vs.

Table 7.—INTERACTION BETWEEN GENES DIFFERENTIATING AND ASSOCIATED IN INHERITANCE WITH ADHERENCE OF GLUME AND COLOR OF GLUME AS THEY AFFECT THREE QUANTITATIVE CHARACTERS.

Genotypes	Number of spikes per plant		Height per plant		Weight of seed per plant	
	Diff.	t	Diff.	t	Diff.	t
Covered (NN) vs: Naked (nn)						
Black (BB) vs: Black (Bb)	-1.35	3.321*	-5.35	12.305*	1.62	2.106*
Black (BB) vs: White (bb)	-.21	.304	.30	.405	-3.57	4.998*
Black (Bb) vs: White (bb)	-1.56	2.340*	5.65	20.905*	-5.19	8.304*
Covered (Nn) vs: Naked (nn)						
Black (BB) vs: Black (Bb)	-.78	1.357	.31	1.798	-.93	1.721
Black (BB) vs: White (bb)	2.47	3.458*	1.25	3.338*	-8.05	12.075*
Black (Bb) vs: White (bb)	1.69	3.042*	1.56	8.424*	-7.12	12.460*
Covered (NN) vs: Covered (Nn)						
Black (BB) vs: Black (Bb)	-2.13	4.158*	+5.04	24.696*	-2.55	5.100*
Black (BB) vs: White (bb)	-2.26	3.616*	-.98	4.410*	-4.48	7.168*
Black (Bb) vs: White (bb)	-.13	.234	-6.02	29.498*	-1.93	3.088*

* t test gives $P > .05$

nn in combination with BB is the same as in combination with Bb. This was found by comparing the differences as obtained from Table 6. A value of 1.62 was obtained for the difference between the BB and Bb genotypes in combination with NN vs. nn segregates for weight of seed. This value was obtained by finding the difference between the differences of 1.09 for the BB genotype and a difference of -.53 for the Bb genotype. The difference between these values is 1.62.

As can be seen in Table 6, the Nabb genotype was the high producing combination. It showed a significant difference of 2.63 over its NN allele and 7.29 over the nn allele. The NnBB and NnBb were the low producing genotypes. It was desirable to know if the genes bb, favorable for increased yield over their alleles in the high producing genotypes, also showed increased yield over their alleles in the low producing genotypes. This was shown in the bb vs. Bb and bb vs. BB segregates, and the genotypes for adherence of glume in Table 6. The NN genotypes showed a significantly greater yield over the Nn genotypes when in combination with the BB genotype, and the nn genotypes showed an increased yield over NN genotypes when combined with the Bb genotypes. The data in Table 6 indicate that those genes associated with high yield in one combination are not necessarily the high producing genes when

associated with the lower non-allelic genotypes in other combinations. Powers (13), 1936, showed that the type of spike genes (Vv) favorable for high yield produce increased yields over their alleles in both high and low yielding genotypes with respect to habit of growth. (Brbr).

The object now is to assemble these genotypes to show the nature of the interactions. Table 7 shows the results of these interactions for the three quantitative characters studied. The data of Table 7 may be explained by showing how the values were obtained. For this example we will consider the calculations for weight of seed per plant. All figures were taken from Table 6 since we were calculating the interaction of covered vs. naked caryopsis, holding the color of glume constant. The values of the interactions in Table 7 showing the difference between the differences for weight of seed were as follows:

$$(NNBB - nnBB) - (NNBb - nnBb) = (1.09) - (-.53) = 1.62 \text{ grams}$$

$$(NNBB - nnBB) - (NNbb - nnbb) = (1.09) - (4.66) = -3.57 \text{ grams}$$

$$(NNBb - nnBb) - (NNbb - nnbb) = (-.53) - (4.66) = -5.19 \text{ grams}$$

$$(NNBB - NnBB) - (NNBb - NnBb) = (1.85) - (-.70) = 2.55 \text{ grams}$$

$$(NNBB - NnBB) - (NNbb - Nnbb) = (1.85) - (-2.63) = 4.48 \text{ grams}$$

$$(NNBb - NnBb) - (NNbb - Nnbb) = (-.70) - (-2.63) = 1.93 \text{ grams}$$

$$(NnBB - nnBB) - (NnBb - nnBb) = (-.76) - (.17) = -.93 \text{ grams}$$

$$(NnBB - nnBB) - (Nnbb - nnbb) = (-.76) - (7.29) = -8.05 \text{ grams}$$

$$(NnBb - nnBb) - (Nnbb - nnbb) = (.17) - (7.29) = -7.12 \text{ grams}$$

An analysis of the genes associated with weight of seed given in Table 7 can be explained more clearly as follows:

BB > Bb when in combination with NN vs. nn segregates.

bb > BB when in combination with NN vs. nn segregates.

bb > Bb when in combination with NN vs. nn segregates.

BB > Bb when in combination with Nn vs. Nn segregates.

BB > bb when in combination with NN vs. Nn segregates.

Bb > bb when in combination with NN vs. Nn segregates.

Bb > BB when in combination with Nn vs. nn segregates.

bb > BB when in combination with Nn vs. nn segregates.

bb > Bb when in combination with Nn vs. nn segregates.

As can be seen from the gene action shown in the above comparisons, there were certain gene pairs in combination with other genes that gave high yields but the same gene pairs in other combinations gave low yields. In other words, the interactions are such that yields cannot be predicted for the different gene combinations, nor can gene interaction itself be predicted.

Comparisons between the black vs. white and the covered vs. naked plants with number of spikes per plant and height per plant were made. As can be seen from Table 5, the only significant differences for spikes per plant are those between BB and bb within the Nn genotype, and between Bb and bb within the Nn and NN genotype. Since the Nnbb combination shows a significantly greater weight of seed per plant, one would also expect Nnbb to show a significantly greater number of spikes per plant. This was shown to be true in Table 5 in the combinations cited above. The combination of genes favorable for high weight of seed were also favorable for number of spikes per plant, and the combination of genes giving lower yields also gave lower number of spikes per plant.

