A GENETIC ANALYSIS OF FLAG LEAF AREA AND OTHER CHARACTERS IN A DIALLEL CROSS INVOLVING SEVEN WINTER WHEAT PARENTS

By

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Bachelor of Science

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1974

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
MASTER OF SCIENCE
July, 1976

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ACKNOWLEDGMENTS

The author wishes to extend his sincere appreciation to Dr. Edward L. Smith, the author's advisor, for the assistance, encouragement and helpful suggestions he gave throughout the course of this study.

Grateful acknowledgments are also extended to other committee members, Dr. Lewis H. Edwards and Dr. Lavoy I. Croy, for their guidance and constructive criticism in the preparation of this thesis.

The author is deeply grateful to Dr. Ronald W. McNew for his assistance in conducting the statistical analysis.

Great appreciation is extended to the Department of Agronomy of Oklahoma State University for the financial support provided to make graduate studies such as this possible.

The assistance given by members of the Small Grains Breeding section in planting, harvesting and threshing of this study and help given by the laboratory assistants in Crop Physiology during the protein analysis is greatly appreciated.

The author wishes to express special thanks to his wife Sharla and daughter Jennifer for their encouragement and exceptional patience given throughout the course of this study.

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CHAPTER I

INTRODUCTION

The ever increasing human population calls for continued increases in the production of the world's basic food crops. Wheat has been a primary source of nutrition for the world for many centuries. One way of increasing wheat grain production is through the development of cultivars with higher grain yield potential.

Since grain yield in wheat is a very complex system under genetic and environmental influence, it may be possible to make larger gains in increasing yield potential by selecting for the more simply inherited components and studying their relationships with other plant characteristics. Using this approach, more effort could be placed on breeding for yield components rather than yield itself. Knowledge of the genetic control of these yield components and their interactions with other plant characters would be useful in breeding for increased yield potential.

Leaf area duration is one of the plant characters which may influence the expression of the yield components. There is a great deal of variation for this character within the species, but little effort has been concentrated on determining the actual contribution to yield or system of genetic control of leaf area duration in wheat. It therefore would seem desirable to study this component-character relationship as a possible means of increasing the yield potential of grain in wheat.

The objective of this study was to investigate the genetic systems controlling leaf area duration and the association of leaf area duration with yield and yield components in a diallel cross involving seven winter wheat cultivars which are presently used in the wheat breeding program at the Oklahoma Agricultural Experiment Station in Stillwater, Oklahoma.

CHAPTER II

LITERATURE REVIEW

In attempts to understand the genetic and physiological systems controlling grain yield in cereal grains, some investigators have considered the role of plant leaves and their relationship to the yield components. Stoy (27) in a study of the translocation of C^{14}, found that only the uppermost one or two leaves of wheat contributed significantly in the direct filling of grains with photosynthetic products. He concluded that a cultivar which has the ability to maintain a sufficient rate of photosynthesis for a relatively long period of time after anthesis would be especially well adapted for producing high grain yield under favorable growing conditions. In a similar study on the movement of C^{14} labeled assimilates in wheat, Quinlan and Sagar (22) found that assimilates from the flag leaf moved predominantly toward the spike, while assimilates from the leaves below the flag leaf moved toward the root system as well as toward the spike.

Thorne (30) found that the weight of CO_2 fixed by the flag leaf was equivalent to 110 to 120% of the grain weight while the ear assimilated CO_2 equal to 17 to 30% of the grain weight but more than this amount was lost through respiration. He states that approximately one half of the actual grain weight came from assimilates produced by the flag leaf of the wheat plant.

Welbank et al. (34) found in a study of leaf area duration that the duration of green parts above the flag leaf node in the wheat plant was the primary internal factor determining grain yield. They also noted that the random variation in yield was decreased when duration was measured from anthesis instead of spike emergence. This was expected because anthesis corresponds more closely to grain filling than does spike emergence.

Watson et al. (33) also found positive relationships between leaf area and grain yield and between leaf area duration and grain yield in wheat. They suggested the possibility of increasing yield if the leaf area index could be at a maximum during grain filling after spike emergence or if senescence could be delayed.

Davidson (4) also noted the correlation of leaf area with yield in wheat when he found that manual reduction of leaf area led to a 50 to 80% reduction in grain yield. This reduction of leaf area had no effect on tiller numbers, but resulted in decreased seed number and kernel weight. They concluded that an increase in leaf area of tillers producing grain could lead to increased grain yields.

Similar results were found by Saghir et al. (24). They noted that removal of the upper leaves led to significant reductions in 1,000 kernel weight in wheat. This reduction was more pronounced when the leaves were removed in the early bloom or anthesis stages. This suggests that the reproductive organs required the photosynthates at this time in order to produce high kernel weight.

In a study by Hsu and Walton (13), leaf area was analyzed as leaf length and width separately. The findings of this work showed that kernels per spike was affected more by flag leaf width while kernel weight was influenced more by flag leaf length. This led to the conclusion that the effects of morphological characters were expressed through their influences on yield components.

Berdahl et al. (1) found that the effects of leaf area on yield in barley was expressed as tiller numbers or kernel weight with large leaf areas favoring higher kernel weight and smaller leaf area associated with the production of more tillers per plant. Their data showed that the effect of leaf area was less direct on tiller number than kernel weight but that it was equally important.

In a study of the inheritance of leaf area in wheat, Kraljevic-Balalic (17) found that the flag leaf comprised 44 to 50% of the total leaf area of the plant and that the inheritance pattern of the flag leaf was similar to the inheritance pattern of the total leaf area. In this investigation, the heritability of total leaf area ranged from 6 to 47% and general combining ability variances were highly significant while specific combining ability variances were not. This indicated that the major portion of the genetic variance for total leaf area is made up of additive gene effects.

Hsu and Walton (12) in an analysis of a five-parent diallel cross of spring wheats, found that the additive genetic variance comprised the bulk of the total genetic variance, and that the components of photosynthetic area above the flag leaf node showed varying degrees of dominance. Flag leaf length and width were associated with overdominance. They also found flag leaf length to be closely correlated to yield.

Leaf area and its inheritance in barley was investigated by Fowler and Rasmusson (6). The heritability estimates for flag leaf area ranged from 23 to 73% on an individual plant basis. Expected genetic advance, calculated for selection on flag leaf area with a 10% selection pressure, showed that the mean flag leaf gain per plant was 41%. They concluded that selection for flag leaf area could be useful with the expectation that the other leaves would be correlated with the flag leaf.

The contribution of yield components was pointed out by Grafius (7) in his representation of yield in oats as the volume of a parallelepiped with the edges being the yield components: panicles per unit area, average number of kernels, and the average kernel weight. He suggested that if one side of the parallelepiped was shorter than the others, maximum yield increases could be gained by lengthening this component.

Knott and Talukdar (16) found, in a study involving large and small seeded lines of wheat, that there was a highly negative correlation between kernel weight and the average number of kernels. However, the increase in kernel weight was found to have a larger effect upon grain yield, thus overriding the decreased number of kernels. They concluded that an increase in kernel weight could lead to an increase in yield.

Rasmusson and Cannell (23) concluded from responses to selection for yield components in barley, that selection for yield components could be effective in certain situations but could not be recommended as routine procedure. They found that the environmental conditions greatly affected the optimum genotypic level for kernels per spike and number of spikes while the optimum for kernel weight was near its genetic maximum. This suggests that kernel weight is the more stable yield component.

Singh and Kandola (25) found that varying degrees of heterosis existed in wheat for spikes per plant, spikelet number per plant and kernel weight. They concluded that the heterosis observed for grain yield was the result of the hybrid vigor displayed by the yield components and that hybrids derived from parents of diverse origin resulted in the greater levels of heterosis.

Fonseca and Patterson (5) studied the inheritance and interrelationships of yield components in wheat. They showed that increased kernel size and tillering were more closely related to increased yield than was number of kernels per spike. The general trend was for tiller number and kernel number to have high heritability estimates while the heritability estimates for kernel weight and grain yield were intermediate or low. To the contrary, McNeal (19) found that in a population of Lemhi x Thatcher, kernel number was more closely correlated to yield than was kernel weight.

