

AN ABSTRACT OF THE THESIS OF

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Title COMBINING ABILITY AND GENE ACTION ESTIMATES AND THE ASSOCIATION OF THE COMPONENTS OF YIELD IN WINTER WHEAT CROSSES.

Abstract approved _____

(Major Professor)

A diallel cross consisting of ten parents was grown on the Hyslop Agronomy Farm near Corvallis, Oregon, in order to obtain estimates of the gene action contributing to yield and its components in wheat. Gene action estimates were obtained by two methods of diallel analysis and from narrow sense heritability values calculated by parent-progeny regressions involving both parental and F_1 data. In addition, path-coefficient analysis was utilized to investigate the direct and indirect associations of five variables on yield. The morphological characters measured were: (1) total yield per plant, (2) weight per kernel, (3) number of kernels per spikelet, (4) number of spikelets per spike, (5) number of spikes per plant and, (6) plant height.

A large portion of the total genetic variation associated with the yield components, weight per kernel, kernels per spikelet, spikelets per spike and spikes per plant was the result of additive gene action.

When the five variables were considered in terms of their associations with yield it was observed that weight per kernel, number of kernels per spikelet and the number of spikelets per

spike mainly exerted direct effects on yield. The number of spikes per plant had no direct effect, but an indirect effect on yield through the other variables. A similar indirect association was noted for plant height. The data obtained from the path-coefficient analysis indicated further that the number of kernels per spikelet had the greatest direct effect on yield.

Results obtained with correlation coefficients suggested that a negative association exists between weight per kernel and kernels per spikelet. Also such a negative association was found between the number of spikes per plant with weight per kernel and kernels per spikelet. These results would suggest the possible existence of a biological limitation between several of the components of yield.

The diallel cross analysis for general and specific combining ability gave similar estimates of gene action when they were compared to narrow sense heritability values. However, when the Jinks-Hayman method was compared with the other two methods of estimating gene action, several discrepancies were observed. This lack of agreement was possibly due to the inability of this experimental material to meet one or all of the genetic assumptions required by the Jinks-Hayman method.

The results of this study indicate that a breeding program with emphasis on increases in yield which considers each of the components separately, or in combination of two or more would offer the most promise. By this procedure the breeder could take advantage of the large amount of additive genetic variance associated with each of the components and at the same time, take into consideration any

biological limitations which may exist. In utilizing the information obtained in this study in such a breeding procedure the plant breeder would be able to better evaluate the methods for selecting the best parents to be hybridized and in selecting the best lines from hybrid progeny.

COMBINING ABILITY AND GENE ACTION ESTIMATES AND THE ASSOCIATION
OF THE COMPONENTS OF YIELD IN WINTER WHEAT CROSSES

by

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COMBINING ABILITY AND GENE ACTION ESTIMATES AND THE ASSOCIATION OF THE COMPONENTS OF YIELD IN WINTER WHEAT CROSSES

INTRODUCTION

The goal of most plant breeding programs is to increase the yielding capacity of a particular crop. This objective is achieved either by breeding for resistance to one of the many adversities which influence the final harvest or by breeding directly for increased yields. Unfortunately in wheat, as with many other crops, the latter approach has not been very successful, particularly after a certain plateau in plant yield has been attained.

Yielding ability of a plant is expressed through the photosynthetic and metabolic processes and since these physiological processes are under the influence of many genes, yield must also be polygenetically inherited. In addition, yield may be considered an exact measure or a final integration of all ecological conditions that have prevailed throughout the life of the plant. Therefore, lack of success in selecting directly for high yielding progeny in segregating populations may be partly attributed to the nature of yield which is complicated by the interrelationships of many genetic and environmental factors.

Yield in the wheat plant may also be considered as the product of several morphological components which, in turn, are influenced by both genetic and environmental factors. Each of these components, however, may not be influenced to the same degree and thereby may respond differently in their contributions to the total yield.

Therefore, in order to make progress in selecting for a complex character as yielding ability in wheat, the breeder must know the portion of the total variation observed in segregating populations that is due to the genetic composition, and the type of gene action contributing predominately to the character. This is of particular importance to the breeder of self-pollinating plants since only additive gene action and epistatic effects which behave in an additive manner can be utilized. Such information for each of the yield components, as well as the relationships between these components and yield, would help in determining the type of selection program to follow to obtain higher yielding varieties of wheat.

The objectives of this study were: (1) to obtain estimates of the predominate types of gene action contributing to each of the yield components of wheat, (2) to determine the relationship between the components and yield, and (3) to compare estimates of gene action obtained from heritability values calculated from parent-progeny regression with estimates calculated from two methods of diallel analysis.

REVIEW OF LITERATURE

Diallel Cross Analysis

According to Lush (31, p. 356-357), Schmidt in 1919 was apparently the first to introduce a diallel crossing system in which each of a group of males was crossed to each of a group of females. This diallel crossing system would compare to the procedure in plants where crosses are made in all possible combinations within a group of parents. Since that time, the theory of diallel crossing and the practical application of diallel crosses has received considerable attention in genetic analysis of populations. These analyses have been utilized for such diverse problems as estimating general and specific combining ability, measuring genotype-environmental interactions, and early generation evaluation of parental materials in breeding programs.

Griffing (16, p. 464) listed four methods of diallel crosses. The type of analysis depends on the presence or absence of the parental inbreds or the reciprocal F_1 's. With this as a basis for classification the four possible methods are: (1) parents, one set of F_1 's and reciprocal F_1 's are included (P^2 combinations); (2) parents, and one set of F_1 's are included $\left[\frac{1}{2} (P + 1) \text{ combinations} \right]$; (3) reciprocal F_1 's are included, but not the parents $\left[P (P - 1) \text{ combinations} \right]$; and (4) one set of F_1 's only is included $\left[\frac{1}{2} P (P - 1) \text{ combinations} \right]$. Matzinger et al. (34, p. 348) pointed out that the interpretation of these four methods depends on two sampling assumptions. In the first, the parental genotypes are assumed to be

a random sample from some population about which inferences are to be made. The other assumption is that the parental genotypes are deliberately chosen and constitute the entire population about which inferences are to be made. With the four experimental methods plus the two sampling assumptions there is a total of eight different situations, each requiring a different analysis.

Parental genotypes are usually homozygous inbred lines, but they can also be individual clones, open-pollinated varieties, or other genetic entities. Matzinger and Kempthorne (33, p. 833) have suggested the use of models depending on the degree of inbreeding of the parental material. Griffing (14, p. 304) suggested that parental and F_1 data have distinct advantages over data from segregating generations in studying quantitative genetic systems, because they are not confounded by segregation and linkage. Therefore, fewer individuals are necessary for efficient estimation of certain genetic parameters.

Sprague and Tatum (40, p. 931-932) utilized a 10×10 diallel cross in developing a technique to determine differences in the ability of corn inbreds to combine well in crosses. Observed variances were divided into that portion involving general combining ability and that portion involving specific combining ability. General combining ability was defined as the average performance of a line in hybrid combinations and assumed to be primarily a measure of additive gene action. The term specific combining ability was used to describe the performance of those crosses in which certain combinations did relatively better or worse than others on the basis of the average performance of the lines involved. Specific

combining ability is, under this definition, a measure of the non-additive genetic variances. Other workers utilizing diallel crosses in investigation of general and specific combining ability have been Henderson (22, p. 606) with swine, Griffing (15, No. 397) with tomatoes, and Matzinger et al. (34, p. 346-350) with corn.

A second application of diallel cross analysis was used by Rojas and Sprague (39, p. 463) in studies of genotypic-environmental interactions. They found with 11x11 and 10x10 diallel crosses involving corn single cross yield trials, repeated at different locations in different years, that the variance of specific combining ability included not only the non-additive deviations due to dominance and epistasis, but also a considerable portion of the genotypic-environmental interaction. Similar findings have been obtained using diallel analysis in corn by Matzinger and Kempthorne (33, p. 833), and Matzinger et al. (34, p. 346) and by Allard (4, p. 305) with lima beans.

Jinks and Hayman (25, p. 48-52) provided still a third application for diallel analysis involving early generation evaluation of parental materials in breeding programs. The genetic assumptions underlying this biometrical model were outlined by Hayman (20, p. 63) as follows: (1) diploid segregation, (2) only environmental differences between reciprocal crosses, (3) independent action of non-allelic genes, (4) no multiple allelism, (5) homozygous parents, and (6) genes independently distributed between parents. The theory and analytical details of this model have been reviewed by Hayman. (17, p. 235-244; 18, p. 789-809; 19, p. 336-355; 20, p. 63-85 and 21, p. 155-172).

Whitehouse et al. (44, p. 153) studied the components of yield with F_1 and F_2 generations of four spring wheat varieties. Information was obtained on the average additive effects of genes, the effects of heterozygosity, the dominance of the genes in each parent, and gene interaction for each of the components.

A similar method of analysis was employed by Crumpacker and Allard (7, p. 275-318) in interpreting genetic information on date of heading in a complete diallel cross of ten selected wheat varieties. Others using this approach have been Allard (3, p. 537-543) with lima beans, Leffel and Weiss (27, p. 528-534) with soybeans, Johnson and Aksel (26, p. 208-265), and Aksel and Johnson (1, p. 242-257) with barley, and Jinks (24, p. 767-788) with tobacco.

A modification of the Jinks-Hayman technique has been provided by Dickinson and Jinks (9, p. 65-78) in which either homozygous or heterozygous parents can be used. By this method estimates can be determined of the overall degree of dominance, inbreeding coefficient or degree of heterozygosity of loci showing dominance, and of the allelic frequency at such loci.

Heritability

Heritability may be regarded as the proportion of the total variation in a population caused by genetic factors. Lush (31, p. 356-357) considered heritability estimates in two ways: (1) in the broad sense, in which the whole genotype functions as a unit and is used in contrast with the environmental effect, and (2) in the

narrow sense in which heritability includes only the average effects of genes transmitted additively from parent to progeny. Information on heritability estimates in the narrow sense are of value to the breeder as a measure of efficiency in selection and as an index of transmissibility in segregating populations.

Warner (42, p. 427) presented an excellent review of the techniques for estimating the degree of heritability in crop plants reported in the literature prior to 1952. These techniques fall in general into three main categories; (1) those based on parent-offspring regressions, (2) those based on variance components from analysis of variance, and (3) those based on approximations of nonheritable variance from genetically uniform populations.

In self-pollinating species, such as wheat, the plant breeder is primarily interested in narrow sense heritability estimates which measure additive gene action, the only portion of the total genetic variability that can be fixed in succeeding generations. Under this definition heritability can be considered as an index of transmissibility and may be obtained using parent-offspring regressions or F_2 and backcross data to estimate the additive genetic variance.

Broad and narrow sense heritability estimates have been obtained in cross and self-pollinating plants by several workers. This review will be limited to those studies of self-pollinated species for which heritability estimates were obtained for each of the yield components.

Narrow sense heritability estimates were obtained by Bartley and Weber (5, p. 487-493) for three soybean crosses from regression of progeny means on their parents in F_2 and F_3 generations. Values for

seed yield varied from 10 to 44 percent. The heritability estimates for plant height were higher, ranging from 49 to 63 percent.

Mahmud and Kramer (32, p. 609) in a study with soybeans, calculated heritability estimates from the variability among spaced F_2 plants in relation to the variability among spaced plants of the non-segregating parents. Regressions of F_3 lines on F_2 plants and F_4 progeny on F_3 lines were used to determine the percent deviations from the means of the respective populations. Heritability values were found to range from 69 to 77 percent for yield and 74 to 91 percent for plant height.

