HERITABILITY AND INTERRELATIONS OF YIELD AND YIELD-RELATED TRAITS IN A HARD RED WINTER WHEAT CROSS (*TRITICUM AESTIVUM* L.)

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CHAPTER I

INTRODUCTION

The human population growth in the world today demands increases in food supplies for the future. Limited land space and energy shortages suggest that increased food supplies will have to come about through more efficient production. Wheat is a major crop in many areas of the world, and increased grain yield in this crop would help alleviate future food shortages.

A major obstacle in the production of high grain yielding wheat varieties is the low heritability of yield in early generations of crosses. Grain yield results from a complex interrelated chain of events of genetic and physiologic factors, acting in time and space to produce an end product. These factors are not a result of haphazard events, but instead follow an integrated pattern, however complex it may be. If selection for the simultaneous improvement of factors contributing to grain yield is to be effective in increasing total grain yield, then a knowledge of the heritability and the interrelationships of these characters is necessary.

Information pertaining to the genetic control of yield and certain yield-related traits, and the associations among these traits is presented in Chapter II. A comparison of the heritability of the several traits is made using narrow-sense as well as broad-sense heritability estimates. Associations among the traits are studied by comparing phenotypic and genetic correlation coefficients for the same characters. The direct and indirect effects of the major yield components, tiller number, kernel weight, and seeds/spike are studied by path-coefficient analysis.

In the third chapter, heritability estimates based on two reference units and genetic advance at two levels of selection intensity are reported. Information on the associations among the several traits is reported in terms of phenotypic and genetic correlation coefficients.

The fourth chapter deals with an evaluation of heritability estimates for the same trait determined by different estimating procedures. Realized heritability estimates and grain yield response in the offspring of parents selected for yield and yield components are also presented.

Chapters II, III, and IV will be presented in a form acceptable to the Crop Science Society of America.[1] Chapter V is a general summary of the three studies.

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[1] Handbook and Style Manual for ASA, CSSA, and SSSA Publications, (1971).

CHAPTER II

The Inheritance and Interrelations of Yield and Yield-Related Traits in a Hard Red Winter Wheat Cross (Triticum aestivum L.)[1]

ABSTRACT

The parents, F_1, F_2, and the two backcrosses derived from two hard red winter wheat cultivars were studied in a space-planted experiment grown on the Agronomy Research Station, Stillwater, Oklahoma, during the 1971-72 crop season. Data were taken on individual plants to estimate gene action, heritability, and interrelationships of yield and certain yield-related traits. The characters studied were: tiller number, kernel weight, seeds/spike, spikelets/spike, seeds/spikelet, and grain yield. The direct and indirect effects of the first three characters on grain yield were also studied.

Nonadditive gene action was more pronounced than additive gene action for all characters except kernel weight. Kernel weight had the highest broad-sense and highest narrow-sense heritability while heritability estimates for the other characters ranged from intermediate to low. In general, narrow-sense heritability estimates were larger than broad-sense heritability estimates for the same character. This was explained as being the result of random variation and unequal environmental influence in the different generations used in computing the estimate.

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[1] To be submitted for publication.

On the basis of gene action and heritability estimates, it was concluded that selection for kernel weight would be more effective than selection for any of the other traits.

Tiller number had a high positive phenotypic correlation with yield and an intermediate genetic correlation with yield. Phenotypic correlations of kernel weight and seeds/spike with yield were low while the genetic correlations of these characters with yield were low and intermediate, respectively. Negative associations were observed between kernel weight and tiller number and between kernel weight and seeds/spike. This suggests that simultaneous improvement of these characters may be difficult to accomplish. Large positive phenotypic and genetic correlations were observed between seeds/spike and spikelets/spike and between seeds/spike and seeds/spikelet.

Path-coefficient analysis at the phenotypic level indicated that the direct effect of tiller number on grain yield was large while the direct effects of kernel weight and seeds/spike on grain yield were intermediate and low, respectively. At the genetic level the direct effects of each component on yield were intermediate and about equal in magnitude. This suggests that the large direct effect of tiller number at the phenotypic level was due largely to nonadditive genetic and/or environmental effects. The direct genetic effect of kernel weight on grain yield was not evident in the genetic correlation between these two characters because of the negative indirect effects of this character via tiller number and seeds/spike.

The results of this study indicated that more advance would be expected by selecting for increased kernel weight in an effort to increase grain yield by early generation selection. However, negative

correlations involving kernel weight may tend to reduce progress in a breeding program.

Additional index words: Additive variance, Nonadditive variance, Broad-sense heritability, Narrow-sense heritability, Phenotypic correlation, Genetic correlation, Path coefficient.

Considerable emphasis is currently being placed on yield improvement in wheat. Yield component breeding, and the possibility of modifying plant architecture, offer possibilities in developing a more efficient system leading to increased yield potential. Consequently, the inheritance and interrelations of characters affecting yield become very important. Grafius (6) introduced a geometrical concept of the components of yield in oats. He suggested that it might be easier to increase total yield by selection for an increase in one of the components, which would presumably be more simply inherited than yield *per se*. Grain yield is the product of kernel weight, seeds/spike, and tiller number when each of these characters is measured without error; therefore, estimates of the relative magnitudes of these components should be a good means of determining the cause of yield fluctuations (7,9,10).

Yield component breeding to increase grain yield potential would be most effective if the components involved were highly heritable, genetically independent, and physiologically unrelated. Heritability estimates are dependent on the method by which they are estimated, the populations from which the estimates are obtained, the unit of measurement, and the environmental conditions encountered during the test. Because of this, a wide range of heritability estimates for the same trait have been reported in wheat. Johnson, et al. (8), using F_2 and backcross variances in a cross between 'Seu Seun 27' and 'Blue Jacket' winter wheats, obtained narrow-sense heritability estimates for spikes/plant, kernel weight, and grain yield of 0.034, 0.547, and 0.102, respectively. Fonseca and Patterson (5) reported narrow-sense heritability estimates from a seven-parent diallel using regression of F_1 and F_2 means on the mid-parent. The magnitude of their estimates varied greatly depending on the generation of the hybrid, but the ranking did not. They found spikes/930 cm^2 and kernels/spike to be highly heritable and kernel weight and grain yield to be intermediate to low.

Negative associations among yield-related traits have been observed in several studies (1,5,7,10). Hsu and Walton (7), using five spring wheat cultivars in a complete diallel, along with the 20 F_2 families and the 20 backcrosses, studied the relationships between yield and its components. They found spike length, tiller number, and seeds/spike to be closely associated with total yield/plant while kernel weight was not. They obtained a significant positive correlation between tiller number and seeds/spike, and a highly significant negative correlation between tiller number and kernel weight. Adams (1) suggested that grain yield components are genetically independent characters which are frequently negatively associated. He speculated that these negative relationships may be due largely to competition for growth substances by simultaneously developing characters.

The present study, involving a winter wheat cross, was conducted to furnish information on the genetic control of yield and certain yield-related traits, and on the associations among these traits. Also, the direct and indirect effects of three yield components on the expression of total grain yield were studied by path-coefficient analysis.

MATERIALS AND METHODS

The parental, F_1, F_2, BC_1, and BC_2 populations studied in this experiment were derived from two hard red winter wheat cultivars, 'Sturdy' and 'Centruk'. These cultivars are being widely used in the crossing program at the Oklahoma Agricultural Experiment Station. Sturdy was developed by the Texas Agricultural Experiment Station and is a true semi-dwarf with strong straw. It has medium maturity and excellent baking qualities. Centurk was developed cooperatively by the Nebraska Agricultural Experiment Station and the Plant Science Research Division of the Agricultural Research Service, USDA. It has medium height, is mid-early with moderately strong straw, and has excellent milling and baking characteristics. These two cultivars were chosen as parents for this study because of their diversity for the characters studied.

Seedlings of the parents, F_1, F_2, and the two backcrosses BC_1 and BC_2 were started in flats and then transplanted to the field on October 29, 1971. Transplanting was made in a randomized complete block design at the Stillwater Agronomy Research Station. The experiment consisted of six replications with each replication composed of 11 experimental rows as follows:

Population	Number of Rows
P_1	1
P_2	1
F_1 (P_1 X P_2)	1
F_2 (F_1 selfed)	4
BC_1 (Backcross of F_1 to P_1)	2
BC_2 (Backcross of F_1 to P_2)	2

Each row was composed of 20 plants spaced 15 cm apart. The rows were spaced 30 cm apart and all measurements made on an individual plant basis. The end plants and the two lowest yielding plants were discarded and the following data collected on the remaining 16 plants in each row:

Grain yield. Total weight in grams of the seed from each plant.