A diallel analysis of yield components in wheat was conducted by Paroda and Joshi (21). They found that 1,000 kernel weight and number of kernels per spike were highly heritable, indicating that breeding for these components could be relatively effective. Kernel weight had the highest heritability estimate of the components studied and showed a preponderance of additive genetic variance. Kernel number showed inconsistent results ranging from overdominance one year to partial dominance another year. This inconsistency led to the conclusion that kernel weight was the most genetically stable component influencing grain yield.

Sun et al. (28) worked with spring wheats and noted that additive genetic variance made up the larger portion of the total genetic variance for kernel weight and that dominance was also important in this character. Heterosis for kernel weight was found to be associated with dominant gene action in the presence of epistasis. Their heritability estimates for kernel weight ranged from 51 to 85%.

Tandon et al. (29) found that grain yield exhibited complete dominance and overdominance while spike number showed complete dominance and kernel weight showed partial dominance patterns of inheritance. Kernels per spike showed a very slight degree of dominance. Combining ability estimates revealed that additive and nonadditive effects were equally important in the genetic control of kernel weight.

In a study involving two spring wheat crosses, Bhatt (3) found that partial dominance controlled heavy kernel weight with additive gene effects being of higher magnitude than dominance gene effects. There was no evidence of significant epiststic effects for kernel weight. However, additive gene effects were important while dominance effects were not. In a separate study, Bhatt (2) found that kernel weight exhibited a high level of heterosis. Significant general and specific combining ability estimates were found for kernel weight but additive gene action was the predominant source of genetic variation.

A study of correlated sequential characters by Lee and Kaltsikes (18) indicated that spikes per plant, kernels per spikelet, spikelets per spike and kernel weight showed predominantly additive genetic effects with some degree of dominance and a general lack of epistasis. Their data also showed that spikes per plant and kernels per spikelet were independent of other characters but spikelets per spike and kernel weight were dependent upon characters developed before them in the developmental sequence of the wheat plant.

Johnson et al. (15) concluded, after comparing yield components and agronomic characteristics in a winter wheat study, that as yields were increased to higher levels, new levels of productivity became increasingly harder to attain. They stated that more increase might be made by giving attention to selection of individual yield components rather than by selecting for yield per se.

CHAPTER III

MATERIALS AND METHODS

This study was conducted on a space-planted nursery during the 1974-75 wheat growing season at Stillwater, Oklahoma. Twenty-one F_1's from a diallel cross involving seven winter wheat cultivars (*Triticum aestivum* L. em Thell) comprised the basic materials in the study. The cultivars used as parents were 'Tam W 101', 'Bezostaia 1', 'Trison', 'OK66V2629', 'Osage', 'Centurk' and 'Tam W 103'. These cultivars were chosen as representative parent stock currently used in the Oklahoma Agricultural Experiment Station wheat breeding program.

The seven cultivars were crossed in all possible combinations in accordance with the diallel crossing system. Crossing was accomplished by hand emasculation and pollination in the greenhouse during the 1973-74 crossing season. Reciprocal crosses were not kept separate. Seed of the resulting 21 F_1's and seven parents were planted in greenhouse flats on October 22, 1974. After germination, the seedlings were placed in cold frames and allowed to vernalize at outside temperatures for approximately one month. During this period, the seedlings were periodically clipped to remove excess top growth and they were appropriately cared for in order to assure maximum plant vigor before being transplanted in the field.

Field Layout and Test Conditions

The seedlings were transplanted by hand to the field on November 26, 1974. The experimental design used was four replications of a randomized complete block. Each replication contained one plot of each of the seven parents and 21 F_1's. The 28 entries were assigned at random to the plots of each replication. Each plot consisted of a single row containing eight test plants with a guard plant at the front and back of the plot to reduce bias by border effect. The distance between plants within a plot was 30 cm and the same distance separated adjacent plots. Each replication was bordered by one guard row on either side in order to reduce bias by border effect. The study was located on the 2100 series at the Agronomy Research Station, Stillwater, Oklahoma. The soil type was a Bethany silt loam which was fallowed the previous year.

A preplant application of 224 kg/ha of 18-46-0 was made on September 9, 1974, and a top dressing of 168 kg/ha of 34-0-0 was applied to the study on March 3, 1975.

Generally favorable conditions prevailed during the growing season. Above average spring temperatures resulted in early growth and good development of yield related traits. There was no problem with disease or pests, however, a hail storm did occur before harvest. This storm did not appear to damage the plants enough to affect the results of the measurements taken later.

The study was harvested on June 18, 19 and 20 by pulling each plant individually.

Characters Evaluated

Ten characters were investigated in the experiment. These were plant height, tillers per plant, total grain yield, seeds per main tiller, grain weight per main tiller, flag leaf area, flag leaf duration, percent protein, leaf area duration and kernel weight.

The measurements of these characters were made as follows.

Plant Height

This measurement was made as the distance from the crown of the plant to the tip of the spike of the tallest tiller, awns excluded. This character was expressed as centimeters per plant.

Tillers per Plant

The number of tillers per plant was taken as the number of fertile spikes collected from each plant at the time of harvest and was expressed on a per plant basis.

Total Grain Yield

Total grain yield was measured as the weight of threshed and cleaned grain from each individual plant and was expressed in grams per plant.

Seeds per Main Tiller

Seeds per main tiller was taken as the number of seed threshed from the tiller which was designated as the main tiller.

Grain Weight per Main Tiller

Grain weight per main tiller was calculated on the basis of the weight of thrashed grain from the main tiller of each individual plant and was expressed as grams per main tiller.

Flag Leaf Area

Flag leaf area was measured using the flag leaf of the main tiller of each individual plant. The measurement was taken with a portable digital readout area meter at the time of anthesis. This observation was expressed in square centimeters per flag leaf.

Flag Leaf Duration

Flag leaf duration was taken as the elapsed time from anthesis to senescence of the flag leaf of the main tiller on each individual plant and was expressed in days. The date of anthesis for the main tiller of each plant was noted. The flag leaf senescence was recorded on a plot basis since there appeared to be very little variation in the time of senescence among plants within a plot.

Percent Protein

Percent protein of the grain was obtained by using the Udy analyses test for ground whole kernels and was measured on a per plant basis.

Leaf Area Duration

Leaf area duration was a mathematical calculation obtained by multiplying the leaf area by the duration of the flag leaf on the main tiller of each individual plant and was recorded as centimeter squared days per plant.

Kernel Weight

This character was obtained by dividing the weight of the seed threshed from the main tiller by the corresponding number of seed from that tiller and was expressed as grams per 1,000 kernels.

Statistical Analysis

Analyses of variance were conducted for each of the traits measured. These analyses were the first stages of the complete statistical analysis of the data. Their purpose is to detect the presence or absence of true differences among the entries for the ten characters which were measured.

Phenotypic correlation coefficients among the ten traits were calculated from the error term of a cross products analysis of variance. Correlation coefficients were calculated for F_1's alone, parents alone and F_1's combined with parents. Tests for significance of these correlations were done in the manner suggested by Steel and Torrie (26).

Diallel Analysis

The data were subjected to the diallel analysis as outlined by Hayman (8, 9, 10, 11) and Jinks and Hayman (14). This system of analysis provides information about the genetic system controlling quantitative characters in the parents involved in a diallel crossing system. The validity of conclusions drawn from the information provided by this method of analysis depends upon the correctness of the following assumptions: 1) diploid segregation, 2) no difference between reciprocal crosses, 3) independent action of non-allelic genes, and in the diallel cross, 4) no multiple allelism, 5) homozygous parents, and 6) genes independently distributed between the parents. Tests were conducted to determine the validity of these assumptions.

To determine if the assumptions were met fully or partially, the broad test of an analysis of variance for the quantity (W_r-V_r) was conducted as outlined by Verhalen and Murray (31, 32). In this quantity, V_r is the variance of all the progeny of each parental array, and W_r is the covariance of the progeny of each array with the non-recurrent parents. If a trait shows significance in this test, it is concluded that the data fails to meet one or more of the assumptions.

The parameters estimated by the diallel analysis are E_0, E_1, D, H_1, H_2 and F. The parameter E_0 is an estimate of the environmental variation associated with the parents while E_1 is the estimate of the F_1 environmental variation.

D is an estimate of additive genetic variance which may include additive by additive epistatic effects. H_1 and H_2 are different estimates of dominance genetic variance and 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.

F serves as an indicator of the relative frequency of dominant and recessive alleles in the parents. An F value of zero indicates that dominant and recessive alleles are equally distributed among the set of parents. A positive F value indicates an excess of dominant alleles while a negative F value indicates an excess of recessive alleles in the parents.

