HETEROSIS, COMBINING ABILITY, AND VARIANCE-COVARIANCE RELATIONSHIPS IN A DIALLEL CROSS AMONG SIX COMMON WHEAT VARIETIES OF DIVERSE ORIGIN

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CHAPTER I

INTRODUCTION

Two of the foremost problems in wheat improvement are the selection of the best possible parents for hybridization and the identification of promising hybrid combinations. Progress in improving production levels has been achieved principally through hybridization of varieties or strains chosen as parents on the basis of phenotypic merit for one or more traits and subsequent isolation of superior lines from segregating populations. Despite the improvements that have been possible, it has become evident that varieties developed by the usual procedures in recent years have not greatly exceeded the performance of the parents going into the crosses.

Significantly higher yields than are currently possible with pure-line varieties may eventually be realized if large-scale production of wheat hybrids becomes economically practical as a result of the recent discovery of cytoplasmic male-sterile and fertility restoring systems in wheat. Where major emphasis is placed on the development of hybrids, techniques are needed that would enable breeders to classify lines according to their ability to perform in hybrid combination since crosses between parents selected on the basis of superior combining ability would reasonably be expected to result in the most outstanding hybrids. Considering that large numbers of desirable lines may be isolated through conventional procedures plus the amount of time and effort required for the conversion of ordinary lines to male-sterile or fertility restoring lines, the value of such techniques is evident.

Currently, there is relatively little information available concerning combining ability in wheat. Combining ability is of interest as it relates to the types of gene action governing expression of quantitative characters. Presumably, only that portion of the genetic variability controlled by additive effects of genes has been exploited through the use of hybrid-derived wheat varieties. The advantages of growing wheat hybrids consequently lie with the possibility of exploiting the additional vigor manifested as a result of non-additive genetic effects associated with hybrid heterozygosity. Assuming that some degree of relationship exists between heterozygosity and the manifestation of hybrid vigor, crosses among varieties or strains of diverse parentage would probably be of greater value than crosses involving related types. While the utility of combining germ plasm from unrelated sources is generally recognized in the production of corn hybrids, little is known of the importance of diversity of germ plasm as a factor in the production of wheat hybrids.

In view of the foregoing, this study was conducted for the purpose of evaluating six hexaploid wheat varieties of diverse geographic origin from the standpoint of heterosis and combining ability relationships for earliness, plant height, yield, and the components of yield. An additional objective was to assess the relative importance of additive and non-additive effects of genes controlling the expression of these traits by means of variance-covariance techniques.

CHAPTER II

REVIEW OF LITERATURE

Heterosis in Wheat

Interest in the degree of heterosis manifested in wheat has been stimulated by the prospect of employing a cytoplasmic male-sterility and fertility restoration system in the commercial production of wheat hybrids. Instances of reported heterosis were recently reviewed in detail by Briggle (5). He emphasized that virtually all heterosis studies in wheat have been carried out under conditions of space-planting, and have involved rather small populations. Briggle et al. (6) studied heterosis under conditions thought to permit accurate evaluation of the potential of hybrids without growing them as in conventional practice. Hill plantings of F_1 seed from two winter wheat crosses were made at rates of one, two, and four seeds per hill. 'Blackhawk' x 'Kharkof' F_1's exceeded the high parent in yield per plot by 17.5, 21.4, and 37.7% at the three planting rates, respectively. Yield heterosis was not expressed in the cross between 'Wabash' and 'Purkof'. Heterosis for weight of grain per spike, number of kernels per spike, weight per 1000 kernels, and plant height were also observed in the former cross, the highest expression in these traits being observed at the lowest planting rate. No heterosis for these traits was observed in the Wabash x Purkof F_1, except for a questionable expression of vigor for weight per 1000 kernels. Since the weight of grain produced per plot at the highest planting rate was significantly greater for both crosses than for the parents, it was suggested that the F_1's had a competitive advantage over the parents.

Observations on heterosis were made by Brown et al. (8) in a study of crosses among seven hard and soft winter wheat varieties. The study was similar to that conducted by Briggle et al. (6) in that hill plantings were used to simulate normal seeding rates. Parents and hybrids were seeded at a rate of eight seeds per hill. Yield heterosis relative to the high parent was observed in five of the 16 hybrids, and 12 exceeded their respective midparent values. The yielding capacity of the hybrids ranged from 96 to 131% of the high parent means. Only one hybrid exceeded the high parent in straw yield, although eight hybrids exceeded the midparent for this trait. It was noted that much less heterosis occurred for number of spikes and kernel weight than was observed for grain and straw yield. In addition, it was observed that the yield heterosis obtained in these crosses was not accompanied by a significant decrease in percent grain protein. In general, their results suggested that considerable heterosis for grain yield may occur in some wheat hybrids, but not in others.

The F_1 and F_2 generations from three spring wheat crosses involving varieties having some germ plasm in common, and therefore a rather narrow genetic base, were evaluated by McNeal et al. (37). Since seedings were made in 10-foot rows at a rate equivalent to about 30 pounds per acre the populations were studied under more or less normal conditions. It was observed that the F_1 and F_2 populations from these crosses did not differ significantly except in two instances. In one cross, the F_2 exceeded the F_1 in number of spikes per row, whereas the F_1 of the same cross exceeded the F_2 in weight per kernel. The performance of the F_1 and F_2 populations was usually found to be intermediate between the parents for both agronomic and quality characteristics, and in no case was it significantly better than that of the high parent. These results suggested that closely related parents may result in little or no heterosis, and the need of genetic diversity was emphasized in the development of vigorous hybrids.

Johnson et al. (23) observed heterosis for yield of grain per plant, kernel weight, and number of spikes per plant in populations from a cross between the hard red winter wheat varieties, 'Seu Seun 27' and 'Bluejacket'. These varieties differ greatly in height, and contrast in spike length, grain yield, maturity, and seed weight as well. The populations studied included the parents, F_1, F_2, and backcrosses, all of which were grown at two-inch spacings of plants within rows. Higher grain yields were observed for the F_1, F_2, and BC_2 (Bluejacket backcross) populations than for either parent, the F_1 yield being 12.9% above that of the better parent. The F_1 mean for kernel weight was significantly greater than that of either parent, and the F_2 mean for this trait approached that of the higher parent. In addition, both the F_1 and F_2 means for spikes per plant exceeded that of either parent. Differences between the parent and hybrid generations for number of kernels per spike were not significant.

The performance of hybrids derived from crosses involving nine hard red winter wheat varieties was evaluated in replicated field tests over a three-year period by Livers and Heyne[1]. The hybrids were grown in

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[1] (Livers, R. W., and E. G. Heyne. 1966. Field performance of Kansas wheat hybrids in 1964, 1965, and 1966. Agron. Abs. p. 11.)

single-row plots three feet in length and were seeded at the rate of 45 pounds per acre. The mean yield of 18 hybrids in 1964 was 37 bushels per acre, or 20% higher than that of the seven parent varieties. In the 1965 test, 36 hybrids averaged 48 bushels, or 37% more than the mean of the nine parents. The mean yield equivalent of the best hybrid in 1964 was 45 bushels, or 33% above that of the best parent, and the best hybrid in 1965 averaged 57 bushels which was 29% above the best variety. On the basis of these results, it was concluded that certain hard red winter wheat hybrids grown under normal planting conditions can express heterosis comparable to that obtained in other crops.

Genetic Variability in Self-Pollinated Crops

Numerous investigations have been conducted in recent years to assess the relative importance of the various types of gene action contributing to variability in quantitative characters in self-pollinated crops. Studies of this sort have employed both diallel cross analyses and analyses based on early segregating generations of crosses between pure lines. In general, additive genetic effects have been shown to be of major importance in quantitative character expression in such studies, although in some instances non-additive effects have also been found to be of some importance. Implications and limitations of investigations of this type have been discussed in relation to breeding methodology by Matzinger (35).

Matzinger et al. (36) found variances of general combining ability to be significant for ten characters studied in a diallel cross among eight tobacco varieties, while variances of specific combining ability were not significant for any of the characters. Robinson et al. (43)

also reported estimates of additive genetic variance of considerable magnitude relative to non-additive variation for days to flower, plant height, leaf number, leaf length and breadth, and leaf yield in F_2 populations of tobacco. Little dominance or epistasis was detected by these workers. Studies by Marani and Sachs (34) involving crosses among nine oriental tobacco varieties of divergent origin showed that the predominant component of genetic variance for a number of traits was of the additive type. However, the occurrence of significant heterotic effects suggested that non-additive genetic effects may also be of importance in materials of this type.

Ramey and Miller (40), working with reciprocal backcross progenies in cotton, studied the relative importance of the additive and dominance portions of the genetic variation present in eleven traits. They found that the magnitude of the additive genetic variation was considerably greater than that of the dominance variation for yield of seed cotton, boll weight, seed index, and several lint and fiber characteristics. The low magnitude of the dominance variance estimates suggested that epistatic effects such as additive x dominance interactions contributed little to the genetic variations. The relative magnitudes of these additive and dominance genetic variances were in agreement with results of Miller and Marani (38) who also found that the major portion of the genetic variance for several agronomic and quality traits in cotton resulted from genes with additive effects as measured by F_1 and F_2 populations derived from a diallel cross involving eight inbred lines.

White and Kohel (46) found mostly additive variation for 14 characters in a five-parent diallel study in cotton, but their results indicated that dominance effects were also influencing yield, seedling height, boll size, bolls per plant, and vegetative weights. Essentially complete dominance was observed for seedling height while partial dominance was indicated for the rest of these traits. The average direction of dominance for yield was toward greater yield, i.e., most of the dominant genes had positive (greater yield) effects. Subsequently, White (45) reported significant additive variation for yield, lint percent, boll size, and lint index in a study of crosses derived from the same five parents. Additive variation was present for earliness and seed index also, but was not significant. Significant dominance components were noted only for yield and boll size, which substantiated the above results.

Marani (32, 33) concluded from five- and six-parent diallel studies in cotton that the most important component of the genetic variance associated with date of flower initiation, date of maturity, plant height, number of flowers, percentage boll retention, lodging, yield, and several yield-related traits was of the additive type for interspecific as well as intraspecific crosses. Significant specific combining ability variances were also noted for yield of seed cotton and lint, number of bolls, and seed index, however, and since a high degree of heterosis was found he suggested that some of the genetic variance for these traits was non-additive (dominance and epistasis).

Niehaus and Pickett (39) studied heterosis and combining ability in crosses among domestic and introduced sorghums. Significant general and specific combining ability variances were observed for all of the eight traits evaluated in the F_1 generation. The component for general combining ability was larger than that for specific combining ability in all cases except 100-seed weight. General combining ability variances for number of heads per row, and specific combining ability variances for grain yield, number of seeds per head, number of heads per row, and threshing percentages were not significant in the F_2 generation. They concluded that there was considerable non-additive gene action in the F_1 generation, much of which was lost in the F_2 generation. Genetic diversity was emphasized in relation to hybrid vigor as crosses between geographically diverse and presumably genetically diverse parents produced high-yielding hybrids.

Component of variance estimates for general and specific combining ability and their interaction with years were determined from 190 grain sorghum hybrids by Kambal and Webster (25). They found general combining ability to be relatively more important and more stable over years than specific combining ability for yield, seed weight, test weight, plant height and days to bloom.

General and specific combining ability variance estimates were obtained by Leffel and Weiss (29) in F_1 populations derived from a 10-parent diallel cross in soybeans. While both general and specific combining ability were of importance for yield, date of flowering, height, oil content of seed, iodine number of oil, and seed quality, general combining ability variances were much larger than specific for maturity, flowering, and seed size. In additional studies which involved F_2 and F_3 bulk populations as well as F_3 lines derived from the above F_1 populations, Leffel and Hanson (28) found general combining ability to be especially prominent for seed yield, seed size, and plant maturity. For plant maturity and height, relatively large specific effects were observed.

Johnson and Aksel (22) presented evidence that overdominance effects were operative in the control of yielding capacity in F_1 and F_2 populations derived from a diallel cross among 15 barley varieties. The apparent degree of overdominance was observed to decline in the F_2 generation. Incomplete dominance was generally observed in analyses of F_2 and F_3 yield component data, although nearly complete dominance was noted for number of heads per plant in certain subdiallel analyses which involved only arrays of six- or two-rowed varieties. Subsequent investigations by these workers (3) led them to conclude that both short sowing-to-heading period and long heading-to-ripening period in F_2 barley populations were inherited with a high average degree of dominance. A long sowing-to-heading period had a tendency to be associated with a short heading-to-ripening period in a given parent, both traits being inherited as recessives. However, despite close relationships between the two periods, and between these periods and yield as well as yield components, each character was found to be controlled by different genes.

Yield and yield components were studied in the F_1 and F_2 generations of a diallel cross among four spring wheat varieties by Whitehouse et al. (47). Primarily additive genetic effects were observed in analyses of each yield component, although indications of slight dominance effects were noted in the F_1 generation for grains per spikelet and spikelets per head. Whereas yield was strongly influenced by non-allelic interaction in both the F_1 and F_2 populations, little evidence of non-additive genetic effects was found in separate analyses of the yield components.

Heading date analyses based on F_1 data from a 10-parent diallel cross among spring wheat varieties were repeated over a three-year period by Crumpacker and Allard (9). Genetic variability was attributed largely to additive and dominance effects of a relatively small number of genes. Three major and numerous minor genes were implicated in the control of heading date. It was suggested that one or two of the major genes had relatively large dominance effects since effects among genes exhibiting dominance were unequal in both direction and magnitude. Averaged over all genes, partial dominance for earliness of heading was observed. Epistasis was not considered to be an important feature of the genetic system.

In a diallel study involving F_1 and F_2 populations derived from crosses among six winter wheat varieties, Lupton (31) found yielding capacity to be influenced by gene interactions. He reported that yield was inherited with a completely dominant relationship within the range of crosses not showing non-allelic interactions, and that high yield expression is in general dominant. Lupton's results contrasted with those of Whitehouse et al. (47) in that interaction effects were detected in yield component analyses, although these could be traced to the presence of certain varieties. Following removal of arrays of crosses involving interacting parents it was noted that 1000-grain weight was controlled by a primarily additive genetic system, but that grains per head and heads per plant were inherited with a relatively high degree of dominance.

Estimates of general and specific combining ability variances and effects were obtained by Kronstad and Foote (27) in a diallel study involving 10 winter wheat varieties. They found general combining ability variances to be considerably greater than specific combining ability variances for all traits studied with the exception of weight per kernel. Significant specific combining ability variances were observed only for yield per plant and plant height. The genetic variation for each measured trait was considered to be largely due to additive gene action, and it was suggested that greater progress might be made if selection were based on yield components rather than yield as a complex trait. The relative magnitudes of general and specific combining ability estimates obtained in a five-parent diallel study conducted by Brown et al. (8) also led to the conclusion that additive genetic effects account for most of the total genetic variability in winter wheat. Percent protein was the only character for which a significant specific combining ability variance was observed in this study.

CHAPTER III

MATERIALS AND METHODS

Varieties

Six varieties of common wheat (*Triticum aestivum* L. em. Thell. ssp. *vulgare* (Vill., Host) MacKey), consisting of four foreign and two indigenous types were selected for crossing. The varieties were chosen to represent germ plasm sources from several different geographic regions, and were therefore assumed to be broadly divergent genetically. Having been developed in widely separate areas of the world, these included types which varied considerably in their degree of adaptation to the local environment. The varieties used, and a brief description of their characteristics and origins insofar as available are as follows:

(Y)[1] -- Yeoman C (C.I. 6722) -- an awnless, pure-line selection from Yeoman, an English variety. Pedigree: Red Fife of Canada x an unknown strain.

(NS) -- Novi Sad 1421/48 (P.I. 221366) -- an awned Yugoslovian variety. Pedigree unavailable.

(P) -- Probus (P.I. 263564) -- an awnless Swiss variety described (26) as being a high yielding type having good tillering ability, lodging resistance, medium winter resistance, and satisfactory quality when

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[1] Letter abbreviations will be used in reference to parent varieties in parts of this report.

grown within certain climatic limitations. Probus was cultivated on a large scale in Switzerland for the first time in 1950. Pedigree: Trubilo x Plantahof.

(R) -- Reichersburger Kolben (P.I. 201137) -- an awnless Austrian variety described (26) as being a late, high yielding and good quality type with resistance to lodging, black rust, and winter conditions. Pedigree: unavailable, although this variety is described (26) as being a derivative from a cross involving Thatcher.

(N) -- C.I. 13678 (Neb. 551146) -- an awned semi-dwarf experimental strain developed at the Nebraska Agricultural Experiment Station. Some agronomic characteristics of this variety have been studied and compared with those of several other varieties by Johnson et al. (24). Pedigree: Norin 16 x Neb. 60-Mediterranean-Hope.

(K) -- Kaw (C.I. 12871) -- an awned hard red winter wheat released jointly by the Kansas and Oklahoma Agricultural Experiment Stations in 1960. A detailed description of this variety is given by Briggle and Reitz (7). Pedigree: Early Blackhull-Tenmarq x Oro-Mediterranean-Hope.

Experimental Procedure

Crosses among the above varieties were made in all possible combinations in the greenhouse during the winter of 1962-63. The study therefore involved a total of 21 entries consisting of the six parent varieties and 15 crosses. Mature spikes from plants used as males or females were harvested in the spring of 1963 and later threshed manually. A separate source number was assigned to the F_0 seed from each different cross, and seed of each cross was maintained separately after threshing.

<u>F_1's and Parents</u>. F_1 and parent seedlings were established under

greenhouse conditions in October 1963 by planting the seeds in plant bands contained in flats. Subsequent transplanting of the seedlings to plots in the field at Stillwater was delayed past normal seeding time due to non-uniform germination and generally unfavorable soil moisture conditions which prevailed in the fall of 1963. Transplantings to all except 15 plots were made from November 5 to 8. The remaining plots, involving seven entries, were planted on November 14.