Fiuzat and Atkins (10, p. 419) determined heritability estimates for six agronomic traits in two barley crosses using the F_2 variance method. The values were high for heading date (92.1 and 90.9 percent) and maturity date (86.3 and 87.3 percent). The values were quite variable between the two crosses for plant height (74.6 and 44.4 percent) and lower for tillers per plant (29.5 and 23.6 percent), grain yield (50.7 and 43.9 percent) and kernel weight (38.5 and 21.2 percent).

Heritability values were determined in three wheat crosses for date of heading, plant height and number of tillers by Nandpuri (36, p. 70-71). These values were determined by the F_2 variance method and from regression of F_3 progeny means on F_2 plants. The following estimates were obtained, date of heading 93.2 percent, plant height 88.4 percent, and number of tillers per plant 24.4 percent. McNeal (35, p. 349) calculated the heritability values for yield and components of yield from the regression of F_3 lines

on F_2 plants. The regression coefficients were so low that the author concluded that selection for these characters in the F_2 generation is of doubtful value. In contrast to the other cited experiments tillers per plant had the highest value of 35.6 percent.

Components of Yield

Yield is generally considered to be a complex heritable character showing continuous variation; however, Grafius (12, p. 419) suggests that yield is an artifact and that, consequently, there could be no genes for yield. Therefore, there can be no dominance effects, no over-dominance effects, no additive effects and in turn, no heritability of yield. Under this assumption yield is the end result of several components that are in turn quantitatively inherited.

In studies with the components of yield in barley Grafius (13, p. 552) concluded that vigor of an F_1 was due to epistasis. A large portion of this vigor of the F_1 was shown to be fixable in a true breeding form. In another study involving the components of yield in barley, Johnson and Aksel (26, p. 259) found that the number of kernels per spike had a predominant effect in determining yield. Also the general similarity of inheritance of all three yield components (weight per kernel, number of kernels per spike and number of tillers per plant) may represent different physiologically controlled expressions of the same genes.

Immer (23, p. 205) considered the amount of heterosis in F_1 crosses between varieties of barley and the reduction in yield during successive generations of natural selfing. Heterosis was

expressed as F_1 performance in percent of the parental mean. Yield per plant was the highest with 27.3 percent, followed by the components of yield with kernels per spike 11.1 percent, tillers per plant 8.3 percent and weight per kernel 4.9 percent.

In considering the major components of yield in corn, Leng (28, p. 502) found that the hybrids exceeded their best parent by consistent amounts for total grain yield, weight of kernels per ear, number of kernels per ear, and number of kernels per row. With the component, ears per plant, hybrids were significantly lower than their best parent. Heterosis was considered to have been manifested in any F_1 hybrid in which the mean value of the component being studied exceeded that of the higher parental inbred line.

Several studies have been conducted on the components of yield in wheat. McNeal (35, p. 349) observed that only kernels per plant were highly associated with yield in F_2 plants and in F_3 progenies. Spikes per plant and kernels per spike were more highly correlated with plant yield than was kernel weight. This is in contrast to the findings of Whitehouse, et al. (44, p. 147). A correlation coefficient of $r = 0.500$ in this latter study was observed for weight per kernel and plant yield. A smaller value of $r = 0.364$ was obtained between spikelets per spike and plot yield. Kernels per spikelet and tillers per plant showed little or no association with yield. A negative correlation was found between tillers per plant and weight per kernel, kernels per spikelet, and spikelets per spike. Also a negative association was obtained between weight

per kernel and kernels per spikelet. Sprague (41, p. 992) analyzed results obtained from studies with bread wheats and found a high positive correlation between yield per unit area and average number of spikes per area. Smaller positive correlation was obtained between yield per unit area and grain yield per spike and weight per kernel. In a similar study Weibel (43, p. 100) found positive correlations between plant height and number of heads and between plant height and grain yield. Numerous studies have indicated a small correlation between plant height and number of tillers per plant (Poehlman 37, p. 430).

By the use of path-coefficient analysis Quisenberry (38, p. 493) measured the direct influence of one variable (component) upon another and was able to separate the correlation coefficient into direct and indirect effects. From this analysis it was determined that the number of spikes per unit area was one of the most important factors in determining yield, closely followed by the number of kernels per spike or size of spike. Weight of 1,000 kernels was not as important in determining yield as the other two factors mentioned. There was very little relationship between number of spikes per area and size of spikes or plumpness of grain.

Path-coefficient analyses were also employed by Dewey and Lu (8, p. 517) to establish the relative importance of seed size, fertility and plant size as determiners of seed yield in crested wheatgrass. Fertility and plant size were found to have strong influences, directly and indirectly, upon seed yield, whereas seed

size and spikelets per spike were relatively unimportant.

This method of measuring the direct and indirect effects has rather diverse application, being employed by Frakes et al. (11, p. 210-212) to determine the effects of leaf weight, stem weight and stem number on forage yield of alfalfa. In addition, Brooks (6, p. 192-196) used this analysis in determining direct and indirect effects of alpha and beta acid on total hop-acid in male hops.

MATERIALS AND METHODS

Eight varieties and two experimental selections of winter wheat were chosen for this study. These included the varieties Nord Desprez, Heines VII, Dual, Panter, Alba, Druchamp, Burt, Omar, Pullman Selection 1, and Corvallis Selection 55-1744. A detailed description and pedigree of each of the parental lines is given in the Appendix Table 1. Panter, Alba and Druchamp were developed in Europe, and the exact degree of relationship between them is uncertain. Nord Desprez and Heines VII were also developed in Europe and have a common parent in Vilmorin 27. The varieties Omar, Burt, and Pullman Selection 1 were products of the breeding program at Washington State University and have several parents in common. Corvallis Selection 55-1744 is thought to be related to Pullman Selection 1, having a common parent in the Japanese variety Norin 10. Dual does not appear to be related to any of the other nine winter wheats.

These varieties and selections clearly do not constitute a random sample from any population. Rather they are a selected high yielding sample and constitute the entire population about which inferences can be made.

The 45 possible crosses involving the ten parental lines and the ten parents were grown in a randomized block trial in 1959 on the Hyslop Agronomy Farm, Corvallis, Oregon. There was sufficient hybrid seed to plant two complete replications using five and six plants per plot in replications one and two respectively. To avoid

losses due to poor emergence and to obtain uniformity, the plants were grown in plant bands in the greenhouse and transplanted into the field. The individual plants were spaced planted one foot apart within and between plots. Barley plants were grown at the end of each row to control differential growth adjacent to the alleys and they were removed prior to harvest.

Examination of individual plants indicated that root rot organisms of undetermined species, probably of Fusarium, Cercospora, Ophiobolus, or Rhizoctonia were present. Those plants showing severe disease symptoms were omitted from the study.

The plants were harvested individually and the following data were obtained: (1) number of spikes per plant, (2) total number of spikelets per spike, (3) total number of kernels, (4) total weight of kernels per plant to the nearest 50 milligrams, and (5) average plant height from ground level to the tip of the tallest spike to the nearest inch. From these data three additional values were computed: (6) the average number of spikelets per spike, (7) average number of kernels per spikelet, and (8) the average weight of a single kernel. Each character was analyzed on a plot mean basis.

The data obtained from the ten parents, 45 F_1 crosses were analyzed separately and together by the analysis of variance for the characters measured.

Estimates of general and specific combining ability were obtained by the technique proposed by Griffing (16, p. 463-493), where one set of F_1 's are included in a matrix, and neither parents nor reciprocal

F_1 's are used. These estimates were obtained for the following six characters and for each parental effect: X_1 = total yield per plant, X_2 = weight per kernel, X_3 = number of kernels per spikelet, X_4 = number of spikelets per spike, X_5 = number of spikes per plant, and X_6 = plant height.

In using this approach, general combining ability is interpreted as the relative performance due primarily to the additive effects of polygenes, whereas specific combining ability is considered to be the relative performance due primarily to deviations from the additive scheme. The method for computing the analysis of variance for combining ability is given in Table 1.

General and specific combining ability effects for each parent were estimated by the following procedure.

General combining ability of the i^{th} (j^{th}) parent

$$g_i = \frac{1}{P(P-2)} [PX_{i.} - 2X_{..}]$$

Specific combining ability of i^{th} and j^{th} parent such that $S_{ij} =$
 S_{ji}

$$s_{ij} = X_{ij} - \frac{1}{P-2} (X_{i.} + X_{j.}) + \frac{2}{(P-1)(P-2)} X_{..}$$

To estimate the nature of gene action governing the characters measured, the diallel cross analysis outlined by Jinks and Hayman (25, p. 48-52) was employed. For this analysis the mean values are arranged in arrays as illustrated in Table 2. In this procedure an array is defined as one variety (P) and all the F_1 crosses involving this parent.

Table 1. Analysis of variance and the expected mean squares for a modified diallel analysis.

Source of variation	d.f.	Sum of squares	Mean square	F	Expected mean square
Replication	N-1	$2 \frac{\sum X_{..} K^2}{P(P+1)} - \frac{2X_{..}^2}{NP(P+1)}$			
Genotype	$\frac{P(P+1)-1}{2}$	$\frac{\sum X_{ij.}^2}{N} - \frac{2X_{..}^2}{NP(P+1)}$	M_1	M_1/M_4	
GCA	P-1	$\frac{1}{P-2} \sum X_{i.}^2 - \frac{4}{P(P-2)} X_{..}^2$	M_2	M_2/M_3	$\sigma^2 + \sigma_S^2 + (P-2) \sigma_G^2$
SCA	$\frac{P(P-1)}{2}$	$\sum \sum X_{ij}^2 - \frac{1}{P-2} \sum X_{i.}^2 + \frac{2}{(P-1)(P-2)} X_{..}^2$	M_3	M_3/M_4	$\sigma^2 + \sigma_S^2$
Replication X Genotype	$\left[\frac{P(P+1)-1}{2} \right]$ $\left[N-1 \right]$	$\sum X_{ijk}^2 - 2 \frac{\sum X_{..} K^2}{P(P+1)} \frac{\sum X_{ij.}^2 + 2X_{..}^2}{N NP(P+1)}$	M_4		σ^2

Table 2. Symbolic representation of mean values of the different genotypes arranged in a diallel table.

	P ₁	P ₂	P ₃	P ₁₀
P ₁	$\bar{X}_{1,1}$	$\bar{X}_{1,2}$	$\bar{X}_{1,3}$	$\bar{X}_{1,10}$
P ₂	$\bar{X}_{2,1}$	$\bar{X}_{2,2}$	$\bar{X}_{2,3}$	$\bar{X}_{2,10}$
P ₃	$\bar{X}_{3,1}$	$\bar{X}_{3,2}$	$\bar{X}_{3,3}$	$\bar{X}_{3,10}$
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P ₁₀	$\bar{X}_{10,1}$	$\bar{X}_{10,2}$	$\bar{X}_{10,3}$	$\bar{X}_{10,10}$

From the table the following symbols are defined and computed:

Vr is the variance for each F₁ array and is obtained for the first parent (P₁) by the formula.

$$Vr = \frac{\bar{X}_{1,1}^2 + \bar{X}_{1,2}^2 + \bar{X}_{1,3}^2 + \dots + \bar{X}_{1,10}^2 - \frac{(\bar{X}_{1,1} + \bar{X}_{1,2} + \bar{X}_{1,3} + \dots + \bar{X}_{1,10})^2}{P}}{P-1}$$

Wr is the covariance between the individual F₁'s in the arrays and the variable parent. The Wr value for the first parent (P₁) is obtained by the formula:

$$Wr = \frac{\bar{X}_{1,1}^2 + \bar{X}_{1,2} \cdot \bar{X}_{2,2} + \bar{X}_{1,3} \cdot \bar{X}_{3,3} + \dots + \bar{X}_{1,10} \cdot \bar{X}_{10,10} - \frac{(\bar{X}_{1,1} + \bar{X}_{2,2} + \bar{X}_{3,3} + \dots + \bar{X}_{10,10})(\bar{X}_{1,1} + \bar{X}_{1,2} + \bar{X}_{1,3} + \dots + \bar{X}_{1,10})}{P}}{P-1}$$

V_p is the variance of parental means and is determined as follows:

$$V_p = \frac{\bar{x}_{1,1}^2 + \bar{x}_{2,2}^2 + \bar{x}_{3,3}^2 + \dots + \bar{x}_{10,10}^2 - \frac{(\bar{x}_{1,1} + \bar{x}_{2,2} + \bar{x}_{3,3} + \dots + \bar{x}_{10,10})^2}{P}}{P-1}$$

Once the values for V_r , W_r and V_p have been determined, the variance (V_r) and covariance (W_r) for each parental array are plotted on a graph showing the linear regression (V_r , W_r) and the limiting parabola $W_r^2 = V_p V_r$. The slope of the regression line should not be significantly different from one if epistasis is absent. The limiting parabola marks the limits within which the points (V_r , W_r) should lie. The type of gene system is indicated by where the regression line interrupts the vertical (W_r) or horizontal (V_r) axis as illustrated in Figure 1.