The parameters were calculated from an analysis based on data from individual plants and each replication was analysed separately as suggested by Nedler (20). The variation of the replication 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 ten traits measured are presented in Table I. An analysis of variance was conducted for F_1's and parents separately and a combined analysis involving both was conducted as well. Highly significant entry (genotype) mean squares were obtained for nine of the ten traits in the three types of analyses. The exception was total grain yield per plant. Mean squares for this trait were found to be significant at the .01 level of probability for the combined analysis and for the analysis of F_1's alone, but significant at the .05 level of probability when parents were analyzed alone.

The mean squares for replications from the combined analysis, as shown in Table I, were statistically significant in eight of the ten traits indicating that the blocking of replications was effective in removing some of the nonessential variation from treatment effects and hence increasing the precision of the analysis.

When the replication by entry interaction is considered, it can be seen that there was a significant interaction for the ten traits from the combined analysis and from the analysis for F_1's alone. The analysis for parents alone showed no statistically significant

TABLE I

MEAN SQUARES OF 10 CHARACTERS FOR THE PARENTS AND F_1'S FROM A 7-PARENT DIALLEL CROSS OF WINTER WHEAT

Source of Variation		df	Flag Leaf Area	Plant Height	Tillers per Plant	Total Grain Yield	Seeds per Main Tiller	Grain Yield per Main Tiller	Flag Leaf Duration	Percent Protein	Leaf Area Duration	Kernel Weight
Rep	a	3	225.03**	671.92**	37.41	100.80*	85.96	0.290*	10.56**	57.13**	181238.0**	108.98**
	b	3	133.87**	406.84**	3.49	42.38	53.67	0.115	11.02**	34.77**	78798.0*	78.55**
	c	3	117.15*	345.17**	113.18**	128.07**	64.30	0.295*	1.03	25.56**	136804.0**	60.97*
Entry	a	27	509.17**	1354.75**	427.55**	405.43**	806.57**	1.550**	168.13**	35.83**	715044.0**	549.99**
	b	20	378.16**	982.29**	396.56**	382.49**	755.05**	1.374**	165.14**	30.18**	543422.0**	431.23**
	c	6	976.56**	2307.09**	591.56**	190.72*	1035.51**	0.563**	196.31**	27.47**	1334014.0**	583.74**
Rep x Entry	a	81	57.87**	58.50**	72.32**	109.72**	99.07**	0.225**	6.86**	4.55**	66498.0**	34.74**
	b	60	58.20**	59.96**	85.56**	125.77**	109.38**	0.264**	8.06**	4.40**	65035.0**	37.29**
	c	18	62.08**	50.06**	27.03	62.90**	75.90*	0.114	3.77**	5.27**	76728.0**	26.93
Plant (Rep Entry)	a	784	29.57	12.16	20.72	27.62	50.06	0.094	0.735	1.09	27425.0	19.72
	b	588	28.27	13.00	19.87	29.72	52.83	0.100	0.736	1.06	25908.0	19.80
	c	196	33.44	9.64	23.26	21.30	41.77	0.079	0.735	1.20	31975.0	19.47
Corrected Total	a	895	47.25	59.07	37.72	46.69	77.44	0.151	6.37	2.64	52220.0	37.37
	b	671	41.85	47.85	36.90	48.88	78.82	0.152	6.34	2.37	45068.0	33.89
	c	223	62.26	79.23	40.07	30.65	71.56	0.098	6.25	2.56	72030.0	35.81

*,** 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

replication by entry interaction for tillers per plant, grain yield per main tiller and kernel weight.

Comparison Among Means

The means for each trait measured in the 28 genotypes are presented in Table II. Since each plot consisted of eight plants from which individual measurements were taken and there were four replications in this study, each mean is based on 32 observations.

The leaf area means ranged from 19.58 cm^2 for Tam W 103 to 34.50 cm^2 for Bezostaia 1/Tam W 101 F_1. Bezostaia 1 was the parent having the largest flag leaf area with a mean of 33.75 cm^2. The overall mean values of the seven parents and 21 F_1's were 27.87 cm^2 and 29.26 cm^2, respectively. This comparison would indicate that larger flag leaf area is incompletely dominant to the alternate condition, assuming that this difference is real.

Plant height ranged from 65.50 cm for Tam W 103 to 89.25 cm for OK66V2629/Centurk F_1. Centurk, the tallest parent, had a height of 88.50 cm. The overall mean values of the parents and F_1 hybrids were 79.22 cm and 83.57 cm, respectively. These comparisons suggest that taller plant height is incompletely dominant to the shorter plant stature.

The number of tillers per plant varied from 15.12 for Bezostaia 1 to 31.00 for Tam W 101/Tam W 103 F_1. The parent with the largest average number of tillers was Tam W 103 with 27.15. The overall mean value for the parents was 21.19 and for the F_1's the mean value was 21.80. Thus, indicating that larger numbers of tiller per plant is incompletely dominant to the condition of smaller tiller numbers per

TABLE II

MEANS OF 10 CHARACTERS IN A 7-PARENT DIALLEL CROSS OF WINTER WHEAT

Entry	Flag Leaf Area (cm^2)	Plant Height (cm)	Tillers per Plant	Total Grain Yield (cm)	Seeds per Main Tiller	Grain Yield per Main Tiller (gm)	Flag Leaf Duration (days)	Percent Protein	Leaf Area Duration (cm^2 days)	Kernel Weight (gm/1000 kernels)
Parents										
Tam W 101	32.23	73.71	22.81	18.01	42.43	1.338	29.96	13.21	968.6	31.51
Bezostaia 1	33.75	73.03	15.12	13.54	48.71	1.347	29.90	14.91	1012.4	27.70
Trison	23.21	83.50	16.59	14.47	44.43	1.353	26.50	11.90	615.2	30.44
OK66V2629	30.94	84.50	23.62	17.52	43.90	1.197	25.25	13.99	783.3	27.23
Osage	31.52	85.81	19.43	17.08	44.31	1.438	31.78	13.83	1010.3	32.21
Centurk	23.82	88.50	23.59	20.83	59.03	1.350	25.68	13.92	613.2	22.82
Tam W 103	19.58	65.50	27.15	15.59	48.81	1.041	27.96	13.93	548.3	21.13
Overall Parental Mean	27.87	79.22	21.19	16.72	47.37	1.295	28.15	13.67	793.1	27.58
F_1 Hybrids										
Tam W 101/Trison	26.05	79.81	18.18	17.10	42.96	1.466	28.56	11.80	744.8	33.69
Tam W 101/OK66V2629	34.19	88.00	26.09	26.15	51.00	1.784	28.40	12.17	971.0	34.98
Tam W 101/Osage	29.57	82.18	22.46	14.66	36.68	1.034	32.18	13.23	954.0	28.21
Tam W 101/Centurk	32.50	85.40	22.62	22.90	50.18	1.722	28.75	12.71	937.8	34.19
Tam W 101/Tam W 103	28.00	69.18	31.00	26.90	49.78	1.728	29.75	11.09	832.8	34.92
Bezostaia 1/Tam W 101	34.50	79.15	19.56	19.48	52.06	1.666	28.87	13.01	995.7	32.03
Bezostaia 1/Trison	30.03	85.50	18.43	18.08	49.12	1.591	26.81	11.93	807.7	32.45
Bezostaia 1/OK66V2629	32.53	87.06	22.62	20.02	44.53	1.419	28.12	13.22	914.9	31.71
Bezostaia 1/Osage	33.65	88.71	18.15	22.90	51.90	2.013	33.71	12.97	1138.4	38.69
Trison/OK66V2629	27.24	85.65	22.90	21.60	47.62	1.550	26.84	11.60	730.5	32.77
Trison/Centurk	24.90	88.87	16.03	14.97	53.00	1.553	26.00	11.35	648.1	29.13
Trison/Tam W 103	23.65	76.15	20.78	17.54	48.87	1.444	26.62	10.83	631.5	29.30
OK66V2629/Osage	32.11	88.81	21.00	19.81	48.53	1.503	29.87	13.64	961.8	31.05
OK66V2629/Centurk	29.48	89.25	19.65	16.91	50.50	1.388	25.43	13.75	753.3	27.28
OK66V2629/Tam W 103	32.45	87.90	25.78	23.05	47.00	1.553	27.68	12.63	898.5	32.74
Osage/Trison	26.77	86.75	22.28	23.13	49.59	1.734	31.03	11.65	832.4	35.04
Osage/Centurk	28.81	88.50	21.78	21.86	53.31	1.759	30.53	14.00	882.7	32.63
Centurk/Bezostaia 1	29.50	81.93	16.50	15.59	51.09	1.456	25.43	14.25	752.5	28.57
Centurk/Tam W 103	23.10	74.84	23.43	18.96	51.71	1.266	27.50	12.73	635.4	24.00
Tam W 103/Bezostaia 1	29.83	79.09	24.12	22.04	59.71	1.491	29.40	12.33	877.0	24.84
Tam W 103/Osage	25.52	80.93	24.50	22.66	40.62	1.438	32.06	13.26	820.3	35.42
Overall F_1 Mean	29.26	83.51	21.80	20.30	49.04	1.550	28.74	12.58	843.9	31.60
$\bar{F}_1$ percent of $\bar{p}$	105.0	105.4	102.9	121.4	103.5	119.7	102.1	92.0	106.4	114.6

plant if this small difference is due only to genotype.