There were only three of the nine differences involving BB, Bb, and bb genotypes (Table 5) that were statistically significant for greater height per plant. In two cases the Bb

genotypes in combination with NN genotype gave taller plants than its alleles (BB and bb). The other significant difference showed that bb in combination with Nn produced a greater height of plant than Bb in the same combination. It was only in this latter case that the gene combination (Nnbb) producing greater yield and increased number of spikes per plant was also responsible for the production of greater height over its Bb allele.

As can be seen in Table 6 of the analysis of the NN, Nn, and the nn genotypes, the differences were significant in all nine comparisons. The data showed that the nn segregates produced taller plants than did NN or Nn segregates when in combination with BB and bb, but not in combination with Bb genotype.

The same general conclusions can be drawn for height of plant and number of spikes per plant as was drawn for weight of seed. That is, there were some genes favorable for height or greater number of spikes per plant in one combination, but the same genes were not favorable in other combinations.

Genes Associated with Inheritance of Color of Plant and Length of Rachilla Hairs

The data in Table 8 show the differences of the FF vs. ff, FF vs. Ff, and the Ff vs. ff genotypes in combination with the

SS, Ss and ss genes. The FF genotypes produced greater effects than did the ff genotypes for each of the three quantitative characters. The Ff genotypes produced greater effects than the FF and ff genotypes except in the FFSS and ffSS combination for height of plant. For each of these three quantitative characters the differences between the genotypes were significant, except for the difference between the FF and Ff genotypes in combination with the SS genotypes for weight of seed per plant. The data indicated that the FfSs combination was the most favorable for the greatest number of spikes, height of plant, and yield of seed. The FFSS genotype was less than the FfSs genotype, but greater than any combination of the ff genes with genes governing the length of rachilla hairs. One may conclude that the genotype Ff which was favorable for high yield was more favorable than its alleles (FF and ff) when found in all combinations with SS, Ss, and ss. However, this does not hold true when considering the other two quantitative characters, i.e., spikes per plant and height per plant.

The difference between the SS, Ss and ss genotypes in combination with the FF, Ff, and ff genotypes is shown in Table 9. There was statistical significance between the means of SS vs. ss with the Ff genotypes, and between SS vs. Ss in the Ff genotypes for height of plant. Only two combinations showed significance

Table 8.—GENES DIFFERENTIATING AND ASSOCIATED IN INHERITANCE WITH COLOR OF PLANT AND LENGTH OF RACHILLA HAIRS.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Green (FF)												
vs:												
Chlorina (ff)												
Long hair (SS)	28.08	14.07	14.01	14.28*	31.07	26.85	4.22	4.599*	24.11	10.97	13.14	12.672*
Long hair (Ss)	28.67	12.36	16.31	17.78*	30.86	26.28	4.58	11.317*	25.19	10.47	14.72	20.814*
Short hair (ss)	27.82	13.86	13.96	19.68*	31.36	26.41	4.95	15.142*	24.21	14.11	10.10	11.241*
Green (Ff)												
vs:												
Chlorina (ff)												
Long hair (SS)	29.54	14.07	15.47	15.930*	25.77	26.85	-1.08	3.033*	24.87	10.97	13.90	14.247*
Long hair (Ss)	30.64	12.36	18.28	19.010*	32.26	26.28	5.98	22.305*	28.06	10.47	17.59	25.786*
Short hair (ss)	29.90	13.86	16.04	22.135*	32.25	26.41	5.84	18.466*	26.93	14.11	12.82	12.294*
Green (FF)												
vs:												
Green (Ff)												
Long hair (SS)	28.08	29.54	-1.46	2.015*	31.07	25.77	5.30	9.667*	24.11	24.87	-.76	0.842
Long hair (Ss)	28.67	30.64	-1.97	3.400*	30.86	32.26	-1.40	5.601*	25.19	28.06	-2.87	4.698*
Short hair (ss)	27.82	29.90	-2.08	2.433*	31.36	32.25	-.89	3.399*	24.21	26.93	-2.72	3.440*

* t test gives $P > .05$

Table 9.—GENES DIFFERENTIATING AND ASSOCIATED IN INHERITANCE WITH RACHILLA HAIR LENGTH AND COLOR OF PLANTS.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant				
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t	
Long hair (SS)													
vs:													
Short hair (ss)													
Green (FF)	28.08	27.82	.26	0.274	31.07	31.36	-.29	0.430	24.11	24.21	-.10	0.108	
Green (Ff)	29.54	29.90	-.36	0.492	25.77	32.25	-6.48	8.689*	24.87	26.93	-2.06	0.886	
Chlorina (ff)	14.07	13.86	.21	0.358	26.85	26.41	.44	1.218	10.97	14.11	-3.14	1.633	
Long hair (Ss)													
vs:													
Short hair (ss)													
Green (FF)	28.67	27.82	.85	0.940	30.86	31.36	-.50	1.254	25.19	24.21	.98	1.205	
Green (Ff)	30.64	29.90	.74	1.043	32.26	32.25	.01	0.049	28.06	26.93	1.13	1.774	
Chlorina (ff)	12.36	13.86	-1.50	2.562*	26.28	26.41	-.13	0.290	10.47	14.11	-3.64	6.035*	
Long hair (SS)													
vs:													
Long (Ss)													
Green (FF)	28.08	28.67	-.59	0.640	31.07	30.86	-.21	0.361	24.11	25.19	-1.08	1.188	
Green (Ff)	29.54	30.64	-1.10	1.535	25.77	32.26	-6.49	29.737*	24.87	28.06	-3.19	4.785*	
Chlorina (ff)	14.07	12.36	1.71	1.848	26.85	26.28	.57	1.184	10.97	10.47	.50	.280	

* t test gives $P > .05$

Table 10.—INTERACTION OF RACHILLA HAIR LENGTH AND COLOR OF PLANT.