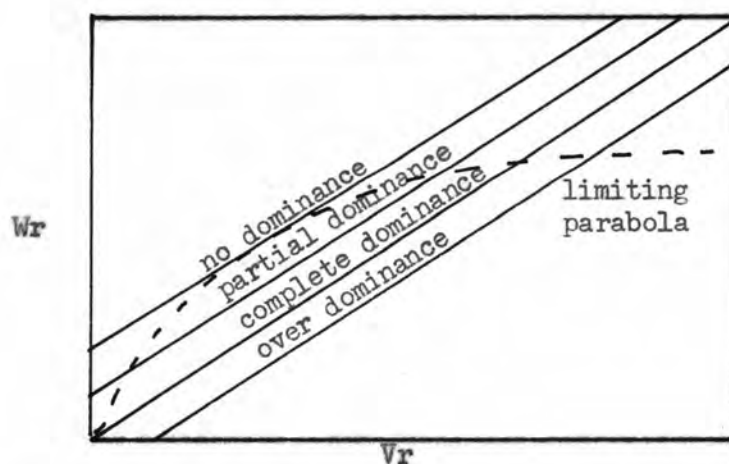


Figure 1. Geometrical interpretation of regression of W_r on V_r .

Heritability values in the narrow sense were obtained by the regression of the F_1 means on the means of the two parents along with

correlation coefficients for the six characters studied.

In addition, simple correlation coefficients were computed for the six measured traits in all possible combinations. This included $n=10$ for the parents, $n=45$ for the single crosses and $n=55$ for both parents and F_1 's together. This was done to determine if the associations were similar in all three populations.

The correlation coefficients for the 45 single crosses were further analyzed by the path-coefficient analysis outlined by Wright (45, p. 557-585). Detailed discussions of the theory and application of path-coefficient analysis are given by Wright (45, p. 557-585) and Li (29, p. 144-171). By this method direct and indirect relationships were determined for the yield components and yield. Where all direct and indirect effects are accounted for in this type of analysis the combined total effect will equal unity. If there are unknown variables which have direct and indirect effects, the combined effect of those measured will not equal unity, but a residual effect will remain. The path diagram and association of all characters studied in this experiment are present in Figure 2. In the diagram the single-arrowed lines indicate the direct effect of one character on another, and the double-arrowed lines indicate the correlation between two characters.

The path coefficients (P = standardized partial regression coefficients) were obtained by the simultaneous solution of the following equations, which indicate the basic relationships between correlation and path-coefficients.

$$r_{2,1} = P_{2,1} + r_{2,3} P_{3,1} + r_{2,4} P_{4,1} + r_{2,5} P_{5,1} + r_{2,6} P_{6,1}$$

$$r_{3,1} = P_{3,1} + r_{2,3} P_{2,1} + r_{3,4} P_{4,1} + r_{3,5} P_{5,1} + r_{3,6} P_{6,1}$$

$$r_{4,1} = P_{4,1} + r_{2,4} P_{2,1} + r_{3,4} P_{3,1} + r_{4,5} P_{5,1} + r_{4,6} P_{6,1}$$

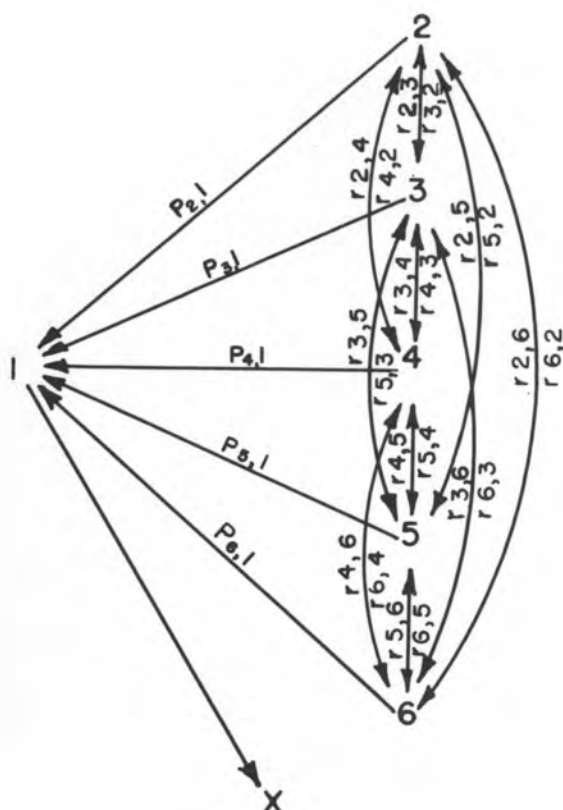
$$r_{5,1} = P_{5,1} + r_{2,5} P_{2,1} + r_{3,5} P_{3,1} + r_{4,5} P_{4,1} + r_{5,6} P_{6,1}$$

$$r_{6,1} = P_{6,1} + r_{2,6} P_{2,1} + r_{3,6} P_{3,1} + r_{4,6} P_{4,1} + r_{5,6} P_{5,1}$$

The variation in yield unaccounted for by these associations is calculated from the formula, $1-R^2$, where:

$$R^2 = P_{2,1} r_{2,1} + P_{3,1} r_{3,1} + P_{4,1} r_{4,1} + P_{5,1} r_{5,1} + P_{6,1} r_{6,1}$$

R^2 is the squared multiple correlation coefficient and is the amount of variation in yield that can be accounted for by the five characters.



1= YIELD PER PLANT.

2= WEIGHT PER KERNEL.

3=NUMBER OF KERNELS PER SPIKELET. 6= PLANT HEIGHT.

4= NUMBER OF SPIKELETS PER SPIKE.

5= NUMBER OF SPIKES PER PLANT.

P= PATH COEFFICIENT.

r = CORRELATION COEFFICIENT.

X= RESIDUAL FACTORS.

Figure 2. Path diagram and association of all characters studied.

EXPERIMENTAL RESULTS

Analysis of Variance

The per plant mean values for all measured characters for each population studied are found in the Appendix Tables 2 and 3. The mean squares for the various sources of variation for the characters measured are presented in Tables 3, 4 and 5. The tables represent the three populations involved in this study with a separate analysis of variance provided for the parents, the F_1 crosses and the parents and F_1 crosses considered together. These will be referred to as Populations I, II and III, respectively, in experimental results and discussion.

In comparing these three populations, significant differences among phenotypes were observed for yield per plant, kernels per spikelet, spikelets per spike and plant height. Spikes per plant differed significantly in Population I, and this character also differed significantly in Populations II and III. A significant difference for weight per kernel was found in Population I, but not in the other two populations.

Coefficients of variation were rather high for tillers per plant, ranging from 10.5 percent for Population II to 15.3 percent for Population I. The coefficient of variation for the other characters measured was below 10 percent, spikelets per spike having the lowest value of 2.1 percent in Population I and 4.4 and 4.1 percent, respectively, in Populations II and III.

Table 3. Observed mean squares from randomized block analysis of variance for all characters measured involving the ten parents (population I, n = 10).

Source of variation	D.F.	Yield per plant	Weight per kernel	Kernels per spikelet	Spikelets per spike	Spikes per plant	Plant height
Parents	9	7.7022**	.0033**	.2635**	13.2984**	27.5781*	110.16**
Replication	1	19.1493**	.0020*	.2354**	.0186	191.7043	2.45
Parents x replication	9	.8994	.0004	.0143	.2714	27.4952	.78
Total	19	--	--	--	--	--	--
Coefficient of variation		6.3	4.0	4.5	2.1	15.3	2.0

* Significant at the five percent level.

** Significant at the one percent level.

Table 4. Observed mean squares from randomized block analysis of variance for all characters measured involving the 45 single crosses (population II, n = 45).

Source of variation	D.F.	Yield per plant	Weight per kernel	Kernels per spikelet	Spikelets per spike	Spikes per plant	Plant height
Crosses	44	13.5891**	.0015	.2080**	9.7375**	37.0114**	39.99**
Replication	1	114.9662**	.0077*	1.4440**	.0185	894.2855**	139.38**
Crosses x replication	44	3.0753	.0018	.0792	1.2747	16.3447	2.63
Total	89	--	--	--	--	--	--
Coefficient of variation		10.3	8.9	10.3	4.4	10.5	3.4

* Significant at the five percent level.

** Significant at the one percent level.

Table 5. Observed mean squares from randomized block analysis of variance for all characters measured involving both parents and F_1 single crosses (population III, n = 55).

Source of variation	D.F.	Yield per plant	Weight per kernel	Kernels per spikelet	Spikelets per spike	Spikes per plant	Plant height
Parents and crosses	54	13.4751**	.0018	.2168**	10.4759**	39.6474**	56.19**
Replication	1	133.7388**	.0097	1.6740**	.0328	1085.9380**	128.73**
Parents and crosses x replication	54	2.6627	.0015	.0670	1.0839	17.9014	2.51
Total	109	--	--	--	--	--	--
Coefficient of variation		9.8	8.3	9.5	4.1	11.2	3.4

* Significant at the five percent level.

** Significant at the one percent level.

General and Specific Combining Ability

Since in the general analysis of variance a highly significant F ratio was obtained for all characters, with the exception of weight per kernel in Populations II and III (Tables 4 and 5), an analysis of variance for combining ability was computed using Griffing's method (16, p. 464), and the results are presented in Table 6. The variances associated with general combining ability were found to be significant for yield, weight per kernel, kernels per spikelet, spikelets per spike, spikes per plant, and plant height. No differences were detected for the variances associated with specific combining ability for any of the variables measured in this study.

Direct comparisons of the general combining ability performances of individual varieties and selections along with corresponding standard errors for each character are shown in Table 7. When yield per plant is considered, Omar and Selection 55-1744 had a significantly greater positive general combining ability effect than the other eight parental lines. A similar observation can be made for kernels per spikelet with Omar and Corvallis Selection 55-1744 again having significant positive effects. Omar also had a significant positive general combining ability effect for spikelets per spike, and, Panter, Heines VII and Corvallis Selection 55-1744 had smaller positive, but significant effects, in contrast to the other lines. The largest positive effects for spikes per plant was contributed by Pullman Selection 1, followed closely by Burt, both

Table 6. Observed mean squares from general and specific combining ability analysis for all characters measured involving the 45 single crosses (n = 45).

Source	D.F.	Yield per plant	Weight per kernel	Kernels per spikelet	Spikelets per spike	Spikes per plant	Plant height
General combining ability	9	14.10**	.00174*	.343**	19.37**	59.53**	79.67**
Specific combining ability	35	4.91	.00050	.042	1.14	7.95	4.62
Error	44	3.08	.00185	.079	1.27	16.34	2.63

* Significant at the five percent level.