Tiller number. Total number of seed-bearing culms for each plant.

Kernel weight. The weight in grams of 100 randomly selected kernels. This was expressed as 1000-kernel weight.

Seeds/spike. Total number of seeds on one representative head from each plant.

Spikelets/spike. Total number of seed-bearing spikelets on one representative head from each plant.

Seeds/spikelet. This character was determined for each plant by dividing the number of seeds/spike by the number of spikelets/spike.

Broad-sense heritabilities were computed using the method of Burton (2) and are reported for each character as the mean of the estimates calculated for each of six replications. The broad-sense estimates ($\hat{h}^2_{bs}$), on a plant basis, were calculated as

$$\hat{h}^2_{bs} = \frac{\mathrm{var}(x)_{F_2} - [\mathrm{var}(x)_{P_1} + \mathrm{var}(x)_{P_2} + \mathrm{var}(x)_{F_1}]/3}{\mathrm{var}(x)_{F_2}}$$

where $\mathrm{var}(x)_{F_2}$, $\mathrm{var}(x)_{P_1}$, $\mathrm{var}(x)_{P_2}$, and $\mathrm{var}(x)_{F_1}$ represent the variance of character x in the F_2, P_1, P_2, and F_1 generations, respectively. To increase the precision of the heritability estimate, each variance term in the numerator was based on an estimate of the within row variance component and $\mathrm{var}(x)_{F_2}$ in the denominator was based on the sum of the estimates of the variance components within and between rows in the F_2 generation. Narrow-sense heritability estimates were calculated by the method described by Warner (13) and are also reported as a mean based on six replications. The narrow-sense estimates ($\hat{h}^2_{ns}$), on a plant basis, were calculated as

$$\hat{h}^2_{ns} = \frac{2\text{var}(x)_{F_2} - [\text{var}(x)_{BC_1} + \text{var}(x)_{BC_2}]}{\text{var}(x)_{F_2}}$$

where $\text{var}(x)_{F_2}$, $\text{var}(x)_{BC_1}$, and $\text{var}(x)_{BC_2}$ represent the variance of character x in the F_2, BC_1, and BC_2 generations, respectively, and the variance terms in the numerator and denominator were based on estimates of variance components as previously discussed for the broad-sense heritability estimate. When calculating the broad-sense and narrow-sense heritabilities, values falling outside the range of 0.0 to 1.0 were adjusted to 0.0 and 1.0, respectively. The standard errors for the broad-sense and narrow-sense heritability estimates were estimated by computing the standard error of the mean based on heritability estimates calculated for each replication.

Estimates of additive and nonadditive variances were obtained for each replication using variances of the F_2 and backcross generations, and are reported as the mean of the estimates calculated for each of six replications. The following formulas were used in estimating the additive and nonadditive variances

$$\hat{\sigma}^2_A(x) = 2\text{var}(x)_{F_2} - [\text{var}(x)_{BC_1} + \text{var}(x)_{BC_2}]$$

$$\hat{\sigma}^2_{NA}(x) = \text{var}(x)_{F_2} - \hat{\sigma}^2_A(x)$$

where $\hat{\sigma}^2_A(x)$ represents an estimate of the additive genetic variance of character x, and $\hat{\sigma}^2_{NA}(x)$ denotes an estimate of the nonadditive variance of the same character and contains the nonadditive genetic as well as the environmental variance. From this point on, the nonadditive genetic variance and the environmental variance will be referred to as nonadditive variance (σ^2_{NA}) to avoid unnecessary repetition. Each variance term in the above formulas was based on an estimate of the within row variance component. The standard errors for the additive and nonadditive variance estimates were obtained by computing the standard error of the mean based on estimates calculated for each replication.

The interrelationships among the plant characters were studied by computing phenotypic and genetic correlation coefficients among all pairs of variables. Phenotypic correlations were calculated using variances and covariances of the F_2 generation. Genetic correlations were computed using variances and covariances of the F_2 and backcrosses assuming equal environmental influences in these generations. Under this assumption, environmental correlations cancel out in the formula used to estimate the genetic correlation coefficients. The phenotypic (r_p) and genetic (r_g) correlations, on a plant basis, were calculated as

$$r_p = \frac{\mathrm{cov}(x,y)_{F_2}}{[\mathrm{var}(x)_{F_2} \cdot \mathrm{var}(y)_{F_2}]^{1/2}}$$

$$r_g = \frac{2\mathrm{cov}(x,y)_{F_2} - [\mathrm{cov}(x,y)_{BC_1} + \mathrm{cov}(x,y)_{BC_2}]}{[\hat{\sigma}^2_A(x) \cdot \hat{\sigma}^2_A(y)]^{1/2}}$$

where $\mathrm{cov}(x,y)_{F_2}$, $\mathrm{cov}(x,y)_{BC_1}$, and $\mathrm{cov}(x,y)_{BC_2}$ represent the covariances between characters x and y in the F_2 and backcross generations, respectively, $\mathrm{var}(x)_{F_2}$ and $\mathrm{var}(y)_{F_2}$ represent the variances of x and y, respectively, and $\hat{\sigma}^2_A(x)$ and $\hat{\sigma}^2_A(y)$ denote an estimate of the additive variance (as previously discussed) for x and y, respectively. Phenotypic correlation coefficients were single values based on individual plants over six replications using total mean squares and total mean products, while the genetic correlation coefficients were mean values based on estimates calculated for each of six replications using within row mean squares and within row mean products. When calculating the genetic correlation coefficients, values falling outside the range of -1.0 to 1.0 were adjusted to -1.0 and 1.0, respectively. All correlations reported in this study were calculated using logarithmic transformations of the original data; however, correlation coefficients based on the original data were very similar in magnitude to those found by using the logarithmic transformations. Statistical significance of the phenotypic correlation coefficients were determined in the usual way (12), but tests for the significance of the genetic correlation coefficients, as calculated above, are not available; however, the relative magnitude of the genetic correlation should reflect the degree of genetic association between two given characters. Standard errors of the estimate of the genetic correlation coefficients were estimated by computing the standard error of the mean based on estimates calculated for each replication.

The correlations were further analyzed by determining both phenotypic and genetic path-coefficients. The use of the path analysis requires an additive cause and effect situation among the variables, and the experimenter must assign direction in the cause and effect system based on prior knowledge of the variables involved. For a more detailed description of the path analysis system the reader is referred to Li (11), Dewey and Lu (3), and Duarte and Adams (4). The data were converted to logarithms so that the assumption of additivity of the path systems would be satisfied.

RESULTS AND DISCUSSION

The parental mean values, their respective standard errors, and coefficients of variation for the six characters studied are presented in Table 1. Centurk was slightly higher yielding, had more tillers per plant, and had a higher number of seeds/spike, spikelets/spike, and seeds/spikelet, while Sturdy had a greater kernel weight per 1000 kernels. Due to dry conditions encountered during the growing season, supplemental applications of water were applied to the experiment. Stress conditions did not appear to adversely affect the expression of any of the characters studied.

Gene Action and Heritability

Estimates of additive and nonadditive variances as well as narrow-sense and broad-sense heritability estimates are presented in Table 2. Nonadditive gene action was more important than additive gene action for grain yield, tiller number, seeds/spike, spikelets/spike, and seeds/spikelet. Additive and nonadditive gene action were about equally important for kernel weight. These findings indicate that selection for kernel weight would be more effective than selection for the other traits in the development of pure line cultivars.

Heritability estimates were much higher for some traits than for others. Kernel weight had the highest broad-sense as well as the highest narrow-sense heritability estimate (.409 and .411, respectively), while heritability estimates for the other characters ranged from intermediate to low. The narrow-sense heritability estimate for kernel weight would be expected to be larger than the narrow-sense heritability estimates for the other traits because of the comparable magnitudes of the additive and nonadditive variances for this trait. Johnson, et al. (8) also reported a high narrow-sense heritability estimate for kernel weight (.547). The narrow-sense heritability estimate for tiller number was intermediate (.316), while the narrow-sense estimates for grain yield and seeds/spike were low (.285 and .239, respectively). The narrow-sense estimates for these traits were characterized by rather large standard errors. The broad-sense heritability estimates for tiller number, seeds/spike, and grain yield were low (.206, .197, and .163, respectively).

Narrow-sense heritability estimates were larger than the broad-sense estimates for all characters except spikelets/spike. In calculating the heritabilities, the environmental components for the F_2 and the two backcross generations were assumed to be equal. If the environmental variation for the mean of the parents and F_1 was larger than the environmental component of the F_2, then the genotypic variance would have been underestimated. The additive genetic variance would have been overestimated if the environmental variation of the backcrosses was less than that of the F_2. Except for the F_2, different generations were involved in calculating the broad-sense and narrow-sense estimates. Therefore, the difference between the broad-sense and narrow-sense heritability estimates for the same character may be explained by random variation and unequal environmental variances in the different generations.