The total grain yield per plant ranged from 13.54 g for Bezostaia 1 to 26.90 g for Tam W 101/Tam W 103 F_1 which was nearly a two-fold difference. Centurk was the highest yielding parent with a mean of 20.83 g. The overall mean values for the parents and F_1's were 16.72 and 20.30 g, respectively. This comparison of means suggests that high grain yield is incompletely dominant to the condition of low grain yield. However, it should be noted that statements made on the basis of mean comparisons may not necessarily be statistically valid.

The means for number of seeds per main tiller ranged from 36.68 for Tam W 101/Osage F_1 to 59.71 for Tam W 103/Bezostaia 1 F_1. The highest parental mean was 59.03 for Centurk. The overall mean values for the parents and F_1's were 47.37 and 49.04, respectively. The comparison of means suggests a lack of dominance or slight partial dominance for larger number of seeds per main tiller.

Grain yield per main tiller ranged from 1.034 g for Tam W 101/Osage F_1 to 2.031 g for Bezostaia 1/Osage F_1. The highest parent was Osage with a mean value of 1.438 g. The overall mean values for the parents and F_1's were 1.295 and 1.550 g, respectively. This comparison indicates incomplete dominance for higher grain yield over low grain yield per main tiller.

Flag leaf duration means ranged from 25.25 days for OK66V2629 to 33.71 days for Bezostaia 1/Osage F_1. The parent with the longest flag leaf duration was Osage with a mean of 31.78 days. The overall mean values for the seven parents and 21 F_1's were 28.15 and 28.74 days, respectively. The comparison of means indicates a general lack of dominance or slight partial dominance for longer flag leaf duration. Again, it should be recognized that these comparisons may not be statistically valid as will be discussed in a future chapter.

The mean values for percent protein varied from 10.83 for Trison/Tam W 103 F_1 to 14.91 for the parent Bezostaia 1. The F_1 with the highest protein percent was Centurk/Bezostaia 1 F_1 with a mean of 14.25. The overall mean values for the parents and F_1's were 13.67 and 12.58%, respectively. Thus the difference 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 lower protein percentage. However, this difference may be due to the difference between the yields of F_1's and parents.

The means for leaf area duration ranged from 548.3 cm^2 days for Tam W 103 to 1138.4 cm^2 days for Bezostaia 1/Osage. The parent with the largest leaf area duration was Bezostaia 1 with 1012.4 cm^2 days. The overall mean values for the parents and F_1's were 793.1 and 843.9 cm^2 days, respectively. The duration of the mean F_1 value from the midparent value suggests a genetic system of partial dominance in favor of larger leaf area duration as opposed to the alternate condition.

The means for average 1,000 kernel weight ranged from 21.13 g for Centurk to 38.69 g for Bezostaia 1/Osage F_1. The parent with the highest 1,000 kernel weight was Osage with a mean value of 32.21 g. The overall mean values for the parents and F_1's were 27.58 and 31.60 g, respectively. This difference between the mean values for the F_1 and midparent indicates partial dominance in favor of high kernel weight.

The parental arrays were compared with the corresponding parental values for the various traits under investigation in this study (Table III). For this comparison, an array is defined as all the crosses involving a common parent, but the array does not include the parent itself. This type of comparison gives additional information about the traits and their expected behavior in crosses. A case where the array means and their corresponding parental values have close agreement in their relative ranking would indicate that the behavior of this trait in crosses could be predicted on the basis of the parental value alone. The reverse situation suggests that the parental value is not a good indicator of the behavior of the trait in crosses.

The correspondence between parental values and parental arrays was relatively close for flag leaf area, plant height, tillers per plant, seeds per main tiller, flag leaf duration, leaf area duration and kernel weight. Less agreement was noted for total grain yield per plant, grain yield per main tiller and percent protein. In the case of total grain yield, Centurk was found to have the top ranking parental value while the parental array ranked fifth and the parental value for Tam W 103 was ranked fifth and the parental array was ranked first. Grain yield per main tiller was noted to have relatively large disagreement between the ranking of parental values and parental arrays of Bezostaia 1, Trison and Centurk. Disagreement among the rankings of parental values and parental arrays was noted for OK66V2629, Osage, Centurk and Tam W 103 in the comparisons for percent protein.

The degree of disagreement in the ranking of parental values and parental arrays would suggest that the prediction of the behavior of these three traits could not be accurately based on parental values alone.

TABLE III

PARENTAL VALUES AND ARRAY MEANS OF 10 TRAITS FROM A 7-PARENT DIALLEL CROSS OF WINTER WHEAT

Parental Array a) and Value b)	Flag Leaf Area (cm^2)		Plant Height (cm)		Tillers per Plant		Total Grain Yield (gm/plant)		Seeds per Main Tiller		Grain Yield per Main Tiller		Flag Leaf Duration (days)		Percent Protein		Leaf Area Duration (cm^2 days)		Kernel Weight (gm/1000 kernels)	
	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)	Mean	Rank c)
Tam W 101																				
Parental array	31.01	3	79.64	6	23.25	2	20.75	2	46.45	6	1.534	3	29.50	2	12.46	5	915.0	3	32.80	2
Parental value	32.23	2	73.71	5	22.81	4	18.01	2	42.43	7	1.338	5	29.96	2	13.21	6	968.6	3	31.51	2
Bezostaia 1																				
Parental array	31.98	1	82.07	5	19.22	7	18.81	6	51.02	2	1.569	1	28.90	3	13.24	2	928.4	2	30.86	5
Parental value	33.75	1	73.03	6	15.12	7	13.54	7	48.71	3	1.347	4	29.90	3	14.91	1	1012.4	1	27.70	4
Trison																				
Parental array	25.98	7	83.75	4	19.32	6	18.13	7	47.95	4	1.527	4	27.48	5	11.59	7	715.8	7	31.84	3
Parental value	23.21	6	83.50	4	16.59	6	14.47	6	44.43	4	1.353	2	26.50	5	11.90	7	615.2	5	30.44	3
OK66V2629																				
Parental array	31.28	2	87.31	1	23.10	3	20.73	3	47.59	5	1.485	6	27.83	6	13.01	4	859.1	4	31.12	4
Parental value	30.94	4	84.50	3	23.62	2	17.52	3	43.90	6	1.197	6	25.25	7	13.99	2	783.3	4	27.23	5
Osage																				
Parental array	29.71	4	85.96	2	21.38	4	20.30	4	46.42	7	1.560	2	31.60	1	13.23	3	942.9	1	33.33	1
Parental value	31.52	3	85.81	2	19.43	5	17.08	4	44.31	5	1.438	1	31.78	1	13.83	5	1010.3	2	32.21	1
Centurk																				
Parental array	27.45	5	85.33	3	20.52	5	18.87	5	52.69	1	1.499	5	27.05	7	13.25	1	746.2	6	28.38	7
Parental value	23.83	5	88.50	1	23.59	3	20.83	1	59.03	1	1.350	3	25.68	6	13.92	3	613.2	6	22.82	6
Tam W 103																				
Parental array	26.03	6	76.23	7	25.25	1	20.97	1	49.50	3	1.423	7	28.71	4	12.40	6	749.2	5	28.91	6
Parental value	19.58	7	65.50	7	27.15	1	15.59	5	48.81	2	1.041	7	27.96	4	13.93	4	548.3	7	21.13	7

a) In this comparison, an array consists of all the crosses 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.