Genotypes and phenotypes	Number of Spikes		Height per plant		Weight of seed	
	Diff.	t	Diff.	t	Diff.	t
Long (SS) vs: Short (ss)						
Green (FF) vs: Green (Ff)	.62	1.073	6.19	21.417*	1.96	3.430*
Green (FF) vs: Chlorina (ff)	.05	.077	.73	1.621	3.04	4.730*
Green (Ff) vs: Chlorina (ff)	-.57	.997	-6.92	11.0028*	1.08	1.847
Long (Ss) vs: Short (ss)						
Green (FF) vs: Green (Ff)	.11	.197	-.51	2.601	-.15	.300
Green (FF) vs: Chlorina (ff)	2.35	3.854*	-.37	1.228	4.62	7.900*
Green (Ff) vs: Chlorina (ff)	2.24	4.032*	-.14	.741	4.77	9.302*
Long (SS) vs: Long (Ss)						
Green (FF) vs: Green (Ff)	.51	.861	6.28	7.913*	2.11	3.988*
Green (FF) vs: Chlorina (ff)	-2.30	3.650*	-.78	1.895	-1.58	2.598*
Green (Ff) vs: Chlorina (ff)	-2.81	4.974*	-7.06	35.300*	-3.69	8.266*

* t test gives $P > .05$

when considering yield. They were the differences between SS vs. Ss in combination with Ff and Ss vs. ss with the ff genotypes. Table 10 presents data showing that the gene (Ss) favorable for high yield in certain combinations was not significantly higher over its alleles in other combinations.

Confirmation of this was brought out further in a study of the interaction of genes governing rachilla length in combination with the genes governing color of plant. The combinations studied were:

SS > ss when in combination with FF vs. Ff

SS > ss when in combination with FF vs. ff

SS > ss when in combination with Ff vs. ff

SS > Ss when in combination with FF vs. Ff

Ss > SS when in combination with FF vs. ff

Ss > SS when in combination with Ff vs. ff

ss > Ss when in combination with FF vs. Ff

Ss > ss when in combination with FF vs. ff

Ss > ss when in combination with Ff vs. ff

The above values reveal that the SS genes produced better yield than the ss genes in combination with any set of genes

governing color of plant. However, SS was not more favorable than Ss in all combinations, nor was Ss greater than ss. Therefore, certain genes were favorable in some combinations, but were not favorable in other combinations; which is similar to the results obtained when the genes Bb for color of glumes were studied in all combinations with the Nn genes for covered vs. naked caryopsis.

Genes Differentiating and Associated in Inheritance with Length of Rachilla Hair and Color of Glumes

The genes responsible for rachilla hair length, and their association with genes governing the color of glume as they influence the three quantitative characters, are shown in Tables 11, 12, and 13. As can be seen from these tables, the genes responsible for high yield in certain combinations were not necessarily high yielding genes when in other combinations. As was cited before, there were various gene interactions. These interactions were different for the different gene combinations. The manner of the gene interactions affecting yield was somewhat more definite than the previous examples. Table 13 indicates that the BB genes produced a greater yield than did the bb genes in all combinations with long-hair vs. short-hair rachilla. Likewise, the Bb genes produce greater yield than the bb genes with the same combinations. However, there was one case where the BB did not produce greater

Table 11.--GENES DIFFERENTIATING AND ASSOCIATED IN INHERITANCE WITH LENGTH OF RACHILLA HAIRS AND COLOR OF GLUMES.

Genotypes	Spikes per plant				Height per Plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Long hair (SS) vs: Short (ss)												
Black (BB)	28.64	26.58	2.06	2.800*	31.30	31.18	+.12	.384	24.52	23.15	1.37	1.354
Black (Bb)	25.56	25.73	-.17	.238	30.59	30.92	-.33	1.320	22.13	22.65	-.52	.791
White (bb)	26.78	27.91	-1.13	.961	30.53	30.85	-.32	1.056	20.65	27.12	-6.47	6.146*
Long hair (Ss) vs: Short hair (ss)												
Black (BB)	26.46	26.58	-.12	.109	30.99	31.18	-.19	.665	23.51	23.15	.36	.424
Black (Bb)	26.97	25.73	1.24	.062	30.75	30.92	-.17	.629	24.10	22.65	+1.45	2.211*
White (bb)	27.37	27.91	-.54	.594	30.87	30.85	.02	.058	24.42	27.12	-2.70	3.086*
Long hair (SS) vs: Long hair (Ss)												
Black (BB)	28.64	26.46	2.18	1.940	31.30	30.99	.31	.930	24.52	23.51	1.01	1.054
Black (Bb)	25.56	26.97	-1.41	2.129*	30.59	30.75	-.16	.598	22.13	24.10	-1.97	3.021*
White (bb)	26.78	27.37	-.59	.678	30.53	30.87	-.34	.949	20.63	24.42	-3.79	4.286*

* t test gives $P > .05$

Table 12.—GENES DIFFERENTIATING AND ASSOCIATED IN INHERITANCE WITH COLOR OF GLUME AND LENGTH OF RACHILLA HAIRS.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Black (BB)												
vs:												
White (bb)												
Long hair (SS)	28.64	26.78	1.86	2.129*	31.30	30.53	.77	2.216*	24.52	20.65	3.87	3.610*
Long hair (Ss)	26.46	27.37	-.91	1.092	30.99	30.87	.12	0.135	23.51	24.42	-.91	1.302
Short hair (ss)	26.57	27.91	-1.34	0.407	31.18	30.85	.33	0.124	23.15	27.12	-3.97	4.005*
Black (Bb)												
vs:												
White (bb)												
Long hair (SS)	25.56	26.78	-1.22	1.307	30.59	30.53	.06	0.063	22.13	20.65	1.48	1.706
Long hair (Ss)	26.97	27.37	-.40	0.663	30.75	30.87	-.12	0.447	24.10	24.42	-.32	0.511
Short hair (ss)	25.73	27.91	-2.18	2.350*	30.92	30.85	.07	0.238	22.65	27.12	-4.47	5.735*
Black (BB)												
vs:												
Black (Bb)												
Long hair (SS)	28.64	25.56	3.08	3.671*	31.30	30.59	.71	2.232*	24.52	22.13	2.39	2.583*
Long hair (Ss)	26.46	26.97	-.51	0.695	30.99	30.75	.24	0.274	23.51	24.10	-.59	0.871
Short hair (ss)	26.57	25.73	.84	1.032	31.18	30.92	.26	0.937	23.15	22.65	.50	1.548

* t test gives $P > .05$

Table 13.—INTERACTION OF COLOR OF GLUME WITH LENGTH OF RACHILLA HAIRS.