** Significant at the one percent level.

Table 7. Estimates of general combining ability effects for all characters measured from all possible single crosses involving the ten parents.

Parent	Yield per plant	Weight per kernel	General Combining Ability Effects		Spikes per plant	Plant height
			Kernels per spikelet	Spikelets per spike		
Nord Desprez	-0.794	0.022	-0.263	0.521	-0.208	-2.200
Heines VII	-0.398	0.009	-0.145	0.692	0.618	-0.575
Dual	0.411	0.006	0.182	-1.456	-1.432	4.800
Omar	2.140	-0.027	0.340	2.496	-2.423	4.600
Selection 1	-1.062	-0.015	-0.044	-0.392	5.546	-2.575
Burt	-1.347	-0.005	0.050	-2.913	3.079	0.425
Druchamp	-1.554	0.015	-0.240	-1.306	1.619	-0.450
Panter	0.844	-0.005	0.008	1.337	-1.792	1.925
Alba	-0.284	0.006	-0.142	0.389	-2.496	-0.700
Selection 55-1744	2.044	-0.004	0.254	0.635	-2.514	-5.325
Standard error	0.876	0.019	0.141	0.564	2.021	0.811

parental lines being significantly different from the others, except Druchamp. For plant height significant effects were noted with Omar and Dual and to a lesser extent by Panter. Significant negative values were also noted for general combining ability effects for certain parental lines depending on the character being measured.

Estimation of effects of specific combining ability involving each F_1 mean along with the standard errors for each character are found in Table 8. The greatest effect on yield was detected in crosses of Omar and either Druchamp or Panter. There were no significant specific combining ability effects observed for weight per kernel (X2), kernels per spikelet (X3) or spikes per plant (X5). A significant effect for spikelets per spike (X4) was noted only in the cross Heines VII x Omar. Several crosses, however, showed significant effects for plant height (X6). In addition, negative values were observed for several of the crosses involving all six characters measured.

To determine how the average specific combining ability of the series of crosses involving one line compared with the average specific combining ability of a different line, associated variances for each parent were computed (Table 9). Omar had the largest associated variance for yield (X1) followed by Panter. No positive values were obtained in the parental line for kernels per spikelet (X3) and spikes per plant (X5). This was also true for spikelets per spike (X4) for each parent with the exception of Heines VII and Omar and for weight per kernel (X2) except for Nord Desprez.

Table 8. Estimates of specific combining ability effects for all characters measured from all possible single crosses involving ten wheat parents. X1 = yield per plant, X2 = weight per kernel, X3 = kernels per spikelet, X4 = spikelets per spike, X5 = spikes per plant, and X6 = plant height. P1 = Nord Desprez, P2 = Heines VII, P3 = Dual, P4 = Omar, P5 = Selection 1, P6 = Burt, P7 = Druchamp, P8 = Panter, P9 = Alba, and P10 = Selection 55-1744.

Parent	Variable	P10	P9	P8	P7	P6	P5	P4	P3	P2
P1	X1	-.29	-2.28	-3.72	-.85	1.08	2.64	-.15	2.45	1.15
	X2	.004	-.024	-.019	-.033	.001	.025	.026	.004	.019
	X3	-.10	-.12	-.40	.07	.16	-.06	.04	.34	.06
	X4	.12	-1.33	1.39	-.18	.51	.31	-.07	-.17	-.60
	X5	3.53	-1.10	-1.84	1.37	.37	-5.93	1.29	2.42	-.13
	X6	.91	-.72	-3.35	-.97	2.15	2.15	-.09	-.22	.15
P2	X1	2.44	-1.52	-2.34	-1.37	1.05	.78	.03	-.20	
	X2	.003	-.011	-.001	-.007	.014	-.006	.009	-.017	
	X3	.21	-.13	-.15	-.15	.07	.10	-.11	.09	
	X4	1.11	-.92	-2.30	-.37	.35	.19	2.78	-.24	
	X5	3.42	1.83	-1.71	1.30	-2.46	1.72	1.17	-5.14	
	X6	.28	-2.35	1.03	-1.59	3.53	1.53	.28	-2.85	
P3	X1	-1.29	-1.19	1.27	1.37	.15	.87	-3.41		
	X2	-.023	.015	.017	.024	-.002	.014	-.028		
	X3	-.02	-.27	-.16	.15	.03	.10	-.28		
	X4	.21	.16	.42	.17	1.17	.00	-1.73		
	X5	-3.47	2.38	-1.20	-1.78	4.76	-.75	2.77		
	X6	2.91	-.72	1.65	1.03	.15	-.85	-1.09		
P4	X1	-1.05	2.69	4.30	4.26	-2.45	-4.21			
	X2	-.005	-.005	.031	.024	-.037	-.010			
	X3	-.02	.30	.25	.29	-.15	-.32			
	X4	-1.48	.59	.72	1.18	-.36	-1.65			
	X5	-6.25	1.20	-1.24	1.56	.60	-1.11			
	X6	-.97	2.41	2.78	1.15	-2.72	-1.72			
P5	X1	-.78	.52	2.07	.65	-2.52				
	X2	-.024	.014	-.003	-.011	.006				
	X3	-.04	.10	.33	.14	-.35				
	X4	1.01	.16	.35	.47	-.84				
	X5	2.43	-1.05	2.86	.38	1.46				
	X6	-3.72	1.65	1.03	2.41	-2.47				
P6	X1	.57	1.34	-.56	1.37					
	X2	-.001	-.013	-.006	.043					
	X3	.04	.13	.02	.05					
	X4	-.86	1.38	.24	-1.61					
	X5	-2.38	.62	-1.63	-1.36					
	X6	-.72	2.65	-3.97	1.41					
P7	X1	-1.06	-2.48	-1.86						
	X2	.005	-.026	-.015						
	X3	-.18	-.24	-.13						
	X4	.38	.37	-.42						
	X5	-.18	-1.34	.03						
	X6	.15	-2.47	-1.09						
P8	X1	-.29	1.16							
	X2	-.004	.004							
	X3	.05	.19							
	X4	-.24	-.16							
	X5	5.09	-.37							
	X6	1.78	-.85							
P9	X1	1.78								
	X2	.049								
	X3	.04								
	X4	-.25								
	X5	-2.18								
	X6	-.59								
Standard Error				X1	X2	X3	X4	X5	X6	
				2.320	.051	.372	1.493	5.348	2.145	

Table. 9. Estimates of general and specific combining ability variances associated with each parent and estimates of the environmental variance on a mean basis. X1 = yield per plant, X2 = weight per kernel, X3 = kernels per spikelet, X4 = spikelets per spike, X5 = spikes per plant, and X6 = plant height.

Parent	Variable	$\hat{\sigma}_{gi}^2$	$\hat{\sigma}_{si}^2$	$\hat{\sigma}^2$
Nord Desprez	X1	.2845	1.7250	3.0753
	X2	.0003	.0452	.0015
	X3	.0602	-.0267	.0792
	X4	.1280	-.5526	1.2747
	X5	-1.7955	-6.5800	16.3447
	X6	4.5441	.5530	2.6300
Heines VII	X1	-.1876	-.3544	3.0753
	X2	0	0	.0015
	X3	.0122	-.0510	.0792
	X4	.3357	.8678	1.2747
	X5	-1.4568	-7.2422	16.3447
	X6	.0347	1.7257	2.6300
Dual	X1	-.1770	.4392	3.0753
	X2	0	0	.0015
	X3	.0243	-.0274	.0792
	X4	1.9780	-.5245	1.2747
	X5	.2118	-3.6163	16.3447
	X6	22.7441	.5580	2.6300
Omar	X1	4.2336	7.3534	3.0753
	X2	0	0	.0015
	X3	.1066	-.0123	.0792
	X4	6.0866	1.1441	1.2747
	X5	4.0322	-7.2052	16.3447
	X6	20.8641	1.1277	2.6300
Selection 1	X1	.7819	2.0586	3.0753
	X2	0	-.0011	.0015
	X3	-.0070	-.0205	.0792
	X4	.0109	-.4967	1.2747
	X5	28.9193	-7.1290	16.3447
	X6	6.3347	2.7207	2.6300
Burt	X1	1.4684	-.3215	3.0753
	X2	0	0	.0015
	X3	-.0060	-.0441	.0792
	X4	8.3480	-.1300	1.2747
	X5	7.6415	-9.0650	16.3447
	X6	-.1153	4.6857	2.6300
Druchamp	X1	2.0689	1.7663	3.0753
	X2	0	0	.0015
	X3	.0488	-.0365	.0792
	X4	1.5635	-.5077	1.2747
	X5	.7824	-12.0810	16.3447
	X6	-.0934	.3188	2.6300
Panter	X1	.3672	3.4221	3.0753
	X2	0	-.0011	.0015
	X3	-.0090	-.0149	.0792
	X4	1.6447	-.0708	1.2747
	X5	1.3725	-8.5304	16.3447
	X6	3.4097	3.1907	2.6300
Alba	X1	-.2653	.9205	3.0753
	X2	0	0	.0015
	X3	.0110	-.0295	.0792
	X4	.0075	-.4724	1.2747
	X5	4.3912	-11.8222	16.3447
	X6	.1941	1.2718	2.6300
Selection 55-1744	X1	3.8340	-.9267	3.0753
	X2	0	0	.0015
	X3	.0554	-.0573	.0792
	X4	.2596	-.4272	1.2747
	X5	4.4814	-3.8851	16.3447
	X6	28.0597	1.2252	2.6300

It is also interesting to compare the relative magnitudes of the associated variances for general and specific combining ability with that of the environmental variances. The appropriate statistics for these comparisons are also presented in Table 9. Environmental variances were larger than those for general and specific combining ability for all traits measured for the varieties Heines VII and Alba. The variances for general combining ability involving spikelets per spike were greater with the parental lines Dual, Omar, Burt, Druchamp and Panter. This was also true for plant height with Dual, Omar, Selection 1, Panter, Nord Desprez and Selection 55-1744. Higher general combining ability variances for yield were noted for Selection 55-1744 and Omar. This was true for the latter variety, also for kernel number per spikelet and with Selection 1 when the number of spikes per plant was considered. Variances for specific combining ability were found to be larger than environmental variances with Omar and Panter for plant yield, Panter, Selection 1 and Burt for plant height and with Nord Desprez for weight per kernel.