Correlations

Correlation coefficients for the F_1 data are presented in Table IV. Correlation coefficients were calculated for all three sets of data, (F_1's and parents combined, F_1's alone and parents alone). Because of the close agreement in magnitude and sign of the three data sets, only those for the F_1 data are presented in order to reduce confusion which might arise from the sets of coefficients. The correlations of particular interest were those involving leaf measurements and yield and yield components.

Flag leaf area was found to have a high coefficient of correlation (r = 0.984) in the comparison with leaf area duration. This association was expected due to the fact that flag leaf area makes the largest contribution in the calculation of leaf area duration. In the comparison involving flag leaf duration and leaf area duration, an r value of 0.366 was observed. This correlation was relatively low but expected because leaf duration makes the smallest contribution in the calculation of leaf area duration. Even though the two components of leaf area duration differed widely in their respective correlations to leaf area duration, no one of the two can be said to be more important to leaf area duration than the other. Leaf area duration was observed to have a significant positive correlation with total grain yield with an r value of 0.397. This r value would fall in the intermediate range of magnitude for correlations and would seem to indicate that leaf area duration does have a positive relationship with higher grain yield. Welbank et al. (34) noted that grain yields were nearly proportional to the leaf area duration. The greatest correlation of leaf

TABLE IV

COEFFICIENTS OF CORRELATION AMONG 10 TRAITS FROM F_1'S OF A 7-PARENT DIALLEL CROSS OF WINTER WHEAT

	Plant Height	Tillers per Plant	Total Grain Yield	Seeds per Main Tiller	Grain Yield per Main Tiller	Flag Leaf Duration	Percent Protein	Leaf Area Duration	Kernel Weight
Flag Leaf Area	0.250**	0.218**	0.345**	0.363**	0.335**	0.219**	-0.025	0.984**	0.119**
Plant Height		0.158**	0.413**	0.415**	0.439**	0.026	-0.190**	0.240**	0.221**
Tillers per Plant			0.795**	0.226**	0.214**	0.412**	-0.184**	0.271**	0.101*
Total Grain Yield				0.423**	0.502**	0.427**	-0.401**	0.397**	0.306**
Seeds per Main Tiller					0.733**	0.237**	-0.160**	0.380**	0.073
Grain Yield per Main Tiller						0.256**	-0.242**	0.357**	0.713**
Flag Leaf Duration							-0.156**	0.366**	0.153**
Percent Protein								-0.047	-0.187**
Leaf Area Duration									0.136**

*,** 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.

df(n-2) = 587 The significant value (.05) = .086
df(n-2) = 587 The significant value (.01) = .113

area duration and a yield component was observed in the comparison between leaf area duration and seeds per main tiller with an r value of 0.380. The comparisons involving leaf area duration and the yield components: tillers per plant and kernel weight showed correlation coefficients of r = 0.271 and r = 0.136, respectively. If the assumption of a cause and effect relationship is made between leaf area duration and yield, it would seem that leaf area duration makes a larger contribution to yield through its effect upon seed per main tiller than the other yield components. In the comparison between leaf area duration and grain yield per main tiller, an r value of 0.357 was observed. Since all leaf area measurements were taken on the main tiller of each individual plant, this correlation could be a reliable indication of the relationship of leaf area duration to grain yield if the assumption of a cause and effect relationship is true. Leaf area duration was found to have a low correlation with plant height and a low, nonsignificant, negative correlation to percent protein.

Total grain yield was observed to have a high correlation in the comparison with tillers per plant, r = 0.795. This was the largest r value observed in any comparison involving total grain yield, indicating that in this study total grain yield was most highly dependent upon the number of tillers per plant. This association is to be expected in space planted material when a cause and effect assumption is made. Similar results were reported by Hsu and Walton (13). It was noted that the r value in the comparison between total grain yield and grain yield per main tiller was the second highest value observed in comparisons involving total grain yield, r = 0.502.

Total grain yield was found to have correlation coefficients of intermediate magnitude in the comparisons with flag leaf area and flag leaf duration, r = 0.345 and r = 0.427, respectively. From Table IV, it can be seen that among the comparisons in which total grain yield is involved with a measurement of the flag leaf, flag leaf duration was observed to be the most highly correlated with total grain yield. This supports what is known about yield and maturity relationships, but here again, one of these traits cannot be said to be more important to total grain yield than the others. Comparisons involving total grain yield with seeds per main tiller and kernel weight were found to have r values of 0.423 and 0.306, respectively. Total grain yield was observed to have an intermediate negative correlation with percent protein.

Seed per main tiller and kernel weight were noted to have high correlation coefficient values in the comparisons with grain yield per main tiller. Previous work has shown similar relationships between grain yield and seeds per spike and kernel weight (5, 16).

Diallel Analysis

The Jinks-Hayman diallel analysis provides information about the genetic systems controlling the behavior of a given trait in a set of parents. One of the first steps in conducting a diallel analysis is to test the validity of the assumptions stated in the diallel analysis model.

The test used in this study is the Wr-Vr homogeneity check. The statistic Wr is the covariance of the progeny of each array with the nonrecurrent parent, and Vr is the variance of all the progeny of each parental array. In this test, an array includes the parent itself as well as the crosses derived from it. In the analysis of variance for the quantity Wr-Vr, statistical significance for a trait would indicate that the trait failed to meet one or more of the assumptions of the diallel model. Testing for the failure to meet a specific assumption cannot be accomplished when only parents and F_1's are studied.

The Wr-Vr homogeneity check was conducted for the ten characters measures in this study and the results are presented in Table V. The results from the test indicate that the characters flag leaf area, tillers per plant, total grain yield, protein percent and leaf area duration met all the assumptions as specified by the diallel analysis model. Failure of one or more assumptions was indicated for plant height, number of seeds per main tiller, grain yield per main tiller, flag leaf duration and kernel weight.

Even though a trait fails to meet all of the assumptions, parameter estimates can still be made. However, the estimates concerning the genetic systems may not be as reliable as if the assumptions had been met.

Parameter Estimates

The parameters estimated by the Jinks-Hayman model were D, H, H_2, F, E_0 and E_1. The computed estimates of these parameters are shown in Table VI. The estimates of additive genetic variance (D) were found to be significantly different from zero for seven of the traits measured. These were plant height, tillers per plant, grain yield, seeds per main tiller, flag leaf duration, percent protein and kernel weight.

TABLE V

MEAN SQUARES FROM AN ANALYSIS OF VARIANCE OF THE Wr-Vr QUANTITY OF PARENTAL ARRAYS FOR 10 CHARACTERS FROM A 7-PARENT DIALLEL CROSS OF WINTER WHEAT

Source of Variation	df	Flag Leaf Area	Plant Height	Tillers per Plant	Total Grain Yield	Seeds per Main Tiller	Grain Yield per Main Tiller	Flag Leaf Duration	Percent Protein	Leaf Area Duration	Kernel Weight
Replications	3	175.18*	1504.05**	262.78**	504.26**	77.35	0.0037**	10.24**	1.02*	862965092.00	83.29**
Array (Wr-Vr)	6	35.76	508.93**	73.69	141.82	593.88*	0.0053**	4.83**	0.21	45441834.00	192.53**
Error	18	38.11	102.73	36.05	77.02	194.00	0.0007	1.14	0.27	77664347.00	15.39

*,** 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 the offspring of each array with the nonrecurrent parents.
Vr is the variance of all the offspring of each parental array.

TABLE VI

PARAMETER ESTIMATES OF GENETIC AND ENVIRONMENTAL VARIANCE COMPONENTS OF 10 CHARACTERS FROM A 7-PARENT DIALLEL CROSS OF WINTER WHEAT

Parameter	Flag Leaf Area	Plant Height	Tillers per Plant	Total Grain Yield	Seeds per Main Tiller	Grain Yield per Main Tiller	Flag Leaf Duration	Percent Protein	Leaf Area Duration	Kernel Weight
D	32.16	75.58 **	18.11 **	9.195*	34.25 *	0.018	6.396*	1.203*	44884.0	18.33 **
H_1	22.74**	78.10 *	40.83	86.12 *	83.95 **	0.243*	7.148*	3.478*	30251.0*	48.65 **
H_2	18.43**	63.25 *	34.77	73.89 *	73.88 **	0.228*	5.564**	2.765*	25507.0*	45.96 **
F	9.86	28.79 **	1.868	13.74 *	18.93	0.019	-2.262	0.276*	11061.0	6.494
E_o	4.18**	1.205**	2.908**	2.663**	5.221**	0.010**	0.092*	0.150**	3997.0**	2.434**
E_1	3.53**	1.625**	2.484**	3.716**	6.604**	0.013**	0.092**	0.132**	3239.0**	2.475**

*,** Significantly different from zero at the 0.05 and 0.01 probability levels, 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_o and E_1 = environmental variance.

