A GENETIC ANALYSIS OF KERNEL WEIGHT AND OTHER CHARACTERS IN A DIALLEL CROSS INVOLVING FIVE WINTER WHEAT PARENTS

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CHAPTER I

INTRODUCTION

The current and projected requirements for food resources in the world call for all-out efforts for increasing the production of man's basic food crops. Wheat is one of the crops that occupies a front line position in the fight against hunger. One of the ways of increasing wheat production is through the development of cultivars with higher grain yield potential.

Grain yield in wheat is a complex character resulting from the interaction of many different genetic - physiologic systems in the plant, which are influenced to a greater or lesser degree by fluctuations in the environment under which the plant is grown. More effective increases in grain yield potential may be possible by visualizing yield as the end result of more simply inherited yield components. Breeding efforts could then be concentrated not on yield itself but upon one or more of the components (9). Knowledge of the genetic control of these yield components and their inter-relationships would be useful in breeding for increased grain yield potential.

One of the major yield components in wheat is kernel weight. A considerable range in degree of expression of this trait exists within the species but so far, very little breeding effort has been applied to kernel weight, particularly with North American winter wheats (29). It would, therefore, appear desirable to re-examine kernel weight as a possible means of increasing grain yield.

The objective of this study was to investigate the genetic systems controlling kernel weight and other yield components in a diallel cross involving five winter wheat cultivars that are being utilized in the Oklahoma Agricultural Experiment Station breeding program.

CHAPTER II

LITERATURE REVIEW

It was pointed out by Grafius (9) that grain yield can be represented by a geometric figure (parallelpiped) on which three components are represented. He listed the components as tillers per unit area, average number of seeds per spike, and average weight of the kernels. If one leg of the parallepiped is shorter than the others then this is the one which should be modified for maximum increases in yield.

The importance of kernel weight as a component of grain yield of wheat has been stressed by Lee and Kaltsikes (19), Knott and Talukder (17) and McNeal (21). Lee and Kaltsikes (19) found that the initial heads per plant and grain per spikelet develop before kernel weight and have a strong influence on the expression of seed weight. Knott and Talukdar (17) reported that the yield components had a compensating effect. That is, if there were few tillers formed, then yield could be compensated for by more seeds per spike or heavier seed weight.

Several investigators have reported that kernel weight in wheat was under the control of only a few major genes. Boyce (5) found one gene in one cross and two or three genes in another cross which controlled seed weight. Copp and Wright (6) were of the opinion that, when widely different parents were used, only a few major genes were involved since both parental types were easily recovered. Reddi and Heyne (25) working with winter wheat found that two major genes appeared to be responsible for differences in kernel weight while Sharma and Knott (27) concluded that seed weight was highly heritable and controlled by as few as four genes.

Transgressive segregation for kernel weight in wheat was reported by Bhatt (3), Reddi and Heyne (25), but Sharma and Knott (27) were unable to detect such segregation in their study which involved a cross of two widely different wheat parents one of which was from India and the other from Canada.

Johnson et al. (15) found kernel weight to be highly heritable in a winter wheat cross as did Paroda and Joshi (23) with Indian wheats. Weibel (36) found similar results in winter wheat. In a study of three winter wheats Ketata (16) showed that kernel weight was the component of yield least subject to environment influences. Other workers (15,23,36) have also indicated that kernel weight was more stable than either tiller number or number of seeds per spike in terms of environmental effects.

In crosses involving two spring wheats, Bhatt (3) found kernel weight to be partially dominant in the direction of the heavy-seed parent. Similar results were reported by Bitzer and Fu (4) and by Paroda and Joshi (23). Tandon et al. (33) stated that dominant genes controlled the expression of higher yield and greater kernel weight whereas recessive genes conditioned higher tiller number and increased number of kernels per spike.

On the other hand, several investigators have suggested that kernel weight is due to the effects of many genes. Kuspira and Unrau (18) used wheat substitution lines to study the genes controlling various plant and seed characters. They found that maturity was conditioned by major genes as well as modifier genes. Plant height and spike density appeared to be controlled by minor genes. Other characters such as grain yield and 1000-kernel weight were governed by multiple genes situated on many chromosomes. Bitzer and Fu (4) found that for all characters investigated (including yield and yield components) general combining ability was much more important than specific combining ability in a diallel cross involving six soft red winter wheats; indicating major control by additive gene effects. In durum wheat, Lee and Kaltsikes (19) reported that kernel weight in a diallel cross was primarily controlled by additive gene effects. In a diallel cross of four spring wheat varieties, Sun et al. (32) showed that additive effects were important in kernel weight although other types of genetic variance were also detected. Gill, et al. (8) studied the inheritance of several agronomic characters in the F_1 generation of a diallel cross involving ten wheat lines of diverse origin. They reported that additive genetic variance was important for kernels per spike and dominance variance was important for 100-kernel weight, and tiller number.

Bhatt (3) reported additive genetic variance to be larger than the dominance component for kernel weight in two spring wheat crosses. Paroda and Joshi (23) believed that the additive genetic component for kernel weight was sufficiently large in their study of six bread wheats to justify its inclusion in breeding for yield improvement. Sharma and Knott (27) also reported that large amounts of additive genetic variance was detected in a cross of Selkirk, a large-seeded Canadian wheat with Chargot, a small-seeded Indian wheat.

The importance of dominance genetic variance on kernel weight has been reported by Bhatt (3) and Sun et al. (32). The latter authors stated that even though dominance effects tended to be smaller than the additive effects, they were important especially in crosses of medium X low and heavy X low seed weight parents.

Very few studies have been reported on epistatic genetic variance for kernel weight but in the paper of Sun et al. (32) epistatic effects were noted in all crosses in at least one year of a four year study when the parents differed in kernel weight. The authors suggested that epistasis is more important when the parents are genetically diverse. In the study reported by Bhatt (3), no significant epistatic gene effects were observed for kernel weight. However, the design of his experiment may not have been sensitive enough to detect epistatic effects. Gill et al. (8) working with Indian wheats stated that epistasis was detected for kernel weight as well as for kernels per spike and tiller number.

Heritability scores for kernel weight have been reported by numerous investigators. Bhatt (3) obtained narrow-sense estimates of 55 and 69% for two wheat crosses. Gill et al. (8) reported estimates of narrow sense heritability that were high for kernels per spike and plant height, moderate for kernel weight, and low for number of tillers. Johnson et al. (15) reported high heritability estimates for kernel weight but low estimates for tiller number and grain yield. For kernel weight their estimates were 55 and 61% for the narrow-and broad-sense heritabilities, respectively. McNeal (21) estimated heritability in a spring wheat cross by regressing F_3 means on F_2 values. He found that among the yield components, heads per plant had the highest heritability score. However, he noted that heritability estimates were in general low for all characters measured.