Plots in 1963-64 consisted of two 10-foot rows, each of which included 10 plants. All plants from which data were collected were thereby spaced at one-foot intervals due to the presence of adjacent plants in the same plot and in adjoining plots or border rows. Plants at the ends of the plots were not included in sampling. Where necessary, dead or weak seedlings were replaced with healthy plants to maintain uniform competition. All replications received supplemental irrigation twice in November. In March 1964, all plots were topdressed with nitrogen as urea in pelled form at a rate of approximately 30 pounds of N per acre. All F_1 and parent plants harvested were pulled at maturity, the spikes being bagged to prevent seed loss.

F_2's and Parents. Sufficient seed from F_1 plants having the same source number was bulked in the fall of 1964 for the purpose of growing the F_2 populations. The F_2 bulks were subsequently seeded along with the parents at Stillwater on October 5. Plots in 1964-65 consisted of two 10-foot rows spaced one foot apart and seeded at a rate of one bushel per acre. The plots were arranged in a randomized complete block design with four replications. Weather and soil moisture conditions during the establishment period were considered excellent. A topdressing of nitrogen in the form of pelled urea was applied early in March at a rate of

45 pounds of N per acre.

In June, all F_2 and parent plots were shortened to a length of eight feet. As the plants matured, samples consisting of all spikes within a linear foot of row were pulled to facilitate collection of yield component data on a unit area basis. Two samples in tandem were taken randomly from each row, making a total of four samples per plot. The spikes of plants pulled in this manner were bagged to prevent seed loss during storage, and the remainder of each plot was cut and handled separately. All grain from samples and from the part of each plot remaining after sampling was retained separately after threshing.

Agronomic Characters

F_1's and Parents. All pre- and post-harvest observations were recorded on a per plant basis in 1963-64. The following characters were studied:

Maturity. Heading date was used as a measure of the relative maturity of the parents and hybrids, and was recorded as the number of days from March 31 until the first head of each plant had completely emerged from the boot.

Plant Height. Height observations were obtained in the field. Measurements were taken in centimeters from the soil surface to the tip of the tallest spike of each plant, exclusive of awns if present.

Yield. Yield observations consisted of the weight of threshed, cleaned seed from each plant and was expressed in grams.

Tiller Number. This character was determined on the basis of a direct count of the number of tillers bearing fertile spikes on each plant.

Kernel Number. Kernel number was obtained by direct count of all kernels produced by each plant.

Kernel Weight. Kernel weight was calculated as (yield per plant) ÷ (number of seeds per plant) and was expressed in grams per 1000 kernels.

F_2's and Parents. The same traits measured in 1963-64 were also studied in the F_2 and parent populations grown in 1964-65. Sampling techniques differed, however, since the plots were seeded in solid stands. The procedures used in sampling from these plots for the various characters follow:

Maturity. Heading date observations were made on entire plots in April and May 1965, and were expressed on the basis of the number of days after March 31 until emergence of approximately 75% of the spikes in each plot.

Plant Height. Height observations were obtained on individual plants which were separated from each sample and measured in centimeters from the crown to the tip of the tallest spike. A total of 23 observations per plot were used in the analyses.

Yield. Total grain yield observations were based on the yields of entire plots (16 ft.^{2}) and were expressed in grams.

Tiller Number. Tiller counts were based on a direct count of the number of tillers having fertile spikes in each sample and were expressed as tillers per square foot.

Kernel Number. Kernel number was obtained by direct count of all seeds from each sample and was expressed as kernels per square foot.

Kernel Weight. Kernel weight was computed as (sample yield) ÷ (number of kernels per sample) and was expressed in grams per 1000 kernels.

Quality Tests

Samples of grain from all populations grown in 1963-64 and in 1964-65 were subjected to routine quality micro-tests in order to evaluate their relative milling and baking properties. The samples consisted of 125 gram composites of seed from each F_1, F_2, or parent population. Approximately equal amounts of seed from each replication made up the composites. Wheat and flour protein determinations were made by standard Kjeldahl analysis. Sedimentation tests were run on the milled flour as an indicator of the dough-mixing tolerance and general bread baking strength of the various genotypes (10, 48). Mixograms were obtained using flour from the F_2's and parents grown in 1964-65 as an index of physical dough properties. Due to low flour extraction, the F_1's and parents were not evaluated in mixograph tests.

Analyses of Variance

Standard analyses of variance were conducted on data from the populations grown in 1963-64 and 1964-65 for days to head, plant height, yield, and the three yield components. Analyses of the 1963-64 F_1 and parent data were based on only three of the five replications grown since approximately one-third of the plants in two replications were visibly stunted. The cause of this stunting was undetermined, although the only plants affected were those near fallow which had been cropped the previous year. In addition, data from a number of obviously stunted or weak plants from the three unaffected replications were not used in the analyses. Thus, all analyses of data from the F_1 and parent space-plants were conducted on unweighted means based on 12 observations per plot for all entries except C.I. 13678. Plot means of C.I. 13678 were based on 4, 5, and 12 observations respectively for the three replications involved. Means of all F_1 and parent entries were therefore based on 36 observations, except for the latter which was based on 21. Quality characters were not analyzed statistically because of the necessity of compositing replications to obtain sufficient seed for quality tests.

Heterosis Analyses

Heterosis was measured for all F_1 and F_2 populations with respect to both the midparent and high parent values. Adjusted LSD values were used to test each hybrid-midparent contrast due to the fact that hybrid means are based on only half as many observations as midparent values. Since the variance of a hybrid-midparent contrast may be defined as (6) (EMS) ÷ (4) (rn), where EMS = experimental error mean square and rn = the number of observations per entry mean, LSD values calculated by the usual method were multiplied by $\sqrt{3/4}$ to account for this difference in number of observations.[2] Thus, in the present case, LSD = $t_{(\alpha, \text{[illegible]} t - 1)} S_{\bar{d}} \sqrt{3/4}$.

Duncan's new multiple range tests were used to determine the significance of differences among means of the F_1 and parent populations grown in 1963-64, and among means of the F_2 and parent populations grown in 1964-65.

Combining Ability Analyses

Combining ability analyses were conducted with F_1 data for all agronomic characters according to the procedure outlined by Griffing (12),

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[2] (This procedure was suggested by Dr. Robert D. Morrison, Professor of Mathematics and Statistics, Oklahoma State University, Department of Mathematics and Statistics.)

and designated as method 4, model I. Inferences in this case are restricted to the varieties entering into the diallel cross since they are considered as a fixed set rather than a random sample from a population of lines. The form of the analysis provides for partitioning the sum of squares due to genotypes (crosses) into general and specific combining ability sums of squares associated with P-1 and P(P-3) ÷ 2 degrees of freedom respectively, where P represents the number of parents involved in the diallel cross. Neither parents nor reciprocal crosses are included in the analysis. A similar analysis was presented originally by Sprague and Tatum (44).

Preliminary analyses of variance were conducted with F_1 data based on 12 observations per plot for all traits. Experimental error variances were used to test significance of mean squares associated with genotypes in all analyses. General and specific combining ability estimates were obtained using the University of Illinois program (30) converted to run on the IBM 7040.

Vr, Wr Regression Analyses

Variance-covariance regression analyses were applied to F_1 and F_2 data to obtain an overall evaluation of the genetic systems controlling heading date, height, yield, and the yield components of the six varieties used in the diallel cross. The method employed was that proposed by Jinks and Hayman (21). Theoretical and procedural aspects of this method of analysis have been illustrated and discussed by a number of workers (2, 11, 13, 14, 16, 17, 18, 19, 20, 21). The analysis provides a means of identifying the potentially superior crosses. Also, since the method can be used with data from the early hybrid generations (F_1,

F_2, backcross), it is theoretically possible to identify the parental combinations having the best selection potential for a trait in a much shorter period of time than would be required by growing and evaluating advanced generations of the crosses.

The statistics generated by the Jinks-Hayman technique may be interpreted in terms of defined genetic parameters. The necessary computations, based on parent and F_1 or F_2 family means in the present study, include the variance of the parents entering into the diallel cross ($V_{\bar{p}}$), the variance of the rth array corresponding to each of the r parents (Vr), and the covariance of the progeny in each array with the non-recurring parents (Wr). An array in the context of the diallel cross consists of the means of all crosses involving a given parent, including the mean of the parent itself. Thus, inferences regarding the relative dominance properties of the parents of a diallel set are dependent upon estimates of parameters for additive, dominance, and environmental effects. The analysis also permits detection of non-allelic interaction and provides information about the relative proportions of dominant and recessive alleles possessed by each of the parents for a given trait.

The interpretation is based on a number of hypotheses or simplifying assumptions regarding a genetic system. These include: i) homozygous parents, ii) diploid segregation, iii) no reciprocal differences (i.e., no maternal effects), iv) no epistasis (i.e., no non-allelic gene interaction), v) no multiple allelism, vi) genes independently distributed in the parents (no linkage), vii) no genotype-environment interaction. An approximate test of the validity of the basic assumptions is obtained in the simplest form of the analysis by fitting a regression line to the array points having coordinates Vr, Wr. The array points will lie within the limits of a parabola defined by $Wr^2 = V_{\bar{p}}Vr$, and if all assumptions are valid, a regression line having unit slope is expected. Failure of one or more of the basic assumptions is indicated by either a non-significant regression, or by a significant deviation of the slope from unity (21).

Certain of the assumptions may be considered valid for the materials used in the present study, hence the regression of Wr on Vr provides a test of those remaining. Parental homozygosity, for instance, is essentially assured due to the self-pollinating habit of wheat. Diploid segregation may also be assumed since 21 bivalents are normally observed at meiosis, despite the hexaploid chromosome complement of common wheat. The genetic basis for diploid segregation and disomic inheritance in wheat has recently been established by Riley et al. (41, 42). While strict validity of assumption (iii) regarding the absence of reciprocal cross differences is not assured, maternal influences on the expression of most traits studied in wheat crosses are unusual. Thus, it is unlikely that such effects could bias the analysis in any significant way. Some bias to the analysis is possible in view of the difficulty in obtaining independent evaluations of assumptions (iv), (v), and (vi). However, Crumpacker and Allard (9) considered this bias insignificant so long as no distortion of the Vr, Wr graph resulted. According to Hayman (15), the measure of the average degree of dominance, at least, is not invalidated by graphical disturbances caused by multiple allelism and non-independent distribution of genes in the parents.

Although Vr and Wr contain environmental components (1, 9, 13), no gross disturbance in the Vr, Wr analysis is expected if the non-heritable variation in a character is small relative to the heritable variation.

Where environmental effects are not removed, slight displacement of the regression line is possible, but bias with regard to its slope is improbable (1). In general, a sufficient degree of accuracy appears to be obtainable with the graphical analysis to provide a reasonable assessment of the genetic system controlling a given trait, despite partial failure of one or more of the basic assumptions.

CHAPTER IV

RESULTS AND DISCUSSION

Analyses of Variance

Mean squares from the randomized complete block analyses of variance conducted on data from all entries grown in 1963-64 and in 1964-65 for days to head, plant height, yield, number of tillers, number of kernels, and weight per 1000 kernels are presented in Tables I and II. Differences among genotypes were highly significant for each character, and accounted for the major portion of the observed variation in both years of the study. This result was expected because of the basis on which the parent varieties were selected, and because of variations in adaptive characteristics of both parent and F_1 or F_2 populations. In these, and in subsequent analyses, the standard notation for significance is used, i.e., * = significance at the 5% level of probability and ** = significance at the 1% level.

Heterosis

Means of the F_1, F_2, and parent populations are presented in Appendix Tables XIII - XVIII along with appropriate significance tests of heterosis for all of the above characters. In addition, means of the F_1 and F_2 populations are expressed in percent of their respective high parent means in Appendix Tables XIX and XX.

TABLE I

MEAN SQUARES FROM ANALYSES OF VARIANCE OF DATA FROM PARENT AND F_1 POPULATIONS GROWN IN 1963-64

Source of Variation	d.f.	Days to Head	Plant Height	Yield	Number of Tillers	Number of Kernels	Weight Per 1000 Kernels
Total	62	-	-	-	-	-	-
Replicate	2	4.104	24.678*	28.214**	6.244	26866.885*	18.104**
Population	20	97.403**	103.760**	96.388**	50.764**	80593.795**	72.997**
Error	40	1.362	5.877	3.264	5.084	5905.539	1.288

TABLE II

MEAN SQUARES FROM ANALYSES OF VARIANCE OF DATA FROM PARENT AND F_2 POPULATIONS GROWN IN 1964-65

Source of	Days to Head		Plant Height		Yield		Number of Tillers		Number of Kernels		Weight Per 1000 Kernels	
Variation	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Total	83	-	1931	-	83	-	335	-	335	-	335	-
Replicate	3	2.41**	3	866.38	3	15398.13**	3	55.11	3	159971.55**	3	151.18**
Population	20	106.41**	20	2077.05**	20	39049.40**	20	852.31**	20	454610.04**	20	266.35**
Error	60	0.53	60	369.47**	60	1575.29	60	61.56	60	24495.86	60	13.51
Sampling Error	-	-	1848	37.17	-	-	252	49.34	252	24906.12	252	3.08

Significant midparent heterosis was observed in all but two of the F_1 populations and in all but four of the F_2 populations for one or more of the characters studied. Heterosis for earliness of heading was observed in six F_1 and six F_2 populations, but in either generation was significant only in relation to the respective midparent values (Appendix Table XIII). All except four F_1 and four F_2 populations headed significantly later than their respective earlier parents.

Ten of the F_1 populations exceeded their respective taller parents in mean plant height, although significant high-parent heterosis was observed only in the Y x N population (Appendix Table XIV). Significant midparent heterosis for plant height occurred in all but two of the F_1 populations. While the means of nine of the F_2 populations exceeded those of their respective high parents, only one population exhibited significant high-parent heterosis for plant height. Seven of the F_2 populations exhibited significant midparent heterosis for plant height.

The most striking heterotic effects for yield and the components of yield were observed in the P x N, NS x N, N x K, and R x N F_1 populations. Significant high-parent heterosis was observed for yield per plant and weight per 1000 kernels in the P x N F_1 population, and for weight per 1000 kernels in the NS x N F_1. None of the F_2 populations exhibited high-parent heterosis for yield or for any of the yield components, although the mean yields of three of the F_2's did exceed their respective high-parent means (Appendix Table XVIII). However, significant midparent heterosis was observed in the P x K and Y x N F_2 populations for yield, in the N x K, Y x N, Y x K, P x K, and Y x P F_2 populations for number of kernels, and in the Y x N and R x N F_2 populations for weight per 1000 kernels. Midparent heterosis for number of tillers did not occur in any of the F_1 or F_2 populations. Yield per plant and 1000-kernel weight means of the P x N F_1 populations averaged 141 and 123% respectively of the corresponding means of C.I. 13678, the high parent of this cross for both characters. In addition, the average number of kernels produced per plant in the P x N F_1 population was 117% of the average number produced by C.I. 13678. Heterosis for this component was significant only in relation to the midparent value, however.

Although the average weight per 1000 kernels in the NS x N F_1 population was 122% of that of the high parent, C.I. 13678, yield heterosis for this cross was barely significant with respect to the midparent value due to its relatively poor performance in terms of numbers of tillers and kernels produced. Heterosis for yield per plant in the cross R x N was also largely accounted for by significant midparent heterosis for 1000-kernel weight. The mean yield of this cross was 114% of that of C.I. 13678, the higher yielding parent. Yield heterosis was manifested primarily through increased kernel numbers in the cross N x K, the F_1 means for yield and kernel numbers per plant both being significant relative to the midparent value and both 13% greater than the corresponding means of Kaw, the high parent of this hybrid. The average weight per 1000 kernels in the N x K F_1 population was also significant in relation to the midparent, but was essentially equal to the high parent mean. Higher yield and kernel number means were observed for this population than for any of the other F_1's or parents even though certain of the other hybrids exhibited greater heterotic effects for yield and the yield components. The fact that the parents of the highest yielding cross among those of the present diallel set, viz. C.I. 13678 and Kaw, were locally well adapted types would not seem to preclude the possibility of obtaining higher yielding hybrids than N x K by employing more diverse parents than these. The present evidence appears to indicate that reasonably high expression in terms of one or more yield components may be expected even in crosses involving parents of varying degrees of adaptation. It may be noted in this regard that the differences between 1000-kernel weight means of the N x K, P x N, and NS x N F_1populations (Appendix Table XVII) and between the N x K, NS x K, and P x N F_1 means for number of kernels per plant (Appendix Table XVI) were not significant. In addition, the mean yields of the P x N and NS x K F_1 populations did not differ significantly from that of Kaw, the highest yielding parent variety, although these crosses involved indigenous x foreign genotypes.

Quality characteristics of the F_1 and F_2 populations did not differ appreciably from those of the parent varieties (Appendix Table XXI). Protein percentages, sedimentation scores, and mixing times ranged from values lower than those observed for the lower parents to values somewhat in excess of the high parents.

Combining Ability Analyses

Mean squares from the combining ability analyses of variance conducted on F_1 data for days to head, plant height, yield per plant and the three components of yield are presented in Tables III and IV. Variances due to differences among genotypes were highly significant for all characters. The genetic variability for all characters was largely accounted for by highly significant general combining ability although significant specific combining ability variances were also observed for all traits. Ratios of variances due to general and specific combining ability for days to head and plant height were respectively 21:1 and 10:1.

TABLE III

MEAN SQUARES FROM PRELIMINARY ANALYSES OF VARIANCE OF DATA FROM F_1 POPULATIONS GROWN IN 1963-64

Source of Variation	d.f.	Days to Head	Plant Height	Yield	Number of Tillers	Number of Kernels	Weight Per 1000 Kernels
Replicates	2	1.451	8.056*	8.604**	3.068	11,356.807**	4.923**
Crosses	14	24.630**	19.394**	30.865**	12.659**	24,136.976**	23.241**
Error	28	0.504**	1.976**	0.851**	1.561**	1,508.436**	0.494**
Sampling Error	495	0.050	0.481	0.307	0.334	422.823	0.136

TABLE IV

OBSERVED MEAN SQUARES AND RELATIVE MAGNITUDES OF GENERAL AND SPECIFIC COMBINING ABILITIES FOR SIX CHARACTERS 1/

Character	Gca	Sca	Gca:Sca
Days to Head	63.524**	3.036**	21:1
Plant Height	46.232**	4.493*	10:1
Yield/Plant	75.013**	6.340**	12:1
No. Tillers/Plant	25.170**	5.714**	4:1
No. Kernels/Plant	55,468.275**	6,725.958**	8:1
Wt./1000 Kernels	60.431**	2.567**	23:1

1/F tests based on experimental error mean square.