Correlations Among Characters

Phenotypic and genetic correlation coefficients for all pairs of the six traits are presented in Table 3. The phenotypic and genetic coeffcients agree in sign but not necessarily in magnitude. The values obtained for the genetic correlation coefficients indicate that yield components may not be genetically independent as suggested by Adams (1). Tiller number had the highest positive phenotypic correlation with yield

(.6804), but an intermediate genetic correlation with yield (.3393). The phenotypic correlation of kernel weight with yield was higher than the genetic correlation between these two characters (.2814 vs. .0948), although both were low. A higher phenotypic correlation than genetic correlation, indicates that environmental effects and/or nonadditive genetic effects are acting on the two characters in the same direction.

The largest negative phenotypic and genetic correlation obtained occurred between kernel weight and tiller number, -.3009 and -.4791, respectively, indicating that simultaneous improvement of these two characters may not be possible. Hsu and Walton (7) also found these two traits to be highly negatively associated. Kernel weight was also negatively associated with seeds/spike as indicated by the phenotypic and genetic correlations between these two characters. The largest positive phenotypic and genetic correlations obtained occurred between seeds/spikelet and seeds/spike, .7941 and .4946, respectively, and were about equal to the phenotypic and genetic correlations between spikelets/spike and seeds/spike, .7242 and .4838, respectively. This indicates that seeds/spikelet and spikelets/spike are equally important in the determination of seeds/spike which is equal to the product of seeds/spikelet and spikelets/spike when each of these characters is measured without error. Therefore, an increase in the number of seeds/spike should be possible by selecting for an increase in the number of spikelets/spike or the number of seeds/spikelet, both of which should be more readily noticeable than increased seeds/spike under field conditions.

Path-Coefficient Analysis

Further information on the nature of the interrelations among the various characters was obtained by the path-coefficient analysis of the phenotypic and genetic correlations. This was done by assigning direct and indirect effects to the yield components as their contribution to total grain yield. Grain yield was considered as the resultant variable and tiller number, kernel weight, and seeds/spike as the causal vari ables. Spikelets/spike and seeds/spikelet were omitted from the analysis since they are components of seeds/spike.

The path diagram based on the phenotypic correlations is presented in Figure 1, where P represents the direct effect (path-coefficient) and r denotes the correlation between the characters involved in the system. The residual, X, was assumed to be independent of the other variables and is in effect measuring the failure of the sum of the three components to exactly equal total grain yield. The components each had a direct influence acting alone, and an indirect influence acting in combination with the other variables with which it was correlated. The amount of variation in the dependent variable (yield) accounted for by path-coefficient analysis was determined as $(1-R^2)$, where R is the path-coefficient of the residual. The phenotypic measurement of the three components in this analysis accounted for 76% of the total variation in yield. Had the product of these components exactly equaled yield, 100% of the variation in yield would have been accounted for in the phenotypic path diagram, and the value of the residual path would have been zero.

A summary of the direct and indrect phenotypic effects of each component is presented in Table 4. Tiller number had the largest direct effect on yield (.8354), but a negative indirect effect via kernel weight (-.1699). The direct effect of kernel weight was intermediate (.5647), but because of negative indirect effects via tiller number (-.2514) and seeds/spike (-.0319) the total correlation of kernel weight with yield was low (.2814). The direct and indirect effects involving seeds/spike were low. These results are in general agreement with Fonseca and Patterson (5).

A genetic path analysis also has application but its interpretation is somewhat different. Besides the obvious difference between genetic and phenotypic effects, the residual has different interpretation. In the genetic system, the residual is a measure of the failure of the estimated genetic correlations among the variables to account for the total genetic variation in yield. The correlations calculated for this system accounted for 36% of the genetic variation in the dependent variable, yield. Had the genetic correlations been calculated without error, 100% of the genetic variation in yield would have been accounted for by the three components, and the value for the residual would have been zero.

A summary of the direct and indirect genetic effects of each variable is presented in Table 5. The genetic path analysis of these data presents a somewhat different picture than did the phenotypic path analysis. The direct genetic influences of the three components on grain yield were intermediate and similar in magnitude. The total correlations between yield and tiller number, and yield and seeds/spike were very close to the direct effects of these components on yield. This was due to the counter-balancing of the indirect effects associated with these two components. The direct effect of kernel weight was .4192 while its total correlation with yield was .0948. The negative indirect effects of kernel weight counter-balanced its rather large direct effect, making its over-all correlation with yield very small.

The direct effect of tiller number on grain yield in the phenotypic path analysis was much larger than its direct effect in the genetic path analysis. This indicates that a large portion of the direct effect of tiller number on grain yield was due to nonadditive genetic and/or environmental effects. There was very little decrease in the direct effect of kernel weight at the genetic level compared to the phenotypic level, and a large increase in the direct effect of seeds/spike. This suggests that these two characters are affected less by nonadditive genetic and/or environmental effects.

The results of the path-coefficient analysis and heritability estimates indicate that more emphasis should be placed on kernel weight in an effort to increase grain yield by early generation selection. However, progress in breeding by selection for this component may be somewhat limited by the negative genetic correlations between kernel weight and tiller number, and between kernel weight and seeds/spike.

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Table 1. Parental means and coefficients of variation for the six characters studied.

Character	Sturdy (P_1)		Centurk (P_2)	
	Mean	C.V. (%)	Mean	C.V. (%)
Grain yield	15.97 ± 3.60	22.53	17.95 ± 4.10	22.86
Kernel weight	27.80 ± 2.54	9.13	25.35 ± 1.86	7.32
Tiller number	20.34 ± 4.16	20.46	23.26 ± 4.41	18.96
Seeds/spike	35.15 ± 6.93	19.73	41.18 ± 4.80	11.67
Spikelets/spike	15.22 ± 1.39	9.16	17.19 ± 1.11	6.43
Seeds/spikelet	2.30 ± 0.32	14.03	2.39 ± 0.21	8.64

Table 2. Estimates of additive and nonadditive variance and heritability estimates for six characters in a hard red winter wheat cross.

Character	Additive Variance	Nonadditive Variance	h^2 Broad-sense	h^2 Narrow-sense
Grain yield	6.106 ± 3.540	15.128 ± 3.992	.163 ± .044	.285 ± .159
Kernel weight	5.864 ± 3.425	4.821 ± 2.395	.409 ± .079	.511 ± .130
Tiller number	7.645 ± 1.656	19.873 ± 5.523	.206 ± .049	.316 ± .142
Seeds/spike	9.527 ± 6.517	31.505 ± 7.307	.197 ± .076	.239 ± .158
Spikelets/spike	0.812 ± 0.339	1.735 ± 0.348	.339 ± .059	.294 ± .112
Seeds/spikelet	0.016 ± 0.010	0.075 ± 0.020	.110 ± .006	.219 ± .128

Table 3. Simple phenotypic and genetic correlations between six characters in a hard red winter wheat cross.

Character		Kernel weight	Tiller number	Seeds/spike	Spikelets/spike	Seeds/spikelet
Grain yield	(a) (b)	.2814** .0948 ± .1421	.6804** .3393 ± .1665	.1767** .4273 ± .2019	.0812 ns .1669 ± .1060	.1815** .1737 ± .1099
Kernel weight			-.3009** -.4791 ± .1634	-.1566** -.3116 ± .3244	-.1552** -.2074 ± .1762	-.0876 ns -.0495 ± .1213
Tiller number				.0736 ns .3293 ± .2121	.0316 ns .0877 ± .0900	.0776 ns .1192 ± .1398
Seeds/spike					.7242** .4838 ± .2169	.7941** .4946 ± .2213
Spikelets/spike						.1559** .1277 ± .1277

(a) The upper value in each cell is the phenotypic correlation coefficient with df (n-2) = 382, and must exceed .101 and .132 to be significant at the .05 and .01 levels, respectively.

(b) The lower value in each cell is the genetic correlation coefficient and is shown with its standard error.

Table 4. Phenotypic path analysis of factors influencing grain yield in a hard red winter wheat cross.

Pathway	Direct Effect	Indirect Effect	Correlation Coefficient
Yield vs. tiller number			
Direct effect	.8354		
Indirect effect via kernel weight		-.1699	
Indirect effect via seeds/spike		.0150	
Total			.6804
Yield vs. kernel weight			
Direct effect	.5647		
Indirect effect via tiller number		-.2514	
Indirect effect via seeds/spike		-.0319	
Total			.2814
Yield vs. seeds/spike			
Direct effect	.2036		
Indirect effect via tiller number		.0615	
Indirect effect via kernel weight		-.0884	
Total			.1767
Residual			.4865

Table 5. Genetic path analysis of factors influencing grain yield in a hard red winter wheat cross.