In two winter wheat crosses, Reddi and Heyne (25) reported heritability estimates of 48 and 22% for kernel weight in two wheat crosses. Their estimates were obtained by regressing F_4 progeny means on F_3 plants. Sun et al. (32) found that heritability scores for kernel weight ranged from 51 to 85% for five of the six spring wheat crosses studied. One cross involving heavy X heavy seeded parents gave a heritability estimate of only 9%. Sharma and Knott (27) obtained a heritability value of 70% for seed weight from the cross of an Indian X Canadian variety after the data had been transformed. Weibel (36) found a heritability estimate of 45% for kernel weight in a study of quantitative characters in five crosses of hard red winter wheat.

Heterosis for kernel weight was reported by Sun et al. (32) as the percent increase of the F_1's over the parents. Heterosis varied from minus 4 to plus 31% depending on the hybrid and the year grown. The greatest expression of heterosis was noted in the cross involving medium X low seed weight parents. Singh and Kandola (28) studied heterosis in a diallel cross involving seven wheat parents. They found that heterosis as measured by the difference between the F_1 and the higher parent was present for yield and components of yield on a plant basis. Grain yield showed the greatest amount of heterosis and was followed by tiller number, number of spikelets per spike and 100-kernel weight. Negative heterosis was found for plant height and earing date.

Several studies have dealt with the associations among various agronomic traits in an attempt to elucidate those relationships which may help the plant breeder decide on the priorities to be given to certain characters. Grafius (10) examined the behavior of yield components in 36 oat varieties. He stated that intercomponent competition occurs when the component characters share a common source of environmental resources. Johnson et al. (15) studied the relationship between plant height and several other traits in a cross of winter wheat. Plant height was found to be positively correlated with kernel weight, number of spikes per plant, and grain yield. McNeal (21) investigated correlations between grain yield and other characters in the F_2 and F_3 generations of a cross involving a white soft and a hard red wheat. Although all correlations were positive and significant, the correlation coefficient between kernel weight and yield was lower than that between yield and spikes per plant or kernels per spike.

Associations among six characteristics in five winter wheat crosses were studied by Weibel (36). He found that plant height was positively correlated with grain yield, spikes per plant, and kernel weight. Grain yield was also positively correlated with number of heads per plant and kernel weight. However, since number of heads per plant and grain yield had low heritabilities, it was concluded that the association between the two may be of little value to the plant breeder. Knott and Talukdar (17) found a highly significant positive correlation between kernel weight and grain yield in a study on spring wheat.

Tewari et al. (35) studied the genetic association between various traits in bread wheat. They found that the association between plant height, spike length and number of spikelets was due to linkage whereas the association between spikelet number and number of kernels per spike was due to both pleiotropy and linkage. Lee et al. (19) stated that heads per plant and grains per spikelet which develop before kernel weight is established had a strong influence on the expression of seed weight in durum wheat.

CHAPTER III

MATERIALS AND METHODS

This study was conducted on a spaced-planted nursery in the 1972-73 wheat growing season at Stillwater, Oklahoma. A diallel cross involving five winter wheat cultivars (Triticum aestivum L.) was used in this experiment to study the genetic systems controlling kernel weight and other seed and plant characteristics. The cultivars used were 'Centurk', 'Lovrin 6', 'Nicoma', 'Sturdy', and 'Tamwheat 102'.

Parent Cultivars

Centurk was developed by the Nebraska Agricultural Experiment Station in cooperation with the Agricultural Research Service, U.S.D.A., and was released in 1971 by several agencies including the Oklahoma Agricultural Experiment Station (26). It was selected from the cross: Ky58-Nth-Hope-Tk2-Cnn X Prk. This cultivar has a medium plant height, a high tillering capacity and relatively small kernels.

Lovrin 6 is a Romanian experimental line which resulted from a cross of 'Fiorella' X 'Bezostaia 1'. It is a winter wheat characterized by large kernels but is not well adapted to Oklahoma growing conditions. It is being utilized as germplasm in the Oklahoma Agricultural Experiment Station wheat breeding program because of its large kernel size (29).

Nicoma was developed and released in 1971 by the Oklahoma Agricultural Experiment Station (30). It resulted from a cross between

'Triumph' and 'C.I. 12406', a Mq1-Oro-Oro-Tm selection. Nicoma is characterized by early maturity, midtall straw and medium sized kernels.

Sturdy, resulting from a cross of Sinvalocho-Wi X Hope-Cnn-Wi X Sen Seun 27, is a semidwarf cultivar which was released by the Texas Agricultural Experiment Station in 1966. It was developed for irrigated culture systems and has shown good response to fertilizer applications. It has relatively large spikes and medium-sized kernels (1).

Tamwheat 102, a selection from Sinvalocho-Wi X Hope-Cnn X 2*Wichita X Sen Seun-Tcs, was developed at the Texas Agricultural Experiment Station and released as germplasm in 1971. It is a semidwarf winter wheat characterized by a short stature, relatively large spikes and a potential for high yield. However, it has a low test weight and only fair quality (24).

These five cultivars were intermated in all possible combinations according to a diallel crossing system. Crossing was accomplished by hand emasculation and pollination in the greenhouse during February and March, 1972. Reciprocal crosses were not kept separate. Seed of the ten F_1's and five parents were planted in flats containing a greenhouse soil mixture on October 1, 1972. After germination, the seedlings were allowed to vernalize at outside temperatures for approximately three months. During this period, the seedlings were occassionally clipped to reduce excessive top growth.

Field Layout and Test Conditions

The seedlings were transplanted to the field on December 28, 1972. Four replications were used in a randomized complete block design. Each replication contained one plot each of the five parents and ten

F_1's. The fifteen entries were assigned at random to plots. Each plot consisted of a single row containing nine test plants. The first and last test plant in each row was bordered by a guard plant to reduce bias. The distance between the plants within a row was 30 cm and the same distance separated adjacent rows. A guard row bordered the first and last row in each replication. The study was grown on a Norge loam soil in field series 2200 at the Agronomy Research Station, Stillwater.

A preplant application of 20 kg/ha of N and 23 kg/ha of P was made. Another application of 56 kg/ha of N was made on February 21, 1973. The plots received a final application of 20 kg/ha of N and 23 kg/ha of P on April 20, 1973.

Growing conditions were favorable throughout the season. Above-average precipitation and moderate temperatures in late winter and early spring resulted in vigorous plant growth and good development of yield-related characters. There were no problems with disease or insect pests but some bird damage was experienced in the test just prior to harvest. However, this did not appear serious enough to affect results of the measurements on the traits investigated. The plots were harvested on June 23, 1973 by pulling each plant individually.