Evaluation of Parental Lines

An attempt was made to evaluate the parental lines using the model proposed by Jinks and Hayman (25, p. 48-52). The values of the variances within each array (V_r), the covariances (W_r) and the variance of the parental means ($V_{\bar{p}}$) together with linear regression ($V_r W_r$) and the parabola $W_r^2 = V_{\bar{p}} V_r$ are presented in Figures 3, 4, 5, 6, 7 and 8. It is clear from these figures that the regression

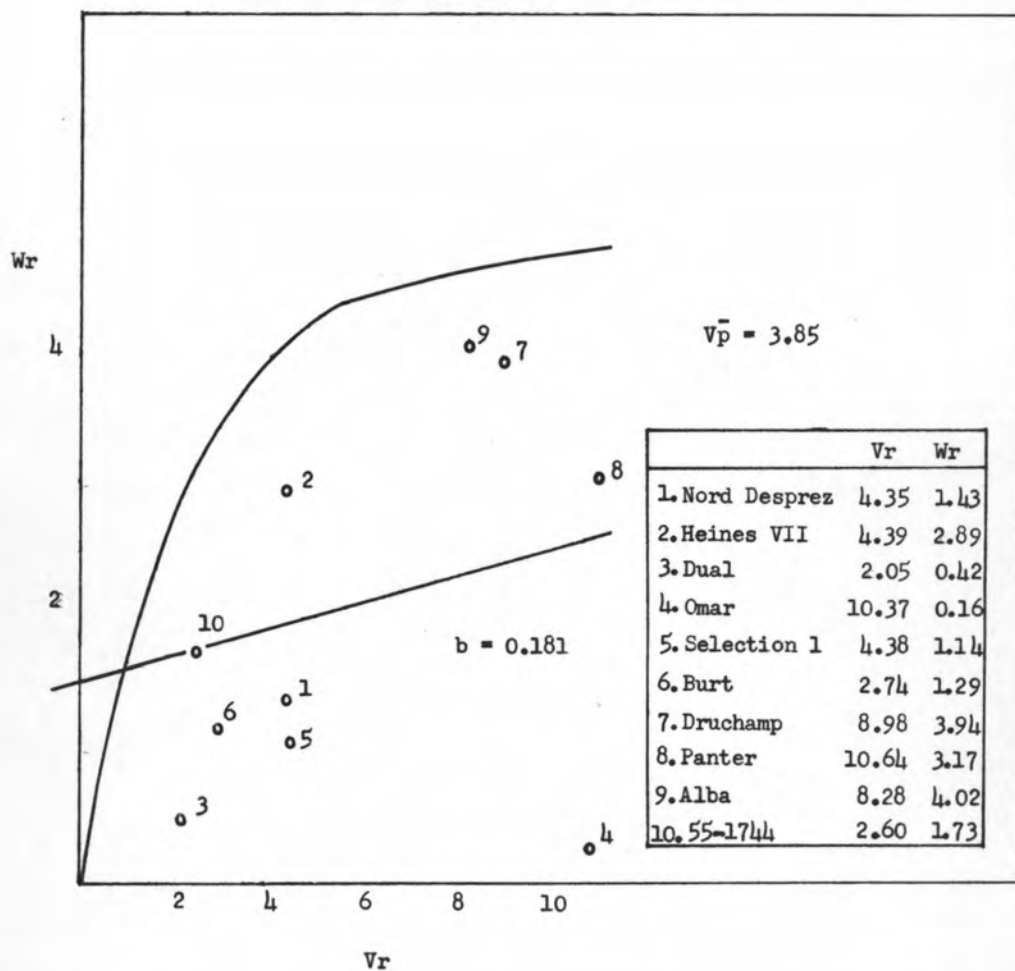


Figure 3. Regression of the variances (V_r) and the covariances (W_r) for each F_1 parental array for yield per plant (X_1).

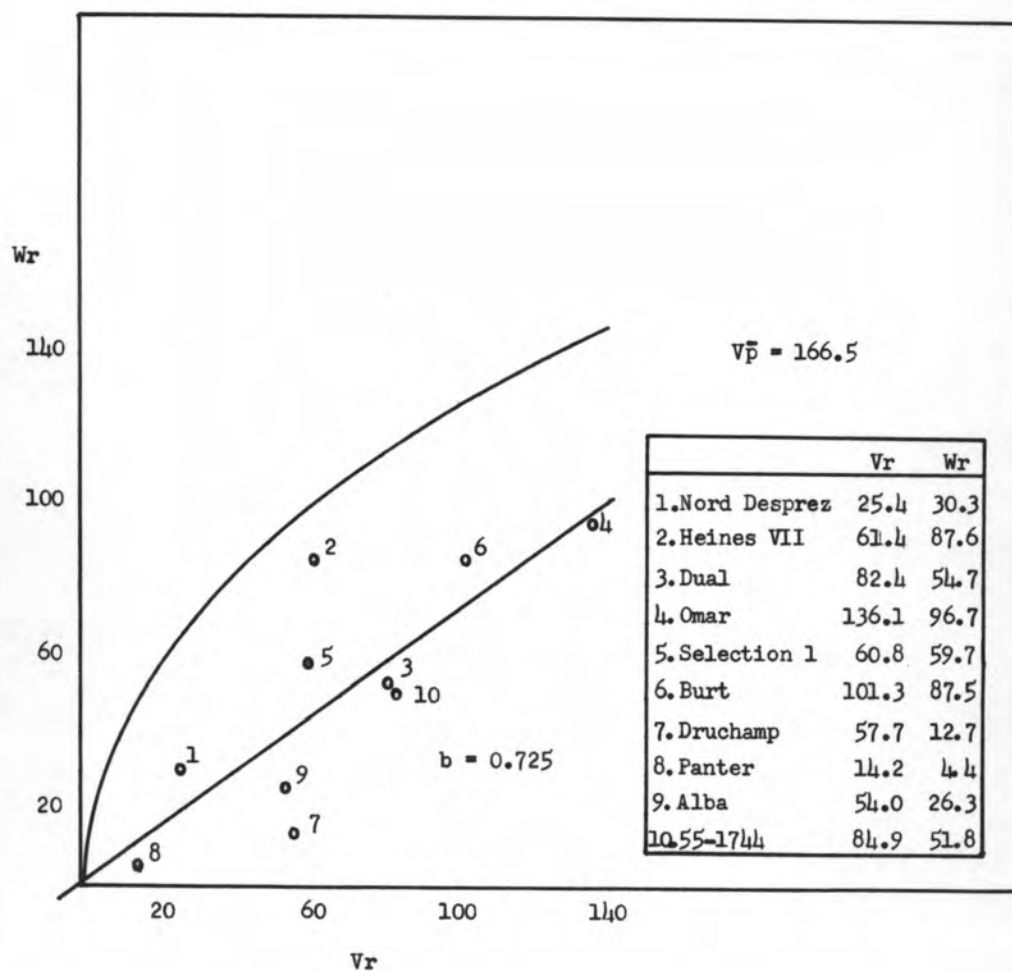


Figure 4. Regression of the variances (V_r) and the covariances (W_r) for each F_1 parental array for weight per kernel (X_2).

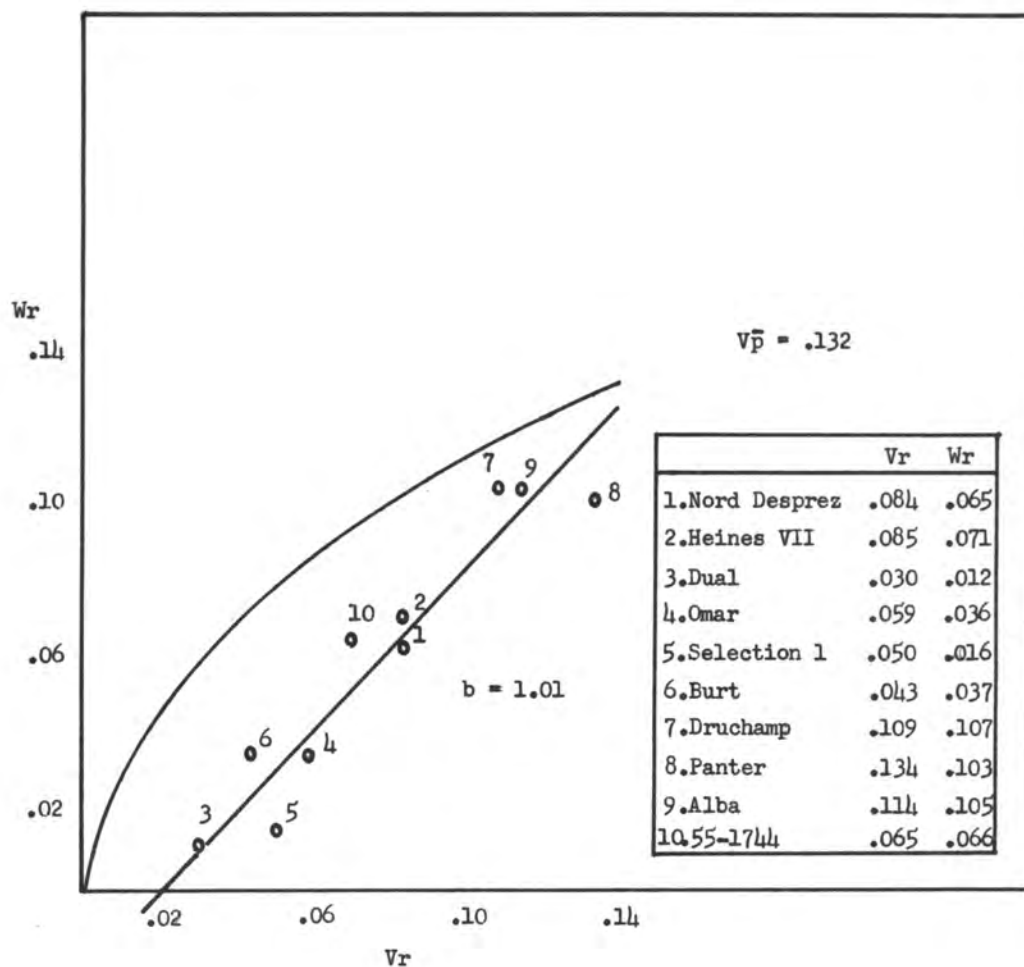


Figure 5. Regression of the variances (V_r) and the covariances (W_r) for each F_1 parental array for kernel per spikelet (X_3).

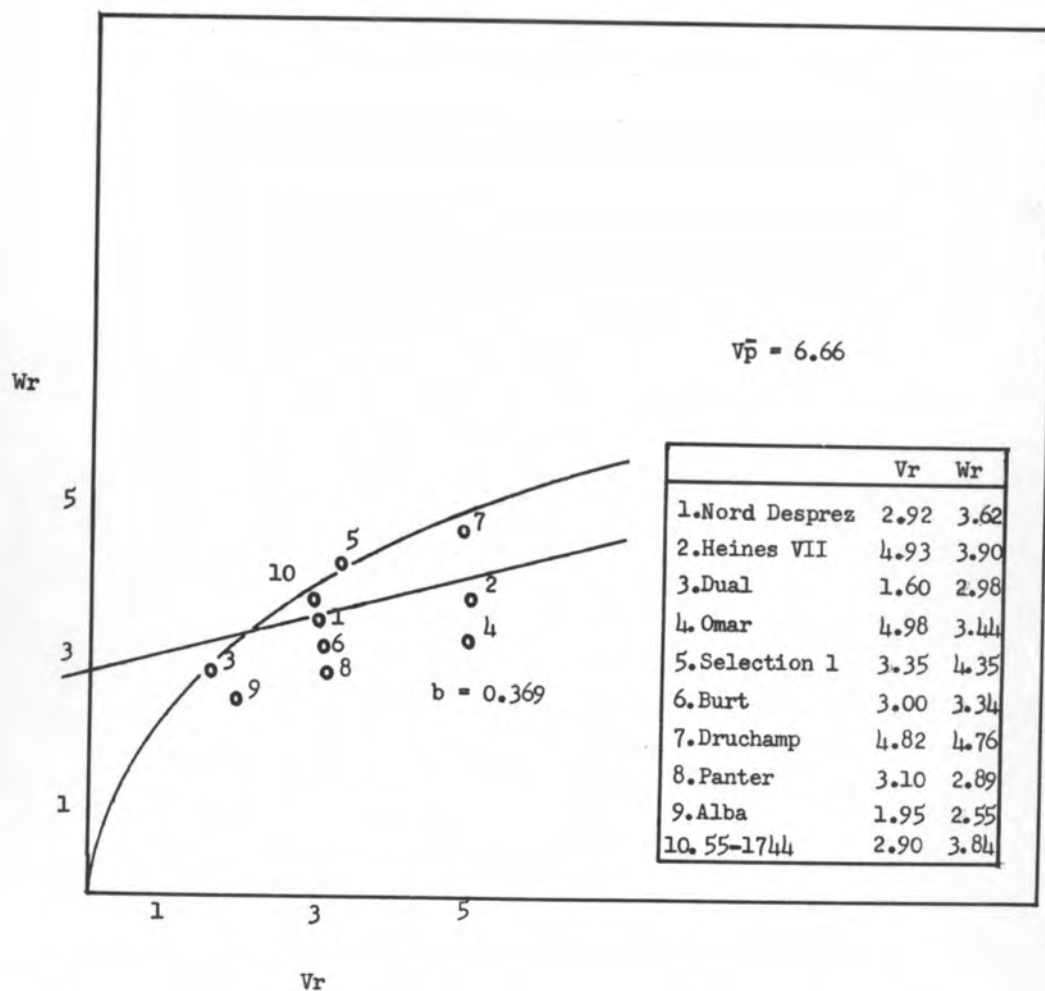


Figure 6. Regression of the variances (V_r) and the covariances (W_r) for each F_1 parental array for spikelets per spike (X_4).