Pathway	Direct Effect	Indirect Effect	Correlation Coefficient
Yield vs. tiller number			
Direct effect	.3997		
Indirect effect via kernel weight		-.2008	
Indirect effect via seeds/spike		.1404	
Total			.3393
Yield vs. kernel weight			
Direct effect	.4192		
Indirect effect via tiller number		-.1915	
Indirect effect via seeds/spike		-.1328	
Total			.0948
Yield vs. seeds/spike			
Direct effect	.4263		
Indirect effect via tiller number		.1316	
Indirect effect via kernel weight		-.1306	
Total			.4273
Residual			.8000

LIST OF FIGURES

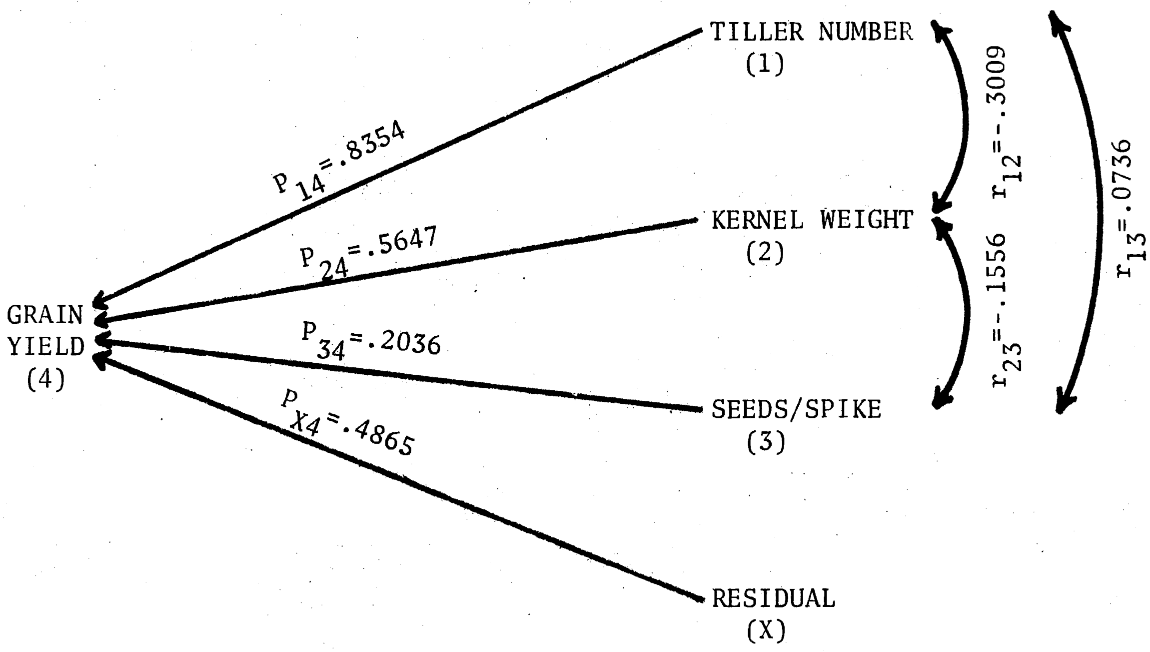

Figure 1. A phenotypic path diagram of yield and some factors influencing yield in a hard red winter wheat cross.

CHAPTER III

Heritability, Genetic Advance, and Interrelations of Certain Agronomic Traits in the F_3 Generation of a Hard Red Winter Wheat Cross (*Triticum aestivum* L.)[1]

ABSTRACT

The F_3 families of 158 F_2 random plant selections, generated from two cultivars of hard red winter wheat, were studied in an experiment conducted during the 1972-73 crop season on the Agronomy Research Station, Stillwater, Oklahoma. Data were taken on individual families to estimate heritability, genetic advance, and interrelationships among certain agronomic characters. The characters studied were: grain yield, tiller number, kernel weight, seeds/spike, yield/spike, heading date, and plant height.

Heritability estimates were based on two types of reference units; one on families based on their individual performance (heritability for single-rep selection), and the other on families based on means over three replications (heritability for multiple-rep selection). Heritability estimates for multiple-rep selection were nearly twice the magnitude of heritability estimates for single-rep selection for yield, tiller number, and yield/spike. Less difference in heritability estimates was

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[1] To be submitted for publication.

noted for the other traits as the reference unit changed. Heading date, plant height, and kernel weight were highly heritable, while heritability estimates for the other traits ranged from intermediate to low.

Estimates of genetic gain via selection for 5% and 10% levels of selection intensity were obtained for single-rep as well as multiple-rep selection. As the reference unit changed from the multiple-rep to the single-rep unit, the predicted genetic gain decreased less than the heritability estimates. This indicates that even though there was a large increase in the heritability, especially with the lower heritable traits, as the reference unit changed, we should expect only slight increases in genetic advance with multiple-rep selection as compared to single-rep selection. Estimates of genetic gain, when selecting for earlier heading date and shorter plant stature, were larger with single-rep selection than with multiple-rep selection.

Phenotypic and genetic correlation coefficients were estimated from the variance and covariance analysis for all possible pairs of characters. The highest positive correlation involving yield occurred with tiller number. Heading date was negatively associated with yield in both estimates. The largest negative genetic correlation occurred between kernel weight and seeds/spike. Based on estimates of heritability and genetic correlation coefficients, more emphasis should be placed on kernel weight to increase grain yield by indirect selection in early generations.

Additional index words: Heritability, Genetic advance, Phenotypic correlation, Genetic correlation.

The effectiveness of selection depends on the heritability of the trait under selection, the intensity of selection, and the phenotypic variation in the population under consideration. If one considers the improvement in a trait which may be brought about by selection of another trait, then the genetic correlation of the selected trait with the character to be improved also becomes important. Selection should therefore be most effective if the trait being selected was highly heritable, and the genetic correlation of the selected trait with the character to be improved was highly positive.

Heritability estimates are dependent on the method by which they are estimated, the genetic populations from which the estimates are obtained, the unit of measurement, and the environmental conditions encountered during the test. Johnson, et al. (9), using F_2 and backcross variances in a cross between 'Seu Seun 27' and 'Blue Jacket' winter wheats, obtained narrow-sense heritability estimates for spikes/plant, kernel weight, and grain yield of 0.034, 0.547, and 0.102, respectively. Fonseca and Patterson (6) reported narrow-sense heritability estimates from a seven-parent diallel using regression of F_1 and F_2 means on the midparent. The magnitude of their estimates varied greatly depending on the generation of the hybrid, but the ranking did not. They found spikes/930 cm^2 and kernels/spike to be highly heritable and kernel weight and grain yield to be intermediate to low in heritability.

The magnitude of the heritability estimate obtained depends to a great extent on the experimental units considered and the population of inference. Experimental units such as single plants, single plots, and a sample of replicated plots have been used to obtain heritability estimates which impose limitations as to the type of selection to be practiced. Hanson (7) points out that heritability estimates based on single plots have limited utility, but that estimates based on a large sample of environments and plots within environments also have limited usefulness since the heritability for any character could be made as close to 1.0 as desired by unlimited sampling. He states: "'Heritability' is the fraction of the selection differential expected to be gained when selection is practiced on a defined reference unit." Therefore, reports of heritability estimates should be accompanied by descriptions of the material used in obtaining the estimates and the reference unit upon which the heritability estimate is based.

Some of the characters affecting grain yield are most often found to be negatively correlated (6,8,11), thus not rendering themselves to maximum simultaneous improvement through selection. Adams (1) suggested that grain yield components are genetically independent characters which are frequently negatively associated. He speculated that these negative relationships may be due largely to competition for growth substances by simultaneously developing characters.

The present study was conducted to compare heritability estimates for certain agronomic traits in a winter wheat cross, based on two reference units, and to obtain estimates of genetic advance at two levels of selection intensity. Information on the association between all the characters studied was also obtained by computing estimates of phenotypic and genetic correlation coefficients.