Characters Evaluated

Five characters were investigated. These were plant height, number of fertile tillers per plant, kernels per spike, average kernel weight, and grain yield per plant. The measurements on these characters were made as follows.

Plant Height

This measurement on this character was taken as the distance in centimeters between the crown and the tip of the spike in the tallest tiller, awns excluded. This character was expressed as centimeters per plant.

Tiller Number

Tillers per plant corresponded to the number of seed-bearing spikes collected from each plant during harvest and was expressed on a per plant basis.

Kernels per Spike

The number of kernels per spike was determined by taking the three best heads from each plant. These were then threshed in bulk, and seeds counted to determine the average number of kernels per spike.

Kernel Weight

This character was obtained by dividing the weight of the seeds from the three selected heads by the number of seeds produced on same three heads. This character was expressed as grams per 1,000 kernels.

Grain Yield

Grain yield was taken as the weight of the threshed grain from each individual plant and was expressed as grams per plant.

Statistical Analysis

Analyses of variance for each character were conducted for the parents, the F_1 hybrids, and the parents and F_1's combined. These analyses are the primary steps in the statistical treatment of the data since they indicate the presence or absence of true differences among the entries for the various characters.

All two way phenotypic correlation coefficients among the five characters were calculated using the relation

$$r_{xy} = \frac{\text{cov }(x,y)}{(\text{var }(x)\ \text{var }(y))^{\frac{1}{2}}}$$

In this formula, x and y are the characters being correlated. The statistics var(x) and var(y) are variances associated with x and y while cov (x,y) is the covariance between x and y. These variances and covariances were computed from the sums of squares for the total degrees of freedom line from the analysis of variance table. Tests for significance of these correlation coefficients were made in the usual way as outlined by Steel and Torrie (31).

Diallel Analysis

In order to investigate the genetic system of the five characters measured in this study, the data were subjected to the Jinks-Hayman diallel cross analysis as outlined in several papers (11,12,13,14). This analysis provides genetic information about the parents utilized in the diallel cross. The diallel analysis is based on the following assumptions: 1) no genotype by environment interaction, 2) homozygous parents, 3) diploid segregation, 4) no reciprocal differences, 5) no epistasis, 6) no multiple alleles, and 7) uncorrelated gene distribution. The validity of the conclusions obtained from this analysis is invalidated to some degree by the failure of any of these assumptions.

The parameters estimated by the diallel analysis are D, H_1, H_2, F, E_0, and E_1. The parameter D is an estimate of additive genetic variance while H_1 and H_2 are different estimates of dominance genetic variance. D may include additive by additive epistatic effects while H_1 and H_2 may include additive by additive, additive by dominance, and dominance by dominance epistatic effects. Since D, H_1, and H_2 are variances, they are expected to be positive values. The parameter F indicates the relative frequency of dominant and recessive alleles in the parents. A positive F value indicates as excess of dominant alleles while a negative F value indicates an excess of recessive alleles in the parents. An F value of zero indicates that the dominant and recessive alleles are equally distributed among the set of parents. The parameter E_0 estimates the environmental variation associated with the parents in the test while E_1 estimates the environmental variation associated with the F_1's.

The parameters were calculated from parental and F_1 data by equations adapted to diallel cross analyses which involved the variances and covariances of parents and parental arrays (7,12). Each parameter was estimated from an analysis based on data from individual plants. Each block (replication) in the test was analyzed separately (22) and the variation of the block means around the overall mean was used to calculate the standard error of the mean in order to make tests of significance.

All analyses were performed by computer at the Oklahoma State University Computer Center.

CHAPTER IV

RESULTS AND DISCUSSION

Analysis of Variance

Mean squares from the analysis of variance of the five traits are presented in Table I. Parents and F_1's were analyzed separately as well as together in a combined entry procedure. Highly significant entry mean squares were noted for four of the five traits in the three types of analyses. Grain yield was an exception. Mean squares for grain yield were significant at the .01 probability level for the combined analysis and for the analysis of the F_1's. However, the entry mean square for grain yield was not statistically significant when the parents were analyzed alone.

The analyses of variance showed that the ten F_1's of the diallel cross differed in each of the five traits investigated. The parents differed in all traits except grain yield.

As shown in Table I, the replication effects were statistically significant in most cases. This indicates that the blocking of replications was effective in removing environmental variation and increasing the precision of the experiment.

If the analysis of variance for all entries is considered (Table I), it can be seen that the replication by entry interaction is significant for kernels per spike. This suggests that measuring this trait on an individual plant basis is to be recommended. The same reasoning applies

TABLE I

MEAN SQUARES OF FIVE CHARACTERS FOR THE PARENTS AND F_1'S FROM A 5X5 DIALLEL CROSS OF WINTER WHEAT

Source of Variation	df	Plant Height	Tillers per Plant	Kernels per Spike	Kernel Weight	Grain Yield
Replications	a 3	68.24**	124.2**	652.03**	136.13*	567.60**
	b 3	63.12	106.82**	504.04**	100.97**	474.14**
	c 3	32.04	26.92	179.50*	37.25*	121.01
Entries	a 14	1545.68**	188.11**	2389.74**	1398.40**	97.18**
	b 9	806.12**	94.70**	974.42**	792.28**	94.36**
	c 4	2789.65**	415.33**	6160.28**	2978.61**	114.75
Replications X entries	a 42	25.58	18.30	45.50*	6.36	35.44
	b 27	22.19*	18.77	47.28	6.55	24.23
	c 12	32.85	19.42	44.64	6.98	62.62*
Plants within entries within replications	a 480	13.38	14.07	31.00	4.67	27.06
	b 320	13.23	14.27	31.26	4.45	29.88
	c 160	13.67	13.67	30.48	5.12	21.43

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

a (upper line) = analysis of variance of parents and F_1's combined

b (middle line) = analysis of variance of F_1's alone

c (lower line) = analysis of variance of Parents alone to plant height and grain yield from the analysis of the F_1's and parents, respectively.

Comparisons Among Means

The magnitude of the differences among the 15 entries for each trait can be seen in Table II. Since each plot consisted of nine plants and measurements were taken on an individual plant basis, each mean is based on thirty-six observations. To facilitate comparisons, entries were ranked from highest to lowest for each trait.

Plant height ranged from 69.3 cm for Sturdy to 92.9 cm for Centurk/Nicoma F_1. Nicoma, the tallest parent, had a height of 87.9 cm. The mean values of the five parents and ten F_1 hybrids were 79.3 cm and 84.5 cm respectively. Thus it would appear, for material evaluated in this study, that taller plant stature is in general incompletely dominant over shorter plant stature.