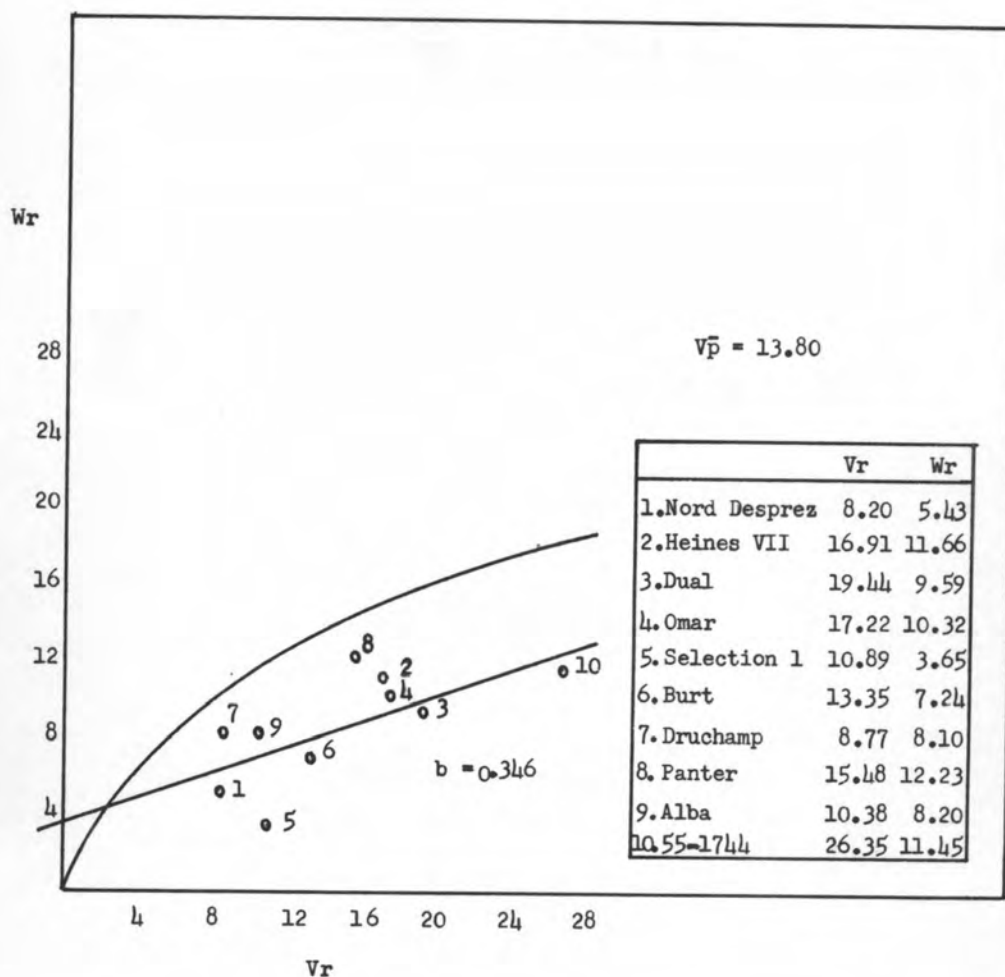


Figure 7. Regression of the variance (V_r) and the covariance (W_r) for each F_1 parental array for spikes per plant (X_5).

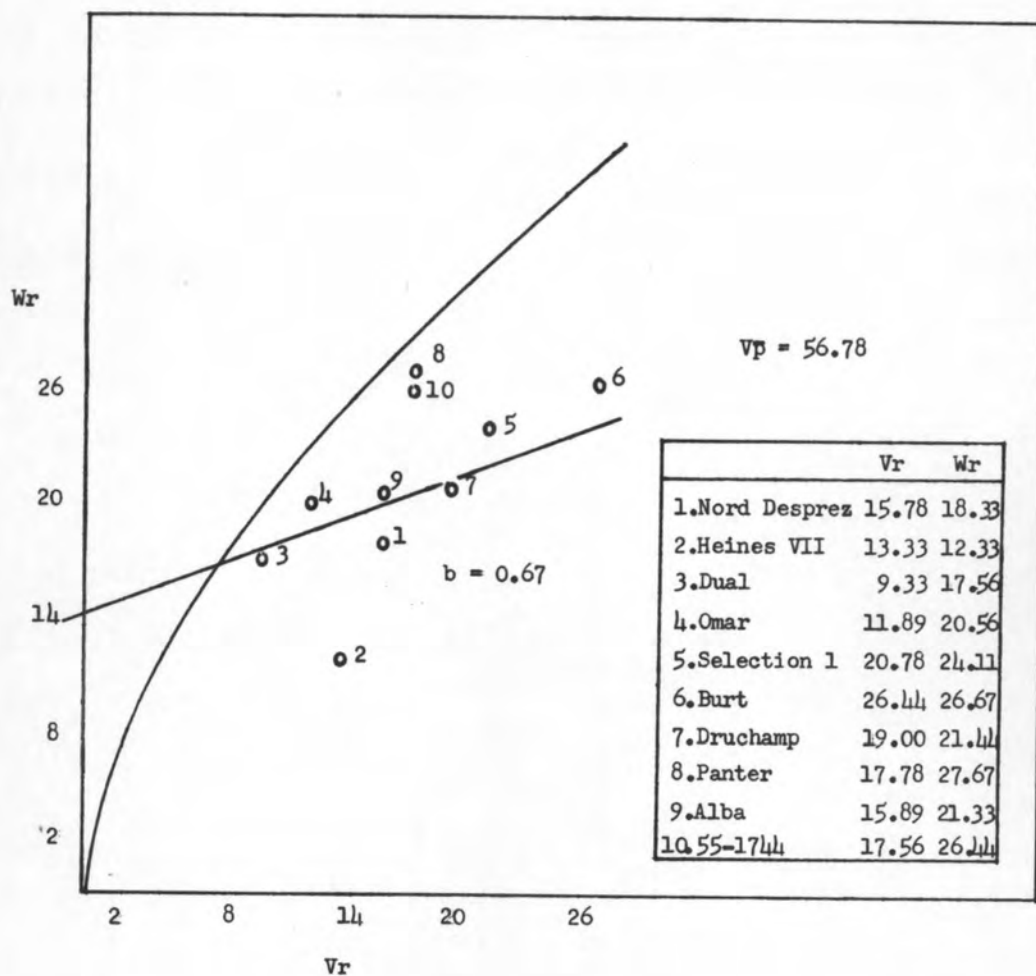


Figure 8. Regression of the variance (V_r) and the covariances (W_r) for each F_1 parental array for plant height (X_6).

values (b) do not equal one for the characters except kernels per spikelet where $b=1.01$ and for weight per kernel with $b=0.725$. Therefore, it is not possible to interpret the results for the characters where b does not equal one because the assumption of no epistasis cannot be met. The character showing the greatest deviation from one is plant yield (Figure 3) with a value of $b=0.18$ which indicates that a large epistatic effect is present.

Since the analysis of kernels per spikelet (Figure 5) shows practically no epistatic effects, certain genetic information concerning the type of gene action involved can be obtained. The relationship of the regression line to the parabola suggests that over-dominance plays a small part in the determination of kernels per spikelet. Furthermore, due to the position of the points for their arrays, the varieties Dual and Pullman Selection 1 possess more dominant genes, and by the same measure, Druchamp, Panter and Alba contain most of the recessive genes.

Heritability

Heritability estimates in the narrow sense were obtained by parent-progeny regressions. These values along with parent-progeny correlation coefficients for the six characters studied are presented in Table 10. The highest parent-progeny regression of $b=0.829$ was obtained for plant height, followed by spikelets per spike with a value of $b=0.607$. Similar values were obtained for kernels per spikelet ($b=0.478$) and weight per kernel ($b=0.472$), while

Table 10. Parent-progeny regression and correlation coefficients for six characters as determined by the mean values of the 45 F_1 crosses and the mean value of the two parents.

Character	Parent-progeny regression	Parent-progeny correlations
Yield per plant	0.2591	0.523
Weight per kernel	0.4720	0.449
Kernels per spikelet	0.4783	0.664
Spikelets per spike	0.6074	0.811
Spikes per plant	0.4011	0.623
Plant height	0.8292	0.762

Significant r with $n = 45$ is 0.296 at five percent and 0.382 at one percent levels of significance.

spikes per plant had a somewhat lower estimate of $b=0.401$, with the lowest value being $b=0.259$ for plant yield.

When parent-progeny correlations are considered, a somewhat different result is obtained. The highest value was found for spikelets per spike ($r=0.811$) followed closely by plant height ($r=0.762$). Yield per plant again had the lowest value of $r=0.523$.

In order to determine if the associations between the six measured characters were of the same magnitude for all three populations, simple correlation coefficients were computed for each. These coefficients, with the corresponding significant values for five and one percent levels, are given in Table 11. In general there was close agreement in the magnitude and sign of the values among the three populations. High positive values were obtained between yield per plant and with kernels per spikelet and spikelets per spike. Smaller associations were observed between yield and weight per kernel and plant height, while a negative value was found between yield and spikes per plant. In addition, spikes per plant were found to have either a negative or no association with the other characters measured. A negative association was also noted between kernel weight with kernel number and also with plant height. A comparison among the other characters resulted in very small positive or negative values.

Table 11. Correlation coefficient values between five characters and yield involving ten parents, 45 single crosses, and both parents and single crosses in winter wheat.

	N	Plant height	Weight per kernel	Kernels per spikelet	Spikelets per spike	Spikes per plant
Plant yield	10	0.249	-0.123	0.548	0.784	-0.744
	45	0.326	0.104	0.802	0.540	-0.387
	55	0.357	0.104	0.754	0.588	-0.283
Spikes per plant	10	-0.551	0.008	-0.313	-0.643	
	45	-0.198	-0.081	-0.217	-0.359	
	55	-0.131	0.002	-0.171	-0.312	
Spikelets per spike	10	0.108	-0.064	0.115		
	45	0.092	-0.181	0.235		
	55	0.143	-0.116	0.227		
Kernels per spikelet	10	0.528	-0.739			
	45	0.395	-0.298			
	55	0.440	-0.379			
Weight per kernel	10	-0.458				
	45	-0.038				
	55	-0.118				

Significant r with $n = 10$ is 0.632 at five percent and 0.765 at one percent levels of significance.

Significant r with $n = 45$ is 0.296 at five percent and 0.385 at one percent levels of significance.

Significant r with $n = 55$ is 0.263 at five percent and 0.342 at one percent levels of significance.

Path-Coefficient Analysis

Direct and indirect effects of the five characters on total plant yield for the 45 F_1 crosses are presented in Table 12. It can be readily observed that the correlation between weight per kernel and yield of $r=0.104$ is made up almost entirely by the direct effect of kernel weight on yield (0.425), however, the indirect effects by way of the other characters are negative or of small magnitude which cancels out this large direct effect. The association ($r=0.802$) between kernels per spikelet and yield is determined almost completely by the direct effect of kernel number on yield (0.838), while only small positive or negative effects are exerted indirectly. This association is also found for the correlation value of $r=0.540$ between spikelets per spike and yield, where the greatest effect (0.412) was exerted directly by spikelet number on yield with only a small influence coming indirectly by way of the other characters. The negative correlation between spikes per plant and yield of $r=-.387$ was the result of the negative indirect effects of spike number by way of kernel number and spikelet number. The correlation value of $r=0.326$ between plant height and yield was primarily due to a positive indirect effect of plant height by way of kernel number, since the direct effects of plant height on yield were small.