MATERIALS AND METHODS

The material for this study consisted of 158 F_3 families, randomly selected from a space-planted F_2 population generated from a cross of two hard red winter wheat cultivars, 'Sturdy' and 'Centurk'. These cultivars are being widely used as parental stock in the breeding program at the Oklahoma Agricultural Experiment Station. Sturdy was developed by the Texas Agricultural Experiment Station and is a semi-dwarf with strong straw. It has medium maturity and excellent baking qualities. Centurk was developed cooperatively by the Nebraska Agricultural Experiment Station and the Plant Science Research Division of the Agricultural Research Service, USDA. It has medium height, is mid-early with moderately strong straw, and has excellent milling and baking characteristics. These two cultivars were chosen as parents because of their diversity for the characters studied. The maturity and height relations between these two cultivars are as pointed out above. Centurk is characterized by a greater number of tillers and seeds/spike, while Sturdy has greater kernel weight. Based on 1968-72 state-wide yield trials, Sturdy has a slight yield advantage over Centurk.

The F_3 families were planted on October 12, 1972 at the Agronomy Research Station, Stillwater, Oklahoma. Families were grown in single row plots in a randomized complete block design with three replications. The nursery was seeded with a tractor-mounted cone planter at the rate of 100 seeds per 1.33 m of row. This is comparable to the standard seeding rate for wheat in Oklahoma of approximately 67 kg/ha (1 bu/A).

Each 1.33 m row was spaced 30 cm apart and trimmed back to 1 m at harvest time in an effort to remove the border effect. The following data were collected on each 1 m row:

Grain yield. Total weight of threshed, cleaned seed from 1 m of row. This was expressed in gm/plot.

Tiller number. The number of seed-bearing culms per 30 cm of a representative section of row.

Seeds/spike. This character was determined by taking a random sample of 10 heads from each row and calculating the mean number of seeds/spike.

Yield/spike. This character was determined by threshing the above 10 heads and calculating the mean yield in gm/spike.

Kernel weight. Calculated as (yield/spike) ÷ (seeds/spike), and expressed as grams per 1000 kernels.

Plant height. The height was measured for each plot as the distance in centimeters from the soil level to the tip of the spikes in the plot, awns excluded.

Heading date. Days to heading was measured as the number of days from March 31 to the date when 50% of the spikes in each plot had completely emerged from the boot.

Growing conditions were generally favorable throughout the growing season and plant development was considered normal.

Heritability estimates based on two reference units were obtained for each character following the variance component method proposed by Comstock and Robinson (4). The heritability estimates obtained in this study were considered as narrow-sense estimates, but because of the method of calculation they contain a portion of the dominance variance and may be biased upward. For further discussion on this point, the reader is referred to Fanous, et al. (5), and Chapter IV of this manuscript. Epistatic effects and genotype by environment interaction were assumed to be negligible.

One method of estimating heritability in the F_3 generation was by the use of single plot values as the reference unit. From this point on, this will be referred to as the heritability for single-rep selection ($\hat{h}^2_{SRS}$) to avoid unnecessary repetition. This heritability estimate is applicable to selection of F_3 families based on their phenotypic performance in a single replication. Assuming no dominance, the heritability for single-rep selection in terms of variance components would be

$$h^2_{SRS} = \frac{\sigma^2_A}{\sigma^2_{P_{SRS}}} = \frac{\sigma^2_A}{\frac{3}{2}\sigma^2_A + \sigma^2_E} = \frac{\sigma^2_A}{\sigma^2_A + [\frac{1}{2}\sigma^2_A + \sigma^2_E]}$$

where σ^2_A is the additive genetic variance, $\sigma^2_{P_{SRS}}$ is the phenotypic variance based on single plot values, and σ^2_E is the environmental variance. Heritability estimates for single-rep selection ($\hat{h}^2_{SRS}$) were calculated from F_3 family data as

$$\hat{h}^2_{SRS} = \frac{[\text{var}(x)_F - \text{var}(x)_{RXF}]/3}{[(\text{var}(x)_F - \text{var}(x)_{RXF})/3] + \text{var}(x)_{RXF}}$$

where $\text{var}(x)_F$ represents the variance of character x based on the measurement of individual families and $\text{var}(x)_{RXF}$ denotes the rep by family interaction for character x and is estimating $[\frac{1}{2}\sigma^2_A + \sigma^2_E]$.

The other method of estimating heritability was by the use of plot means over three replications as the reference unit. From this point on, this will be referred to as the heritability for multiple-rep selection ($\hat{h}^2_{MRS}$). This type of heritability is applicable to selection of F_3 families based on their mean phenotypic performance over three replications. Assuming no dominance, the heritability for multiple-rep selection in terms of variance components would be

$$h^2_{MRS} = \frac{\sigma^2_A}{\sigma^2_{P_{MRS}}} = \frac{\sigma^2_A}{\frac{7}{6}\sigma^2_A + \frac{1}{3}\sigma^2_E} = \frac{\sigma^2_A}{\sigma^2_A + \frac{1}{3}[\frac{1}{2}\sigma^2_A + \sigma^2_E]}$$

where σ^2_A is the additive genetic variance, $\sigma^2_{P_{MRS}}$ is the phenotypic variance based on plot means over three replications, and σ^2_E is the environmental variance. Heritability estimates for multiple-rep selection ($\hat{h}^2_{MRS}$) were calculated from F_3 family data as

$$\hat{h}^2_{MRS} = \frac{[\mathrm{var}(x)_F - \mathrm{var}(x)_{RXF}]}{[\mathrm{var}(x)_F - \mathrm{var}(x)_{RXF}] + [\mathrm{var}(x)_{RXE}]}$$

where $\mathrm{var}(x)_F$ and $\mathrm{var}(x)_{RXF}$ have the same meaning as they did in calculating the heritability estimate for single-rep selection.

Standard errors for heritability for single-rep selection and heritability for multiple-rep selection were estimated by an approximation formula discussed by Kempthorne (10). The estimation formula may be presented as

$$\mathrm{var}(\hat{\theta}) = \frac{\mathrm{var}(a)}{b^2} - 2\,\frac{a\,\mathrm{cov}(a,b)}{b^3} + \frac{a^2}{b^4}\,\mathrm{var}(b)$$

where $(\hat{\theta})$ represents the heritability estimate in the form of a ratio, $\frac{a}{b}$, and var(a) and var(b) represent the variance of a and b, respectively, and cov(a,b) represents the covariance between a and b.

Estimates of genetic advance, at the 5% and 10% levels of selection, for each trait via selection of superior individuals were obtained by the procedure outlined below, where early heading was considered as desirable to late heading and short plant stature was considered as desirable to tall plant stature. The best 5% and 10% of the F_3 families, based on phenotypic values, were selected for each trait based on single-rep selection and based on multiple-rep selection. Selection differentials at each level of selection pressure for both single-rep and multiple-rep selection were determined for each trait by subracting the mean of the original population from the mean of the selected population. Estimates of genetic advance based on single-rep selection ($\hat{GA}_{SRS}$) and genetic advance based on multiple-rep selection ($\hat{GA}_{MRS}$) for both the 5% and 10% levels of selection were then calculated using the following formulas.

$$\hat{GA}_{SRS} = \hat{h}^2_{SRS}(SD_{SRS})$$

and

$$\hat{GA}_{MRS} = \hat{h}^2_{MRS}(SD_{MRS})$$

where $\hat{h}^2_{SRS}$ and $\hat{h}^2_{MRS}$ represent heritability estimates as previously discussed, and SD_{SRS} and SD_{MRS} are the selection differentials for single-rep selection and multiple-rep selection, respectively. Estimates of genetic gain for single-rep selection are reported for each character as the mean of the estimates calculated for each of three replications. The standard errors for the estimates of genetic advance, based on single-rep selection, were estimated by computing the standard error of the mean based on estimates calculated for each replication. Estimates of genetic gain for multiple-rep selection are reported as individual estimates without standard errors.

The interrelationships among all characters were studied by estimating phenotypic and genetic correlation coefficients following the method employed by Anand and Torrie (2). The phenotypic correlations (r_p), on an individual plot basis, were estimated using total mean squares and total mean products as

$$r_p = \frac{\mathrm{cov}(x,y)_F}{[\mathrm{var}(x)_F \cdot \mathrm{var}(y)_F]^{1/2}}$$

where $\mathrm{cov}(x,y)_F$ represents the covariance between characters x and y, and $\mathrm{var}(x)_F$ and $\mathrm{var}(y)_F$ denotes the variance of x and y, respectively. Variances and covariances were based on measurements taken on individual F_3 families.