Genotypes and phenotypes	Number of spikes		Height per plant		Weight of Seed	
	Diff.	t	Diff.	t	Diff.	t
Black (BB) vs: White (bb)						
Long (SS) vs: short (ss)	3.20	4.646*	.44	2.055*	7.84	10.819*
Long (Ss) vs: short (ss)	.43	.243	-.21	1.006	3.06	5.355*
Long (SS) vs: long (Ss)	2.77	2.035*	.65	2.901*	4.78	8.876*
Black (Bb) vs: White (bb)						
Long (SS) vs: short (ss)	.96	1.469	-.01	.048	5.95	9.972*
Long (Ss) vs: short (ss)	1.78	3.524*	-.19	.929	4.15	8.258*
Long (SS) vs: long (Ss)	-.82	1.624	.18	.864	1.80	2.754*
Black (BB) vs: Black (Bb)						
Long (SS) vs: short (ss)	2.24	3.808*	.45	2.146*	1.89	3.194*
Long (Ss) vs: short (ss)	-1.35	2.444	-.02	.097	-1.09	2.101*
Long (SS) vs: long (Ss)	3.59	5.349	.47	2.115*	2.98	5.534*

* t test gives $P > .05$

yields than the Bb genes. Therefore, the BB genes were not associated with the genes for high yield in all gene combinations, when considering the interaction of genes governing color of glumes vs. length of rachilla.

The results of different gene combinations for weight of seed as shown in Table 13 are summarized as follows:

BB > bb when in combination with SS vs. ss

BB > bb when in combination with Ss vs. ss

BB > bb when in combination with SS vs. Ss

Bb > bb when in combination with SS vs. ss

Bb > bb when in combination with Ss vs. ss

Bb > bb when in combination with SS vs. Ss

BB > Bb when in combination with SS vs. ss

Bb > BB when in combination with Ss vs. ss

BB > Bb when in combination with SS vs. Ss

Genes Associated with Color of Plants and Adherence of Glumes to the Carvepis

The data showing the interaction of genes associated with color of plants and adherence of glumes are shown in Tables 14, 15, and 16. Table 14 shows that the Ff genotype was more favorable than either the FF or ff genotypes in all combinations

Table 14.—GENES DIFFERENTIATING AND ASSOCIATED IN INHERITANCE OF COLOR OF PLANT AND ADHERENCE OF GLUMES TO CARYOPSIS.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Green (FF)												
vs:												
Chlorina (ff)												
Covered (NN)	27.24	14.19	13.05	11.745*	29.24	26.39	2.85	4.343*	25.12	11.43	13.69	12.403*
Covered (Nn)	28.59	13.03	15.56	23.946*	31.33	26.42	4.91	18.265*	25.36	11.77	13.59	20.847*
Naked (nn)	28.72	11.90	16.82	15.289*	32.69	26.59	6.10	18.348*	24.37	7.46	16.91	12.240*
Green (Ff)												
vs:												
Chlorina (ff)												
Covered (NN)	30.02	14.19	15.83	17.903*	30.81	26.39	4.42	12.411*	27.20	11.43	15.77	19.239*
Covered (Nn)	30.26	13.03	17.23	23.381*	32.33	26.42	5.91	25.082*	27.98	11.77	16.21	23.844*
Naked (nn)	30.28	11.90	18.38	16.045*	33.18	26.59	6.59	17.634*	24.90	7.46	17.44	14.492*
Green (FF)												
vs:												
Green (Ff)												
Covered (NN)	27.24	30.02	-2.78	3.252*	29.24	30.81	-1.57	3.826*	25.12	27.20	-2.08	2.504*
Covered (Nn)	28.59	30.26	-1.67	2.464*	31.33	32.33	-1.00	5.150*	25.36	27.98	-2.62	4.336*
Naked (nn)	28.72	30.28	-1.56	1.708	32.69	33.18	-.49	1.705	24.37	24.90	-.53	0.537

* t test gives $P > .05$

Table 15.—GENES DIFFERENTIATING AND ASSOCIATED IN INHERITANCE WITH ADHERENCE OF GLUMES AND COLOR OF PLANT.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Covered (NN)												
vs:												
Naked (nn)												
Green (FF)	27.74	28.72	-.98	.882	29.24	32.69	-3.45	6.396*	25.12	24.37	.75	2.271*
Green (Ff)	30.02	30.28	-.26	.373	30.81	33.18	-2.37	9.622*	27.20	24.90	2.30	3.337*
Chlorina (ff)	14.19	11.90	2.29	3.345*	26.39	26.59	-.20	.504	11.43	7.46	3.97	6.467*
Covered (Nn)												
vs:												
Naked (nn)												
Green (FF)	28.59	28.72	-.13	.150	31.33	32.69	-1.36	4.800*	25.36	24.37	.99	1.084
Green (Ff)	30.26	30.28	-.02	.027	32.33	33.18	-.85	1.312	27.98	24.90	3.08	4.669*
Chlorina (ff)	13.03	11.90	1.13	1.560	26.42	26.59	-.17	.394	11.77	7.46	4.31	6.676*
Covered (NN)												
vs:												
Covered (Nn)												
Green (FF)	27.74	28.59	-.85	.976	29.24	31.33	-2.09	5.339*	25.12	25.36	-.24	-.279
Green (Ff)	30.02	30.26	-.24	.346	30.81	32.33	-1.52	.747	27.20	27.98	-.78	-1.276
Chlorina (ff)	14.19	13.03	1.16	1.702	26.39	26.42	-.03	.074	11.43	11.77	-.34	.615

* t test gives $P > .05$

Table 16.--INTERACTION OF ADHERENCE OF GLUMES AND COLOR OF PLANT.