A ratio of 23:1 between general and specific combining ability variances was observed for weight per 1000 kernels. General to specific combining ability ratios for yield, number of heads, and number of kernels per plant were somewhat narrower in comparison, being 12:1, 4:1, and 8:1 respectively.

Estimates of general combining ability effects associated with each of the parent varieties for the six agronomic traits measured are presented in Table V along with appropriate standard errors. The varieties C.I. 13678, Kaw, and Novi Sad 1421/48 had significant negative general effects for earliness of heading, and significant positive effects for yield per plant as well as for each of the three yield components. The remaining parents had significant positive effects for earliness, and significant negative effects for yield and the components of yield. Considerably greater general combining ability was exhibited by the semi-dwarf parent C.I. 13678 than by either Novi Sad 1421/48 or Kaw for number of days to head, yield per plant, number of kernels per plant, and weight per 1000 kernels. However, Novi Sad 1421/48 and Kaw had the greatest general combining ability for number of tillers per plant, the effect associated with C.I. 13678 for this trait being barely significant. Also, Novi Sad 1421/48 and Kaw were the only parents exhibiting positive general effects for plant height.

Estimates of specific combining ability effects associated with individual crosses for each of the above characters are presented in Tables VI - XI along with standard errors for comparison of effects of crosses having one parent in common. Significant negative (earlier) specific combining ability effects were observed in four crosses for number of days to head. Two of these crosses involved the semi-dwarf

TABLE V

ESTIMATES OF GENERAL COMBINING ABILITY EFFECTS FOR SIX VARIABLES MEASURED IN THE HYBRID POPULATIONS

Character	Yeoman C	Novi Sad	Probus	R. Kolben	C.I. 13678	Kaw	S.E. $(\hat{g}_i-\hat{g}_j)$
Days to Head	4.06	-2.23	3.77	2.64	-5.29	-2.96	0.502
Plant Height	-3.02	4.71	-0.11	-3.55	-1.45	3.43	0.994
Yield/Plant	-4.00	1.36	-3.67	-3.39	6.22	3.49	0.652
No. Tillers/Plant	-1.32	2.62	-3.67	-1.21	0.91	2.67	0.880
No. Kernels/Plant	-105.72	51.48	-141.77	-56.12	141.56	110.56	27.463
Wt./1000 Kernels	-3.27	1.28	-2.04	-4.26	5.96	2.32	0.497

TABLE VI

ESTIMATES OF SPECIFIC COMBINING ABILITY EFFECTS FOR NUMBER OF DAYS TO HEAD

	Novi Sad	Probus	R. Kolben	C.I. 13678	Kaw
Yeoman C	-0.30	0.70	0.47	1.04	-1.90
Novi Sad		0.38	-2.07	2.30	-0.31
Probus			1.18	-2.34	0.08
R. Kolben				-1.36	1.77
C.I. 13678					0.36

S.E. $(\hat{s}_{ij} - \hat{s}_{ik}) = 0.869$

TABLE VII

ESTIMATES OF SPECIFIC COMBINING ABILITY EFFECTS FOR PLANT HEIGHT

	Novi Sad	Probus	R. Kolben	C.I. 13678	Kaw
Yeoman	3.14	-1.52	-1.71	-1.12	1.21
Novi Sad		0.62	1.03	-1.53	-3.26
Probus			-0.71	2.03	-0.41
R. Kolben				-0.22	1.61
C.I. 13678					0.85

S.E. $(\hat{s}_{ij} - \hat{s}_{ik}) = 1.721$

TABLE VIII

ESTIMATES OF SPECIFIC COMBINING ABILITY EFFECTS FOR YIELD PER PLANT

	Novi Sad	Probus	R. Kolben	C.I. 13678	Kaw
Yeoman C	0.24	0.48	0.61	-3.06	1.72
Novi Sad		-1.80	2.60	-2.29	1.24
Probus			-0.63	3.78	-1.84
R. Kolben				0.06	-2.64
C.I. 13678					1.51

S.E. $(\hat{s}_{ij} - \hat{s}_{ik}) = 1.130$

TABLE IX

ESTIMATES OF SPECIFIC COMBINING ABILITY EFFECTS FOR NUMBER OF TILLERS PER PLANT

	Novi Sad	Probus	R. Kolben	C.I. 13678	Kaw
Yeoman C	1.24	0.58	0.28	-2.56	0.46
Novi Sad		-1.80	1.99	-2.94	1.50
Probus			-0.58	3.82	-2.02
R. Kolben				-0.04	-1.65
C.I. 13678					1.71

S.E. $(\hat{s}_{ij} - \hat{s}_{ik}) = 1.530$

TABLE X

ESTIMATES OF SPECIFIC COMBINING ABILITY EFFECTS FOR NUMBER OF KERNELS PER PLANT

	Novi Sad	Probus	R. Kolben	C.I. 13678	Kaw
Yeoman C	12.46	0.21	-15.94	-77.71	80.98
Novi Sad		-33.19	107.16	-87.31	0.88
Probus			-61.39	137.73	-43.36
R. Kolben				17.98	-47.81
C. I. 13678					9.31

S.E. $(\hat{s}_{ij} - \hat{s}_{ik}) = 47.567$

TABLE XI

ESTIMATES OF SPECIFIC COMBINING ABILITY EFFECTS FOR WEIGHT PER 1000 KERNELS

	Novi Sad	Probus	R. Kolben	C.I. 13678	Kaw
Yeoman C	0.19	-0.09	0.52	-1.57	0.96
Novi Sad		-1.91	1.61	-1.10	1.21
Probus			-0.47	2.38	0.09
R. Kolben				0.45	-2.10
C.I. 13678					-0.15

S.E. $(\hat{s}_{ij} - \hat{s}_{ik}) = 0.860$

parent C.I. 13678, the largest negative effect being noted in the cross P x N. Only two crosses, Y x NS and P x N, exhibited significant positive effects for plant height, and only one cross, NS x K, had a significant negative effect for this trait. The crosses NS x R and P x N had significant positive effects for yield per plant as well as for each yield component. For each of these traits, as well as for earliness of heading, the greatest effect was associated with the cross P x N, and the second largest effect with NS x R. Lesser, although significant, effects were associated with the cross Y x K for yield, number of kernels, and weight per 1000 kernels, with the cross N x K for yield and number of tillers, and with the cross NS x K for yield and weight per 1000 kernels.

As indicated by the ratios of general to specific combining ability obtained in the analyses of variance, the genetic variation for each character was largely accounted for by the variance due to general combining ability. According to Sprague and Tatum (44), general combining ability provides a measure of additive gene action. On the basis of this assumption, the present results are therefore in good agreement with those of Brown et al. (8) and Kronstad and Foote (27) who also found that most of the total genetic variability for a number of characters studied in wheat crosses was due to additive effects of genes. The occurrence of significant specific combining ability variation for all of the agronomic traits measured in the present study suggests that the genetic variation present for each trait was also due in part to nonadditive effects. It should be noted in this connection, however, that tests of the significance of general and specific combining ability variation were based on experimental error. A more conservative test of the relative contributions of additive and non-additive effects to the total genetic variation in the materials used in this study could be obtained by pooling the experimental error and sampling error sums of squares in these analysis.

On the basis of estimates of general combining ability effects for earliness of heading, yield, and the components of yield, the best parents among those of the present set are C.I. 13678, Kaw, and Novi Sad 1421/48. The crosses N x K, NS x K, and NS x N would consequently be expected to provide the best source materials for the selection of segregates superior to the best parents in yielding ability. Direct selection for yield in segregating generations of each of these crosses would presumably result in improvement, although the cross N x K should be the most promising. Improvement in yielding capacity through selection based on yield components may be feasible if selection for high expression in one component does not result in a significant reduction in the expression of another. Thus, selection for increased number of kernels or weight per 1000 kernels within populations arising from the cross N x K might also be expected to result in improved yields since C.I. 13678 and Kaw exhibited the highest general combining ability effects for these traits. The cross between Novi Sad 1421/48 and Kaw should offer the best potential for yield improvement through selection for increased tillering capacity since these parents exhibited the highest general effects for this trait, and also produced the highest average numbers of tillers per plant.

Since Novi Sad 1421/48 and Kaw were the only parents having positive general effects for plant height, the crosses involving these parents with C.I. 13678 should provide a relatively broad range of segregates from which types with desired heights could be selected.

Since the use of hybrids would permit the wheat breeder to take advantage of non-additive as well as additive genetic variation, and since a part of the total genetic variability for each trait measured in the present study was associated with a significant specific combining ability effect, there would appear to be some merit in employing diverse parents for hybridization purposes. As noted earlier, the most prominent example of yield heterosis occurred in the cross P x N which exceeded the high parent in yield by 41%, and which exhibited larger specific combining ability effects than any of the other hybrids for all traits except plant height. The fact that a large part of the general combining ability in the analyses of heading date, yield, number of kernels, and weight per 1000 kernels was due to the presence of C.I. 13678 suggests that this parent would be of considerable value in a hybrid wheat program. It is of interest to note that the number of crosses in the present study exhibiting significant specific combining ability for yield was proportionately rather high. If the parents used can be considered a random sample of lines, then the chances of obtaining favorable combinations that will give a high level of yield heterosis seem reasonably good.

Vr, Wr Regression Analyses

Days to Head. Graphical analyses of number of days to head for the F_1 and F_2 generations are presented in Figure 1. Highly significant regression coefficients were obtained for both generations, and since both regression lines are in agreement with a line of unit slope the gene system controlling number of days to head may be considered almost exclu-

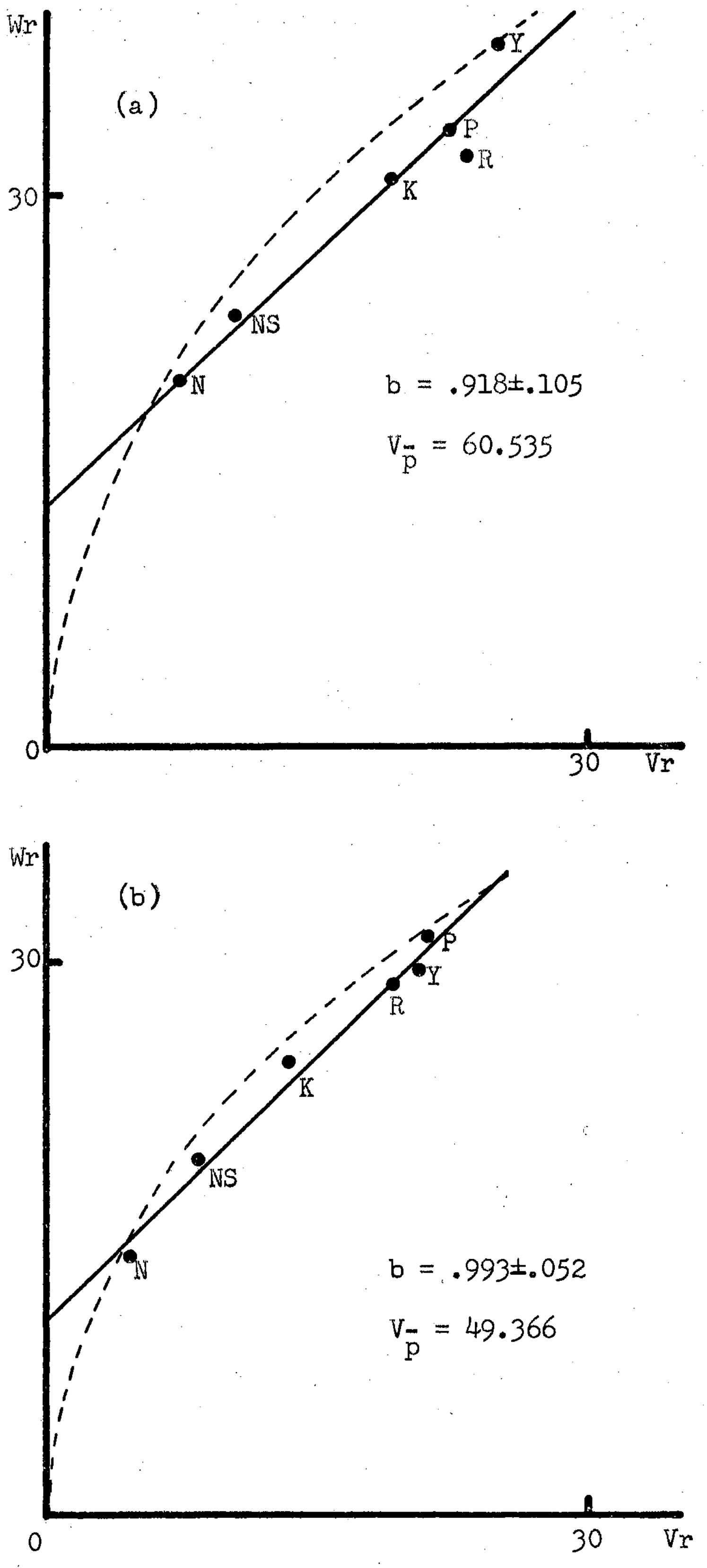

Figure 1. Vr, Wr graphs of F_1 (a) and F_2 (b) families for days to head.

sively additive. The proximity of the regression lines to their limiting parabolas in both graphs indicates that the average degree of dominance at loci influencing the heading period is only partial, since with full dominance at all loci involved the line of regression should pass through the origin.

According to the relative positions of the array points along the regression lines in Figure 1, C.I. 13678 is the parent variety most obviously exhibiting strong dominance effects at some or all loci affecting number of days to head. In both graphs, the array points corresponding to this parent are positioned nearest the lower intersections of the regression lines with their respective limiting parabolas, or closest to the position that would be taken by an array point corresponding to a parent variety possessing the highest possible proportion of dominant alleles for the character. Parents having array points positioned near the upper part of the regression lines presumably possess the least proportions of dominant alleles, hence the period of time required for heading of R. Kolben, Probus, and Yeoman C is apparently controlled primarily by recessives. While it is expected that the relative positions of the array points in the graphs reflect the true proportions of dominant and recessive genes possessed by each parent, the possibility should not be overlooked that unequal dominance effects of the involved genes may cause the positions of some array points to be weighted in favor of genes with large dominance effects. The extent to which the varieties used as parents in the present study exhibit diversity in the genetic system controlling heading date, as is shown by the distance between array points, could therefore depend upon whether dominant or recessive alleles are present at a relatively few loci.

Except for minor shifts, the positions of the array points are the same in Figure 1b as in 1a. Thus, the dominance order of the parent varieties remained essentially constant over both years of the study despite the considerable difference in environmental conditions under which the F_1 and F_2 generations were grown.

In view of the fact that most of the F_1 and F_2 populations means (Appendix Table XIII) deviated negatively from their respective midparent values in terms of number of days to head, dominance clearly lies in the direction of earliness rather than lateness. The closeness of the association between earliness and dominance is equally evident from results of the graphical analyses in which C.I. 13678, a characteristically early type, is singled out as being the top dominant variety among those comprising the present parental group. In addition, it will be noted that the array means (Table XII) of the parents considered to possess mostly recessives substantially exceeded those of the more dominant parents as would be expected if dominants rather than recessives confer earliness. In general, the foregoing observations are consistent with those of Blair and Patterson (4) and Crumpacker and Allard (9) who also found partial dominance for earliness in common wheat.

The prominence of additivity as a feature of the genetic system governing number of days to head suggests that the hybrid populations most likely to yield segregates heading earlier than the best of the parent varieties used for crossing are those which were earliest in the F_1 and F_2 generations. The varieties having the lowest array means in F_1 and F_2 were C.I. 13678, Kaw, and Novi Sad 1421/48, hence certain crosses within the respective arrays of these parents should provide the best source materials. Apparently, selection could be limited to the

TABLE XII

ARRAY MEANS OF THE SIX-PARENT DIALLEL FOR THE F_1 AND F_2 GENERATIONS

		Arrays					
Character		Yeoman C	Novi Sad	Probus	R. Kolben	C.I. 13678	Kaw
Days to Head	F_1	43.0	36.4	42.0	41.1	33.8	35.1
	F_2	42.4	36.6	40.5	40.2	33.0	35.2
Plant Height	F_1	85.0	93.0	88.8	86.0	86.1	91.7
	F_2	94.1	96.5	96.2	96.1	89.9	95.1
Yield	F_1	7.57	13.21	8.30	8.63	15.98	15.41
	F_2	259.72	335.44	278.52	273.02	391.55	422.19
Number of Heads	F_1	15.1	19.6	13.6	15.2	16.5	19.0
	F_2	38.7	46.1	39.3	42.8	47.0	51.3
Number of Kernels	F_1	399.8	593.3	404.4	480.7	624.3	625.3
	F_2	933.1	973.5	866.6	906.2	1090.2	1129.4
Weight/1000 Kernels	F_1	17.82	21.79	18.83	17.00	25.13	23.85
	F_2	20.36	24.65	22.01	21.09	26.48	26.94

N x K, NS x K, NS x N, P x N, and R x N populations without discarding any crosses likely to yield valuable strains.

Plant Height. Vr, Wr analyses of plant height with all arrays included are presented graphically in Figure 2 for the F_1 and F_2 generations. The slope of the F_1 regression line shown in Figure 2a is highly significantly different from zero (P=.01-.001), but is not significantly different from 1.0. Therefore, the assumptions on which the analysis is based may be considered valid for the F_1 data. Since the F_1 regression line intercepts the Wr axis near the origin, the average degree of dominance at loci governing plant height in the present group of crosses appears to be complete, or nearly so. This result generally accords with expectation in that, with only one exception, no significant difference was observed (Appendix Table XIV) between the mean height of each of the F_1 populations and that of each of their respective taller parents. Averaged over all parents then, dominance is complete, or nearly so, and lies in the direction of greater stature.