The genetic correlations (r_g), on an individual plot basis, were estimated as

$$r_g = \frac{[\mathrm{cov}(x,y)_F - \mathrm{cov}(x,y)_{RXF}]}{[\mathrm{var}(x)_F - \mathrm{var}(x)_{RXF}]^{1/2}[\mathrm{var}(y)_F - \mathrm{var}(y)_{RXF}]^{1/2}}$$

where $\mathrm{cov}(x,y)_F$, $\mathrm{var}(x)_F$, and $\mathrm{var}(y)_F$ have the same meaning as in the previous equation and $\mathrm{cov}(x,y)_{RXF}$ represents the rep by family interaction covariance between characters x and y, and $\mathrm{var}(x)_{RXF}$ and $\mathrm{var}(y)_{RXF}$ denote the rep by family interaction variances for x and y, respectively. Variances and covariances were based on measurements taken on individual F_3 families. Correlations calculated by the above formula will be referred to as genetic correlation coefficients in this paper, but it should be noted that the estimate contains a portion of the correlation between the dominance effects for characters x and y, which may cause an upward bias in the estimate.

Significance of the phenotypic correlation coefficients were determined in the usual way (12), but tests for the significance of the genetic correlation coefficients, as calculated above, are not available; however, the relative magnitude of the genetic correlations should reflect the degree of genetic association between two given characters.

RESULTS AND DISCUSSION

Heritability

Estimates of heritability for each character studied are presented in Table 1. In general, kernel weight, heading date, and plant height were highly heritable while heritability estimates for the other characters ranged from intermediate to low. These results are in general agreement with Johnson, et al. (9) and Bhatt (3). Heritability estimates for multiple-rep selection were nearly twice the magnitude of heritability estimates for single-rep selection for the lower heritable traits: grain yield, tiller number, seeds/spike, and yield/spike. On the other hand, the more highly heritable traits showed less reduction in heritability as the reference unit changed. The changes in the heritability estimates for grain yield, yield/spike, and tiller number represent a 44%, 56%, and 63% reduction, respectively, as the reference unit changed from the multiple-rep to the single-rep unit. However, the reduction in heritability for kernel weight was 23%. The reduction in heritability of plant height was 14%. The most highly heritable trait, heading date, was least affected (12% reduction) as the reference unit changed.

In general, the heritability estimates for multiple-rep selection were higher than estimates for single-rep selection. This was due to the reduction in the phenotypic variance of plot means over three replications as compared to the phenotypic variance of individual plot values. The heritability estimates obtained in this study indicate that a sizeable increase in the heritability for lower heritable traits can be expected with the reference unit being means over replications as compared to the reference unit being individual plot values in single replication. This was as expected because traits exhibiting low heritabilities have a large phenotypic variance in relation to the genetic variance, and it was the phenotypic variance that was reduced when the reference unit changed from means over replications to individual plot values with single replication.

Genetic Advance

Estimates of genetic advance expressed in the original units of measurement are presented in Table 2. The estimates indicate that a reduction in progress is encountered with single-rep selection (selection based on a single replication) as compared to multiple-rep selection (selection based on means over three replications). The estimated genetic advance for yield, at the 5% level of selection intensity, with single-rep selection, was 12.236 gm/plot and represents a 25% reduction compared to the estimate for multiple-rep selection, which was 16.308 gm/plot. The reduction of genetic advance was much less than the reduction of the heritability estimates as the reference unit for selection changed. The reason for this is that there was a reduction in the population variance when considering plot means over three replications as compared to individual plot values, thus reducing the selection differential used in calculating the genetic advance. The reduction of the selection differentials was slightly overcome by the large increases in heritabilities; therefore, a slight advantage was indicated with multiple-rep selection as compared to single-rep selection.

Single-rep selection resulted in a slightly greater predicted genetic advance than multiple-rep selection for heading date and plant height at both levels of selection. This was due to the larger selection differential for single-rep selection. Also, the magnitude of the heritability estimates of these two traits with multiple-rep selection were close to the magnitude of the heritability estimates with single-rep selection, thus not overcoming the increase of the selection differentials. The estimated genetic advance for heading date, with single-rep selection was the same for the 5% and 10% levels of selection. This was due to the absence of variation in the top 5% and 10% of the families selected for early maturity.

Selection of F_3 families would include all individuals in the family, some of which may be less desirable types. From a breeding standpoint, within-family selection could be practiced to select superior individuals from promising families identified by single-rep or multiple-rep selection procedures. Genetic advance in this type of breeding program would be expected to be greater than the genetic advance in a program where entire families were selected with no within-family selection practiced to remove less desirable types.

Correlations Among Characters

Estimates of the phenotypic and genetic correlations between all possible two-way combinations of characters studied are presented in Table 3. In general, the genetic correlations were higher than the phenotypic correlations indicating that yield components may not be genetically independent as suggested by Adams (1). The phenotypic and genetic correlations agreed in sign in all cases except for the correlation between plant height and tiller number, and the phenotypic value in this case was judged to be nonsignificant.

Tiller number was the character most highly associated with grain yield as indicated by the phenotypic as well as the genetic correlation coefficients. Heading date was negatively associated with yield in both estimates. The genetic correlations of heading date with all other characters were positive except for its correlation with tiller number (-.6077), and it was this negative relationship that was the main cause of the rather large negative genetic association between grain yield and heading date (-.6767). The negative genetic association between heading date and tiller number, and between heading date and grain yield indicates that the earlier genotypes had a greater tiller number and were characterized by greater yields than the later genotypes. Except for grain yield and the insignificant phenotypic correlation with plant height, tiller number was found to be negatively associated with each character in this study. Fonseca and Patterson (6) also found tiller number to be negatively correlated with most characters in one year of their study.

Other large negative genetic associations occurred between kernel weight and seeds/spike, and between seeds/spike and plant height (-.7796 and -.6287, respectively), while the genetic correlation between kernel weight and plant height was positive (.5845), indicating that taller genotypes with heavier kernels possessed fewer seeds/spike. Kernel weight was negatively associated with tiller number, but the correlation coefficient was nonsignificant at the phenotypic level. The genetic correlation between these two characters was also negative (-.4657).

Total grain yield is the product of kernel weight, tiller number, and seeds/spike when each of these traits is measured without error. Based on the heritability estimates of kernel weight (.848 and .651) and its genetic correlation with yield (.2750), an increase in total grain yield should be possible by selecting in early generations for increased kernel weight. However, progress in breeding by selection for kernel weight may be somewhat limited by the negative genetic correlation of this trait with tiller number. Due to the rather low heritability of tiller number (.134 and .049), selection for this character would seem less likely to increase yield. Seeds/spike was negatively associated with total grain yield; therefore, selection for an increase in this character would not be expected to increase grain yield. It should be remembered, however, that the heritabilities and genetic correlations reported in this study may be biased by dominance effects and therefore should be used with caution.

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Table 1. Estimates of heritability for single-rep selection ($\hat{h}^2_{SRS}$) and for multiple-rep selection ($\hat{h}^2_{MRS}$) for seven agronomic characters, based on F_3 data.

Character	$\hat{h}^2_{MRS}$	$\hat{h}^2_{SRS}$	$\hat{h}^2_{MRS}-\hat{h}^2_{SRS}$	% Change
Grain yield	.605 ± .067	.338 ± .358	.267	44
Tiller number	.134 ± .123	.049 ± .169	.085	63
Kernel weight	.848 ± .035	.651 ± .057	.197	23
Seeds/spike	.661 ± .060	.394 ± .213	.267	40
Yield/spike	.374 ± .095	.166 ± .489	.208	56
Heading date	.934 ± .022	.824 ± .023	.110	12
Plant height	.921 ± .024	.794 ± .028	.127	14

Table 2. Estimates of genetic advance for single-rep selection $(\widehat{GA}_{SRS})$ and for multiple-rep selection $(\widehat{GA}_{MRS})$ for 5% and 10% levels of selection, based on F_3 data.

Character	$\widehat{GA}_{SRS}$		$\widehat{GA}_{MRS}$	
	5%	10%	5%	10%
Grain yield	12.236 ± .620	10.418 ± .449	16.308	14.132
Tiller number	1.270 ± .101	1.093 ± .069	2.076	1.868
Kernel weight	1.316 ± .226	1.019 ± .287	3.651	3.080
Seeds/spike	2.852 ± .065	2.299 ± .065	3.939	3.014
Yield/spike	0.032 ± .003	0.028 ± .022	0.052	0.043
Heading date	4.470 ± .241	4.470 ± .241	4.392	4.003
Plant height	12.597 ± .527	10.987 ± .161	12.521	10.737

Table 3. Phenotypic and genetic correlation coefficients among seven agronomic characters, based on F_3 data.