The estimates for H_1 and H_2 (dominance variance) were both significant at the .05 level of probability for plant height, grain yield, grain yield per main tiller, percent protein and leaf area duration. Significance for both H_1 and H_2 at the 0.1 level of probability was observed for flag leaf area, seeds per main tiller and kernel weight, while neither H_1 or H_2 was significant for tillers per plant. In the case of flag leaf duration, H_1 was found to be significant at .05 and H_2 was significant at the .01 level of probability.

The results presented in Table VI indicate that additive genetic effects are relatively more important than dominance effects for tillers per plant, while dominance genetic effects seemed to be most important for flag leaf area, grain yield per main tiller and leaf area duration. Both additive and dominance genetic systems were indicated for plant height, total grain yield, seeds per main tiller, flag leaf duration, percent protein and kernel weight.

Although both H_1 and H_2 are estimates of dominance genetic variance, 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 be equal to H_2. For all 10 traits in this study, H_1 was always greater than H_2.

Significant positive F values were found for plant height, total grain yield and percent protein (Table VI). A positive F value which is significantly different from zero indicates an excess of dominant alleles among the parents for the traits in question. Nonsignificant F values, indicating that the dominance and recessive alleles are equally distributed among the parents, were observed for the seven other traits as shown in Table VI.

Genetic Ratios

After the parameters D, H_1, H_2 and F were estimated, various ratios were calculated to gain additional information about the genetic systems controlling each trait. Standard errors and confidence limits of these ratios were also determined.

The ratios H_1/D, $(H_1/D)^{\frac{1}{2}}$, and $(D+H_1-F)/(2D-F)$ or $(V_{1L1}-E)/(W_{0L02}-E/n)$ are weighted measures of the average degree of dominance at each locus. Under a system of no dominance the estimates are zero. Under partial dominance, the estimates are expected to fall in a range from zero to one, and in the case of complete dominance, the estimates are expected to equal one. Values greater than one indicate over-dominance.

The quantity $(\bar{F}_1-\bar{P})$ is an indicator of the average direction of dominance. If no dominance exists, the estimate is zero. If the value is greater than zero, the direction of dominance is in favor of the parent with the higher value for the trait in question. If the value is less than zero, the direction of dominance is in favor of the parent with the lower value.

The ratio $(\frac{1}{4}H_2/H_1)$ estimates the average frequency of the negative alleles as opposed to the positive alleles in the parents showing some degree of dominance. The ratio is expected to be 0.25 when the distribution is equal and less than 0.25 when the distribution is unequal.

The ratio K_D/K_R is used as a measure of the ratio of dominant alleles to recessive alleles in a parent for a given trait.

The number of effective factors is defined as being the smallest unit of hereditary material that is capable of being recognized by the methods of biometrical genetics. This may be a single gene or a group of closely linked genes. The statistic K is an estimate of the lower limit of the actual number of genes controlling a given trait and showing some degree of dominance.

Narrow-sense heritability, h_2, was estimated by $\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1 - \frac{1}{4}F+E)$. The results of the estimates concerning the genetic systems will be discussed for each trait individually.

Flag Leaf Area

The estimates of the average degree of dominance for flag leaf area (Table VII) do not seem to be completely reliable with one estimate not being statistically significant from zero and the other two falling in the range of incomplete dominance. The overall direction of dominance shows a tendency to be in the direction of larger flag leaf area as indicated by $\bar{F}_1-\bar{P}$ having a value of 1.391 ± 0.393.

The value $\frac{1}{4}H_2/H_1$ was not significantly different from 0.25 indicating that alleles determining larger or smaller flag leaf area are equally distributed among the parents. The estimate of K_D/K_R was found to be not significantly different from zero, indicating that the parents contain equal numbers of dominance and recessive alleles for this trait. The estimate of the number of effective factors, K, was less than one and hence this estimate was assumed to be unreliable. Flag leaf area was found to have a heritability estimate of 0.519 ± 0.173, but this estimate was not significantly different from zero according to the confidence limits. Heritability estimates for total leaf area ranging from 6% to 47% were reported by Kraljevic-Balalic (17). The results found for flag leaf area tend to indicate that this

TABLE VII

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF FLAG LEAF AREA

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1D	1.016	0.381	2.228-(-0.196)
1b) $(H_1/D)^{½}$	0.960	0.176	1.520-0.400
1c) $(D+H_1-F)/(2D-F)$	0.940	0.187	1.535-0.345
2) $\bar{F}_1-\bar{P}$	1.391	0.393	2.642-0.140
3) $¼H_2/H_1$	0.207	0.016	0.258-0.156
4) K_D/K_R	1.432	0.548	3.176-(-0.312)
5) K	0.509	0.363	1.664-(-0.646)
6) h^2	0.519	0.173	1.069-(-0.031)

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.

trait is affected by the environment and/or nonadditive genetic effects to such a degree that significant values for most estimates cannot be easily detected. The nonsignificant additive genetic variance estimate (Table VI) and the nonsignificant parameter estimates (Table VII) tend to support this conclusion.

Plant Height

The estimates of the average degree of dominance for plant height (Table VIII) seem to vary, with one estimate being not significantly different from zero and the other two estimates being in the range indicating overdominance action. A large $\bar{F}_1-\bar{P}$ value of 4.286 ± 0.690 shows that the dominance involved was in the direction of taller plant stature. The estimate of $\frac{1}{4}H_2/H_1$ was significantly different from 0.25, indicating that positive and negative alleles for this trait are not equally distributed among the parents.

The value of the ratio of dominant to recessive alleles for plant height ($K_D/K_R = 1.586 \pm 0.210$) suggests that on the average there are more dominant than recessive alleles controlling plant height. The estimate of the number of effective factors ($K = 0.985 \pm 0.247$) indicates that plant height was controlled by a single gene. The heritability of plant height was found to be relatively high, $h_2 = 0.636 \pm 0.145$.

Tillers per Plant

The estimates of the average degree of dominance for tillers per plant with values from 1.433 to 2.128 all fell within the range of overdominance, (Table IX). The estimate of $\bar{F}_1-\bar{P}$ was not significantly

TABLE VIII

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF PLANT HEIGHT

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	1.168	0.454	2.613-(-0.277)
1b) $(H_1/D)^{1/2}$	1.022	0.203	1.668-0.376
1c) $(D+H_1-F)/(2D-F)$	1.110	0.293	2.042-0.178
2) $\bar{F}_1-\bar{P}$	4.289	0.690	6.485-2.093
3) $\frac{1}{4}H_2/H_1$	0.201	0.006	0.220-0.182
4) K_D/K_R	1.586	0.210	2.254-0.918
5) K	0.985	0.247	1.771-0.199
6) h^2	0.636	0.145	1.097-0.175

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.

TABLE IX

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

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	2.128	0.492	3.694-0.562
1b) $(H_1/D)^{\frac{1}{2}}$	1.433	0.157	1.933-0.933
1c) $(D+H_1-F)/(2D-F)$	1.656	0.348	2.763-0.549
2) $\bar{F}_1-\bar{P}$	0.615	0.687	2.801-(-1.571)
3) $\frac{1}{4}H_2/H_1$	0.206	0.007	0.228-0.184
4) K_D/K_R	1.024	0.102	1.349-0.699
5) K	0.072	0.066	0.282-(-0.138)
6) h^2	0.274	0.024	0.350-0.198

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.

different from zero suggesting an absence of a consistent trend in the direction of dominance. The value for $\frac{1}{4}H_2/H_1$ (0.206 ± 0.007) was significantly different from 0.25 which is consistent with the observation that H_1 was larger than H_2 (Table VI). Therefore, positive and negative alleles were not equally distributed among the parents.