The positions of the Novi Sad 1421/48 and Kaw array points in Figure 2a indicate that these varieties both possess nearly complete complements of dominant genes of similar effectiveness, or possibly a proportion of alleles with dominance effects large enough to cause the positions of the points to be weighted toward the origin, simulating complete dominance. Conversely, the points corresponding to Yeoman C and C.I. 13678 lie farthest from the origin suggesting that these parents possess relatively high proportions of recessive genes which condition plant height.

Analysis of the F_2 data gives only the random scatter of array points plotted in Figure 2b when all arrays are considered. The dis-

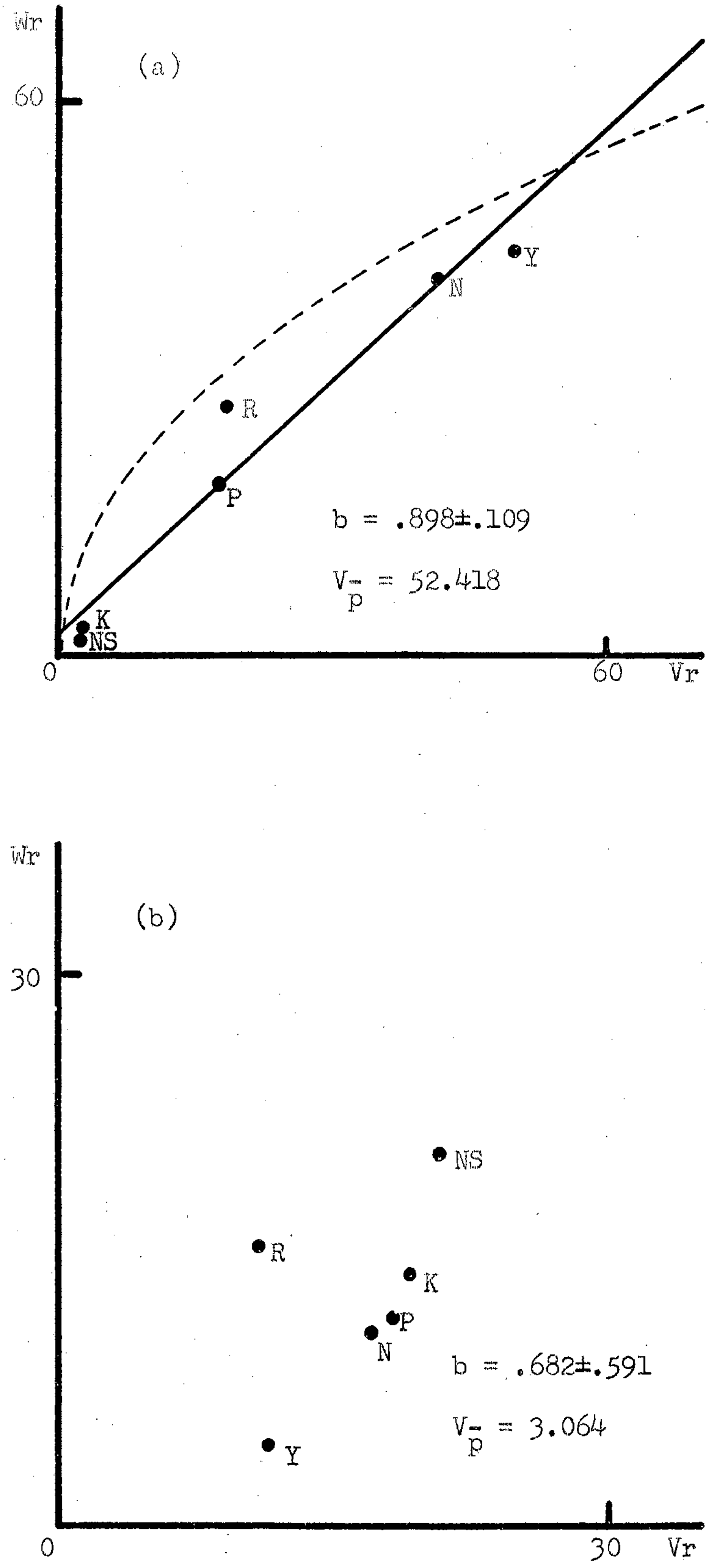

Figure 2. Vr, Wr graphs of F_1 (a) and F_2 (b) families for plant height.

turbance in this graph relates to the fact that several F_2 populations deriving mostly, but not exclusively, from crosses involving either Kaw or Novi Sad 1421/48 as one of the parents exceeded their respective taller parents in average height (Appendix Table XIV). This suggests the presence of non-allelic interactions tracing primarily to height factors contributed by Kaw and Novi Sad 1421/48, although the excess was significant for only the Y x K F_2 population.

In order to examine the possibility that non-allelic interaction influenced height expression in certain of the F_2 populations, sub-diallel analyses were conducted omitting arrays within which heterotic effects were most evident. Omission of the Kaw and Novi Sad 1421/48 arrays in turn and simultaneously resulted in non-significant regressions (.904±.550,.702±.419,.928±.418) owing to excessively high standard errors, although some improvement was noted over the random scatter of points observed when all arrays were included. Similarly, non-significant regressions were observed upon omission of the Kaw, C.I. 13678, and Novi Sad 1421/48 arrays (.814±.143), and of the Kaw, Novi Sad 1421/48, and Probus arrays (.710±.593) despite the fact that all but one of the F_2 means which exceeded both of their respective parental means were eliminated from these analyses. While a significant regression (.801±.008) was obtained by omitting the Kaw, Probus, and Yeoman C arrays from the analysis, a significant deviation of the line from unit slope was observed indicating the presence of complicating effects due to non-allelic interaction (Figure 3). That failure of the assumption of no non-allelic interaction occurred in the foregoing analyses does not seem improbable since the F_2 population means which exceeded the corresponding taller parent means could not all be removed by elimination of only

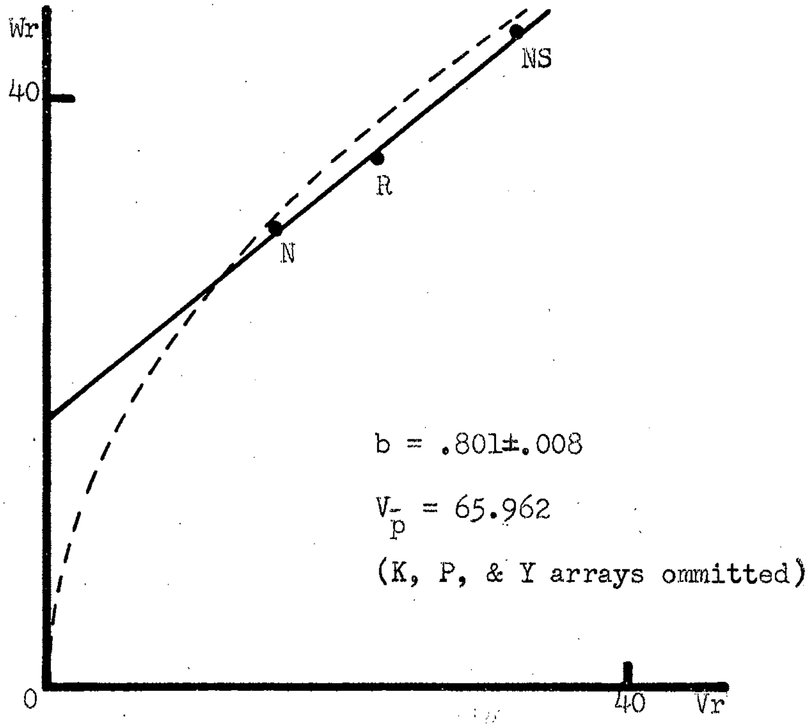

Figure 3. Vr, Wr graph of F_2 families for plant height, K, P, and Y arrays omitted.

three arrays, the maximum number possible in the present study. Apparently, interactions of the complementary type largely underlie the heterotic effects noted in certain of the F_2 populations in view of the improvements toward unit slope that were obtainable in subdiallel analyses. The parents to which disturbing influences can be primarily localized are Kaw, C.I. 13678, and Novi Sad 1421/48. Since the regression line in Figure 3 is in close proximity to the limiting parabola, the genetic system controlling height insofar as C.I. 13678, Novi Sad 1421/48, and R. Kolben are concerned appears to be primarily additive. However, the inclusion of additional arrays in the analysis suggests that the genetic system averaged over all parents is more complex. In the present case, therefore, the F_1 analysis appears to reflect more accurately the nature of the inheritance of plant height. Since C.I. 13678 and Novi Sad 1421/48 contrast both in average height and in relative proportions of dominant versus recessive alleles, selection of a range of types of desirable height from segregating populations derived from the cross between these varieties should be possible.

Tiller Number. The values of the variances and covariances obtained from analysis of F_1 data for tillering capacity when all arrays are included results in a non-significant regression (b=.911±.338) as can be seen in Figure 4a. Despite the fact that the standard error is large, the observed regression is very nearly significant (P=.10-.05). As the b value obtained from analysis of F_2 data (Figure 4b) agrees well with a slope of 1.0, additive rather than non-additive effects are quite likely to be the more prominent feature of the gene system controlling tillering capacity in the present group of crosses. Thus, in what follows it is apparent that the picture presented in Figure 4a is complicated by gene interaction, and that the average degree of dominance is very likely overestimated.

Inspection of the relative positions of the array points in Figure 4a shows that the point corresponding to the variety Probus lies well below the line of regression. Interallelic interaction attributable to the presence of Probus in this group of crosses may therefore be postulated, as this type of interaction causes array points to fall below the line of unit slope, thereby shifting the line of regression downward (11). Analysis of the F_1 data with the Probus array omitted (Figure 5a) results in a significant improvement in the line of regression (b=.930±.246), hence the remaining five-parent diallel satisfies the assumptions on which the analysis is based. Although the standard error of this value is still excessively large, a significant regression which agrees well

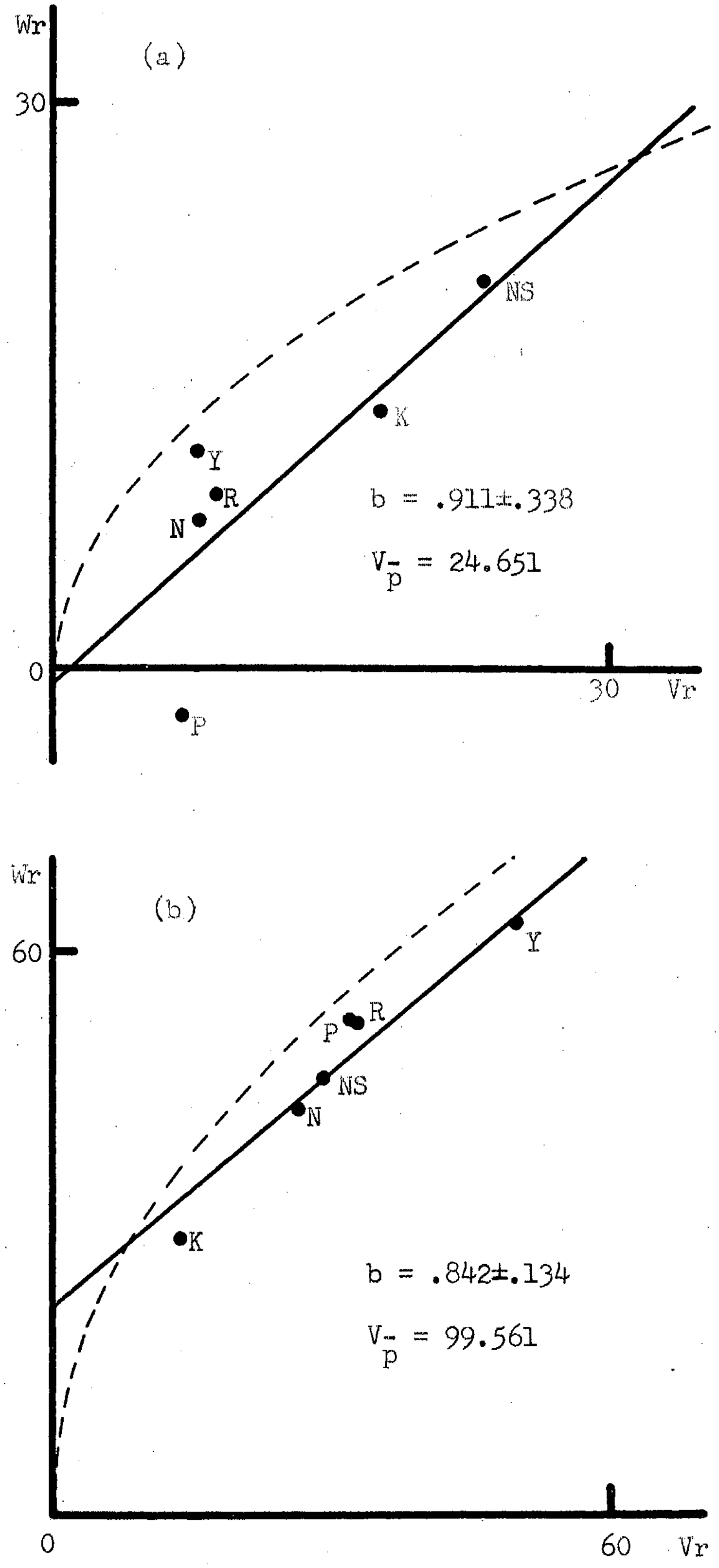

Figure 4. Vr, Wr graphs of F_1 (a) and F_2 (b) families for number of tillers.

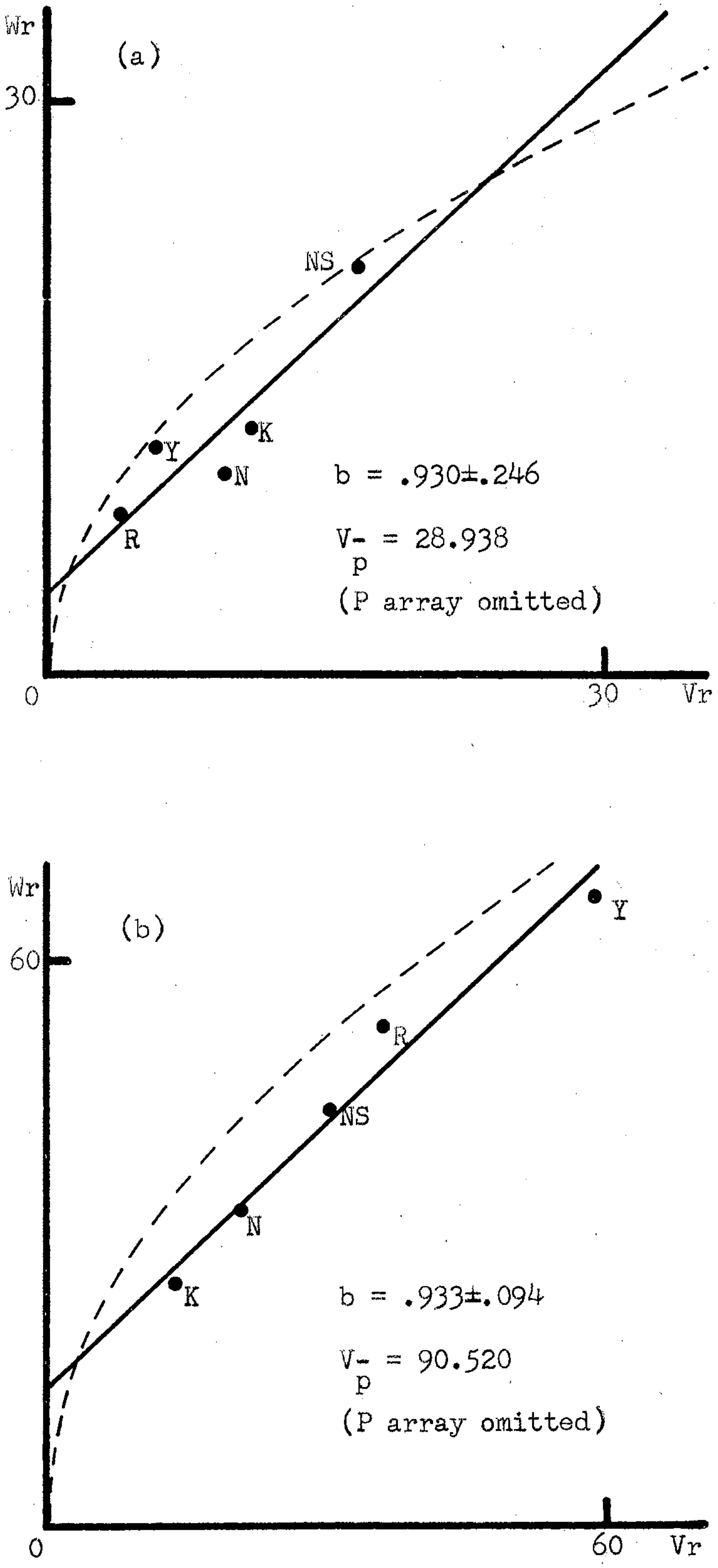

Figure 5. Vr, Wr graphs of F_1 (a) and F_2 (b) families for number of tillers, P array omitted.

with a slope of 1.0 is now evident.

The position of the F_1 regression line with respect to its limiting parabola in Figure 5a indicates the presence of average partial dominance in the gene system controlling tillering capacity. Apparently, positive effects can be attributed to both dominant and recessive alleles insofar as the present group of parents is concerned. It will be noted in this regard that Novi Sad 1421/48 and Kaw had the highest array means (Table XII), and were also the best parents from the standpoint of tilering capacity in the first year of the study when the populations were grown under space-planted conditions. Recessive factors appear to have determined high expression in the case of Novi Sad 1421/48 since the position of the corresponding array point in Figure 5a lies near the upper end of the regression line. However, the more intermediate position occupied by the Kaw array point suggests that the relatively high expression noted in the case of this variety was conditioned by roughly equal proportions of dominant and recessive alleles, or by dominants and recessives of nearly equal effectiveness if some of the involved loci influence tiller development more than others.

Even though analysis of the F_2 data with all arrays included resulted in a significant regression (b=.842±.134) not differing from a slope of 1.0, omission of the Probus array brought about some degree of improvement toward unit slope (b=.933±.094). Apparently, the nonallelic interaction effects previously noted to have a disturbing influence in the F_1 analysis may carry over to some extent into the F_2 generations of certain crosses involving this parent.