Character	Kernel weight	Tiller number	Seeds/spike	Yield/spike	Heading date	Plant height
Grain yield (a) (b)	.1586* .2750	.3356** .6712	-.0215 ns -.1693	.1125 ns .2230	-.4079** -.6767	.1564* .0857
Kernel weight		-.1125 ns -.4657	-.3332** -.7796	.4685** .4311	.0068 ns .0325	.4178** .5845
Tiller number			-.1617* -.0015	-.2367** -.7487	-.1320 ns -.6077	.0102 ns -.2457
Seeds/spike				.6732** .2277	.0632 ns .0900	-.3187** -.6287
Yield/spike					.0611 ns .1699	.0348 ns .0198
Heading date						.0157 ns .0145

[a] The upper value in each cell is the phenotypic correlation coefficient with df (n-2) = 472, and must exceed .156 and .205 to be significant at the .05 and .01 levels, respectively.

[b] The lower value in each cell is the genetic correlation coefficient reported without standard errors.

CHAPTER IV

Heritability Estimates for Yield and Yield Components in a Hard Red Winter Wheat Cross (*Triticum aestivum* L.)[1]

ABSTRACT

The parents, F_1, F_2, and the two backcrosses generated from two hard red winter wheat cultivars were studied in a space-planted experiment grown on the Agronomy Research Station, Stillwater, Oklahoma, during the 1971-72 crop season. Data were taken on an individual plant basis. A total of 158 F_2 plants were randomly selected, and their progenies studied as F_3 families under solid-seeding conditions during the 1972-73 crop season. Data were taken on single 1 m rows.

The characters studied were: grain yield, tiller number, seeds/spike, and kernel weight. Heritability estimates for each character were obtained by three different methods: (a) the narrow-sense method; (b) the single-rep selection method; and (c) the regression method. Realized heritabilities were estimated as the ratio of response in the F_3 generation to the selection differential in the F_2 generation by selecting the upper and lower 10% of the F_2's which were represented in the F_3 generation.

Based on both the narrow-sense and the single-rep selection methods, the heritability estimate for kernel weight was high. The heritability

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[1] To be submitted for publication.

estimate for kernel weight based on the regression method was relatively low, but was characterized by a rather small standard error. Although relatively low, heritability estimates for grain yield in all three methods were higher than expected. However, with each method the estimate was characterized by a rather large standard error. Heritability estimates for the other characters ranged from intermediate to low.

When selecting the upper 10% of the F_2 individuals for each character, kernel weight had the highest realized heritability followed by seeds/spike, tiller number, and grain yield, respectively. However, when the lower 10% of the F_2 individuals were selected for each character, the realized heritability estimate for grain yield was highest followed by tiller number, kernel weight, and seeds/spike, respectively. These results suggested that if kernel weight and seeds/spike are to be improved, direct selection for these characters would be effective. However, if grain yield and tiller number are to be improved, direct selection for these characters should not be applied in F_2 space-plants.

Progeny of F_2 plants selected for each character indicated that individuals selected on the basis of increased kernel weight would produce progeny with a higher mean grain yield than progeny of individuals selected on the basis of the other traits. Based on results of heritability estimates and selection in the F_2 generation, more emphasis should be placed on kernel weight to increase grain yield by indirect selection in early generations.

Additional index words: Heritability, Regression analysis, Variance components, Realized heritability.

Heritability estimates are dependent on the populations from which the estimates are obtained, the unit of measurement, and the environmental conditions encountered during the test as well as the method by which they are estimated. Heritability estimates for the same character, based on different estimating procedures, may present different results. Therefore, the extent to which heritability estimates for the same character are affected by the method of estimation should be of importance to the plant breeder, and he should keep in mind the biases associated with heritability estimates and the assumptions under which the estimates were obtained.

Johnson, et al. (6), using F_2 and backcross variances in a cross between 'Seu Seun 27' and 'Blue Jacket' winter wheats, obtained narrow-sense heritability estimates for spikes/plant, kernel weight, and grain yield of 0.034, 0.547, and 0.102, respectively. Bhatt (1), using F_2 and backcross variances in crosses of 'Timgalen' with 'Sonora 64A' and 'Timgalen' with 'Eagle' obtained narrow-sense estimates for kernel weight of 0.694 and 0.556 for the two crosses, respectively. Fonseca and Patterson (4) reported narrow-sense heritability estimates from a seven-parent diallel using regression of F_1 and F_2 means on the mid-parent. Within the same year the magnitude of their estimates varied greatly depending on the generation of the hybrid but the ranking did not. They found spikes/930 cm^2 and kernels/spike highly heritable and kernel weight and grain yield intermediate to low. McNeal (7), using the regression of F_3 progenies on F_2 parent plants, obtained heritability estimates for tiller number, seeds/spike, kernel weight, and grain yield of 0.356, 0.066, 0.127, and 0.107, respectively. In his study both the F_2 and F_3 generations were evaluated as space-planted populations, and the data collected from F_3 plants were obtained in the same way as those from the F_2 plants. Fanous, et al. (3) studied head length, seed-branch length, node number per head, and 100-seed weight in five crosses of sorghum. They obtained heritability estimates for each character by the regression of F_3 family means on individual F_2 plant values, and by the variance component method proposed by Comstock and Robinson (2). They found heritability estimates based on the variance component method larger than heritability estimates based on regression analysis for each character in each of the five crosses.

Rasmusson and Cannell (9), working with two barley populations, one generated by crossing 'Mars' with 'Larker' and the other by crossing 'Wisc X691' with 'Peatland', obtained realized heritabilities for grain yield, tiller number, seeds/spike, and kernel weight. Realized heritabilities were estimated as the ratio of response in the F_5 generation to the selection differential in the F_4 generation. In general, they found kernel weight and seeds/spike highly heritable, while heritability estimates for grain yield and tiller number were intermediate to low.

The magnitude of the heritability estimate obtained depends to a great extent on the experimental units considered and the population of inference. Experimental units such as single plants, single plots, and a sample of replicated plots have been used to obtain heritability estimates which impose limitations as to the type of selection to be practiced. Hanson (5) points out that heritability estimates based on single plots have limited utility, but that estimates based on a large sample of environments and plots within environments also have limited usefulness since the heritability for any character could be made as close to 1.0 as desired by unlimited sampling. He states: "'Heritability' is the fraction of the selection differential expected to be gained when selection is practiced on a defined reference unit." Therefore, reports of heritability estimates should be accompanied by descriptions of the material used in obtaining the estimates and the reference unit upon which the heritability estimate is based.

In breeding programs designed for grain yield improvement by selecting for yield components, selection of the components needs to be accompanied by a change in grain yield. McNeal (8), beginning with 1000 F_2 plants of 'C.I. 13242' X 'Thatcher', studied yield components as selection criteria in a seven-year program in Montana. He found that average grain yields of progeny from a composite of lines selected for six years on the basis of kernel weight and seeds/spike were significantly higher in grain yield than lines selected on the basis of spikelets/spike, tiller number, and grain yield for the same length of time. Except for tiller number, progeny of lines selected on the basis of each character was significantly greater in grain yield than progeny of lines selected on the basis of grain yield _per se_.

The present study was conducted to examine the heritability estimates of grain yield, tiller number, seeds/spike, and kernel weight, from three different methods of estimation, in a winter wheat cross. Realized heritabilities for each character were estimated, and the response of grain yield in the F_3 generation due to selection for each character in the F_2 generation was also determined.

MATERIALS AND METHODS

The parental, F_1, BC_1, BC_2, F_2, and F_3 populations studied in this experiment were derived from two hard red winter wheat cultivars, 'Sturdy' and 'Centurk'. These cultivars are being widely used in the crossing program at the Oklahoma Agricultural Experiment Station. Sturdy was developed by the Texas Agricultural Experiment Station and is a true semi-dwarf with strong straw. It has medium maturity and excellent baking qualities. Centurk was developed cooperatively by the Nebraska Agricultural Experiment Station and the Plant Science Research Division of the Agricultural Research Service, USDA. It has medium height, is mid-early with moderately strong straw, and has excellent milling and baking characteristics. These two cultivars were chosen as parents for this study because of their diversity for the characters studied. The maturity and height relations between these two cultivars are as pointed out above. Centurk is characterized by a greater number of tillers and seeds/spike, while Sturdy has greater kernel weight. Based on 1968-72 state-wide yield trials, Sturdy has a slight yield advantage over Centurk.

Seedlings of the parents, F_1, F_2, and the two backcrosses BC_1 and BC_2 were started in flats and then transplanted to the field on October 29, 1971. Transplanting was made in a randomized complete block design at the Stillwater Agronomy Research Station. The experiment consisted of six replications with each replication composed of one row of each parent and the F_1, two rows of each backcross generation, and four rows of the F_2. Each row was composed of 20 plants spaced 15 cm apart. The rows were spaced 30 cm apart and all measurements were made on an individual plant basis on 16 bordered plants from each row. For further information on the collection of data the reader is referred to Chapter II.