Genotypes	Number of spikes per plant		Height per plant		Weight of seed per plant	
	Diff.	t	Diff.	t	Diff.	t
Covered (NN) vs: Naked (nn)						
Green (FF) vs: Chlorina (ff)	-3.27	3.855*	-3.25	8.466*	-3.22	3.938*
Green (Ff) vs: Chlorina (ff)	-2.55	6.507*	-2.14	10.165*	-1.67	2.972*
Green (FF) vs: Green (Ff)	.72	1.168	-1.08	4.395*	-1.55	3.723*
Covered (Nn) vs: Naked (nn)						
Green (FF) vs: Chlorina (ff)	-1.26	2.000*	-1.19	5.009*	-3.32	29.377*
Green (Ff) vs: Chlorina (ff)	-1.15	1.955	-.67	3.624*	-1.23	2.140*
Green (FF) vs: Green (Ff)	-.11	.194	-.51	3.075*	-2.09	12.289*
Covered (NN) vs: Covered (Nn)						
Green (FF) vs: Chlorina (ff)	-2.01	4.112*	-2.06	7.168*	.10	.171
Green (Ff) vs: Chlorina (ff)	-1.40	2.585*	-1.49	8.195*	-.44	.915
Green (FF) vs: Green (Ff)	-.61	1.104	-.57	2.969*	.54	1.077

* t test gives $P > .05$

with covered vs. naked caryopsis with respect to the three quantitative characters studied. The *FF* genotypes were more favorable than the *ff* genotype in all combination with covered vs. naked caryopsis. This same trend between the *FF*, *Ff* and *ff* genotypes was observed when considering their association with other qualitative characters, i.e., *Bb* and *ss* genotypes. Table 15 places emphasis on covered vs. naked with respect to color of plants. In this table the *nn* genotype in combination with *FF* and *Ff* was more favorable than its alleles (*NN* and *Nn*) with respect to number of spikes per plant and height per plant. However, the differences for number of spikes per plant were not statistically significant, whereas three out of six combinations were statistically significant for height per plant. The *NN* genotype produced a greater number of spikes per plant than did its alleles (*Nn* and *nn*) in all combinations with the chlorina plant color genes. The *NN* and *Nn* genotypes produced a greater yield than did the *nn* genotype in all combinations with the green and chlorina plant color genes. There was a tendency for the heterozygote (*Nn*) to produce greater yields than either homozygote (*NN* or *nn*). The differences between *Nn* and *NN* in combinations with green and the chlorina plant color genes *FF*, *Ff*, and *ff* for weight of seed were not statistically significant; but there was a significant difference between the *Nn* and *nn* genotypes in combination with the *FF*, *Ff*, and *ff* genotypes.

Table 16 shows the results obtained from the interaction between gene combinations for adherence of glume and all gene combinations for color of plants. The number of spikes per plant was increased by the interaction of the nn genotype. The heterozygous covered (Nn) genotype produced greater effect than the homozygous covered (NN) genotype in all combinations with the green and chlorina plant color genes. This same trend was true with height per plant. Likewise, the genotype (nn) produced greater yield than either NN or Nn genotypes, and these cases were statistically significant. There was no evidence to prove that (NN) produced greater yields than the heterozygote (Nn).

The gene combinations for weight of seed per plant, as shown in Table 16, are summarized as below:

nn > NN in combination with FF vs. ff

nn > NN in combination with Ff vs. ff

nn > Nn in combination with FF vs. ff

nn > Nn in combination with FF vs. ff

nn > Nn in combination with Ff vs. ff

nn > Nn in combination with FF vs. Ff

NN > Nn in combination with FF vs. ff

Nn > NN in combination with Ff vs. ff

NN > Nn in combination with FF vs. Ff

In general, the covered seeds might be expected to produce greater yields than the naked seeds because of the extra weight added by the floral organs which remain on the caryopsis of the covered seed. However, as can be seen from Tables 14 and 16, the plants of genotype (nn) naked caryopsis produced better yields than either Nn or NN plants in combinations with the FF, Ff or ff genotypes.

Genes Associated with Length of Rachilla Hairs and Adherence of Glume to the Caryopsis

The genes associated with length of rachilla hairs in combination with genes governing adherence of glume to the caryopsis are shown in Tables 17, 18, and 19. The SS genotype was more favorable than its ss and Ss alleles in four out of the six combinations for number of spikes per plant. (Table 17). The heterozygote (Ss) was more favorable for number of spikes per plant than its ss allele in all combinations with the genes for covered and naked caryopsis. However, only the interaction of the Ss with the NN genotype showed statistical significance for greater number of spikes when combined with the interaction of the ss and NN genotypes. There was no consistent gene action for height of plant or weight of seed shown by genes associated with length of rachilla hairs in combination with covered or naked.

Table 17.—GENES DIFFERENTIATING AND ASSOCIATED WITH LENGTH OF RACHILLA HAIRS AND ADHERENCE OF GLUMES TO CARYOPSIS.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Long hair (SS) vs: Short hair (ss)												
Covered (HH)	26.99	24.68	2.31	2.772*	29.83	29.89	-.06	.189	22.77	21.66	1.11	1.476
Covered (Hh)	25.33	26.53	-1.20	2.928*	30.53	31.10	-.57	2.394*	22.50	25.14	-2.64	3.696*
Naked (hh)	29.36	26.13	3.23	2.972*	32.80	31.99	.81	2.511*	21.27	22.06	-.79	.785
Long hair (Ss) vs: Short hair (ss)												
Covered (HH)	26.56	24.68	1.88	2.068*	29.36	29.89	-.53	1.166	24.03	21.66	2.37	2.844*
Covered (Hh)	26.97	26.53	.44	.616	31.00	31.10	-.10	.446	24.41	25.14	-.73	1.036
Naked (hh)	27.38	26.13	1.25	1.375	32.04	31.99	.05	.167	23.20	22.06	1.14	1.140
Long hair (SS) vs: Long hair (Ss)												
Covered (HH)	26.99	26.56	.43	.516	29.83	29.36	.47	.987	22.77	24.03	-1.26	1.260
Covered (Hh)	25.33	26.97	-1.64	2.329*	30.53	31.00	-.47	2.115*	22.50	24.41	-1.91	2.865*
Naked (hh)	29.36	27.38	1.98	1.822	32.80	32.04	.76	2.128*	21.27	23.20	-1.93	1.756