The foregoing results agree reasonably well with those of Lupton (31) who also detected interaction among factors determining number of tillers per plant in F_1 and F_2 populations of winter wheat. Analyses involving both F_1 and F_2 generations lead him to conclude that high expression was inherited as a genetic recessive. In the present study, both the six-parent and five-parent F_1 analyses lead to the same conclusion although results obtained in the F_2 analyses suggest that dominant as well as recessive alleles are involved in expression of high tillering capacity. Analyses conducted by Whitehouse et al. (47) on F_1 and F_2 data obtained in a four-parent diallel study involving spring wheat also indicated that both dominants and recessives play a part in determining high tillering. Their results differed from those of Lupton and of the present study in that no definite indications of non-allelic interaction for number of tillers were found.

The fact that the array points in either of the F_2 graphs (Figures 4b, 5b) do not maintain the same relative positions as in the F_1 graphs reflects the failure of certain genotypes to maintain the same relative levels of performance in both years of the study. In the first year, tiller proliferation of a considerable number of the F_1 and parent plants was noticeably suppressed because planting was completed later in the fall than desired, and also because of moisture stress during the period of establishment. The populations most notably affected in terms of inherent capacity to initiate and develop tillers under these circumstances were several of the hybrids having in their parentage either Probus, R. Kolben, or Yeoman C, the varieties least suited to the locality in which the populations were grown. In contrast, the inherent tillering potential of the more adapted varieties and most of the hybrids in which they were involved was in general more fully expressed. As the array variances corresponding to the unadapted varieties were comparatively low, the suppressing effect on tiller proliferation evidently prevented differences among means of those populations having unadapted common parents from being as large as they might have been under more favorable growing conditions. Thus, the positions of the array points representing Probus, R. Kolben, and Yeoman C in Figures 4a and 5a denote the fact that less variation was present among means comprising the arrays involving unadapted varieties as common parents than among means comprising the arrays of the adapted parents.

The position of the C.I. 13678 array in Figure 4a indicates that variation among crosses making up this array was no greater than the variation within the arrays of the unadapted parents. However, in the absence of interaction effects (Figure 5a), the variation within the C.I. 13678 array appears to have increased. Omission of the Probus array from the analysis left the C.I. 13678 array more variable than the R. Kolben and Yeoman C arrays, hence it is probable that the inherent potential of most of the crosses involving this parent was reasonably well expressed.

The conditions under which the F_2's and parents were established were far more favorable than those prevailing in the first year. The extent of tiller development in the second year of the study was presumably affected by plant-to-plant competition since these populations were seeded at a normal rate. As a result, manifestation of the inherent potential of the respective F_2 and parent populations for proliferation of tillers was comparatively normal. In the absence of undue stress, the amount of variability among means of populations related through one or another of the unadapted parents exceeded that among means of populations related through an adapted parent; hence, array variance appears to have been largely a function of the level of adaptation of the particular parent common to the populations of an array. This association between array variance and degree of adaptedness of the parent varieties is apparent from the fact that the array points in Figures 4b and 5b are distributed along the regression lines according to the levels of adaptation of the corresponding common parents. Of the hybrid populations subject to greater degrees of suppression in the F_1, some actually exhibited greater tillering capacity in the F_2 generation than certain related populations which had previously been suppressed to a lesser degree. Comparatively larger differences among population means comprising the arrays of the less well adapted varieties therefore underlie the relatively higher array variances calculated for these varieties and used in plotting the F_2 regressions. Thus, the F_2 data would seem to support the contention that failure on the part of some populations to tiller as well under stress as certain related populations is the primary reason variation among means within the F_1 arrays of the unadapted common parents was less than that among means within the arrays of the adapted parents.

Of the group of F_1 hybrids derived from crosses having Probus as common parent, it may be noted (Appendix Table XV) that only the cross P x N did not show a significant negative deviation from the midparent value. While this particular cross deviated positively in terms of tillering ability, the increase was not significant. Thus, while gene interaction in crosses involving Probus appears to have an important effect on tillering ability, it is unlikely to be useful in obtaining significant yield increases through selection based on tiller number. In view of the heterotic effects noted in the P x N cross for kernel number and kernel weight, selection for high-yielding segregates from this population may be well worthwhile however. In general, since additivity is prominent in the gene system controlling tillering capacity, selection should be limited to the populations producing the largest numbers of tillers in the F_1 and F_2 generations.

Kernel Number. Analyses of number of kernels per plant and per unit area respectively for the F_1 and F_2 generations, with all arrays included, appear in Figure 6. The observed scatter of array points in Figure 6a is essentially random, but the line of regression in Figure 6b, based on F_2 data, does not differ significantly from a line of unit slope. Failure of one or more basic assumptions in the F_1 analysis is evident, and inspection of the F_1 and parent means in Appendix Table XVI shows that, although none of the hybrids exceeded the high parent in number of seeds by a significant margin, five of the hybrids produced either greater or smaller numbers of seeds per plant than both of their respective parents. Consequently, non-allelic interactions appear to exert an important effect on number of seeds, at least in one or more of the following crosses: NS x K, N x K, P x R, P x N, and R x N. Interactions influencing number of kernels should therefore trace primarily to Kaw, C.I. 13678, Novi Sad 1421/48, Probus, or R. Kolben. Of the above crosses, three involve C.I. 13678 as one of the parents, and it may be noted that P x N, R x N, and N x K all produced greater numbers of seeds than their respective better parents. Thus, non-allelic interaction appears to have affected seed production favorably in these crosses. However, the crosses P x R and NS x K produced fewer seeds per plant on the average than either of their respective parents, hence seed number was adversely affected in these crosses.

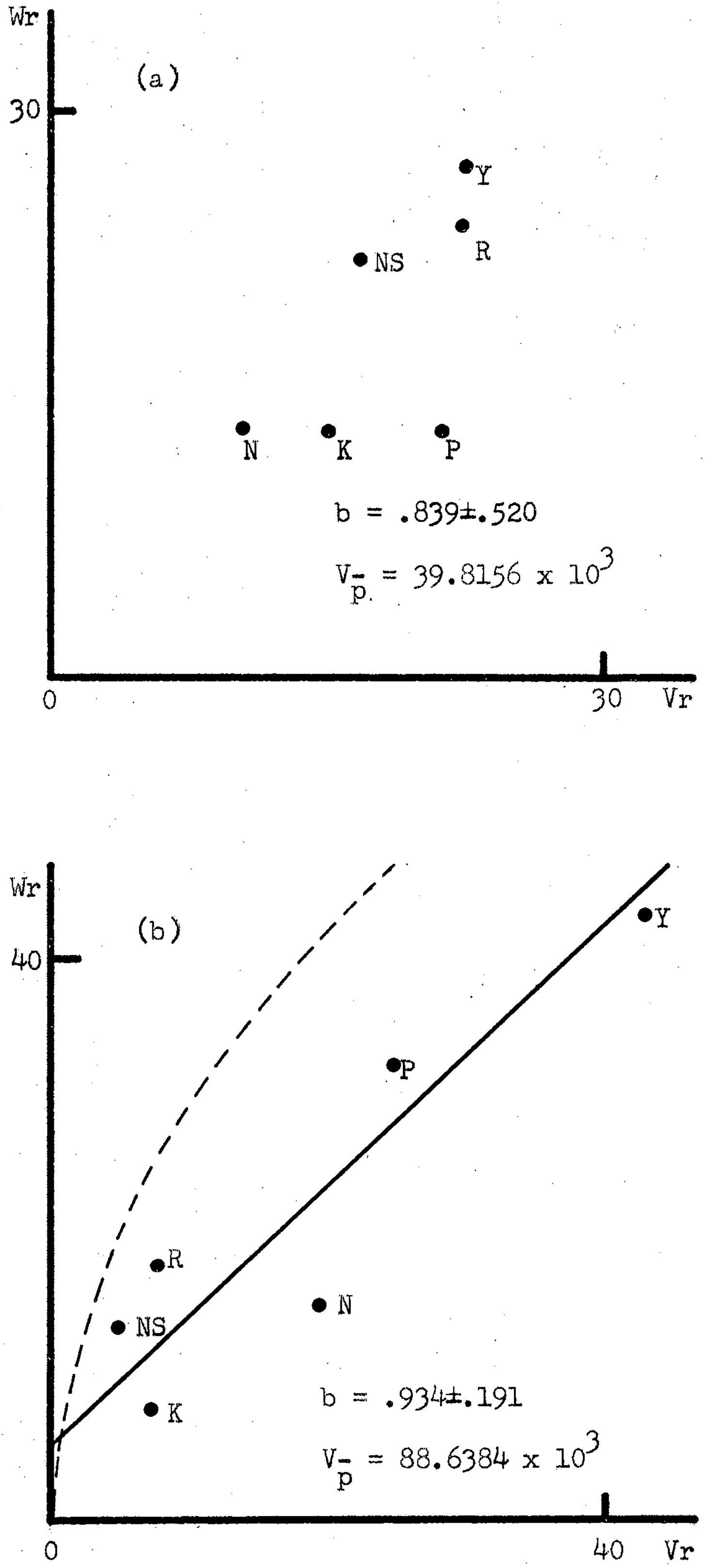

Figure 6. Vr, Wr graphs of F_1 (a) and F_2 (b) families for number of kernels.

With one exception, F_1 analyses conducted with arrays of each of the parent varieties omitted in turn resulted in non-significant regressions. The Vr, Wr regression with the C.I. 13678 array omitted (Figure 7a) is in good agreement with a slope of 1.0 and has positive Wr intercept. Therefore, complementary interactions among loci governing numbers of seeds developed appear to characterize the above three hybrids having C.I. 13678 as a parent. Removal of paired combinations of arrays of the five varieties contributing to interaction resulted in subdiallel groups for which non-significant regression values were obtained. However, significant regressions were obtained in analyses omitting in turn the R. Kolben and C. I. 13678 arrays, the Novi Sad 1421/48 and C.I. 13678 arrays, and the Probus and Kaw arrays (Figures 7b,8). While omission of the C.I. 13678 array alone gave significant improvement in the observed regression ($b=1.133\pm.102$), showing that interaction is largely attributable to the presence of this variety, removal of the above combinations of arrays resulted in values somewhat closer to unity indicating that additional sources of disturbance were eliminated from the analysis. That further improvement in regression was obtained when R. Kolben and Novi Sad 1421/48 were removed along with C.I. 13678 suggests that genes from these varieties also contribute to interactions between loci conditioning seed number in certain of the hybrids involving these parents. Thus, the large negative hybrid-midparent deviation corresponding to the P x R F_1 population (Appendix Table XVI) is apparently attributable to non-allelic interaction which, in this cross, affected seed production in an adverse manner. While the underlying cause of the negative deviation corresponding to the NS x K F_1 population is probably the same, the magnitude of the effect in this case is negligible.

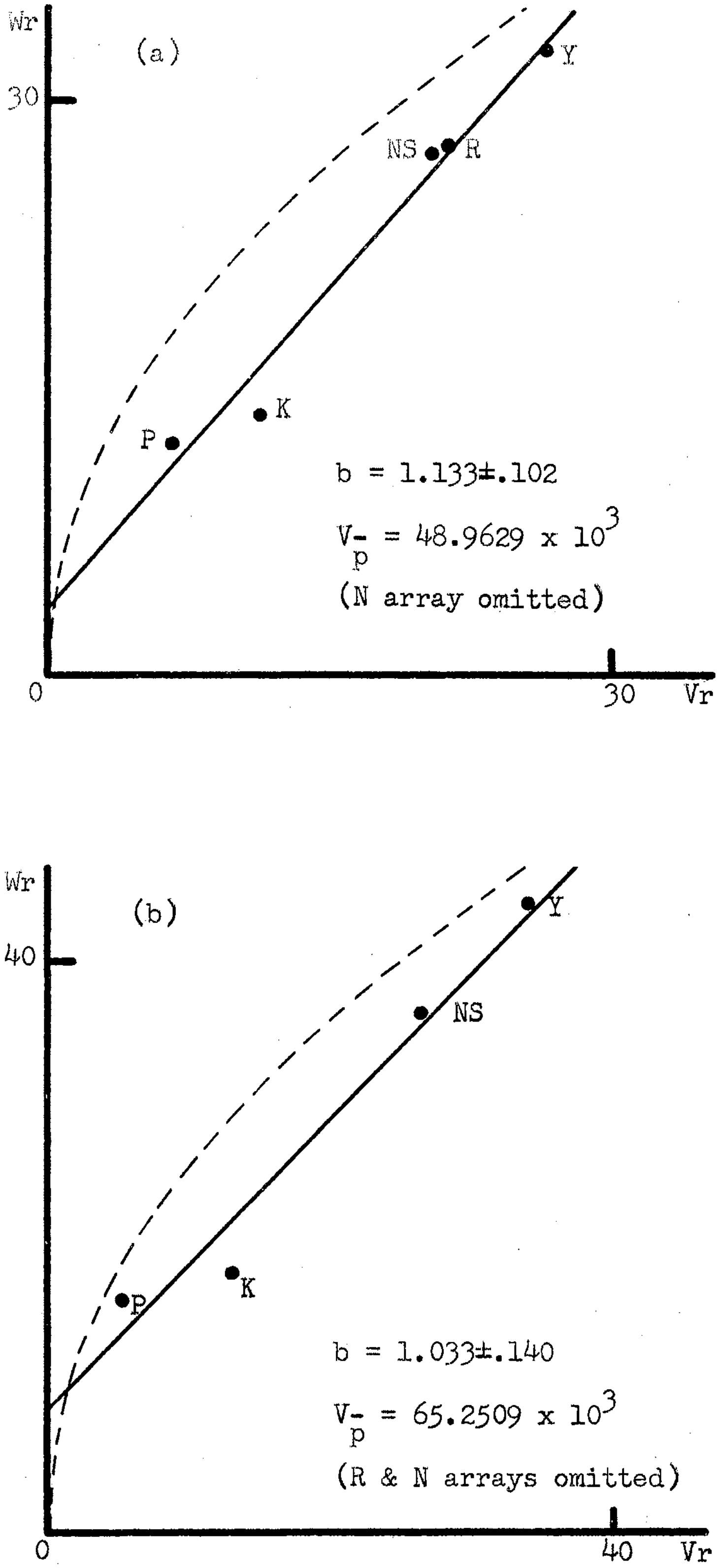

Figure 7. Vr, Wr graphs of F_1 families for number of kernels, (a) N array omitted, (b) R, N arrays omitted.

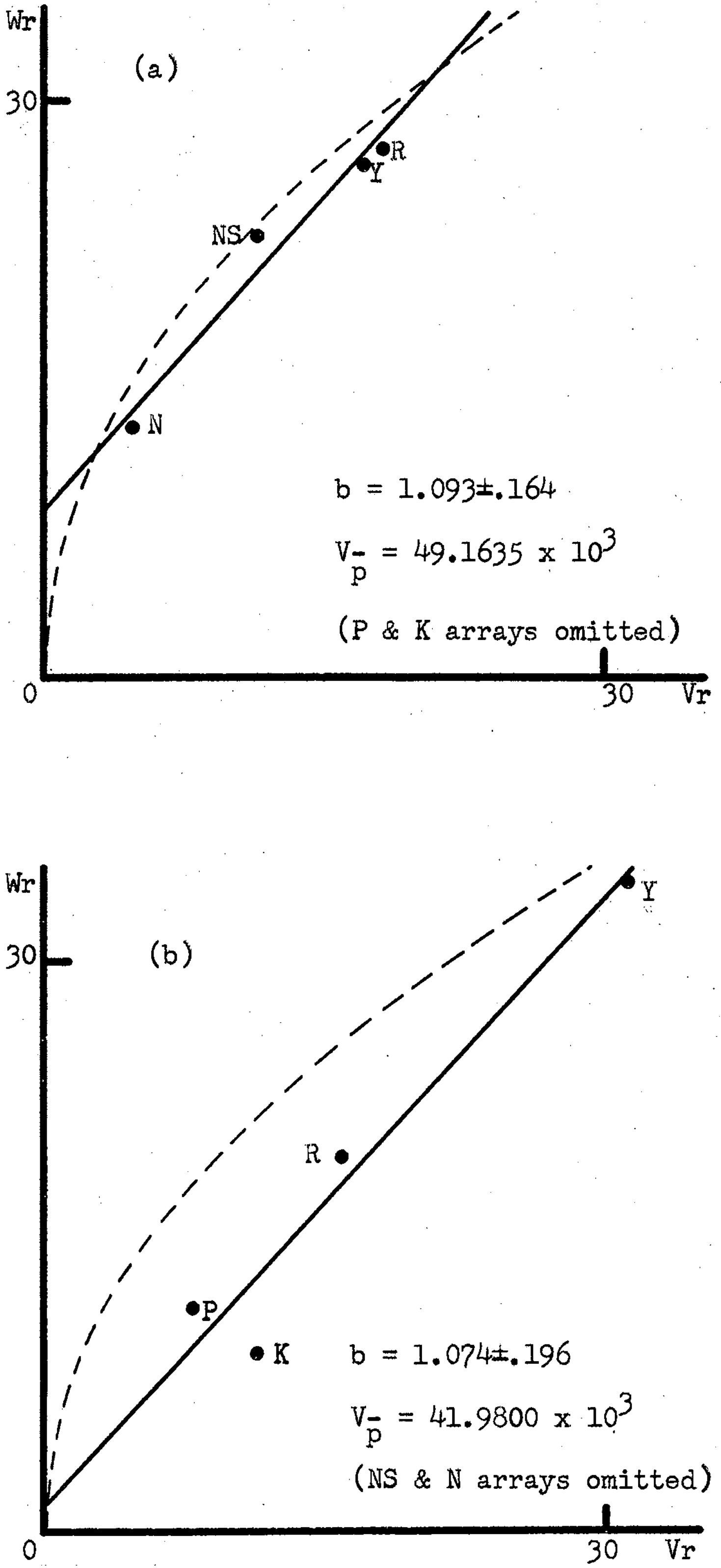

Figure 8. Vr, Wr graphs of F_1 families for number of kernels, (a) P, K array omitted, (b) NS,N arrays omitted.