The number of tillers per plant varied from 11.8 for Lovrin 6 to 21.3 for Centurk. None of the F_1's exceeded the range for tillering set by these two entries. The means of the parents and F_1 hybrids were 17.0 and 16.0, respectively (Table II). These comparisons suggested that low tiller number, on the average, is slightly dominant over the alternative condition. However, this statement may not be statistically valid as will be discussed in another section of this chapter.

The average number of kernels per spike ranged from 46.4 for Lovrin 6 to 78.6 for Tamwheat 102. The F_1 hybrid with highest number of kernels per spike was Centurk/Tamwheat 102 with 64.4, while the F_1 with the lowest value was Lovrin 6/Nicoma with 46.5 (Table II). The means of the five parents and ten F_1's were 56.2 and 55.6, respectively.

TABLE II

MEANS OF FIVE TRAITS FOR PARENTS AND F_1'S OF A DIALLEL CROSS OF WINTER WHEAT[1]

Entry	Plant Height (cms)		Tillers per Plant		Kernels per Spike		Kernel Weight (gms/1000 seeds)		Grain Yield (gms/plant)	
	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank
Parents										
Centurk	87.0	5	21.3	1	55.6	7	27.4	15	18.2	11
Lovrin 6	70.9	14	11.8	15	46.4	15	50.0	1	17.6	13
Nicoma	87.9	4	17.3	4	47.8	13	38.0	7	18.5	10
Sturdy	69.3	15	17.3	5	52.7	10	33.2	11	17.8	12
Tamwheat 102	81.4	11	17.4	3	78.6	1	29.0	14	21.9	2
Overall parental mean	79.3	-	17.0	-	56.2	-	35.5	-	18.8	-
F_1 Hybrids										
Centurk/Lovrin 6	82.8	9	15.8	9	50.3	12	39.2	5	18.6	9
Centurk/Nicoma	92.9	1	17.1	6	51.2	11	34.6	9	17.4	14
Centurk/Sturdy	84.3	7	19.8	2	56.0	6	34.3	10	20.5	4
Centurk/Tamwheat 102	89.2	2	16.2	8	64.4	2	31.4	13	18.9	8
Lovrin 6/Nicoma	83.7	8	14.1	14	46.5	14	46.2	2	19.2	7
Lovrin 6/Sturdy	81.0	12	14.8	12	55.2	9	42.7	3	20.3	5
Lovrin 6/Tamwheat 102	81.6	10	15.2	11	60.0	3	40.8	4	22.1	1
Nicoma/Sturdy	85.1	6	16.6	7	55.3	8	38.1	6	20.9	3
Nicoma/Tamwheat 102	88.2	3	15.8	10	59.1	4	36.1	8	20.0	6
Sturdy/Tamwheat 102	76.1	13	14.7	13	58.0	5	32.8	12	16.7	15
Overall F_1 Mean	84.5	-	16.0	-	55.6	-	37.6	-	19.5	-
$LSD_{.05}$	5.1		5.2		9.6		3.0		7.2	
$LSD_{.01}$	6.7		6.8		12.9		3.9		9.5	

Thus, the deviation of the mean F_1 value from the midparent value indicates that if dominance is involved it would be, on the average, in the direction of fewer kernels per spike.

Kernel weight exhibited the widest relative range among all characters (Table II). The lowest and highest values for this trait were scored for Centurk with 27.4 and Lovrin 6 with 50.0. This was nearly a two-fold difference. The range among the F_1's was from a value of 31.4 (Centurk/Tamwheat 102) to a value of 46.2 (Lovrin 6/ Nicoma). The overall F_1 mean of 37.6 was higher than the parental mean of 35.5 gms/1000 seeds. If epistasis were not involved, this would suggest greater kernel weight is associated with a preponderance of dominant genes. Again, the overall F_1-midparent deviation does not reflect the magnitude of the individual deviations of all the hybrids. However, all of the individual deviations were in the direction of the parents with greater kernel weight as can be observed from Table II.

The range among entries for grain yield was relatively narrow. The lowest and highest means respectively for this character were those of Sturdy/Tamwheat 102 F_1 with 16.7 gms/plant and Lovrin 6/Tamwheat 102 F_1 with 22.1 gms/plant (Table II). The smallest and largest values among the parental means were those of Lovrin 6 with 17.6 and Tamwheat 102 with 22.0 gms/plant. The overall hybrid-midparent deviation was in favor of the F_1's with an average of 19.5 and 18.8 gms/plant, respectively, for the F_1's and parents. However, no test of significance of this deviation is provided in this section of the report. The array means were compared with parental values for the various traits under investigation (Table III). For this comparison, an array is defined as all the crosses involving one parent but does not include the parent

TABLE III

PARENTAL VALUES AND ARRAY MEANS OF FIVE TRAITS
FROM A DIALLEL CROSS OF WINTER WHEAT

Parental Array a) and Value b)	Plant Height (cms)		Tillers per Plant		Kernels per Spike		Kernel Weight (gms/1000 seed)		Grain Yield (gms/plant)	
	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)
Centurk										
Parental array	87.3	2	17.2	1	55.5	3	34.9	5	18.9	5
Parental value	87.0	2	21.3	1	55.6	2	27.4	5	18.2	3
Lovrin 6										
Parental array	82.3	4	15.0	5	53.0	5	42.3	1	20.0	1
Parental Value	70.9	4	11.8	5	46.4	5	50.0	1	17.6	5
Nicoma										
Parental array	87.5	1	15.9	3	53.0	4	38.8	2	19.4	4
Parental value	87.9	1	17.3	3	47.8	4	38.0	2	18.5	2
Sturdy										
Parental array	81.6	5	16.5	2	56.1	2	37.0	3	19.6	2
Parental value	69.3	5	12.3	4	52.7	3	33.2	3	17.8	4
Tamwheat 102										
Parental array	83.8	3	15.5	4	60.3	1	35.3	4	19.4	3
Parental value	81.4	3	17.4	2	78.6	1	29.0	4	21.9	1

a) In this comparison, an array consists of all thecrosses involving one parent but excludes the parent itself.

b) Parental value is the mean value of the parent itself.

c) Array means are ranked separately from parental values.

itself. A comparison of these array means with the parental value provides additional information about the genetic determination of the various traits and their expected behavior in crosses.

For plant height, the parental values and parent arrays as indicated by comparative ranking were in good agreement. This suggests that, with this set of parents, the value of the parent itself for plant height would give a good indication of its performance in crosses with other lines.