The small residual effect indicates that the five traits studied account for 93.9 percent of the total variation in yield.

Table 12. Path-coefficient analysis of factors influencing total yield ($n = 45$).

Pathways of association	Path-coefficient P	Path-coefficient X r value	Correlation (r)
<u>Yield and weight per kernel</u>			
Direct effect ($P_{2,1}$)	.425		
Indirect effect via kernel number ($P_{3,1}$)($r_{2,3}$)		-.250	
Indirect effect via spikelet number ($P_{4,1}$)($r_{2,4}$)		-.075	
Indirect effect via spike number ($P_{5,1}$)($r_{2,5}$)		.002	
Indirect effect via plant height ($P_{6,1}$)($r_{2,6}$)		.001	
Total (r)			.104
<u>Yield and number of kernels per spikelet</u>			
Direct effect ($P_{3,1}$)	.838		
Indirect effect via weight per kernel ($P_{2,1}$)($r_{3,2}$)		-.127	
Indirect effect via spikelet number ($P_{4,1}$)($r_{3,4}$)		.097	
Indirect effect via spike number ($P_{5,1}$)($r_{3,5}$)		.006	
Indirect effect via plant height ($P_{6,1}$)($r_{3,6}$)		-.013	
Total (r)			.802
<u>Yield and number of spikelets per spike</u>			
Direct effect ($P_{4,1}$)	.412		
Indirect effect via weight per kernel ($P_{2,1}$)($r_{4,2}$)		-.077	
Indirect effect via kernel number ($P_{3,1}$)($r_{4,3}$)		.197	
Indirect effect via spike number ($P_{5,1}$)($r_{4,5}$)		.010	
Indirect effect via plant height ($P_{6,1}$)($r_{4,6}$)		-.003	
Total (r)			.540
<u>Yield and spikes per plant</u>			
Direct effect ($P_{5,1}$)	-.029		
Indirect effect via weight per kernel ($P_{2,1}$)($r_{5,2}$)		-.034	
Indirect effect via kernel number ($P_{3,1}$)($r_{5,3}$)		-.182	
Indirect effect via spikelet number ($P_{4,1}$)($r_{5,4}$)		-.148	
Indirect effect via plant height ($P_{6,1}$)($r_{5,6}$)		.006	
Total (r)			-.387
<u>Yield and plant height</u>			
Direct effect ($P_{6,1}$)	-.033		
Indirect effect via weight per kernel ($P_{2,1}$)($r_{6,2}$)		-.016	
Indirect effect via kernel number ($P_{3,1}$)($r_{6,3}$)		.331	
Indirect effect via spikelet number ($P_{4,1}$)($r_{6,4}$)		.038	
Indirect effect via spike number ($P_{5,1}$)($r_{6,5}$)		.006	
Total (r)			.326

$$R^2 = .939$$

$$\text{Residual} = .061$$

DISCUSSION

The total observed variation for all characters within a plant population is the result of: (1) the genetic composition, (2) environment, and (3) the genetic-environmental interaction. Of this variation, the genetic composition is of particular interest to the plant breeder, since it constitutes the basis for which progress can be made in a breeding program. Considering this genetic source of variation, a particular plant character can be described as either qualitatively or quantitatively inherited. Qualitative inheritance involves a small number of genes, and the character exhibits discontinuous variation in segregating populations. Quantitatively inherited characters show continuous variation in segregating populations as they are controlled by a large number of genes which have similar, small and cumulative effects. This latter type of inheritance can be partitioned into component parts which include: (1) that due to additive effect of genes, (2) a dominance component arising from intraactions of alleles, and (3) an epistatic part associated with interactions of nonalleles which do not behave in an additive manner. Quantitatively inherited characters are particularly susceptible to environmental influences; however, like qualitatively inherited characters it is the manner of reaction under particular conditions that is inherited and not the character itself.

Even though the genetic composition provides the basis for plant improvement, the breeder of self-pollinating crops, such as wheat, can utilize only a segment of the total genetic variability

present. This variability includes the additive portion and those epistatic effects which behave in an additive manner, since only this type of gene action can be retained by subsequent inbreeding. It is, therefore, important for the breeder of self-pollinated crops to obtain not only estimates of the total amount of observed variation that is due to the genetic composition, but also to determine the predominate type of gene action which is contributing to a particular character. Such information would be particularly beneficial if it could be obtained for individual crosses in the early generations, preferably the F_1 , thereby helping the plant breeder in choosing the best parents to be hybridized and in selecting the best lines from hybrid progenies. These problems are particularly difficult for a breeder working with a quantitatively inherited character such as yield.

Most advances made for higher yields in wheat have resulted from breeding for resistance to the many adversities that limit the final harvest. This is understandable since yield is generally considered to be a complex character which is quantitatively inherited and influenced greatly by the environment. In this study, yield has been considered as having four component parts, and the ten parents used in the diallel set of crosses were chosen because they were outstanding in terms of one or more of these components. The morphological components of yield are: (1) weight per kernel, (2) number of kernels per spikelet, (3) number of spikelets per spike, and (4) number of spikes per plant. If these are the true components

of yield, an increase in any one of the components would result in an increase in total yield, provided there is no corresponding decrease in the other components. Such a decrease could result if each of the components was predominately controlled by different types of gene action or if a negative association exists between any of the components, such as in the form of a biological limitation. It was the objective of this study to obtain information on the nature of gene action governing each component and to determine the relationship between each of the components and the resulting yield. Further objectives of this experiment were to determine if diallel cross analysis for general and specific combining ability as outlined by Griffing (16, p. 464) and parental evaluation by the Jinks-Hayman method (25, p. 48-52) would provide reliable information on the nature of gene action comparable to that obtained from heritability estimates calculated from parent-progeny regression.

When yield was considered as an individual character the general combining ability analysis indicated that a large part of the total genetic variance was due to additive gene action. This is in agreement with the heritability value obtained from parent-progeny regression for yield. A large non-additive epistatic effect was suggested by the Jinks-Hayman method. The cross between Omar and Corvallis Selection 55-1744, with their high individual general combining ability effects, would appear to provide the greatest probability of giving rise to high yielding progeny lines. It is interesting to note that Omar has also a high specific combining ability effect in crosses involving Alba, Panter

and Druchamp. If such an association exists between general and specific combining ability and the non-additive genetic variance could be utilized, Omar would appear to be a very promising parent. However, the discrepancy between estimates and the small amount of genetic variability present as measured by the analysis of variance for combining ability would make it questionable as to how much would be gained in selecting for yield directly without considering the yield components.

Since the results obtained for weight per kernel failed to meet the requirements for the Jinks-Hayman method, only combining ability analysis and heritability estimates were used in an attempt to measure gene action. These estimates indicate that there is a rather large portion of the total genetic variance which is made up of additive gene action; however, there also appears to be a non-additive epistatic effect which must be taken into consideration in any breeding program.

A similar situation as with weight per kernel is encountered when the number of kernels per spikelet is considered. A high general combining ability estimate and a relatively high heritability value indicated that a large part of the total genetic variance was due to additive gene action. This is in contrast to the Jinks-Hayman analysis which suggested that over-dominance played an important role. It appears again that one of the methods did not give a true estimate of gene action. If the combining ability estimates and the heritability value reflects the true predominate type of gene action, then a cross between Omar and Corvallis

Selection 55-1744 would have the highest probability of producing lines with the greatest number of kernels. It is of interest to note that when yield was considered as a character, the same cross showed the best possibility of producing high yielding lines. This might be interpreted as an indication of the importance of this component to yield and could possibly be used as an index for selecting high yielding lines.

With spikelets per spike, all three methods indicated that gene action was predominately additive. However, a large nonallelic epistatic effect was suggested by the Jinks-Hayman method. This is a further discrepancy between the three types of analyses employed. The parental lines Omar and Panter appear to be the most promising as indicated by their high general combining ability.

Spikes per plant appeared also to be governed primarily by additive gene action as evidenced by high general combining ability and the high heritability value. However, the large environmental variance present would complicate a selection program for this character. The cross between Pullman Selection 1 and Burt appeared the most promising to pursue due to the individual general combining ability effects; however, since both have ancestors in common future improvement may be limited.

The last character analyzed was plant height which generally is not assumed to be a component of yield. However, with the increasing interest in semi-dwarf wheats, information regarding the predominate type of gene action governing this character is of particular

interest. As noted from the significant general combining ability effect in relation to specific combining ability effect and the high heritability value, plant height is controlled primarily by additive gene action with very little environmental influence. Despite the epistatic interaction which is present as suggested by the Jinks-Hayman method a large additive genetic variance was indicated. The parental lines Omar, Dual, Nord Desprez, Corvallis Selection 55-1744, and Pullman Selection 1, which represent extremes in plant height, show the greatest individual general combining ability effects. Therefore, it would appear possible to select individual plants for any desired height level between the extremes in this population.

When the correlation coefficients between each of the components and yield are considered in terms of direct and indirect effects, some very interesting relationships become evident. Number of kernels, weight per kernel and spikelets per spike had the greatest direct effect on plant yield. Multiple R^2 for these three variables alone accounted for 92 percent of the total variation in yield. When all five variables are considered, 93 percent of this variation is accounted for; therefore, spikes per plant and plant height are making only a small contribution towards the total variation in yield. This would appear somewhat illogical since it seems obvious that if there were no spikes per plant there would be no yield. However, in this analysis when all five variables are considered in relation to yield, the effect of spikes per plant is offset by the effect of plant height.

The path-coefficient analysis also indicated that correlation coefficients can be misleading. A large negative value was obtained for the correlation between spikes per plant and yield, but when this value was considered in terms of direct and indirect effects, spikes per plant had very little direct influence on yield. A similar situation was found for plant height and yield where a positive correlation existed, but this correlation was due to the indirect effect by way of kernel number rather than a direct effect of plant height on yield. This also points out the impact of a single variety on the results, as illustrated by the variety Omar which is tall and has a compacted spike with a large number of kernels per spikelet.

Both the path-coefficient and combining ability analyses indicate that kernel number is the most important component in determining yield. This is in agreement with the findings of Johnson and Aksel (26, p. 208) with barley and McNeal (35, p. 349) with wheat. However, Quisenberry (38, p. 493) and Sprague (41, p. 992) found spikes per unit area had the greatest direct effect on yield. Spikes per unit area are influenced by the seeding rate and measure the competitive effect between plants. Kernel number is also influenced by seeding rate, but measures the competitive effect of the other components within the plant as well as the competitive effect between plants.

The data obtained in this study suggest that separate breeding procedures may be useful for several of the components of yield with the final step being synthesis of the desired levels of each

component into one variety. For weight per kernel, number of kernels, spikelets per spike, and spikes per plant, the breeder could utilize the large additive portions of the total genetic variance. However, since there is also some non-additive gene action present plus the environmental influence, phenotypic selection might not provide the desired increase, and a procedure to accumulate the additive type gene action would be required. This would be particularly true for a character such as spikes per plant which is susceptible to environmental factors. In addition, if the components of yield compete for the total amount of metabolic substrate produced by the plant, then conditions which favor the development of one component could have an adverse effect on the other components. Negative relationships were observed between weight per kernel and number of kernels as well as between spikes per plant with kernel number, weight per kernel, and spikelets per spike when simple correlation coefficients were considered. If a biological limitation is present, then certain components may have to be combined in the early phase of a breeding program since a compromise in the desired levels may have to be reached.