Analysis with only the Probus array excluded resulted in a regression value that was very nearly significant ($b=1.038\pm.393$, $P=.10-.05$), owing primarily to removal of means of the F_1 populations in which the magnitude of the apparent interaction effects was greatest, i.e. P x R and P x N. Agreement of the regression line in Figure 8a with a slope of 1.0 indicates that omission of the Probus and Kaw arrays together removes additional non-allelic interaction influencing seed number in the crosses NS x K and N x K. In consequence, if interaction is still present in the subdiallel group remaining after removal of the Probus and Kaw arrays, as seems definite at least for the cross R x N, it is not of sufficient magnitude to seriously disturb the graph plotted from analysis of the remaining arrays. Such inference would accord with expectation if non-allelic interaction is indeed the genetic basis of heterosis for seed number, since the degree of heterosis exhibited by the R x N F_1 population relative to the midparent value was not quite significant, even though the average number of seeds per plant was higher in this population than that of the better parent. Thus, the inference based on observation of means in Appendix Table XVI, that interactions between loci influencing seed number are of importance in several crosses, is apparently substantiated by graphical analysis. Also, detection of interallelic interaction as the basis of the small amount of heterosis in the cross R x N suggests that the degree of sensitivity of the graphs is adequate to give a reasonably accurate assessment of the gene system governing seed number in this group of crosses.

Positions of the array points in Figures 7 and 8 indicate that Probus, Kaw, and C.I. 13678 possess relatively high proportions of dominant genes, and Yeoman C, R. Kolben, and Novi Sad 1421/48 possess relatively high proportions of recessives, which condition seed number. Dominant factors appear to determine high expression in terms of seed numbers since both the F_1 and F_2 array means of Kaw and C.I. 13678 exceeded those corresponding to the other parents. However, the relatively high expression noted in the case of Novi Sad 1421/48 may be more dependent upon a preponderance of recessives, or perhaps nearly equal proportions of dominants and recessives. It may be noted upon inspection of the subdiallel graphs that, with the exception of Figure 8a, the average degree of dominance is in each case overestimated. Omission of the Probus and Kaw arrays, as noted previously, removes the main sources of interaction from the analysis. The proximity of the regression line to its limiting parabola in Figure 8a thus indicates that, in the absence of interaction from these sources, the genetic system conditioning seed number in this group of crosses is primarily additive. Omission of the C.I. 13678 array, the R. Kolben and C.I. 13678 arrays, and the Novi Sad 1421/48 and C.I. 13678 arrays respectively resulted in removal of only part of these sources of disturbance; hence, the characteristic influence of interaction, which is to move the regression line away from the parabola, is quite evident in Figures 7a, 7b, and 8b.

The results obtained in the present study relative to the inheritance of seed number are in relatively good agreement with those of Lupton (31) and of Whitehouse et al. (47). Lupton's analyses were based on number of grains per head while those of Whitehouse et al. were based on number of grains per spikelet and number of spikelets per head. Nonallelic interaction was found by Lupton to influence number of grains per head in both the F_1 and F_2 generations. In the present study there is evidence of interaction in the F_1 analyses, but not in the F_2 analysis.

Whitehouse et al. detected no interaction for grains per spikelet in their analysis of F_1 data obtained from spring wheat populations, and essentially none in the F_2 analysis.

Lupton indicated that, in the populations he studied, grains per head was inherited with a completely dominant relationship in the F_1 generation, but as a recessive in F_2. In contrast, results obtained by Whitehouse et al. suggested that dominance played only a small part in determining either number of grains per spikelet, or number of spikelets per head, implying that most of the genes involved were additive in their effects. In the present study, number of seeds per plant was apparently mediated by a primarily additive genetic system, except in certain crosses in which interactions were present.

As in the present case, Lupton found that dominant factors determine high expression in terms of seed numbers. Whitehouse et al. found that high expression in terms of number of spikelets per ear was determined by dominant factors, but also found that, for number of grains per spikelet, the F_1 and F_2 array means corresponding to the parent possessing the highest proportion of dominants were lower than those of the other parents. In addition, the array points corresponding to the parents having the highest array means for grains per spikelet occupied more or less intermediate positions along the regression lines in both the F_1 and F_2 graphs, hence it is possible that high expression of this trait was dependent upon both dominants and recessives.

Since the present results indicate that seed number is conditioned by a primarily additive genetic system in the absence of non-allelic interaction, the crosses producing the greatest numbers of seeds in the F_1 and F_2 generations should be of greatest interest from the standpoint of improving yield through selection of segregates high in seed productivity. The hybrid populations producing the greatest numbers of seeds in both years of the study were generally those including either Kaw or C.I. 13678 in their parentage, hence it is probable that selection efforts should be limited to crosses within the arrays of these two parents. As noted earlier, both the F_1 and F_2 array means corresponding to C.I. 13678 and Kaw exceeded those of the remaining parents. Thus, the cross N x K would seem to be a particularly valuable source of superior genotypes, especially in view of the fact that the F_1 and F_2 populations deriving from this cross exceeded the better parent, and also ranked highest, in numbers of seeds produced in both years of the study. It may be noted (Appendix Table XVI) that, with the exception of the Y x P F_2 population, the only populations which were more prolific than their respective high parents in either year fell within either the C.I. 13678 or Kaw array. The most valuable lines may therefore be expected to come from populations having one of these varieties as a parent even if fixation of genes which interact in favor of higher seed numbers should be the objective of selection. The occurrence of favorable non-allelic interaction in the N x K, P x N, and R x N F_1 populations suggests that superior segregates may be found within these sources. As noted previously, however, the cross N x K is easily the most promising. The relative productiveness of the F_2 generations of the crosses Y x N, Y x K, and P x K indicate that useful genotypes might be selected from these sources as well, although it is doubtful that such selections would be outstanding from the standpoint of overall yield. Since there was no significant difference between the NS x K F_2 mean and the means of the above populations, useful selections might also be obtained from this source.

Kernel Weight. Analyses of weight per 1000 kernels based on all six arrays appear in Figure 9. Since the Vr, Wr regression lines in Figures 9a and 9b are in close proximity to their limiting parabolas, and are in agreement with a line of unit slope, seed weight in this group of crosses appears to be under the control of a primarily additive genetic system. Dominance at loci influencing this character apparently plays only a very small role in its overall inheritance. While the magnitude of the F_1 regression coefficient (.691±.243) is relatively low, this value is nonetheless barely significant (P=.05-.02).

The array points corresponding to the two parents having the highest mean seed weight expression occupy positions near opposite ends of both the F_1 and F_2 regression lines, indicating that high expression is mediated by both dominant and recessive genes, depending on the variety. Since the array points nearest the lower end of the lines correspond to C.I. 13678, high seed weight in this variety is apparently conditioned either by a preponderance of dominant alleles in this parent, or by dominant alleles having large positive effects which weight the position of the array points. The characteristic high seed weight of Kaw, however, appears to depend on a relatively greater proportion of recessive alleles with positive effects.

While the results presented in Figure 9 give no definite indication of failure of any assumptions underlying the analyses, some basis for heterosis other than overdominance is in evidence. Mean seed weights of the P x N and NS x N F_1 populations were significantly greater than that of C.I. 13678, the better parent of each of these crosses. Also, the R x N F_1 mean was in excess of that of C.I. 13678, but in this case heterosis was significant only in relation to the midparent. The pres-

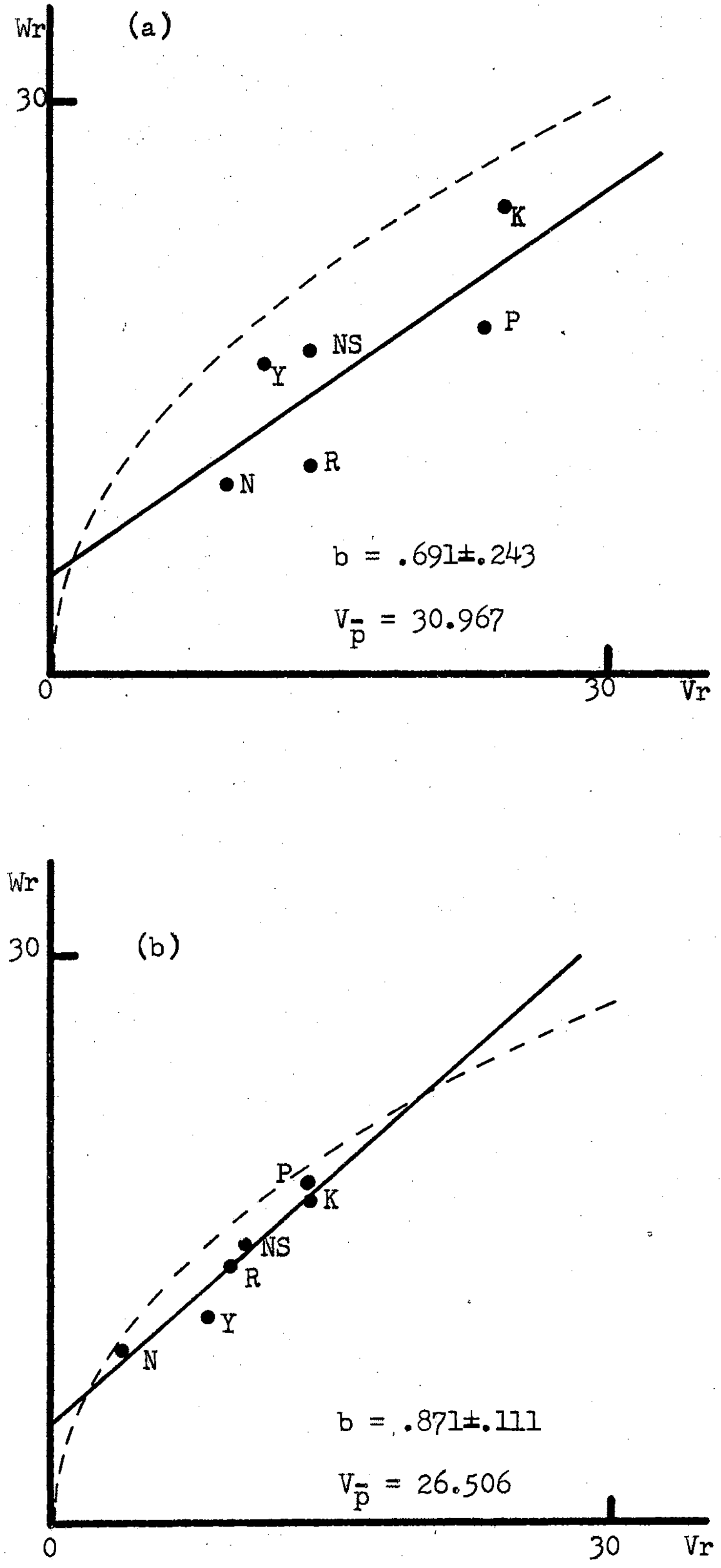

Figure 9. Vr, Wr graphs of F_1 (a) and F_2 (b) families for weight per 1000 kernels.

ence of significant heterosis for seed weight and the rather low F_1 regression coefficient suggest that the F_1 data to not conform to the basic assumption that non-allelic interaction is absent from the hybrid populations. Evidently, interactions of the complementary type among loci affecting seed weight are of importance in the above three crosses, tracing largely to factors contributed by C.I. 13678. Consequently, removal of array means corresponding to this parent and subsequent analysis of the five-parent subdiallel group remaining would be expected to result in a Vr, Wr regression more closely approximating a line of unit slope. As shown in Figure 10, omission of the C.I. 13678 array did result in a considerably improved regression ($b=.885\pm.219$).

The position of the array point representing Kaw in Figure 10 is farthest from the origin and is in fact near the point of intersection of the regression line and limiting parabola. Thus it is probable that, among parents in the present group, Kaw is the only variety having a nearly complete complement of recessive alleles which govern seed weight. Since the array point corresponding to Probus now occupies an intermediate position, this variety is unlikely to possess as high a proportion of recessives as Kaw.

The present results are generally similar to those obtained by Lupton (31) and by Whitehouse et al. (47). Lupton observed non-allelic interaction in an F_1 population, however seed weight was influenced in an unfavorable manner. In the present case, seed weight was apparently influenced favorably in at least three crosses. In the absence of non-allelic interaction Lupton found, as in the present study, that the character, 1000-kernel weight, was inherited with very little dominance. No evidence of non-allelic interaction was observed by Whitehouse et al.

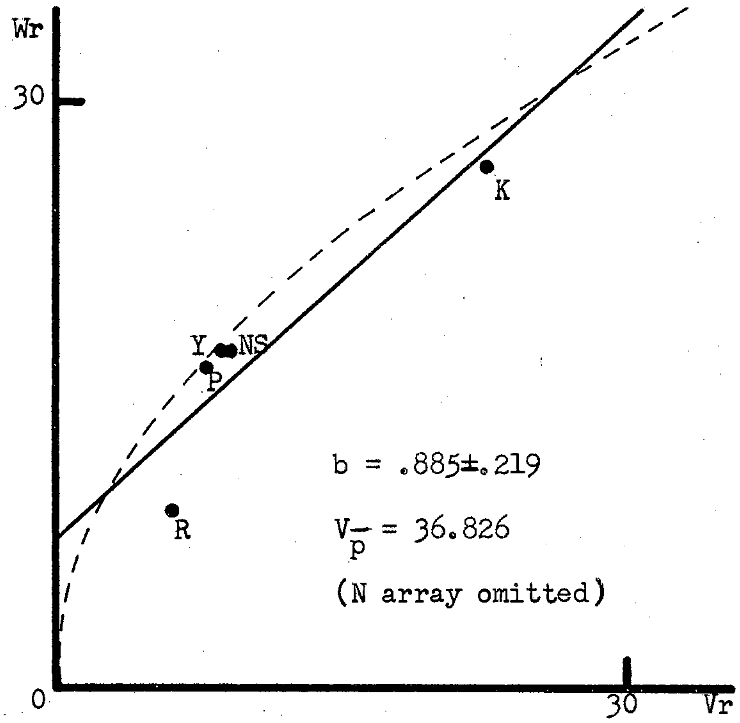

Figure 10. Vr, Wr graph of F_1 families for weight per 1000 kernels, N array omitted.

in either F_1 or F_2 analyses. They concluded that high expression in terms of seed weight was determined by recessive genes. In the present study, and in the study conducted by Lupton, both dominant and recessive alleles were implicated in the control of seed weight depending on the variety considered.

Due to the prevalence of additivity in the gene system controlling seed weight, the crosses with the highest F_1 and F_2 means should provide the best source material for selection of lines superior in test weight. Consequently, the greatest potential for improving this trait apparently lies with the cross between Kaw and C.I. 13678. Inasmuch as C.I. 13678 contrasts with Kaw in having a high proportion of dominant alleles, or a proportion of dominants with relatively large positive effects on seed weight, the best cross derives from the two parents differing most in their gene systems. Parental diversity would seem to favor the chances of obtaining N x K segregates transgressing Kaw in seed weight, especially in view of the fact that the 1000-kernel weight average of the F_2 generation of this cross was essentially equal to that of Kaw. Similarly, selection within the NS x K and P x K populations should result in improvement in seed weight since no significant difference was observed between the F_2 means of these crosses and the N x K F_2 mean. Considering the probability that the interaction effects noted earlier are of significant magnitude, improvement may also be expected to result from selection within the P x N and NS x N populations owing to fixation of alleles interacting favorably toward high seed weight.

Yield. Vr, Wr analyses of yield per plant and per unit area for the F_1 and F_2 generations respectively are presented in Figure 11. The regression coefficient obtained in the F_1 analysis (Figure 11a) does not differ significantly from zero, hence a random scatter of array points is indicated. Average partial dominance is implicated in the inheritance of yielding capacity as indicated by the position of the F_2 regression line (Figure 11b) although its proximity to the limiting parabola suggests that the dominance effect is rather small. This graph also indicates that high yield expression is conditioned by dominant and low expression by recessive genes since array points corresponding to the common parents having the highest array means in both the F_1 and F_2 generations occupy positions nearer the lower end of the F_2 regression line and, conversely, parents having lower array means occupy positions farther from the origin. That dominance lies in the direction of higher yields is further evident upon inspection of the deviation of the mean yields of the hybrids from their respective midparent values

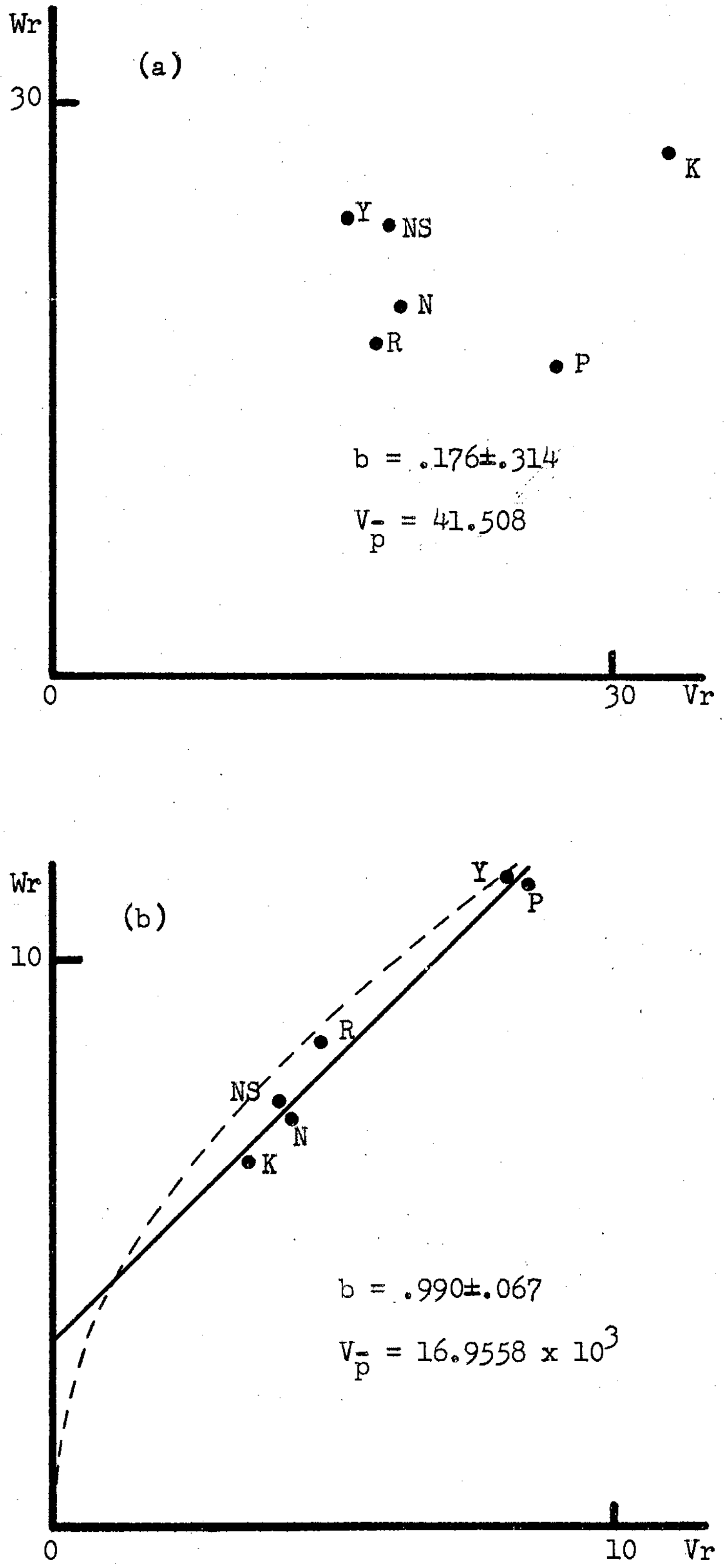

Figure 11. Vr, Wr graphs of F_1 (a) and F_2 (b) families for yield.