For tiller number, the parental values for Centurk, Lovrin 6, and Nicoma agree with their respective parental arrays. However, there was less agreement for Sturdy or Tamwheat 102. The parental array for Sturdy had a higher value than did Sturdy itself. On the other hand, the parental value for Tamwheat 102 was higher than its parental array. Consequently, it appears that the behavior of this trait in crosses cannot always be predicted on the basis of parental values.

The parental values for kernels per spike are in good agreement with their corresponding parental array values. This suggests that the parent value for this trait would be a reliable indicator of its performance in crosses.

The relative ranking of parental values for kernel weight, were in very good agreement with their respective array values. Here again, it appears that parental performance for this trait would serve as a useful indicator of its expected breeding behavior in crosses.

For grain yield, the comparisons between parental values and corresponding parental arrays showed very little agreement (Table III). The performance of the parent itself for this trait as measured by spaced plants apparently would be of little value in predicting its performance in crosses.

Of special interest is the parent Lovrin 6. It was lowest in grain yield among all the parents but its parental array based on the mean of all the F_1's in which it was involved as a parent was the highest yielding of the five parental arrays. It will be noted in Table III that both the parental value and parental array for Lovrin 6 ranked first in kernel weight. It is suggested that the high kernel weight characteristic of this parent made an important contribution to the grain yield performance of its hybrids.

The absence of a consistent relationship between parental values and array means for grain yield (Table III) points out the complexity of this character and leads to the suggestion that additive effects of genes are not the only ones involved. Bitzer and Fu (4) noted that the observed low correlation between the average performance of parents and F_1 arrays would indicate that low yielding parents may give F_1 hybrids of a high performance.

Correlations

As shown in Table IV, the three sets of data (F_1's and parents combined, F_1's alone, and parents alone) used to calculate correlation coefficients were in close agreement in sign, magnitude, and level of statistical significance for most two-way comparisons. All correlation coefficients were statistically significant except for two of the three comparisons between kernel weight and grain yield. The fact that many coefficients were low but statistically significant was no doubt due to the rather large number of degrees of freedom and corresponding low r values required for significance.

TABLE IV

COEFFICIENTS OF CORRELATION AMONG FIVE TRAITS FROM PARENTS AND F_1'S OF A 5X5 DIALLEL CROSS OF WINTER WHEAT

	Tillers per Plant	Kernels per Spike	Kernel Weight	Grain Yield
Plant height	a 0.321**	a 0.159**	a -0.223**	a 0.233**
	b 0.312**	b 0.149**	b -0.167**	b 0.235*
	c 0.454**	c 0.204**	c -0.395**	c 0.237**
Tillers per Plant		a 0.309**	a -0.365**	a 0.718**
		b 0.355**	b -0.182**	b 0.784**
		c 0.270**	c -0.545**	c 0.640**
Kernels per Spike			a -0.469**	a 0.484**
			b -0.344**	b 0.536**
			c -0.560**	c 0.477**
Kernel Weight				a 0.047
				b 0.143**
				c -0.093

*,** Significantly different from zero at the 0.05 and 0.01 probability levels, respectively.

Correlation coefficient based on total number of observations made for each trait.

a (upper line) = Parents and F_1 combined df (n-2) = 538 The significant value (.01) for 538 df is .115.

a (middle line) = F_1's alone df (n-2) = 358 The significant value (.01) for 358 df is .138.

c (lower line) = Parents alone df (n-2) = 178 The significant value (.01) for 178 df is .181.

Low positive correlation coefficients were observed for the comparisons between plant height and kernels per spike, and for the comparisons between plant height and grain yield. The correlation between plant height and kernel weight was low but negative (Table IV). The correlation between tillers per plant and kernels per spike was low and positive.

A negative correlation coefficient was observed for the comparison between tillers per plant and kernel weight. In this comparison, the correlation based on F_1 values was rather low, r = -0.182 while the comparison based on parental data was higher, r = -0.545. This suggests that the parents and F_1's were not behaving in a similar manner with regard to these two traits. The relationship between tiller number and grain yield was relatively high and had a positive r value. This indicates that these two traits were varying in the same direction and they could well have been responding to the same environmental influences.

The correlation coefficients between kernels per spike and kernel weight were negative and intermediate in magnitude (r = -0.344 to -0.560). The correlation coefficients between kernels per spike and grain yield were also intermediate in magnitude but were positive in sign.

The comparisons between kernel weight and yield resulted in low correlation coefficients. These were r = 0.047, r = 0.143**, and r = -0.093 for the combined data, F_1 data, and parental data, respectively.

It is of interest to note (Table IV) that of all the associations with grain yield, tiller number was the highest (r = 0.718, 0.784, 0.640). This was to be expected in space planted material but may also have been the case had the material been evaluated in dense stands.

Kernel weight was negatively associated with plant height, tiller number, and kernels per spike. It appeared not to be correlated with grain yield. Although kernel weight was not closely correlated with grain yield, this character could have had an important effect on grain yield in association with tillers per plant and kernels per spike. In the previous section, the possible influence on yield of Lovrin 6, the high kernel weight parent, was discussed.

Diallel Analysis

The Jinks-Hayman diallel analysis provides information about the genetic system determining the behavior of quantitative characters in a given set of homozygous parents. A first step in such an analysis is the testing of the assumptions of the diallel model. Certain general tests can be made to check the validity of these assumptions (12).

One such test is the analysis of variance of the quantity W_r-V_r. The statistic W_r is the covariance of the offspring of each array with the nonrecurrent parent, and V_r is the variance of all the offsprings of each parental array. For this test, an array includes the parent itself as well as the crosses derived from it.

The quantity W_r-V_r is expected to be constant if all assumptions are met. Inconsistency over arrays of the W_r-V_r values would indicate failure of at least one of the assumptions. It should be noted that no testing of the failure of a specific assumption is available when only F_1's and parents are studied.

The general W_r-V_r test was conducted for the five traits measured in the study reported herein. The results of this test as shown in

Table V indicate that in only two cases (for tillers per plant and grain yield) were all assumptions met. Although partial failure of one or more of the assumptions was indicated for plant height, kernels per spike, and kernel weight, the analysis can still be conducted for these traits but the results would be less reliable than they would have been had all assumptions been met (2,34).

Parameter Estimates

The parameters estimated were D, H_1, H_2, F, E_0, and E_1. Computed values of these parameters are shown in Table VI. The estimates of additive genetic variance (D) were significantly different from zero for plant height, tiller number, kernels/spike, and kernel weight but not for grain yield.

The two estimates for dominance variance (H_1 and H_2) were similar in magnitude and level of significance for each trait. For both H_1 and H_2 significance at the 0.05 probability level were noted for plant height, tiller number, and kernels per spike. Significance at the 0.01 probability was observed for kernel weight for both H_1 and H_2 while neither estimate was significantly different from zero for grain yield.