* t test gives $P > .05$

Table 18.--GENES DIFFERENTIATING AND ASSOCIATED WITH ADHERENCE OF GLUME AND LENGTH OF RACHILLA HAIRS.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Covered (NN)												
vs:												
Naked (nn)												
Long hair (SS)	26.99	29.36	-2.37	2.310*	29.83	32.80	-2.97	9.393*	22.77	21.27	1.50	1.477
Long hair (Ss)	26.56	27.38	-.82	1.045	29.35	32.04	-2.69	7.249*	24.03	23.20	.83	.996
Short hair (ss)	24.68	26.13	-1.45	1.595	29.85	31.99	-2.14	7.591*	21.66	22.06	-.40	.480
Covered (Nn)												
vs:												
Naked (nn)												
Long hair(SS)	25.33	29.36	-4.03	3.953*	30.53	32.80	-2.27	3.859*	22.50	21.27	1.23	1.300
Long hair (Ss)	26.97	27.38	-.41	.565	31.00	32.04	-1.04	4.524*	24.41	23.20	1.21	1.694
Short hair (ss)	26.53	26.13	.40	.456	31.10	31.99	-.89	3.204*	25.14	22.06	3.08	3.696*
Covered (NN)												
vs:												
Covered (Nn)												
Long hair (SS)	26.99	25.33	1.66	2.124*	29.83	30.53	-.70	1.540	22.77	22.50	.27	.324
Long hair (Ss)	26.56	26.97	-.41	.578	29.35	31.00	-1.65	5.940*	24.03	24.41	-.38	.570
Short hair (ss)	24.68	26.53	-1.85	2.164*	29.85	31.10	-1.25	3.500*	21.66	25.14	-3.48	4.698*

* t test gives $P > .05$

Table 19.—INTERACTION OF ADHERENCE OF GLUME AND LENGTH OF RACHILLA HAIRS.

Phenotypes	Number of spikes per plant		Height per plant		Weight of seed per plant	
	Diff.	t	Diff.	t	Diff.	t
Covered (NN) vs: Naked (nn)						
Long (SS) vs: Short (ss)	-.92	1.306	-.83	3.652*	1.90	2.755*
Long (Ss) vs: Short (ss)	.63	1.008	-.55	2.145*	1.23	2.276*
Long (SS) vs: Long (Ss)	-1.55	2.402*	-.28	1.006	.67	1.038
Covered (Nn) vs: Naked (nn)						
Long (SS) vs: Short (ss)	-4.43	6.423*	-1.38	2.002*	-2.25	3.488*
Long (Ss) vs: Short (ss)	-.81	1.418	-.15	.836	-2.27	3.272*
Long (SS) vs: Long (Ss)	-4.44	8.436*	-1.23	6.519*	.02	.034
Covered (NN) vs: Covered (Nn)						
Long (SS) vs: Short (ss)	3.51	5.967*	.45	2.340*	3.75	7.500*
Long (Ss) vs: Short (ss)	1.44	2.534*	-.40	1.960	3.10	6.200*
Long (SS) vs: Long (Ss)	2.07	3.726	.95	4.513*	.65	1.203

* t test gives $P > .05$

Table 18 presents the data of the covered and naked genotypes when in combination with genes governing length of rachilla hairs. The same general conclusions for height per plant and number of spikes per plant in combinations with covered vs. naked and long vs. short hair rachilla, as shown in Table 18, applies to those conclusions drawn from covered vs. naked and green vs. chlorina plants shown in Table 15. That is, the nn genotype in general, produced greater number of spikes and greater height than the NN or Nn genotypes. However, the nn genotype did not produce greater yields than the NN or Nn genotypes when in all combinations of genes for length of rachilla hairs. The following summary taken from Table 19, gives the results of the interaction of Ss and Nn genotypes with weight of seed per plant:

NN > nn when in combination with SS vs. ss

NN > nn when in combination with Ss vs. ss

NN > nn when in combination with SS vs. Ss

nn > Nn when in combination with SS vs. ss

nn > Nn when in combination with Ss vs. ss

Nn > nn when in combination with SS vs. Ss

NN > Nn when in combination with SS vs. ss

NN > Nn when in combination with Ss vs. ss

NN > Nn when in combination with SS vs. Ss

Genes Associated with Color of Plants and the Color of Glumes

The associations of the *FF*, *Ff* and *ff* genotypes with the *BB*, *Bb* and *bb* genotypes are shown in Tables 20, 21, and 22. The *FF* and *Ff* genotypes produced greater effects than the *ff* genotypes in all combinations with black and white glume color. The green plants produced greater effects than did the chlorina plants for each of the three quantitative characters studied. These differences were statistically significant. The *Ff* genotypes produced greater number of spikes per plant, greater height per plant, and greater weight per plant than the *FF* genotypes in all combinations with the black and white genotypes. These results are shown in Table 20.

Table 21 shows the results of the black vs. white genotypes with all combinations with the genotypes for green and chlorina plants. The trend is in favor of the white (*bb*) genotype over the *BB* and *Bb* genotypes. The only significant difference between the *BB* vs. *bb* genotypes was shown in weight of seed per plant where a difference of -3.70 was obtained for the chlorina (*ff*) genotype. The *bb* genotype was significantly greater than the *Bb* genotype when in combination with the *Ff* and *ff* genotypes for spikes per plant and with the *ff* genotype for weight of seed per plant. The differences between *BB* and *Bb* were not statistically significant

Table 20.—GENES DIFFERENTIATED AND ASSOCIATED IN INHERITANCE WITH COLOR OF PLANT AND COLOR OF GLUMES.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Green (FF)												
vs:												
Chlorina (ff)												
Black (BB)	27.73	12.79	14.94	14.327*	31.29	25.88	5.41	14.661*	24.19	9.73	14.46	12.103*
Black (Bb)	29.19	13.12	16.07	20.698*	30.72	26.68	4.04	10.464*	24.74	9.99	14.75	18.408*
White (bb)	29.21	13.35	15.86	16.938*	31.46	26.36	5.10	14.076*	25.11	13.43	11.68	14.904*
Green (Ff)												
vs:												
Chlorina (ff)												
Black (BB)	29.98	12.79	17.19	12.858*	32.26	25.88	6.38	16.779*	26.68	9.73	16.95	16.103*
Black (Bb)	29.63	13.12	16.51	25.029*	32.13	26.68	5.45	23.108*	26.82	9.99	16.83	24.555*
White (bb)	31.52	13.35	18.17	19.406*	32.06	26.36	5.70	15.789*	27.83	13.43	14.40	14.890*
Green (FF)												
vs:												
Green (Ff)												
Black (BB)	27.73	29.98	-2.25	2.315*	31.29	32.26	-.97	3.492*	24.19	26.68	-2.49	2.936*
Black (Bb)	29.19	29.63	-.44	.685	30.72	32.13	-1.41	5.640*	27.74	26.82	-2.08	3.320*
White (bb)	29.21	31.53	-2.32	4.798*	31.46	32.06	-.60	.623	25.11	27.83	-2.72	3.046*

* t test gives $P > .05$

Table 21.—GENES DIFFERENTIATED AND ASSOCIATED IN INHERITANCE WITH COLOR OF GLUMES AND COLOR OF PLANT.