(Appendix Table XVIII). On the average, positive deviations exceeded the negative deviations for both generations as would be expected if dominance favors higher yields. The fact that the array points corresponding to Kaw, C.I. 13678, and Novi Sad 1421/48 in Figure 11b occupy intermediate positions along the F_2 regression line implies that both dominant and recessive alleles determine the yielding capacity of these varieties, although the proportion of dominant alleles present may be somewhat greater than the proportion of recessives.

The F_2 regression coefficient (.990±.067) is highly significantly different from zero, but is not significantly different from 1.0, hence there is no evidence that non-allelic interaction influenced yields in the F_2 populations. However, the scatter of array points in the F_1 graph suggests failure of the basic assumption of no interaction between factors influencing yield. Some type of interaction would appear to condition yielding ability of certain crosses among the group of varieties used in this study since all of the F_1's involving C.I. 13678 exhibited significant heterosis relative to the midparent (Appendix Table XVIII), and all but one of these hybrids exceeded the better parent in average yield per plant. In the case of complete dominance for yielding ability, hybrid performance would be expected to equal but not exceed that of the better parent. Hence, the interaction postulated is probably of the complementary type since it enhanced rather than reduced yields, at least in the P x N population and possibly in others as well.

Insofar as the present group of crosses is concerned, interaction effects are localized primarily within the C.I. 13678 array. This accords with expectation since only one other F_1 population besides those noted in the C.I. 13678 array performed outside of the range of both parents, (viz. P x R). Thus, in a re-analysis involving F_1 means of the subdiallel group remaining after omission of the Probus array, some improvement in the regression coefficient was obtained (b=.394±.315), and a very marked improvement (b=.941±.363) was obtained upon omission of both the Probus and C.I. 13678 arrays (see Appendix Table XXII for a summary of Vr, Wr regression coefficients for the six traits involved in this study). However, excessively high standard errors of the same magnitude as that shown in Figure 11a were in evidence, therefore these regression coefficients are not significant. It is very probable that the unusually high standard errors are due to environmental stress during the period of establishment of the hybrid seedlings. As mentioned earlier, planting in 1963 was completed rather late in the fall and under drouthy conditions, hence real reductions in yield of many of the hybrid and parent plants resulted, most notably from effective curtailment of tillering. The marked influence of the relatively short period between planting and the onset of low winter temperatures was very likely due in part to less direct effects on other components as well, especially in the case of the parent varieties which were not well adapted to the region and some of the crosses involving them.

Results obtained in the present study relative to yield and the components of yield are in general quite similar to those of Lupton (31) and of Whitehouse et al. (47). Lupton's results, based on a diallel study involving six winter wheat varieties, indicated that yielding capacity was inherited with a completely dominant relationship in the absence of non-allelic interaction. Results obtained in the present F_1 analysis, and in F_1 and F_2 analyses conducted by Whitehouse et al., were rather inconclusive insofar as the average degree of dominance involved in the inheritance of yielding capacity is concerned because of the complicating effects of non-allelic interaction. As noted previously, however, average partial dominance for yield was indicated in the present F_2 analysis.

Whitehouse et al. (47) detected non-allelic interaction for yield as an aggregate character in both F_1 and F_2 analyses, but found little indication of such interaction in separate analyses of yield component data obtained from F_1 and F_2 populations. Non-allelic interaction was attributed to the presence of specific parent varieties in their F_2 yield analysis, but could not be confidently localized to particular genotypes in the F_1 analysis. Lupton's evidence was similar to that obtained in the present study in that interaction between factors determining yield was detected in F_1, but not in F_2 analyses. In both of these studies it was possible to localize the observed interaction.

In view of the present evidence, yield heterosis can apparently be attributed, at least in part, to the occurrence of non-allelic interactions probably of the complementary type, in certain of the populations exhibiting hybrid vigor. Considering that the varieties employed as parents in the present study encompassed a diversity of types, having been developed under contrasting environmental conditions and presumably possessing widely variable gene systems as a result, it does not seem improbable that interaction effects are to some extent a function of the degree of divergence among the genetic systems governing yielding capacities of the parents. Lupton (31) and Whitehouse et al. (47) submit that different gene systems may contribute to yield in different environments. Thus, if the divergence in gene systems is greatest among varieties selected in widely different climates, a reasonable basis may exist for expecting relatively greater heterotic responses in crosses between such varieties than between types selected in the same geographical area. In the perspective of present results the foregoing is perhaps provisionally acceptable since all but one of the four F_1 populations having higher average yields per plant than their respective better parents were derived from crosses between indigenous and foreign varieties. Furthermore, the F_1 population exhibiting the greatest heterotic response observed in the present study, and which incidentally exceeded the high parent in average yield per plant by a significant margin despite the adversities described earlier, derived from the cross between Probus, a Swiss variety, and C.I. 13678, an indigenous type.

As the F_1 populations which exceeded their respective better parents in average yield per plant are included within the C.I. 13678 array, it is quite likely that the relatively high array mean corresponding to this variety (Table XII) is attributable to non-allelic interactions favoring higher yields. In the event that the apparent interaction effects are of significant magnitude, the chances of obtaining high yielding selections out of crosses in which C.I. 13678 was involved would seem excellent if factors which interact in a manner favorable to high yield can be fixed in inbred lines. Selection within the N x K, NS x N, P x N, and R x N populations should consequently give the most valuable types. In view of the fact that the NS x K F_2 population mean did not differ significantly from that of Kaw, the high parent (Appendix Table XVIII), selection within segregating generations of this cross should also prove to be worthwhile.

CHAPTER V

SUMMARY AND CONCLUSIONS

Heterosis, combining ability, and certain variance-covariance relationships were studied in a diallel cross involving six common winter wheat varieties of diverse geographical origin. Parental and F_1 populations were grown as space-plants in 1963-64, and F_2 bulk and parent populations were grown in normal stands in 1964-65. Characters for which analyses were conducted included heading date, plant height, yield, number of tillers, number of kernels, and weight per 1000 kernels. Certain quality traits were also evaluated, but were not analyzed statistically.

High-parent and midparent heterosis was evaluated in both the F_1 and F_2 generations. Estimates of general and specific combining ability variances and effects based on F_1 data were obtained to determine the relative importance of additive and non-additive effects of genes influencing character expression. Variance-covariance regression analyses were applied to F_1 and F_2 data to obtain information relative to the over-all genetic systems controlling the various traits, and to identify parental combinations having the greatest selection potential.

Significant midparent heterosis was observed in six F_1 and six F_2 populations for earliness of heading, but none of the F_1 or F_2 populations exhibited heterosis relative to their respective earlier parents. Only two populations, one F_1 and one F_2, exceeded their respective taller parents in mean plant height by a significant margin, although the means of 10 F_1 and 9 F_2 populations were somewhat greater than those of their taller parents. Thirteen F_1 and 7 F_2 populations exhibited significant midparent heterosis for plant height. Mean yields per plant among the F_1 populations ranged from 45 to 141% of the respective high-parent means. Yield heterosis relative to the high parent was found to be significant in only one F_1 population (P x N), and was attributable to high-parent heterosis for seed weight and midparent heterosis for seed number. Four additional hybrids (NS x N, R x N, Y x N, N x K) exhibited significant heterosis for yield per plant, but only in relation to the midparent. In each of these crosses, significant heterosis for seed weight was also observed, although seed numbers appeared to be of greater importance as a yield component than seed weight in the cross N x K. Significant midparent heterosis was observed in certain F_2 populations for yield as well as for number and weight of kernels, but no cases of high-parent heterosis for yield or any of the yield components were found in the F_2. The present results suggest that relatively high yielding wheat hybrids may be obtained from crosses involving broadly diverse genotypes due to high expression in one or more yield components.

Relatively wide ratios of general to specific combining ability variances were obtained for certain traits indicating that the total genetic variability in the F_1 populations was predominately due to additive effects of genes. Significant general combining ability effects were associated with the varieties C.I. 13678, Kaw, and Novi Sad 1421/48 for earliness of heading and yield per plant as well as for each yield component. The variety C.I. 13678 exhibited the greatest general combining ability for earliness, yield, number of kernels, and kernel weight, while Novi Sad 1421/48 and Kaw had the greatest general combining ability for number of tillers per plant. Positive general effects for plant height were exhibited only by Novi Sad 1421/48 and Kaw. Significant negative specific combining ability effects for days to head were exhibited by four crosses, two of which involved the semi-dwarf parent C.I. 13678. Two crosses had significant positive specific effects for plant height, and only one cross had a significant negative specific effect for height. Five of the 15 crosses exhibited significant specific combining ability for yield per plant. The largest positive specific comining ability effects for earliness of heading, yield, and each yield component was associated with the cross P x N and the second largest effects with the cross, NS x R. Lesser, although significant, specific effects were observed for certain other crosses with respect to these traits. In view of the relatively high proportion of crosses exhibiting significant specific combining ability effects for yield, the chances of obtaining favorable combinations that will give a high level of yield heterosis appear to be reasonably good.

Genetic analyses based on variance-covariance regressions were generally in agreement with results obtained in combining ability analyses. The genetic system controlling number of days to head was found to be almost exclusively additive. Average dominance at loci governing plant height was nearly complete in the analysis of F_1 data, but non-allelic interactions appeared to influence height expression in certain F_2 populations. Non-allelic interactions were detected in analyses of F_1 data for yield and for each yield component. Heterosis observed in certain F_1 populations for yield, seed number, and seed weight was thus attributable in part to the occurrence of interactions among loci affecting these traits. In the absence of interaction effects, additivity was found to be prevalent in the genetic system controlling each character. The prevalence of additive genetic variability for the traits studied indicates that selection procedures leading to the isolation of superior homozygous lines could be effectively practiced in breeding for yield improvement. However, the occurrence of significant heterosis and evidence of non-additive genetic effects for yield, seed weight, and seed numbers suggest that the use of F_1 hybrids would also be effective provided that complementary inbreds having a sufficiently broad genetic base can be obtained.

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APPENDIX

TABLE XIII

MEAN NUMBER OF DAYS TO HEADING OF PARENTS, F_1, AND F_2 GENERATIONS, MULTIPLE RANGE COMPARISONS, AND DEVIATIONS OF HYBRID FROM MIDPARENT POPULATION MEANS

F_1's and Parents	Days to Head/1	Rank	Ranges of Ranked Means /2	Deviation of Hybrids from Midparents /3	F_2's and Parents	Days to Head /1	Rank	Ranges of Ranked Means /2	Deviation of Hybrids from Midparents /4
K	30.4	1	1 - 3	-	N	30.2	1	1 - 3	-
N x K	30.6	2	-	-0.42	N x K	31.0	2	-	0.13
N	31.5	3	3 - 5	-	K	31.5	3	3 - 4	-
NS x K	32.9	4	4 - 7	0.17	NS x N	32.7	4	4 - 7	-0.37
NS x N	33.2	5	5 - 8	-0.09	NS x K	34.2	5	5 - 10	0.50
R x N	34.4	6	-	-3.14**	R x N	34.2	6	-	-2.50**
P x N	34.6	7	-	-3.42**	P x N	34.7	7	-	-2.50**
NS	35.1	8	8 - 9	-	Y x N	35.2	8	8 - 11	-3.25**
NS x R	36.8	9	9 - 11	-2.58**	NS	36.0	9	9 - 12	-
Y x K	37.6	10	10 - 12	-2.25**	P x K	36.5	10	-	-1.37**
Y x N	38.2	11	11 - 15	-2.17*	NS x R	37.2	11	11 - 13	-2.37**
P x K	39.3	12	-	1.86*	R x K	38.0	12	-	0.63
R x K	39.9	13	-	2.86**	NS x P	38.7	13	13 - 15	-1.37**
Y x NS	40.0	14	-	-2.25**	Y x K	40.2	14	-	1.13*
NS x P	40.4	15	-	0.56	Y x NS	40.5	15	-	-0.87
R	43.6	16	16 - 18	-	P x R	43.0	16	16 - 18	-0.75
P	44.5	17	17 - 19	-	R	43.2	17	-	-
Y x R	45.6	18	18 - 20	-0.86	P	44.2	18	18 - 20	-
P x R	46.0	19	-	1.97*	Y x R	45.5	19	19 - 21	0.50
Y x P	47.0	20	-	0.06	Y x P	46.0	20	-	0.50
Y	49.3	21	-	-	Y	46.7	21	-	-

/1 Number of days after March 31st.

/2 Means within each range are not significantly different

/3 *--Exceeds LSD .05 = 1.66; **--Exceeds LSD .01 = 2.23.

/4 *--Exceeds LSD .05 = 0.89; **--Exceeds LSD .01 = 1.18.

TABLE XIV

MEAN PLANT HEIGHT OF PARENTS, F_1, AND F_2 GENERATIONS, MULTIPLE RANGE COMPARISONS, AND DEVIATIONS OF HYBRID FROM MIDPARENT POPULATION MEANS

F_1's and Parents	Plant Height (cm.)	Rank	Ranges of Ranked Means/1	Deviation of Hybrids from Midparents/2	F_2's and Parents	Plant Height (cm.)	Rank	Ranges of Ranked Means/1	Deviation of Hybrids from Midparents/3
NS x P	94.7	1	1 - 10	5.7**	NS x P	101.5	1	1 - 11	6.4*
NS x K	94.3	2	2 - 11	3.6*	P x K	100.0	2	2 - 12	9.2**
Y x NS	94.3	3	-	11.0**	NS x R	99.3	3	3 - 14	2.8
P x K	92.4	4	4 - 12	4.6**	Y x NS	98.4	4	4 - 15	5.5*
N x K	92.3	5	-	10.0**	P x R	98.2	5	-	3.0
NS	91.9	6	-	-	Y x K	97.8	6	-	9.1**
NS x R	91.6	7	-	4.1	R x K	97.4	7	7 - 16	5.2*
NS x N	91.2	8	-	7.6**	R	96.6	8	8 - 17	-
Y x K	91.1	9	-	9.1**	NS	96.3	9	-	-
R x K	90.9	10	-	4.6*	NS x K	95.1	10	10 - 18	3.0
P x N	89.9	11	11 - 13	9.3**	Y x R	94.8	11	11 - 19	1.7
K	89.4	12	-	-	P	93.8	12	12 - 20	-
P	86.0	13	13 - 18	-	Y x N	93.1	13	-	7.1**
P x R	85.1	14	14 - 19	0.5	P x N	92.9	14	-	4.8
Y x P	84.8	15	-	4.5*	N x K	92.4	15	-	7.2**
R x N	84.2	16	-	5.0**	Y x P	90.8	16	-	-0.9
Y x N	83.9	17	-	9.0**	R x N	90.0	17	-	0.5
R	83.2	18	-	-	Y	89.6	18	-	-
Y x R	81.2	19	-	2.3	NS x N	88.2	19	19 - 21	-1.2
N	75.2	20	20 - 21	-	K	87.9	20	-	-
Y	74.6	21	-	-	N	82.4	21	-	-

/1 Means within each range are not significantly different.
/2 *--Exceeds LSD .05 = 3.5; **--Exceeds LSD .01 = 4.6.
/3 *--Exceeds LSD .05 = 4.9; **--Exceeds LSD .01 = 6.5.

TABLE XV

MEAN NUMBER OF TILLERS OF PARENTS, F_1, AND F_2 GENERATIONS, MULTIPLE RANGE COMPARISONS, AND DEVIATIONS OF HYBRID FROM MIDPARENT POPULATION MEANS

F_1's and Parents	Tillers Per Plant	Rank	Ranges of Ranked Means /1	Deviation of Hybrids from Midparents /2	F_2's and Parents	Tillers Per Ft.^{2}	Rank	Ranges of Ranked Means /1	Deviation of Hybrids from Midparents /3
NS	26.9	1	1 - 2	-	N x K	55.8	1	1 - 3	3.8
K	23.5	2	2 - 4	-	K	54.9	2	2 - 7	-
NS x K	22.8	3	3 - 5	-2.4	NS x K	52.5	3	3 - 10	0.5
N x K	21.3	4	4 - 7	2.0	Y x K	49.7	4	4 - 12	7.0
NS x R	19.4	5	5 - 14	-2.1	NS x R	49.4	5	-	4.8
Y x NS	18.6	6	6 - 15	-2.8	NS	49.1	6	-	-
Y x K	17.8	7	7 - 16	-1.9	N	49.0	7	-	-
P x N	17.1	8	8 - 19	1.3	P x K	48.1	8	-	4.6
NS x N	16.6	9	-	-4.3**	R x K	46.8	9	9 - 14	-0.8
P	16.5	10	-	-	R x N	46.7	10	-	2.1
R	16.2	11	-	-	NS x N	45.8	11	11 - 15	-3.2
Y	15.9	12	12 - 20	-	Y x N	44.3	12	12 - 17	4.5
R x K	15.8	13	-	-4.0*	NS x P	41.6	13	-	1.1
R x N	15.7	14	-	0.1	P x N	40.6	14	14 - 19	0.1
N	15.0	15	-	-	R	40.2	15	-	-
Y x R	13.8	16	16 - 21	-2.2	P x R	38.8	16	-	2.7
NS x P	13.2	17	-	-9.5**	Y x NS	38.1	17	-	-1.7
Y x N	13.1	18	-	-2.4	Y x P	34.9	18	18 - 21	3.6
P x K	13.0	19	-	-7.0**	Y x R	34.8	19	-	-0.6
Y x P	11.6	20	-	-4.6**	P	32.0	20	-	-
P x R	10.6	21	-	-5.8**	Y	30.6	21	-	-

/1 Means within each range are not significantly different.