Based on the relative magnitudes of the estimates for additive and dominance genetic variance (Table VI), it appears that additive genetic effects are relatively more important than dominance effects (H_1 and H_2) for plant height, kernels/spike, and kernel weight. Gill et al. (8) found that both additive and dominance genetic variances were associated with tiller number, while grains per ear was mostly associated with additive genetic variance. Bhatt (3) stated that additive gene action played a main role in the expression of kernel

TABLE V

MEAN SQUARES FROM AN ANALYSIS OF VARIANCE OF THE Wr-Vr QUANTITY OF PARENTAL ARRAYS FOR FIVE CHARACTERS FROM A 5X5 DIALLEL CROSS OF WINTER WHEAT

Source of Variation	df	Plant Height	Tillers per Plant	Kernels per Spike	Kernel Weight	Grain Yield
Replications	3	60.15	2.20	251.93*	17.99**	28.03
Arrays a) (Wr-Vr)	4	184.99**	2.17	424.01**	3.51**	25.53
Error	12	24.15	3.75	71.64	0.53	23.95

*,** Significant at 0.05 and 0.01 levels of probability, respectively.

Significance for any given trait would indicate that at least one of the assumptions of the diallel analysis is not met, while nonsignificance would indicate that all assumptions are met.

Note: Wr is the covariance of all of the offspring of each array with the non-recurrent parents.
Vr is the variance of all the offspring of each parental array.

TABLE VI

PARAMETER ESTIMATES OF GENETIC AND ENVIRONMENTAL VARIANCE COMPONENTS OF FIVE CHARACTERS FROM A 5X5 DIALLEL CROSS OF WINTER WHEAT

Parameter	Plant Height	Tillers per Plant	Kernels per Spike	Kernel Weight	Grain Yield
D	78.658**	11.645*	171.455**	82.742**	6.018
H_1	43.988*	7.223*	47.238*	6.085**	12.544
H_2	41.714	5.845*	36.144*	5.692**	10.093
F	18.446	6.288	82.421*	11.435**	8.610*
E_0	1.519**	1.519*	3.386**	0.569*	2.381**
E_1	1.470**	1.585**	3.474**	0.495**	3.320**

*,** Significantly different from zero at the .05 and .01 probability levels, respectively.

Note: Estimates of E_0 and E_1 were obtained from the average of within entry mean squares corresponding to the parents and F_1's , respectively.

Explanation of Parameters: D = additive genetic variance, H_1 and H_2 = dominance genetic variance, F = distribution of dominant and recessive alleles among the parents, E_0 and E_1 = environmental variance.

weight in two crosses of spring wheats. The three variances (D, H_1, H_2) for grain yield are of similar magnitude but none is significantly different from zero. This indicates again the complexity of the genetic control for this trait.

Although both H_1 and H_2 are dominance variance estimates, it is expected that H_1 will be greater than H_2 unless the positive and negative alleles are equally distributed among the parents, in which case H_1 will equal H_2. In all cases in this study, H_1 was greater than H_2.

Positive values were found for the parameter F for all five traits (Table VI). These values were significantly different from zero for kernels per spike, kernel weight, and grain yield but not for plant height and tillers per plant. The significant positive F values indicate that there was an excess of dominant alleles among the parents for these three traits. The fact that the F values for plant height and tiller number were not significantly different from zero suggests that dominance and recessive alleles for these two traits were equally distributed among the parents. Similar results concerning tiller number were reported by Gill et al. (8).

Genetic Ratios

In addition to the parameters D, H_1, H_2, and F certain statistics were computed to describe the genetic architecture of the various traits. These statistics included:

1. Ratios for estimating an average degree of dominance. Two of these, H_1/D and $(H_1/D)^{1/2}$ are basically the same. A ratio between 0 and 1 for these two estimators indicates partial dominance, whereas a value of

0 indicates absence of dominance and a value of 1 indicates complete dominance. Finally a value greater than one would be an indication of overdominance. A third ratio $(D + H_1-F)/(2D-F)$ or $(V_{1L1}-E)/(W_{0L01}-E/n)$ was used as another measure of average dominance. Although this statistic measures dominance on a different scale (13), it still has the same properties of being in the range of 0-1 for partial dominance.

2. The difference between the measure of all F_1 hybrids and that of the parents $(\bar{F}_1-\bar{P})$ gives an indication of the overall direction of dominance.

3. The ratio $\frac{1}{4}H_2/H_1$ provides a measure for the average product of the frequencies of the increasing and decreasing alleles over all loci. A value of 0.25 would indicate an equal distribution of the positive and negative alleles in the parental set; a lower value is expected otherwise (7,20).

4. The value K_D/K_R was used as a measure of the average ratio of dominant to recessive alleles in a parent (12).

5. The number of genes or gene blocks referred to as the number of effective factors and denoted by K is a lower limit of the actual number of genes controlling a given trait and showing some degree of dominance (13).

6. Narrow sense heritability h^2 was estimated by $\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E)$ as suggested by Crumpackard and Allard (7). The results concerning the genetic system will now be discussed for each character individually.

Plant Height

All estimates of degree of dominance fell within the range of incomplete dominance (Table VII), ranging from 0.547 to 0.746.

TABLE VII

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF PLANT HEIGHT

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	0.547	0.101	0.226-0.868
1b) $(H_1/D)^{1/2}$	0.730	0.070	0.507-0.953
1c) $(V_{1L1}-E)/(\dot{W}_{0L01}-E/n)$	0.746	0.058	0.561-0.931
2) $\bar{F}_1-\bar{P}$	5.688	0.526	4.014-7.362
3) $\frac{1}{4}\ H_2/H_1$	0.238	0.005	0.222-0.254
4) K_D-K_R	1.401	0.147	0.933-1.869
5) K	2.144	0.270	1.285-3.003
6) h^2	0.730	0.061	0.536-0.924

Note: Estimators 1a, 1b, and 1c = average degree of dominance, 2 = direction of dominance, 3 = distribution of positive and negative alleles, 4 = ratio of dominant to recessive alleles, 5 = number of effective factors, 6 = narrow-sense heritability.

Since $\bar{F}_1-\bar{P}$ was positive (5.688 ± 0.526), the overall dominance was in the direction of the taller plants. This is in agreement with results presented in previous sections of this study.

The value of $\frac{1}{4}H_2/H_1$ was not significantly different from 0.25 (Table VII) suggesting that alleles controlling tallness and dwarfness were equally distributed among the parents.

The estimate of K_D/K_R was not significantly different from one (Table VII) so that the number of dominant and recessive alleles in a parent are equal on the average.