The value for K_D/K_R (1.024 ± 0.102) suggests that on the average the number of dominant alleles and recessive alleles controlling tiller numbers were approximately equal. The low estimate of the number of effective factors (K = 0.072 ± 0.066) is no doubt due to experimental error. The heritability estimate (h^2 = 0.274 ± 0.024) was rather low. This is contrary to the high heritability estimates for tiller number found by Fonseca and Patterson (5).

Total Grain Yield

The estimates of the average degree of dominance for total grain yield (Table X) seem to be unreliable with one estimate being not significant from zero and the other two falling in the range of overdominance. However, Tandon et al (29) found grain yield to be associated with dominance and overdominance. The estimate of the average direction of dominance ($\bar{F}_1-\bar{P}_1$ = 3.580 ± 0.644) indicates that if dominance is involved it is in the direction of higher grain yield on the average.

The value of $\frac{1}{4}H_2/H_1$ (0.211 ± 0.011) was significantly different from 0.25. Here again, this is consistent with the results shown in Table VI, suggesting that positive and negative alleles for this trait were not equally distributed among the parents. The value of K_D/K_R indicates that on the average there are more dominant alleles than

TABLE X

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF TOTAL GRAIN YIELD PER PLANT

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	10.305	1.893	16.329-4.281
1b) $(H_1/D)^{\frac{1}{2}}$	3.161	0.324	4.192-2.130
1c) $(D+H_1-F)/(2D-F)$	-4.711	7.207	18.220-(-27.644)
2) $\bar{F}_1-\bar{P}$	3.580	0.644	5.629-1.531
3) $\frac{1}{4}H_2/H_1$	0.211	0.011	0.246-0.176
4) K_D/K_R	1.825	0.250	2.621-1.030
5) K	0.543	0.106	0.880-0.206
6) h^2	0.100	0.022	0.170-0.030

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.

recessive alleles controlling total grain yield in this set of parents. The unrealistically low estimate of effective factors (K = 0.543 ± 0.106) may be due to large experimental error. The narrow-sense heritability estimate of $h^2 = 0.100 \pm 0.022$ is very low, as may be expected from the results from Table VI, indicating a low degree of additive genetic effects and large nonadditive effects for total grain yield. Fonseca and Patterson (5) also reported grain yield to have low heritability estimates.

Seeds per Main Tiller

The estimates of the average degree of dominance were all in the range of overdominance, but the 95% confidence intervals show that one estimate includes zero which corresponds with no dominance, another includes the value of 1.0 which indicates complete dominance, and the interval for the third estimate shows values greater than 1.0 indicating overdominance (Table XI). These results would seem to indicate that in this study the estimates of the average degree of dominance for seeds per main tiller are not reliable. Paroda and Joshi (21) also found the degree of dominance to be variable for the number of seeds per spike. The $\bar{F}_1-\bar{P}$ value indicates dominance in favor of the highest parent for this trait and the 95% confidence interval supports the validity of this estimate. Therefore, it may be concluded that if some degree of dominance is involved, it would be in the direction of larger numbers of seeds per main tiller.

The ratio $\frac{1}{4}H_2/H_1$ was found to be significantly less than 0.25 for the number of seeds per main tiller, indicating that the distribution of positive and negative alleles was not equal in the parents. The

TABLE XI

ESTIMATES OF VARIOUS STATISTICS DESCRIBING
THE GENETIC CHARACTERISTICS OF
SEEDS PER MAIN TILLER

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	3.334	1.159	7.022-(-0.354)
1b) $(H_1/D)^{\frac{1}{2}}$	1.755	0.290	2.678-0.832
1c) $(D+H_1-F)/(2D-F)$	2.257	0.333	3.317-1.197
2) $\bar{F}_1-\bar{P}$	1.661	0.437	3.052-0.270
3) $\frac{1}{4}H_2/H_1$	0.219	0.007	0.241-0.197
4) K_D/K_R	1.411	0.266	2.257-0.565
5) K	0.127	0.052	0.292-(-0.038)
6) h^2	0.271	0.064	0.475-0.067

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.

K_D/K_R value (1.411 ± 0.266) indicates that dominant alleles occurred at a higher frequency in the parents than did recessive alleles, but the 95% confidence interval includes 1.0. The extremely low estimate of the number of effective factors, K = 0.127 ± 0.052, may be due to large experimental error. The estimate of narrow-sense heritability, h^2 = 0.271 ± 0.064, is relatively low suggesting nonadditive effects of a large magnitude for this character.

Grain Yield per Main Tiller

All of the estimates of the average degree of dominance (Table XII) fell in the range of estimates indicating overdominance, but the 95% confidence intervals for two estimates included the value of zero (no dominance) while the confidence interval for the other included values, for incomplete dominance. The lack of agreement among these estimates and their respective confidence intervals would tend to render them unreliable. The $\bar{F}_1-\bar{P}$ value shows that the overall dominance tends to be in favor of higher grain yield per main tiller.

The estimate of $\frac{1}{4}H_2/H_1$, (0.233 ± 0.003), was found to be significantly different from 0.25, indicating that the distribution of positive and negative alleles for grain yield per main tiller was not equal among the parents. The K_D/K_R value was found to be significantly different from 1.0, indicating a larger number of dominant alleles than recessive alleles were controlling grain yield per main tiller. The estimates of the number of effective factors was found to be not significantly different from 1.0. The narrow-sense heritability estimate, h^2 = 0.070 ± 0.033, was the lowest heritability estimate obtained for the characters measured in this study.

TABLE XII

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF GRAIN YIELD PER MAIN TILLER

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	25.473	11.351	61.592-(-10.646)
1b) $(H_1/D)^{\frac{1}{2}}$	4.619	1.174	8.355-0.883
1c) $(D+H_1-F)/(2D-F)$	63.036	32.974	167.959-(-41.887)
2) $\bar{F}_1-\bar{P}$	0.255	0.027	1.151-0.169
3) $\frac{1}{4}H_2/H_1$	0.233	0.003	0.243-0.223
4) K_D/K_R	1.345	0.096	1.650-1.040
5) K	0.927	0.225	1.643-0.211
6) h^2	0.070	0.033	0.175-(-0.035)

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.

Flag Leaf Duration

Two of the three estimates of the average degrees of dominance (Table XIII) were significantly different from zero, but not from 1.0, indicating that partial dominance was involved in the control of flag leaf duration. The $\bar{F}_1-\bar{P}$ value shows that on the average, dominance was in the direction of longer flag leaf duration.

The ratio $\frac{1}{4}H_2/H_1$ indicates that the average frequency of positive and recessive alleles for flag leaf duration was not equally distributed among the parents used for this study. Among the genes controlling flag leaf duration, the ratio of dominant to recessive alleles was found to be approximately equal as indicated by the K_D/K_R estimator. The unrealistically low estimate of the number of factors was again attributed to large experimental error or a difference in magnitude and sign of the genes controlling this trait. The narrow-sense heritability estimate for flag leaf duration (0.413 ± 0.092) was of intermediate magnitude which would suggest that additive genetic variance did contribute a significant amount to the total variation.

Percent Protein

The three estimates of the average degree of dominance (Table XIV) were observed to have values indicating that percent protein was under a system of overdominance, but the 95% confidence intervals included values ranging from zero to greater than 1.0. This wide range would cause some doubt as to the validity of these estimates. The average direction of dominance was found to be in favor of lower percent protein as indicated by a $\bar{F}_1-\bar{P}$ value of -1.088 ± 0.276.

TABLE XIII

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF FLAG LEAF DURATION

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	1.340	0.428	2.702-(-0.022)
1b) $(H_1/D)^{\frac{1}{2}}$	1.108	0.193	1.722-0.494
1c) $(D+H_1-F)/(2D-F)$	1.100	0.167	1.631-0.569
2) $\bar{F}_1-\bar{P}$	0.592	0.094	0.891-0.293
3) $\frac{1}{4}H_2/H_1$	0.198	0.006	0.217-0.179
4) K_D/K_R	0.725	0.101	1.046-0.404
5) K	0.195	0.045	0.338-0.052
6) h^2	0.413	0.092	0.706-0.120

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.