Genotypes	Spikes per plant				Height per plant				Weight of seed per plant			
	No.	No.	Diff.	t	In.	In.	Diff.	t	Grams	Grams	Diff.	t
Black (BB)												
vs:												
White (bb)												
Green (FF)	27.73	29.21	-1.48	1.510	31.29	31.46	-.17	.182	24.19	25.11	-.92	.973
Green (Ff)	29.98	31.52	-1.54	1.899	32.26	32.06	.20	.790	26.68	27.83	-1.15	1.543
Chlorina (ff)	12.79	13.35	-.56	.605	25.88	26.36	-.48	1.026	9.73	13.43	-3.70	5.698*
Black (Bb)												
vs:												
White (bb)												
Green (FF)	29.19	29.21	-.02	.022	30.72	31.46	-.74	1.825	24.74	25.11	-.37	.414
Green (Ff)	29.63	31.52	-1.89	3.024*	32.13	32.06	.07	.339	26.82	27.83	-1.01	1.576
Chlorina (ff)	13.12	13.35	-.23	3.539*	26.28	26.36	-.08	.202	9.99	13.43	-3.44	6.632*
Black (BB)												
vs:												
Black (Bb)												
Green (FF)	27.73	29.19	-1.46	1.586	31.29	30.72	.57	1.448	24.19	24.74	-.55	.582
Green (Ff)	29.98	29.63	-.35	.508	32.26	32.13	.13	.660	26.68	26.86	-.18	.293
Chlorina (ff)	12.79	13.12	-.33	.559	25.88	26.28	-.40	.888	9.73	9.99	-.26	.418

* t test gives $P > .05$

Table 22.—INTERACTION OF COLOR OF GLUME AND COLOR OF PLANT.

Genotypes and Phenotypes	Number of spikes per plant		Height per plant		Weight of seed per plant	
	Diff.	t	Diff.	t	Diff.	t
Black (BB) vs: White (bb)						
Green (FF) vs: Chlorina (ff)	-.92	1.392	.31	1.244	2.78	3.725*
Green (Ff) vs: Chlorina (ff)	-.98	1.492	.68	2.999*	2.55	4.284*
Green (FF) vs: Green (Ff)	.06	.098	-.37	1.907	.23	.390
Black (Bb) vs: White (bb)						
Green (FF) vs: Chlorina (ff)	.21	.340	-.66	2.203*	3.07	5.210*
Green (Ff) vs: Chlorina (ff)	-1.66	3.370*	.15	.812	2.43	4.877*
Green (FF) vs: Green (Ff)	1.87	3.605*	-.81	4.185*	.64	1.233
Black (BB) vs: Black (Bb)						
Green (FF) vs: Chlorina (ff)	-1.13	1.752	.97	3.117*	-.29	.428
Green (Ff) vs: Chlorina (ff)	-.02	.036	.53	2.910*	.08	.159
Green (FF) vs: Green (Ff)	-1.11	1.817	.44	2.308*	-.37	.713

* t test gives $P > .05$

for any of the three quantitative characters. However, there was a trend in favor of the Bb over the BB genotypes, especially for spikes per plant and weight of seed per plant.

Table 22 presents the data obtained from the interaction of genotypes responsible for glume and plant color. The interactions were inconsistent as far as any certain gene combinations are concerned. For example, let us look at the weight of seed per plant between BB and bb genotypes in Table 1. In every case, the bb genotypes produced greater yields than the BB genotypes. However, the BB genotype produced greater yields than the bb genotypes when we take into account the interactions of genes for green and chlorina plant color as shown in Table 22.

The results for weight of seed per plant as observed in Table 22 are summarized as follows:

BB > bb when in combination with FF vs. ff

BB > bb when in combination with Ff vs. ff

BB > bb when in combination with FF vs. Ff

Bb > bb when in combination with FF vs. ff

Bb > bb when in combination with Ff vs. ff

Bb > bb when in combination with FF vs. Ff

Bb > BB when in combination with FF vs. ff

BB > Bb when in combination with Ff vs. ff

Bb > BB when in combination with FF vs. Ff

Chapter V
DISCUSSION

The results of this study gave evidence that the general nature of the interactions of genes affecting the quantitative characters was extremely variable. Due to the great variations in the nature of these gene interactions, it was not possible to develop a suitable genetic hypothesis accounting for the action of all genes or gene combinations. Data from other workers indicated similar gene interactions. Powers (13), 1936, was unable to formulate a hypothesis due to the great variability of gene interactions between genes that govern the six and two row types of barley, and genes regulating habit of growth. However, he did find some cases in which genes generally favorable for increased yield per additional spike gave greater increased yields when in combination with other genes which also favored the development of this character.

A portion of the data reported in this article concerning the gene action of normal green (FF) genotypes, heterozygous green (Ff) genotypes, and chlorina (ff) genotypes showed that the normal green and the heterozygous green plants were more favorable in the production of greater number of spikes, greater height, and

greater weight of seed per plant than were the chlorina plants. The data also showed that the heterozygous (Ff) genotypes were more efficient than either the homozygous (FF or ff) genotypes. These differences were statistically significant for all combinations of interactions with genes governing color of glumes BB , Bb , and bb adherence of the glumes to the caryopsis NN , Nn , or nn , and were significant in all interactions with genes governing the length of rachilla hairs SS , Ss , and ss except in two cases. These cases were shown in Table 8 for height per plant in which the FF genotype showed greater effect than Ff genotype in combination with the SS genotype. The other case occurred when the ff genotype had a greater effect than the FF genotype when in combination with the SS genotype. However, in general, the heterozygous (Ff) genotype produced a greater number of spikes per plant, greater height, and a greater yield of seed than the homozygous (FF or ff) genotypes.