/2 *--Exceeds LSD .05 = 3.22; **--Exceeds LSD .01 = 4.31.

/3 LSD .05 = 4.805.

TABLE XVI

MEAN NUMBER OF KERNELS OF PARENTS, F_1, AND F_2 GENERATIONS, MULTIPLE RANGE COMPARISONS AND DEVIATIONS OF HYBRID FROM MIDPARENT POPULATION MEANS

F_1's and Parents	Kernels Per Plant	Rank	Ranges of Ranked Means /1	Deviation of Hybrids from Midparents /2	F_2's and Parents	Kernels Per $Ft.^2$	Rank	Ranges of Ranked Means /1	Deviation of Hybrids from Midparents /3
N x K	784.1	1	1 - 5	152.9**	N x K	1266.1	1	1 - 4	105.7*
NS	740.5	2	2 - 9	-	Y x N	1194.7	2	2 - 7	257.0**
K	696.1	3	3 - 10	-	N	1178.5	3	-	-
NS x K	685.6	4	-	-32.7	Y x K	1175.1	4	-	255.5**
P x N	660.2	5	5 - 11	187.0**	K	1142.2	5	5 - 9	-
NS x N	628.4	6	6 - 14	-24.9	P x K	1093.7	6	6 - 10	156.0**
R x N	626.1	7	-	95.4	NS x K	1073.2	7	7 - 12	- 9.8
NS x R	625.2	8	-	7.4	R x K	1026.0	8	8 - 15	27.6
Y x K	608.5	9	-	156.4**	NS	1023.9	9	-	-
N	566.2	10	10 - 15	-	NS x N	990.2	10	-	-110.9*
R x K	529.3	11	11 - 16	-66.3	R x N	962.9	11	11 - 16	- 53.7
R	495.1	12	12 - 17	-	P x N	948.7	12	12 - 17	42.9
Y x NS	480.9	13	13 - 18	6.7	NS x R	942.8	13	-	3.5
Y x N	480.8	14	-	93.7	NS x P	911.9	14	14 - 19	83.4
P x K	448.1	15	-	-90.1	Y x NS	899.1	15	-	38.7
NS x P	399.2	16	16 - 20	-161.2**	R	854.7	16	-	-
P	380.3	17	-	-	Y x R	835.4	17	-	59.5
Y x R	344.9	18	18 - 21	- 6.7	P x R	815.2	18	-	71.3
Y x P	275.4	19	-	-18.7	Y x P	796.9	19	19 - 20	131.8**
P x R	263.4	20	-	-174.3**	Y	697.1	20	20 - 21	-
Y	208.0	21	-	-	P	633.2	21	-	-

/1 Means within each range are not significantly different.
/2 LSD .05 = 109.8; **--Exceeds LSD .01 = 146.9.
/3 *--Exceeds LSD .05 = 95.8; **--Exceeds LSD .01 = 127.5.

TABLE XVII

MEAN WEIGHT PER 1000 KERNELS OF PARENTS, F_1, AND F_2 GENERATIONS, MULTIPLE RANGE COMPARISONS, AND DEVIATIONS OF HYBRID FROM MIDPARENT POPULATION MEANS

F_1's and Parents	Weight Per 1000 Ker. (gms.)	Rank	Ranges of Ranked Means /1	Deviation of Hybrids from Midparents /2	F_2's and Parents	Weight Per 1000 Ker. (gms.)	Rank	Ranges of Ranked Means /1	Deviation of Hybrids from Midparents/3
K	29.09	1	1 - 4	-	K	30.79	1	1 - 2	-
N x K	29.07	2	-	3.42**	N x K	29.97	2	2 - 4	1.31
P x N	27.24	3	3 - 5	7.90**	NS x K	28.84	3	3 - 6	0.52
NS x N	27.08	4	-	5.52**	P x K	27.24	4	4 - 10	1.95
NS x K	25.75	5	-	0.75	NS x N	26.97	5	-	0.78
R x N	23.09	6	6 - 9	4.81**	N	26.53	6	-	-
N	22.22	7	7 - 11	-	NS	25.86	7	7 - 11	-
Y x N	22.06	8	-	3.31**	P x N	25.28	8	8 - 13	2.12
P x K	21.31	9	9 - 12	-1.46	Y x N	25.19	9	-	2.27*
Y x K	20.95	10	10 - 13	-1.24	R x N	24.95	10	-	2.84*
NS	20.91	11	-	-	NS x R	23.55	11	11 - 14	1.77
NS x R	19.57	12	12 - 14	1.95*	R x K	22.82	12	12 - 15	-1.42
Y x NS	19.14	13	-	1.04	NS x P	22.51	13	13 - 16	-0.32
NS x P	18.27	14	14 - 16	-0.41	Y x K	21.98	14	14 - 18	-3.07**
R x K	16.91	15	15 - 18	-4.80**	Y x NS	20.15	15	15 - 21	-2.44*
P	16.45	16	-	-	P	19.80	16	-	-
Y x P	15.54	17	17 - 21	-0.33	P x R	19.61	17	-	0.86
Y	15.29	18	-	-	Y	19.32	18	-	-
R	14.33	19	-	-	Y x R	17.92	19	-	-0.59
P x R	14.17	20	-	-1.22	R	17.70	20	-	-
Y x R	13.93	21	-	-0.88	Y x P	17.63	21	-	-1.93

/1 Means within each range are not significantly different.

/2 *--Exceeds LSD .05 = 1.62; **--Exceeds LSD .01 = 2.17.

/3 *--Exceeds LSD .05 = 2.25; **--Exceeds LSD .01 = 2.99.

TABLE XVIII

MEAN YIELDS OF PARENTS, F_1, AND F_2 GENERATIONS, MULTIPLE RANGE COMPARISONS, AND DEVIATIONS OF HYBRID FROM MIDPARENT POPULATION MEANS

F_1's and Parents	Yield Per Plant (gms.)	Rank	Ranges of Ranked Means /1	Deviation of Hybrids from Midparents /2	F_2's and Parents	Yield Per Plot (gms.)	Rank	Ranges of Ranked Means /1	Deviation of Hybrids from Midparents /3
N x K	22.88	1	1 - 2	6.40**	N x K	497.11	1	1 - 4	44.55
K	20.22	2	2 - 4	-	K	463.71	2	2 - 5	-
P x N	17.98	3	3 - 6	8.49**	N	441.40	3	-	-
NS x K	17.75	4	4 - 7	-0.13	NS x K	438.79	4	-	33.69
NS x N	16.95	5	-	2.82*	P x K	423.65	5	5 - 7	98.43**
NS	15.53	6	6 - 10	-	Y x N	376.02	6	6 - 13	66.44**
R x N	14.54	7	-	4.63**	Y x K	365.65	7	-	44.91
Y x K	12.87	8	8 - 12	1.17	NS x N	361.69	8	-	-32.25
N	12.73	9	-	-	NS	346.48	9	9 - 14	-
NS x R	12.23	10	10 - 14	0.92	R x K	344.22	10	-	7.53
Y x N	10.81	11	11 - 15	2.85*	P x N	340.77	11	-	26.71
P x K	9.64	12	12 - 16	-3.58**	R x N	332.29	12	-	6.75
Y x NS	9.26	13	13 - 17	-0.10	NS x R	325.01	13	-	46.93
R x K	9.12	14	-	-4.54**	NS x P	285.16	14	14 - 16	18.56
NS x P	7.55	15	15 - 19	-3.33*	Y x NS	255.53	15	15 - 18	-6.59
R	7.09	16	16 - 20	-	P x R	239.19	16	16 - 21	40.99
P	6.23	17	17 - 21	-	R	209.67	17	-	-
Y x R	4.87	18	-	-0.27	Y x P	195.61	18	-	13.37
Y x P	4.46	19	-	-0.25	Y x R	187.72	19	-	-6.00
P x R	3.96	20	-	-2.70*	P	186.72	20	-	-
Y	3.18	21	-	-	Y	177.76	21	-	-

/1 Means within each range are not significantly different.

/2 *--Exceeds LSD .05 = 2.58; **--Exceeds LSD .01 = 3.45.

/3 *--Exceeds LSD .05 = 48.61; **--Exceeds LSD .01 = 64.65.

TABLE XIX

MEANS OF F_1 POPULATIONS AS PERCENT OF HIGH PARENT AND RELATIVE RANKINGS FOR SIX CHARACTERS 1963-64

F_1's and Parents	Days to Head		Plant Height		Yield		Number of Heads		Number or Kernels		Weight Per 1000 Kernels	
	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank
Y	-	21	-	21	-	21	-	12	-	21	-	18
NS	-	8	-	6	-	6	-	1	-	2	-	11
P	-	17	-	13	-	17	-	10	-	17	-	16
R	-	16	-	18	-	16	-	11	-	12	-	19
N	-	3	-	20	-	9	-	15	-	10	-	7
K	-	1	-	12	-	2	-	2	-	3	-	1
Y x NS	114	14	102	3	60	13	69	6	65	13	92	13
Y x P	106	20	99	15	72	19	70	20	72	19	94	17
Y x R	105	18	97	19	69	18	85	16	70	18	91	21
Y x N	121	11	112	17	85	11	82	18	85	14	99	8
Y x K	124	10	102	9	64	8	76	7	87	9	72	10
NS x P	115	15	103	1	49	15	49	17	54	16	87	14
NS x R	105	9	100	7	79	10	72	5	84	8	94	12
NS x N	105	5	99	8	109	5	62	9	85	6	122	4
NS x K	108	4	103	2	88	4	85	3	93	4	88	5
P x R	105	19	99	14	56	20	64	21	53	20	86	20
P x N	110	7	105	11	141	3	103	8	117	5	123	3
P x K	129	12	103	4	48	12	55	19	64	15	73	9
R x N	109	6	101	16	114	7	97	14	111	7	104	6
R x K	131	13	102	10	45	14	67	13	76	11	58	15
N x K	101	2	103	5	113	1	91	4	113	1	100	2

TABLE XX

MEANS OF F_2 POPULATIONS AS PERCENT OF HIGH PARENT AND RELATIVE RANKINGS FOR SIX CHARACTERS 1964-65

F_2's and Parents	Days to Head %	Days to Head Rank	Plant Height %	Plant Height Rank	Yield %	Yield Rank	Number of Heads %	Number of Heads Rank	Number of Kernels %	Number of Kernels Rank	Weight Per 1000 Kernels %	Weight Per 1000 Kernels Rank
Y	-	21	-	18	-	21	-	21	-	21	-	18
NS	-	9	-	9	-	9	-	6	-	9	-	7
P	-	18	-	12	-	20	-	20	-	21	-	16
R	-	17	-	8	-	17	-	15	-	16	-	20
N	-	1	-	21	-	3	-	7	-	3	-	6
K	-	3	-	20	-	2	-	2	-	5	-	1
Y x NS	112	15	102	4	74	15	78	17	88	15	78	15
Y x P	104	20	97	16	105	18	109	18	114	19	89	21
Y x R	105	19	98	11	89	19	86	19	98	17	93	19
Y x N	116	8	104	13	85	6	90	12	101	2	95	9
Y x K	128	14	109	6	79	7	91	4	103	4	71	14
NS x P	108	13	105	1	82	14	85	13	89	14	87	13
NS x R	103	11	103	3	94	13	101	5	92	13	91	11
NS x N	108	4	92	19	82	8	93	11	84	10	102	5
NS x K	109	5	99	10	95	4	96	3	94	7	94	3
P x R	99	16	102	5	114	16	96	16	95	18	99	17
P x N	115	7	99	14	77	11	83	14	80	12	95	8
P x K	116	10	107	2	91	5	88	8	96	6	88	4
R x N	113	6	93	17	75	12	95	10	82	11	94	10
R x K	121	12	101	7	74	10	85	9	90	8	74	12
N x K	102	2	105	15	107	1	102	1	107	1	97	2

TABLE XXI

QUALITY CHARACTERISTICS OF PARENTS, F_1, AND F_2 GENERATIONS

Variety or Cross	Entry No. /1	F_1's and Parents 1963-64				F_2's and Parents 1964-65				
		% Protein		Sedimentation		% Protein		Sedimentation		Mixograph
		Wheat	Flour	14% /2	Specific	Wheat	Flour	14% /2	Specific	(Min.)
Y	16	18.0	15.2	29.5	1.94	14.3	12.8	27.8	2.17	1.8
NS	17	15.2	13.5	29.4	2.18	13.5	12.0	28.9	2.41	2.3
P	18	16.0	14.1	34.3	2.43	15.5	13.9	35.1	2.53	3.0
R	19	14.6	12.1	38.5	3.18	13.5	12.0	39.6	3.30	3.3
N	20	13.4	10.7	31.6	2.95	13.5	11.7	35.5	3.03	2.1
K	21	11.8	10.5	26.0	2.48	12.7	11.2	30.9	2.76	3.1
Y x NS	01	15.0	13.5	33.8	2.50	14.0	12.5	30.7	2.46	2.5
Y x P	02	15.3	13.4	37.5	2.80	15.4	13.9	33.4	2.40	2.3
Y x R	03	15.1	12.9	39.6	3.07	14.4	12.0	37.0	3.08	2.8
Y x N	04	14.1	12.1	34.0	2.81	13.3	11.0	25.1	2.28	1.3
Y x K	05	13.0	11.6	30.0	2.59	12.5	11.1	27.0	2.43	3.0
NS x P	06	14.2	12.1	38.9	3.21	12.5	11.1	25.7	2.32	2.3
NS x R	07	14.2	12.1	32.5	2.68	13.3	10.9	25.0	2.29	2.5
NS x N	08	13.6	11.8	31.2	2.64	13.7	11.3	27.6	2.44	2.3
NS x K	09	12.9	11.5	28.8	2.50	12.6	10.8	25.4	2.35	2.9
P x R	10	14.2	11.7	33.3	2.85	14.4	12.4	33.3	2.68	2.2
P x N	11	14.5	12.1	36.0	2.98	14.7	11.1	33.6	3.03	2.0
P x K	12	13.3	12.4	32.9	2.65	12.7	10.9	31.6	2.90	3.2
R x N	13	13.5	11.5	36.2	3.15	13.6	10.6	35.2	3.32	2.1
R x K	14	12.4	11.2	27.3	2.44	12.5	10.8	28.3	2.62	3.0
N x K	15	13.2	11.2	21.8	1.94	13.2	10.9	29.5	2.71	2.3

/1 IBM entry number.

/2 All determinations made on a 14% moisture basis.

TABLE XXII

SUMMARY OF REGRESSION COEFFICIENTS AND TESTS OF SIGNIFICANCE FROM Vr,Wr ANALYSES OF F_1 AND F_2 DATA FOR SIX CHARACTERS

		t tests and significance			
		b=0		b=1	
Character	b	t	P	t	P
Days to Head					
F_1 all arrays	.918±.105	8.76	<.001	0.78	>.50
F_2 " "	.993±.052	19.13	<.001	0.14	>.50
Plant Height					
F_1 all arrays	.898±.109	8.24	.01-.001	0.94	.50-.40
F_2 " "	.682±.591	1.15	.40-.30	0.54	>.50
K array omitted	.702±.149	1.67	.20-.10	0.71	>.50
NS array omitted	.904±.550	1.64	.20-.10	0.17	>.50
K,NS arrays omitted	.928±.418	2.22	.20-.10	0.17	>.50
K,N,NS arrays omitted	.814±.143	5.68	.20-.10	1.30	.50-.40
K,P,NS arrays omitted	.710±.593	1.20	.50-.40	0.49	>.50
K,P,Y arrays omitted	.801±.008	99.66	.01-.001	24.77	.05-.02
Yield					
F_1 all arrays	.176±.314	0.56	>.50	2.63	.10-.05
P array omitted	.394±.315	1.25	.40-.30	1.92	.20-.10
P,N arrays omitted	.941±.363	2.59	.20-.10	0.16	>.50
F_2 all arrays	.990±.067	14.80	<.001	0.15	>.50
Number of Tillers					
F_1 all arrays	.911±.338	2.69	.10-.05	0.56	>.50
P array omitted	.930±.246	3.78	.05-.02	0.29	>.50
F_2 all arrays	.842±.134	6.30	.01-.001	1.18	.40-.30
P array omitted	.933±.094	9.87	.01-.001	0.71	>.50
Number of Kernels					
F_1 all arrays	.839±.520	1.61	.20-.10	0.31	>.50
N array omitted	1.133±.102	11.11	.01-.001	1.30	.30-.20
R,N arrays omitted	1.033±.140	7.39	.02-.01	0.24	>.50
P,K arrays omitted	1.093±.164	6.68	.05-.02	0.57	>.50
N,NS arrays omitted	1.074±.196	5.47	.05-.02	0.38	>.50
F_2 all arrays	.934±.191	4.88	.01-.001	0.34	>.50
Weight/1000 Kernels					
F_1 all arrays	.691±.243	2.84	.05-.02	1.27	.30-.20
N array omitted	.885±.219	4.04	.05-.02	0.52	>.50
F_2 all arrays	.871±.111	7.86	.01-.001	1.17	.40-.30

VITA

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Doctor of Philosophy

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