The value of K indicates that the minimum number of effective factors that show dominance are two or three. In this connection, Johnson et al. (15) reported that plant height was controlled by three major genes in a winter wheat cross.

As shown in Table VII, the narrow sense heritability estimate was of high magnitude ($h^2 = 0.730 \pm 0.061$) as would be expected from the relative magnitudes of D and H_1 as previously discussed. Similar results were obtained by Johnson et al. (15).

Tillers per Plant

The estimates of average degree of dominance were mostly in the range of partial dominance but the upper limits of the 95% confidence interval included the value of 1.0 which corresponds to complete dominance (Table VIII). The overall dominance tends to be in the direction of fewer tillers but in fact the value of $\bar{F}_1-\bar{P}$ was not significantly different from zero.

The estimate of $\frac{1}{4}H_2/H_1$ was not significantly different from 0.25, indicating that alleles determining a smaller or a greater tiller number

TABLE VIII

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF NUMBER OF TILLERS PER PLANT

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	0.615	0.139	0.173-1.057
1b) $(H_1/D)^{1/2}$	0.764	0.101	0.443-1.085
1c) $(V_{1L1}-E)/(W_{0L01}-E/n)$	0.741	0.087	0.464-1.018
2) $\bar{F}_1-\bar{P}$	-0.479	0.275	(-1.354)-0.396
3) $\frac{1}{4}\ H_2/H_1$	0.216	0.015	0.168-0.264
4) K_D/K_R	2.114	0.439	0.717-3.511
5) K	0.185	0.149	(-0.289)-0.659
6) h^2	0.612	0.086	0.338-0.886

Note: Estimators 1a, 1b, and 1c = average degree of dominance, 2 = direction of dominance, 3 = distribution of positive and negative alleles, 4 = ratio of dominant to recessive alleles, 5 = number of effective factors, 6 = narrow-sense heritability.

are equally distributed among the parents (Table VIII). The dominant and recessive alleles controlling number of tillers in a parent are approximately equal in number. The low estimate of the number of effective factors (K = 0.185) may be due to experimental error.

Heritability of this trait was intermediate in magnitude with an estimate of $h^2 = 0.612 \pm 0.086$. Again this is in agreement with the relative magnitudes of the additive and dominance variance parameters and indicates that a considerable portion of the phenotypic variance was additive in nature. This differs somewhat from the findings of Johnson et al. (15) who reported low heritability estimates for tiller number in a winter wheat cross. Although the heritability estimate for tillers per plant in this study was relatively high, it can be noted that it is not as great as those for kernels per spike and kernel weight which will be presented later.

Kernels per Spike

The estimates of the average degree of dominance were within the range of partial dominance with values of 0.271 to 0.564 (Table IX). The estimate of $\bar{F}_1-\bar{P}$ was not significantly different from zero suggesting the absence of a consistent trend in the direction of dominance. Tandon et al. (33) however found that dominant alleles conditioned lower number of kernels per spike. The value of $\frac{1}{4}H_2/H_1$ (0.189 ± 0.015) was significantly different from 0.25 which is consistent with the observation in Table VI that H_1 was much greater than H_2 and suggests that positive and negative alleles were not equally distributed among the parents.

The value of K_D/K_R suggests that on the average there are more

TABLE IX

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF KERNELS PER SPIKE

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	0.271	0.062	0.074-0.468
1b) $(H_1/D)^{1/2}$	0.508	0.065	0.301-0.715
1c) $(V_{1L1}-E)/(W_{0L01}-E/n)$	0.525	0.037	0.407-0.643
2) $\bar{F}_1-\bar{P}$	-0.564	0.513	(-2.196)-1.068
3) $\frac{1}{4} H_2/H_1$	0.189	0.015	0.141-0.237
4) K_D/K_R	2.898	0.422	1.555-4.241
5) K	0.060	0.036	(-0.055)-0.175
6) h^2	1.147	0.100	0.829-1.465

Note: Estimators 1a, 1b, and 1c = average degree of dominance, 2 = direction of dominance, 3 = distribution of positive and negative alleles, 4 = ratio of dominant to recessive alleles, 5 = number of effective factors, 6 = narrow-sense heritability.

dominant than recessive alleles controlling kernels per spike.

The unreasonably low value (K = 0.060 ± 0.036) found for the number of effective factors (Table IX), if not due to experimental error, may be an indication that most of the genes controlling this trait show no dominance. However significant dominance variance parameters were observed for this trait (See Table VI).

The estimate of heritability was very high. The value of h^2 = 1.147 is in fact greater than 1.0 and the estimate may reflect considerable error variation. If the high heritability estimate of this trait is valid, it indicates that a large portion of the genetic variability among the parents is due to additive genetic variation and thus can be fixed rather easily by the plant breeder.

Kernel Weight

The estimates of the average degree of dominance for kernel weight were significantly different from zero but were in general low with values ranging from 0.074 ± 0.004 to 0.502 ± 0.006 (Table X). These estimates were smaller than the same estimates for plant height, tillers per plant and kernels per spike (Tables VII, VIII, IX).

For those loci showing a certain degree of dominance, the direction of dominance was toward greater kernel weight. This is essentially the same trend as discussed in a previous section when means of various traits were discussed. However, a test of significance for the direction of dominance is provided in Table X where the estimator $\bar{F}_1-\bar{P}$ had a value of 2.688 ± 0.151. Similar results were found by Tandon et al. (33). The estimate of $\frac{1}{4}H_2/H_1$ (Table X) was not significantly different from 0.25 indicating that alleles determining greater

TABLE X

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF KERNEL WEIGHT

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	0.074	0.004	0.061-0.087
1b) $(H_1/D)^{1/2}$	0.271	0.007	0.249-0.293
1c) $(V_{1L1}-E)/(W_{0L01}-E/n)$	0.502	0.006	0.483-0.521
2) $\bar{F}_1-\bar{P}$	2.688	0.151	2.208-3.168
3) $\frac{1}{4}\ H_2/H_1$	0.233	0.007	0.211-0.255
4) K_D/K_R	1.715	0.122	1.327-2.103
5) K	3.346	0.489	1.790-4.902
6) h^2	1.043	0.022	0.973-1.113

Note: Estimators 1a, 1b, and 1c = average degree of dominance, 2 = direction of dominance, 3 = distribution of positive and negative alleles, 4 = ratio of dominant to recessive alleles, 5 = number of effective factors, 6 = narrow-sense heritability.

and smaller kernel weight were equally distributed among the parents. This suggests that selection for high or low kernel weight would be effective in a breeding program. Gill et al. (8), in a wheat study, reported a value of 0.170 for $\frac{1}{4} H_2/H_1$ but their estimate was not tested for significance.