TABLE XIV

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF PERCENT PROTEIN

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	3.264	2.131	10.045-3.517
1b) $(H_1/D)^{\frac{1}{2}}$	1.743	0.547	3.484-0.002
1c) $(D+H_1-F)/(2D-F)$	2.265	1.166	3.710-(-1.445)
2) $\bar{F}_1-\bar{P}$	-1.088	0.276	(-0.210)-(-1.966)
3) $\frac{1}{4}H_2/H_1$	0.199	0.014	0.244-0.154
4) K_D/K_R	1.152	0.053	1.321-0.983
5) K	1.443	0.590	3.320-(-0.434)
6) h^2	0.255	0.097	0.564-(-0.054)

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.

The quantity $\frac{1}{4}H_2/H_1$ was observed to be significantly less than 0.25, suggesting that the average frequency of positive and negative alleles controlling percent protein were not equally distributed among the parental lines showing some degree of dominance. The estimate of the ratio of dominant to recessive alleles was found to be not significantly different from 1.0; therefore, the frequency of dominant alleles was approximately equal to the frequency of recessive alleles controlling percent protein. The estimate of the number of effective factors controlling percent protein was observed to be K = 1.443 ± 0.590. However, the 95% confidence interval included zero. The heritability of percent protein was estimated to be 0.255 ± 0.097, but here again, the 95% confidence interval included zero. This would seem to indicate that environmental factors played a large role in the expression of this trait.

Leaf Area Duration

Two of the three estimates obtained for the average degree of dominance (Table XV) were found to be not significantly different from 1.0. This would suggest that the genes controlling leaf area duration are under a system of complete dominance. The large $\bar{F}_1-\bar{P}$ value (50.807 ± 14.302) indicates the direction of dominance is strongly in favor of the parents having larger leaf area duration values.

The ratio $\frac{1}{4}H_2/H_1$ was not significantly different from 0.25, indicating that the average frequency of negative alleles is equal to the average frequency of positive alleles in parents exhibiting some degree of dominance for this character. The K_D/K_R estimate (1.474 ± 0.550) indicates that on the average there are more dominant alleles

TABLE XV

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF LEAF AREA DURATION

Estimator		Mean	Standard Error	95% Confidence Limits
1a)	H_1/D	1.312	0.666	3.431-(-0.807)
1b)	$(H_1/D)^{\frac{1}{2}}$	1.030	0.290	1.953-0.107
1c)	$(D+H_1-F)/(2D-F)$	1.003	0.278	1.888-0.118
2)	$\bar{F}_1-\bar{P}$	50.807	14.302	96.316-5.298
3)	$\frac{1}{4}H_2/H_1$	0.209	0.006	0.228-0.190
4)	K_D/K_R	1.474	0.550	3.224-(-1.318)
5)	K	0.432	0.216	1.119-(-0.255)
6	h^2	0.580	0.222	1.286-(-0.126)

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.

than recessive alleles involved with the genes which control leaf area duration. However, the 95% confidence interval for this estimator includes zero which casts some doubt on the accuracy of this value. The impossibly low estimate of the number of effective factors, $K = 0.432 \pm 0.216$, may be due to large experimental error or a lack of dominance among the genes controlling this trait. However, it can be seen in Table VI that dominance genetic variance was significant. The narrow-sense heritability estimate for leaf area duration was one of the highest obtained in this study, but the 95% confidence interval for this estimate does include the value of zero. There seems to be a lack of ability to obtain meaningful estimates for this trait. This suggests a large environmental influence upon the expression which was observed.

Kernel Weight

All three of the estimates for the average degree of dominance (Table XVI) were observed to have values which fell in the range of overdominance. Some previous reports have shown kernel weight to be controlled by partial dominance (3, 29). The $\bar{F}_1-\bar{P}$ value obtained for kernel weight indicates that the average direction of dominance is largely in favor of the parents with higher kernel weight.

The estimate of the average frequency of negative versus positive alleles, $\frac{1}{4}H_2/H_1 = 0.235 \pm 0.006$, was found to be not significantly different from 0.25. This suggests that on the average the frequency of negative alleles is equal to the frequency of positive alleles in the genes controlling kernel weight in parents which show some degree of dominance. The observed K_D/K_R value indicates that on the average

TABLE XVI

ESTIMATES OF VARIOUS STATISTICS DESCRIBING THE GENETIC CHARACTERISTICS OF KERNEL WEIGHT

Estimator	Mean	Standard Error	95% Confidence Limits
1a) H_1/D	2.679	0.402	3.958-1.400
1b) $(H_1/D)^{\frac{1}{2}}$	1.623	0.123	2.014-1.232
1c) $(D+H_1-F)/(2D-F)$	1.996	0.125	2.394-1.598
2) $\bar{F}_1-\bar{P}$	4.026	0.426	5.382-2.670
3) $\frac{1}{4}H_2/H_1$	0.235	0.006	0.254-0.216
4) K_D/K_R	1.377	0.269	2.233-0.521
5) K	1.126	0.219	1.823-0.429
6) h^2	0.281	0.046	0.427-0.135

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.

there are more dominant alleles that recessive alleles among the genes controlling kernel weight in the parents used for this study. The number of effective factors for kernel weight was K = 1.126 ± 0.219, but the 95% confidence interval includes values from two to less than one. The narrow-sense heritability estimate was found to be relatively low with a value of 0.281 ± 0.046. This low heritability estimate may be the result of a lack of extremes for kernel weight in the material used in this study. Parameter estimates (Table XVI) were usually within the 95% confidence interval. This suggests that kernel weight is a relatively stable character in comparison to the other characters measured in this study. The stability of kernel weight was also noted by Rasmusson and Cannell (23).

CHAPTER V

SUMMARY AND CONCLUSIONS

A diallel cross involving seven winter wheat parents was analyzed in order to study the genetic systems controlling flag leaf area, flag leaf duration, leaf area duration, plant height, tillers per plant, total grain yield, seeds per main tiller, grain yield per main tiller, percent protein and kernel weight. Measurements and observations were made on the seven parents and 21 F_1's which were grown in a space planted nursery at the Agronomy Research Station, Stillwater, Oklahoma, during the 1974-75 wheat growing season.

Analysis of variance computations were conducted for three different data sets: F_1's and parents combined, F_1's alone and parents alone. Statistically significant differences existed for all traits measured in each of the three different data sets.

Comparisons were made between parental values and their respective array means in order to gain some knowledge about the breeding behavior of each trait. In this study, the parental value accurately estimated the behavior of flag leaf area, plant height, tillers per plant, seeds per main tiller, flag leaf duration, leaf area duration and kernel weight in the F_1 hybrids. The comparisons for total grain yield, grain yield per main tiller and percent protein indicate that parental values are less reliable in indicating the behavior of these traits in crosses.

All two-way phenotypic correlations were computed for the ten traits measured in this study. Flag leaf area, flag leaf duration and leaf area duration were found to have significant positive correlations with total grain yield. All of these correlations were of an intermediate magnitude, with the highest correlation being between flag leaf duration and total grain yield. Leaf area duration was also positively associated with tillers per plant, kernel weight and seeds per main tiller.

Tillers per plant had the highest correlation with total grain yield as should be expected in space planted material. A correlation of particular interest was found to exist between total grain yield and grain yield per main tiller. This correlation was of a high intermediate magnitude.

The final step was to submit the data to the Jinks-Hayman diallel analysis system in order to obtain genetic parameter estimates for each trait. The results obtained from the Jinks-Hayman analysis should be interpreted with caution since there seemed to be a general lack of precision in obtaining genetic estimators as indicated by high standard errors and the magnitude of the confidence intervals.

Additive genetic variance was found to be more important than dominance genetic variance in the number of tillers per plant, while dominance genetic variance seemed to be most important in the genetic control of flag leaf area, grain yield per main tiller and leaf area duration. Both additive and dominance genetic systems were noted for plant height, total grain yield, seeds per main tiller, flag leaf duration, percent protein and kernel weight.

Narrow-sense heritability estimates in descending order of magnitude were: plant height (0.636), leaf area duration (0.580), flag leaf area (0.519), flag leaf duration (0.413), kernel weight (0.281), tillers per plant (0.274), seeds per main tiller (0.271), percent protein (0.255), total grain yield (0.100) and grain yield per main tiller (0.070).

The data obtained from this study would indicate that progress can be made with respect to increasing flag leaf area, leaf area duration and flag leaf duration. If there is a cause and effect relationship between these characters and grain yield in wheat, it should be possible to increase grain yields by using properly designed and conducted breeding programs which make the maximum use of these flag leaf characters. However, the interrelationships of other yield components must be considered at the same time in order to make optimum progress in increasing the grain yield of wheat.

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