If male sterility and fertility restoring genes can be utilized for the production of hybrid wheat, the breeder of self-pollinating annual crops may be able to capitalize on the non-additive as well as the additive portion of the total genetic variance. Under this circumstance a breeding program could be developed whereby certain lines would be selected for their

general combining ability first and then a second selection made on the basis of specific combining ability as is done with hybrid corn. The data in this study indicate that primarily only additive gene action was present; however, in certain crosses the F_1 means were higher than the best parent for all characters studied. A variety such as Omar which has both high general and specific combining ability would be of particular value in this type of breeding procedure. A further possibility would be to accumulate the additive type of gene action for those components which respond to it and then make specific crosses for the components which respond to non-additive gene action as a final step. Of course, this depends on whether sterility and fertility restoring genes can be utilized.

Some discrepancies were noted in the results in estimating gene action obtained from the two diallel cross methods and the parent-progeny regression method. Griffing's procedure (16, p. 464) which measures gene action in terms of general and specific combining abilities agrees rather closely with the heritability estimates for all characters studied.

The estimates of gene action obtained by the Jinks-Hayman method (25, p. 48) were different from both the heritability values and the combining ability analysis. Perhaps the most logical reason for this difference is the fact that one or all of the genetic assumptions outlined by Hayman (20, p. 63) could not be met. The most obvious assumption not fulfilled is that no interactions

or epistasis is present. However, it is very clear that nonallelic interactions were involved in four of the components as illustrated by the distortion in the graphs. Allard (2, p. 87) indicates that gene interaction can be of two types: (1) a localized interaction which can be removed by the omission of one or two crosses and (2) a generalized interaction which can be removed only by subjecting the data to some type of scaling. Both approaches were attempted in this study, but not enough of the interaction could be removed by either method to satisfy the assumption. Furthermore it would seem unrealistic to remove a different cross for each of the components in determining gene action for several components since the resulting genetic estimates would be for different populations. No satisfactory scaling method has yet been devised in biometrical genetics as pointed out by Allard (2, p. 87). It would appear, however, that the Jinks-Hayman method would be useful in studying simply inherited characters as was done by Grumpacker (7, p. 275) on date of heading of wheat or by Whitehouse et al. (44, p. 147-169) where the original 19 varieties of wheat were narrowed to four in order to meet the assumptions. However, for quantitatively inherited characters where epistatic effects are involved, this method is of questionable value.

SUMMARY AND CONCLUSIONS

The objectives of this study were to gain information about the predominate type of gene action involving the components of yield in wheat and to determine the relationships between these components. In addition, two methods of diallel cross analysis were compared with heritability values obtained from parent-progeny regressions in estimating gene action. Data were obtained from a diallel cross consisting of ten parents and the resulting 45 F_1 single crosses. The ten parents were chosen because they were high yielding and outstanding in terms of one or more of the yield components. Morphological characters measured were: (1) total yield per plant, (2) weight per kernel, (3) number of kernels per spikelet, (4) number of spikelets per spike, (5) number of spikes per plant and (6) plant height.

Information concerning the predominate type of gene action for each component was estimated by two methods of diallel cross analysis and by heritability values calculated from parent-progeny regressions. Path-coefficient analysis was used to determine the direct and indirect relationships between the components and yield.

From the data resulting from this experiment the following conclusions were made:

1. The yielding capacity of the wheat plant is quantitatively inherited and is composed of morphological components which are also quantitatively inherited.

2. The major components of yield in wheat are weight per kernel, number of kernels per spikelet, number of spikelets per spike and the number of spikes per plant. Plant height does not appear to be a component of yield.

3. Both the diallel cross and path-coefficient analysis indicated that the number of kernels per spikelet had the greatest effect on yield.

4. A large part of the total genetic variation associated with the yield components, weight per kernel, number of kernels per spikelet, number of spikelets per spike, and number of spikes per plant, was the result of additive gene action. This was also true for plant height.

5. Weight per kernel, number of kernels per spikelet and the number of spikelets per spike appeared to exert mainly direct and independent effects on plant yield. The number of spikes per plant had little direct effect but an indirect effect on yield through the other components. A similar indirect relationship was noted for plant height.

6. A small biological limitation may exist between weight per kernel and kernel number. Also such a limitation appears likely between the number of spikes per plant with weight per kernel, kernel number, and spikelets per spike.

7. Simple correlation coefficients can be very misleading unless the direct and indirect effects making up these coefficients are considered. With such an approach, the biological relationships

between the variables measured must not be overlooked and the variables used must be considered.

8. A breeding program for increased yield whereby each component of yield could be considered separately or perhaps in combination with other components followed by a combination of all components as a final step would be the most rewarding. The type of gene action and any resulting biological limitations could be taken into consideration by such a procedure.

9. If the non-additive portion of the total genetic variance can be utilized in producing hybrid wheat through the use of male sterility and fertility restoring genes, it may be possible to obtain hybrid vigor or heterosis in the single crosses as evidenced by the increase of the F_1 over the best parent in certain crosses measured in this study.

10. With the large amount of additive gene action present in plant height, phenotypic selection would be useful in obtaining the desired height level.

11. The diallel cross analysis for general and specific combining ability gave reliable estimates of gene action when compared to heritability estimates.

12. Jinks-Hayman method of evaluating gene action is of questionable value for quantitative characters where the genetic assumptions underlying the method cannot be met.

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APPENDIX

Appendix Table 1. Pedigrees and description of the ten parental winter wheat lines.

Parent	Pedigree	Grain	Straw	Yield	Origin
Nord Desprez	Vilmorin 27 x Joniquois	Red	Short, Stiff	High	Europe
Heines VII	Svalof Kronen x (Ble 205 x Vilmorin 27)	Red	Medium, Stiff	High	Europe
Dual	Fultz Selection Hung-W38-Wabash	Red	Tall, Weak	Low	United States
Omar	(Brevor x Elgin) x (Elgin 19 x Elmar)	White	Tall, Moderate	Medium	United States
Selection 1	[Norin 10 x Brevor) x (Orfed x Brevor) x Burt]	White	Short, Stiff	High	United States
Burt	Brevor x Rio-Rex	White	Medium, Moderate	Medium	United States
Druchamp	Unknown	White	Medium, Stiff	High	Europe
Panter	Pantser III x Alther	Red	Medium, Stiff	High	Europe
Alba	Tr'esor x Jacob Cats	White	Medium, Moderate	Medium	Europe
Selection 55-1744	Norin 10 x Staring	Red	Short, Stiff	High	United States

Appendix Table 2. Mean plot values for six characters measured in ten parental wheat lines used in the 10x10 diallel cross.

Parent	Total yield X1	Weight per kernel X2	Kernels per spikelet X3	Spikelets per spike X4	Spikes per plant X5	Plant height X6
Nord Desprez	15.77	0.508	2.44	25.30	33.07	37
Heines VII	16.02	0.540	2.24	26.38	32.92	42
Dual	14.51	0.457	2.86	22.17	32.30	57
Omar	17.81	0.382	3.43	27.20	31.66	53
Selection 1	13.90	0.452	2.66	23.10	41.50	37
Burt	13.93	0.476	2.81	20.81	36.98	36
Druchamp	10.72	0.455	2.11	22.26	39.71	40
Panter	15.77	0.465	2.62	27.38	31.62	48
Alba	15.11	0.454	2.62	25.22	31.03	41
Selection 55-1744	16.90	0.458	2.60	28.32	32.40	37

Appendix Table 3. Mean plot values of 45 F₁ crosses obtained from a 10x10 diallel cross.
X₁ = total yield, X₂ = weight per kernel, X₃ = kernels per spikelet,
X₄ = spikelets per spike, X₅ = spikes per plant, X₆ = plant height.
P₁ = Nord Desprez, P₂ = Heines VII, P₃ = Dual, P₄ = Omar, P₅ = Selection
1, P₆ = Burt, P₇ = Druchamp, P₈ = Panter, P₉ = Alba, P₁₀ = Selection
55-1744.

Parent	Variable	P ₁₀	P ₉	P ₈	P ₇	P ₆	P ₅	P ₄	P ₃	P ₂
P ₁	X ₁	17.92	13.61	13.29	13.76	15.90	17.75	18.16	19.03	16.92
	X ₂	.500	.482	.476	.482	.496	.510	.498	.510	.528
	X ₃	2.64	2.22	2.09	2.31	2.69	2.38	2.86	3.01	2.40
	X ₄	27.12	25.44	29.10	24.88	23.97	26.29	28.80	24.74	26.46
	X ₅	39.15	34.54	34.50	41.12	41.58	37.75	37.00	39.12	38.62
	X ₆	41.00	44.00	44.00	44.00	48.00	45.00	50.00	50.00	45.00
P ₂	X ₁	21.05	14.76	15.07	13.64	16.27	16.28	18.74	16.78	
	X ₂	.486	.482	.480	.494	.496	.465	.467	.475	
	X ₃	3.06	2.33	2.46	2.21	2.72	2.66	2.83	2.87	
	X ₄	28.28	26.01	25.58	24.86	23.98	26.34	31.82	24.84	
	X ₅	39.86	38.29	35.45	41.88	39.58	46.22	37.70	32.38	
	X ₆	42.00	44.00	50.00	45.00	51.00	46.00	52.00	49.00	
P ₃	X ₁	18.13	15.90	19.49	17.19	16.18	17.18	16.10		
	X ₂	.456	.504	.495	.522	.476	.481	.427		
	X ₃	3.16	2.52	2.78	2.84	3.01	2.98	2.99		
	X ₄	25.24	24.94	26.15	23.26	22.65	24.00	25.16		
	X ₅	30.92	36.79	33.92	36.75	44.75	41.70	37.25		
	X ₆	50.00	51.00	56.00	53.00	53.00	49.00	56.00		
P ₄	X ₁	20.10	21.51	24.25	21.81	15.31	13.83			
	X ₂	.441	.450	.475	.488	.407	.424			
	X ₃	3.32	3.24	3.34	3.14	2.98	2.72			
	X ₄	27.50	29.32	30.40	28.22	25.08	26.30			
	X ₅	27.15	34.62	32.88	39.10	39.60	40.35			
	X ₆	46.00	54.00	57.00	53.00	50.00	48.00			
P ₅	X ₁	17.17	16.14	18.82	15.00	12.03				
	X ₂	.434	.482	.454	.466	.463				
	X ₃	2.91	2.66	3.04	2.60	2.40				
	X ₄	27.10	26.00	27.14	24.62	21.70				
	X ₅	43.80	40.34	44.95	45.88	48.42				
	X ₆	36.00	46.00	48.00	47.00	43.00				
P ₆	X ₁	18.23	16.67	15.90	15.43					
	X ₂	.468	.465	.461	.531					
	X ₃	3.10	2.78	2.82	2.60					
	X ₄	22.71	24.70	24.51	20.02					
	X ₅	36.52	39.54	38.00	41.68					
	X ₆	42.00	50.00	46.00	49.00					
P ₇	X ₁	16.39	12.65	14.39						
	X ₂	.494	.472	.472						
	X ₃	2.58	2.12	2.38						
	X ₄	25.56	25.30	25.46						
	X ₅	37.26	36.12	38.20						
	X ₆	42.00	44.00	48.00						
P ₈	X ₁	19.56	18.68							
	X ₂	.464	.482							
	X ₃	3.06	2.80							
	X ₄	27.58	27.41							
	X ₅	39.12	33.68							
	X ₆	46.00	49.00							
P ₉	X ₁	20.50								
	X ₂	.539								
	X ₃	2.90								
	X ₄	26.62								
	X ₅	31.15								
	X ₆	41.00								