The estimate of K_D/K_R indicates an excess of dominant over recessive alleles in a parent for those loci showing a certain degree of dominance.

The computed value of K indicates that about three to four effective factors control kernel weight. This agrees with the work of Sharma and Knott (27) who stated that as few as four genes may control the inheritance of seed weight in a cross involving two spring wheats. It should be emphasized that the estimate of gene number provided by K is only a lower limit which involves only those loci showing dominance.

The heritability of kernel weight in the narrow sense was found to be very high. The observed estimate of 1.043 ± 0.022 was slightly greater than unity. The estimate appears to be reliable due to the relative narrow confidence interval associated with it as shown in Table X. This high heritability estimate indicates that a major part of the genetic variability that exists between the parents for this trait is primarily due to additive gene effects. Consequently, this trait should be rather easy to modify in a breeding program.

There is an overwhelming evidence from other studies (3,15,27,32) that kernel weight is highly heritable.

These results show that kernel weight should be considered as one of the yield components of major importance to the plant breeder, not only because of its contribution to yield, either directly or indirectly (see Lovrin 6 parental array in Table III), but also because of its' high heritability scores.

Grain Yield

The estimates of the average degree of dominance for grain yield do not appear to be very reliable because of the large standard errors and confidence intervals associated with them (Table XI). Each of the three statistics estimating average degree of dominance exceeded the value of 1.0 indicating overdominance gene action. However, two of the estimators were not significantly different from zero (no dominance) and the third was not significantly different from partial dominance values.

Although it was pointed out in a previous section that the dominance deviation $\bar{F}_1-\bar{P}$ was in favor of the F_1's, the values presented in Table XI show that this deviation was not statistically significant. Thus there was no obvious trend in the overall direction of dominance. The estimate of $\frac{1}{4} H_2/H_1$ (Table XI) was not significantly different from 0.25, which indicates that increasing and decreasing alleles are equally present in the parents. Among the genes contributing to yield, the number of dominant alleles is about 3-4 times as great as the number of recessives as shown by the K_D/K_R estimator.

The impossibly low estimate of the number of effective factors ($K = 0.859 \pm 0.571$) controlling grain yield (Table XI) must be partly the result of large error variations associated with this estimate. Also the absence of dominance of loci controlling grain yield could have contributed to the low K value.

Grain yield had the lowest heritability estimate ($h^2 = 0.297 \pm 0.102$)

TABLE XI

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF GRAIN YIELD

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	3.225	1.492	(-1.523)-7.973
1b) $(H_1/D)^{\frac{1}{2}}$	1.624	0.442	0.128-3.030
1c) $(V_{1L1}-E)/(W_{0L01}-E/n)$	1.058	0.545	(-5.867)-7.983
2) $\bar{F}_1-\bar{P}$	1.164	0.489	(-0.392)-2.720
3) $\frac{1}{4}\ H_2/H_1$	0.206	0.015	0.158-0.254
4) K_D/K_R	3.890	0.585	2.029-5.751
5) K	0.859	0.577	(-0.977)-2.695
6) h^2	0.297	0.102	(-0.028)-0.622

Note: Estimators 1a, 1b, and 1c = average degree of dominance, 2 = direction of dominance, 3 = distribution of positive and negative alleles, 4 = ratio of dominant to recessive alleles, 5 = number of effective factors, 6 = narrow-sense heritability.

among the traits studied in this experiment. The results reported for grain yield tend to indicate that it is influenced by environmental factors and non-additive genetic effects to the extent that it was not easy to detect significant values for most of the parameters and estimators examined in this study. The magnitude of the dominance variance in relation to the additive variance (Table VI) and the relatively low heritability estimate (Table XI) tend to support this contention. Similar results with regard to the genetic control of grain yield in wheat were reported by Tandon et al. (33) and Johnson et al. (15).

In view of this, breeding for increased grain yield potential could perhaps best be accomplished through selection not for yield per se but for changes in yield components such as kernel weight which appears to have major effects on yield and which are highly heritable.

CHAPTER V

SUMMARY AND CONCLUSIONS

Five winter wheat cultivars were used in a diallel crossing system to study the nature of the genetic systems controlling kernel weight, kernels per spike, tillers per plant, plant height, and grain yield. Parents and F_1's were evaluated in a space-planted experiment conducted at the Agronomy Research Station, Stillwater, Oklahoma during the 1972-73 growing season.

Analyses of variance tests indicated that significant differences existed among the F_1's for the five characters measured. Significant differences among the parents were observed for all characters except grain yield per plant.

Parental values were compared with array means to determine the breeding behavior of each trait and phenotypic correlation coefficients among the five traits were computed to elucidate their inter-relationships. Finally, the Jinks-Hayman diallel analysis was applied to the data in order to estimate genetic parameters associated with each trait.

Parental performance _per se_ accurately predicted the average behavior of F_1 hybrid for kernel weight, kernels per spike, and plant height. Predictions were less reliable for tillers per plant and were completely unreliable for grain yield.

Tillers per plant were positively associated with grain yield and had the highest correlation coefficient of all comparisons. This type of association would be expected in space-planted material. Correlation coefficients between kernels per spike and grain yield were positive and of intermediate magnitude, while those between kernel weight and grain yield were very low. Kernel weight was negatively associated with tillers per plant and kernels per spike with low to intermediate correlation coefficient values. The association between tillers per plant and kernels per spike were positive but low.

The diallel analysis indicated that additive genetic effects were more important than dominance effects for kernel weight, kernels per spike, tillers per plant, and plant height. Additive and dominance effects were of similar magnitude for grain yield but, perhaps because of large environmental errors for this trait, the estimates of genetic effects were not significantly different from zero. Grain yield had the lowest heritability estimate of all characters studied, while kernel weight and kernels per spike had the highest estimates.

The results showed that differences in kernel weight among the parents were due primarily to additive genetic variance. This finding, together with the high heritability estimate, indicates that genetic improvement in kernel weight could be made rather easily as long as genetic diversity for this trait existed in the source material.

It can be concluded from the comparison of parental values with their corresponding array means that kernel weight is an important component of grain yield. Lovrin 6, the parent with the heaviest kernel weight had the lowest grain yield but its crosses averaged higher in grain yield than those of any other parent in the study.

If, as indicated, kernel weight contributes substantially to grain yield, then breeding procedures that concentrate primarily on kernel weight should be more effective in increasing grain yield potential than selection for grain yield itself. Of course, the inter-relationships of the other yield components must be considered as well. For the particular set of parents utilized in this study, the results indicate that perhaps the most effective method of increasing grain yield potential would be to select for high tiller number in those crosses involving Lovrin 6, the heavy-seeded parent. This would appear to result in the best balance for all three components in contributing to high grain yield performance.

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