The interactions of dominant favorable growth genes suggested by Jones (8), 1917, is the most generally accepted genetic interpretation as an explanation of heterosis. Jones assumed that there are large numbers of at least partially dominant linked genes which govern the rate and magnitude of the developmental processes. It may be assumed that a series of favorable growth genes are linked with the F allele which, when in combination

with another different series of favorable growth genes in the chromosome with the *f* allele, interacts to produce greater values in the *Ff* combination than either homozygote (*FF* or *ff*).

Martin (10), 1936, found in hybrids between different grain sorghums that certain quantitative characters were due to the interaction of a few genes. The interaction of dominants at two loci accounted for internode length. A similar incident was reported by Quinby and Karper (17), 1945, in which the photoperiod response in milo was controlled by interaction of two genes for internode length and three genes responsible for internode number.

Concepts developed by East (3), 1907, Shull (23), 1910, East and Hayes (4), 1912, and later by East (2), 1936, have a direct bearing on the interpretation of the green vs. chlorina gene reactions in barley providing intra-allelic interactions are assumed, and that each allele produces a different function. These workers have accounted for heterosis as being due to heterozygosity rather than the action of partially dominant linked genes. It has been assumed that heterozygotes have greater advantages, possibly because of greater physiological efficiency, and that alleles have a less weakening or unfavorable effect when heterozygous than when homozygous. (1), (2), (3), (23).

The effect of heterozygosity has been studied by Gustafsson (5), 1946, in which he studied heterozygous barley plants of albina 7, and xantha 3. He found that plants in the heterozygous condition were more favorable than homozygous plants for length of ear, number of culms, and weight of seed. Also the heterozygous seeds of albina 7 remained viable longer than did homozygous seeds.

The Ma gene in sorghum was studied by Quinby and Karper (16), 1946, in which they showed that when the Ma gene was in the heterozygous condition Ma-ma, it produced plants which matured differently than plants possessing the gene in the homozygous condition. They also found that these heterozygous plants produced plants that were larger and tillered more than homozygous plants.

The genes responsible for the chlorina plant color reported in this paper may be classified as physiological defective genes as was suggested by East (1), 1935. The effect of the ff genotype was depressing in every combination with the other three qualitative genotypes. The normal green plants would be classified as non-defective in comparison to the chlorina plants.

Regardless of how the data are interpreted, whether it be due to the action of dominant linked favorable growth factors or to physiological effects due to heterozygosity, it would be evident that the genes responsible for chlorina color in plants are

extremely important in the study of inheritance of quantitative characters. When such genes are involved in a breeding program, in any combination with the other qualitative characters reported on in this paper, one could expect a depressing effect for number of tillers, height per plant, and weight of seed per plant. However, a combination of desirable factors from both green and chlorina plants may be obtained, producing an F_1 more suitable than either parent.

Suggestions for Further Study

There is much information to be gathered from the study of quantitative characters. Special methods have been developed with such crops as tomatoes and squash which are also applicable to many other economic crops. Such methods may be used to analyze data dealing with quantitative inheritance in barley. Another study may be developed in which the parents are used in the analysis of the quantitative characters. Since one parent was unfortunately eliminated in the material of this study the writer was unable to compare the parental genotypes with similar genotypes from the F_2 population. A back-crossing program may be used in which the F_1 generation is back-crossed to both parents. By such a method additional information could be gathered by comparing the back-cross genotypes with the F_2 genotypes.

Chapter VI

SUMMARY

A study was made of the effects of certain quantitative characters associated with known qualitative characters from a cross of Hordeum distichon Nigrinudum and Minnesota 84-7 barley. The quantitative characters studied were: (1) number of spikes, (2) height, and (3) weight of seed per plant. The four qualitative characters studied were: (1) black vs. white glume color (Bb), (2) long vs. short haired rachilla (Ss), (3) covered vs. naked caryopsis (Nn), and (4) green vs. chlorina plant color (Ff). The data were separated into 81 genotypes on the basis of the four factor pairs differentiating the qualitative characters. The sums of squares, regression coefficients, and variances were obtained for each genotype. The variances used to calculate the "t" values were corrected on the basis of the regression coefficients. The linkage relations were determined for the four qualitative characters studied. It was found that the genes governing the inheritance of the four quantitative characters were independently inherited. The means of the three quantitative characters were calculated and it was shown that the means of the three genotypes

for each of the four quantitative characters studied were such that there was no evidence of heterosis in the plants having the genes for the qualitative characters in the heterozygous condition.

The effects of qualitative characters on the three quantitative characters were studied by testing each of the four qualitative characters in all possible combinations two at a time. The results of this study gave evidence that the general nature of the genes affecting the quantitative characters was extremely variable. Due to the great variations in the nature of the gene interactions, it was not possible to develop a suitable genetic hypothesis accounting for the action of all genes or gene combinations. However, a portion of the data followed a definite trend. It was generally true that the normal green (FF) genotypes and the heterozygous green (Ff) genotypes were more favorable for the production of number of spikes per plant, height of plant, and weight of seed per plant than were the chlorina (ff) genotypes in all combinations with the other three qualitative characters. However, the heterozygous (Ff) was more efficient than either homozygous (FF or ff) genotypes. The ff genotype may be classified as physiologically deficient.

The interpretation of such gene reactions may be accounted for by Jones' theory of partially dominant linked genes in which

there is a series of genes linked with the F allele and another series of linked genes with the f allele. The heterozygote (Ff), in this case, will be the product of the interaction between linked genes closely associated with the F and f alleles.

The heterozygosity hypothesis may also account for the green vs. chlorina gene reactions if we assume only the intra-allelic interactions. However, the parents used in this cross were not isogenic and other gene pairs could have been involved.

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