One hundred and fifty-eight F_3 families, generated from the space planted F_2 population described above, were planted on October 12, 1972. The criteria for selection of the F_2 space-plants to be represented in the F_3 generation was that approximately equal numbers of the F_2 plants be randomly selected from each of the six replications and that a minimum of 300 seeds was available from each plant. The F_3 families were grown in single-row plots in a randomized complete block design with three replications. The nursery was seeded with a tractor-mounted cone planter at the rate of 100 seeds per 1.33 m of row. This is comparable to the standard seeding rate for wheat in Oklahoma of approximately 67 kg/ha (1 bu/A). Each 1.33 m row was trimmed back to 1 m at harvest time to eliminate border effect bias. The rows were spaced 30 cm apart and all measurements were made on each 1 m row.

The characters studied were: grain yield, tiller number, kernel weight, and seeds/spike. Grain yield was measured as the total weight in grams of the seed harvested from an individual space plant in the F_2 generation and from a one meter row in the F_3 generation. Tiller number in the F_2 space-planted population was the number of seed-bearing culms for each plant and in the F_3 generation this character was for a 30 cm section of row. The number of seeds/spike in the F_2 generation was taken as the total number of seeds on one head selected from each plant, and in the F_3 generation this character was determined by taking a sample of 10 heads from each experimental row and calculating the mean number of seeds/spike. Kernel weight in the F_3 generation was estimated using the same 10 heads used in calculating the number of seeds/spike. All seeds were weighed and a mean kernel weight determined. For the F_2 generation, kernel weight was determined in a similar manner using the one head which was used to estimate seeds/spike. Kernel weight for both generations was expressed as grams per 1000 kernels.

Heritability estimates obtained by three different methods were examined in this study. The three methods were: (a) the method proposed by Warner (10) using F_2 and backcross variances. The reference unit for this method was individual F_2 plants, and the estimate will be referred to as narrow-sense heritability ($\hat{h}^2_{ns}$); (b) the method proposed by Comstock and Robinson (2) using F_3 family variances. The reference unit for this method was F_3 families in single replication, and the estimate will be referred to as heritability for single-rep selection ($\hat{h}^2_{SRS}$); and (c) the method of parent-offspring regression using F_2 plants (parent) and F_3 families (offspring). The reference unit for this method was individual F_2 plants, and the estimate will be referred to as heritability based on regression ($\hat{h}^2_{Reg}$).

Epistatic effects and genotype by environment interaction were assumed to be negligible in obtaining heritability estimates by each of the three methods.

The narrow-sense heritability estimates (method a) reported in this study, were taken from Chapter II where further discussion on the estimating procedure is presented. In terms of variance components, heritability estimates from this method would be estimating

$$h^2_{ns} = \frac{\sigma^2_A}{\sigma^2_A + \sigma^2_D + \sigma^2_E}$$

where σ^2_A and σ^2_D represent additive and dominance variances, respectively, in the F_2 generation, and σ^2_E denotes the environmental variance in the F_2 generation. For this method of estimation, measurements were based on individual space-plant values.

The heritability estimates for single-rep selection (method b) reported in this study were taken from Chapter III where further discussion on the estimating procedure is presented. In terms of variance components, heritability estimates from this method would be estimating

$$h^2_{SRS} = \frac{\sigma^2_A + (\sigma^2_D/4)}{\sigma^2_A + (\sigma^2_D/4) + [(\sigma^2_A/2) + (\sigma^2_D/2) + \sigma^2_E]} = \frac{\sigma^2_A + (\sigma^2_D/4)}{(3\sigma^2_A/2) + (3\sigma^2_D/4) + \sigma^2_E}$$

where σ^2_A and σ^2_D have the same meaning as before and σ^2_E represents the environmental variance in the F_3 generation. The quantity $[(\sigma^2_A/2) + (\sigma^2_D/2) + \sigma^2_E]$ represents the plot error variance as measured in the F_3 generation. For this method of estimation, measurements were based on single-row plot values.

Heritability estimates based on regression (method c) were obtained by regressing F_3 family means, based on three replications, on their parental F_2 space-plant values. In terms of variance components, heritability estimates from this method would be estimating

$$h^2_{Reg} = \frac{\sigma^2_A + (\sigma^2_D/2)}{\sigma^2_A + \sigma^2_D + \sigma^2_E}$$

where σ^2_A and σ^2_D have the same meaning as before and σ^2_E denotes the environmental variance in the F_2 generation considering only the 158 F_2's represented by offspring in the F_3 generation. Heritability estimates based on regression were calculated as

$$\hat{h}^2_{Reg} = \frac{\text{cov}(x,y)}{\text{var}(x)_{F_2}}$$

where cov(x,y) represents the covariance between x and y, where x denotes the value of a character in the F_2 generation and y denotes the mean value of the same character in the F_3 generation. Also, $\text{var}(x)_{F_2}$ represents the variance of the same character in the F_2 generation considering only the 158 F_2's represented by offspring in the F_3 generation. Heritability estimates based on regression are equal to the estimated slopes of the regression line (b_1) for the various characters. Therefore, the standard errors of the heritability estimates were the standard errors of the b_1 values.

Estimates of realized heritability were obtained for each character, via selection of the upper 10% and the lower 10% of the 158 F_2's represented by offspring in the F_3 generation. Realized heritability estimates based on selection of the upper 10% of the F_2's ($\hat{h}^2_U$) were calculated as

$$\hat{h}^2_U = \frac{\text{Resp}(F_3)_U}{\text{SD}(F_2)_U}$$

where $\text{Resp}(F_3)_U$ represents response in the F_3 generation due to selection of the upper 10% of the F_2's, and $\text{SD}(F_2)_U$ denotes the selection differential in the F_2 generation. Response in the F_3 generation was determined by subtracting the mean of all F_3 families from the mean of the families of selected F_2 individuals (upper 10%). The selection differential in the F_2 generation was determined by subtracting the mean of the 158 F_2's represented in the F_3 generation, from the mean of the selected F_2 individuals (upper 10%). Realized heritability estimates based on selection of the lower 10% of the F_2's ($\hat{h}^2_L$) were calculated as

$$\hat{h}^2_L = \frac{\text{Resp}(F_3)_L}{\text{SD}(F_2)_L}$$

where $\text{Resp}(F_3)_L$ represents response in the F_3 generation due to selection of the lower 10% of the F_2's, and $SD(F_2)_L$ denotes the selection differential in the F_2 generation. $Resp(F_3)_L$ and $SD(F_2)_L$ were determined as per $Resp(F_3)_U$ and $SD(F_2)_U$, respectively, using means of the lower 10% instead of the upper 10%. Realized heritability estimates were calculated for each of three replications, and are reported as the mean of these three estimates. Standard errors for the realized heritability estimates were estimated by computing the standard error of the mean based on estimates calculated for each replication.

The mean grain yield of F_3 families tracing to F_2 space-plants selected for the upper and lower 10% for each character, was determined for each of three replications and reported as the mean of these three estimates. Standard errors for these means were estimated by computing the standard error of the mean based on estimates calculated for each of three replications.

RESULTS AND DISCUSSION

The means for grain yield, tiller number, seeds/spike, and kernel weight as measured in the F_2 and F_3 generations are presented in Table 1. The relative magnitude of the means should be an indication of the performance of each character in each generation. Direct comparison of means for the same character in the F_2 and F_3 generations should not be made due to the difference in planting rate (space-planting vs. solid-seeding). However, in the two generations the same unit of measure was used for seeds/spike and kernel weight, respectively. Due to dry conditions encountered during the growing season, supplemental applications of water were applied to the study conducted during the 1971-72 season. Stress conditions did not appear to adversely affect the expression of any of the characters studied during the 1971-72 and the 1972-73 growing seasons.

Heritability

Heritability estimates for each of the three methods of calculation are presented in Table 2. Heritability estimates for grain yield were higher than expected in all three methods; however, in each case the heritability estimate was characterized by a rather large standard error. Based on the single-rep selection method and the narrow-sense method, heritability estimates for kernel weight were high (.651 and .511, respectively). The regression method resulted in a relatively small heritability estimate for this character (.255), but this estimate was characterized by a rather small standard error. The relatively small heritability estimate for kernel weight obtained from the regression method could be due to a smaller genetic and environmental variance of this trait in the F_3 generation than in the F_2 generation (solid-seeding vs. space-planting). An examination of the variances of kernel weight in the F_2 and F_3 generations supports the above explanation. The heritability estimate for tiller number obtained from the narrow-sense method was intermediate (.316), while estimates for this trait using the regression method and the single-rep selection method were low (.122 and .049, respectively). Estimates of heritability for seeds/spike based on the regression method and the narrow-sense method were low (.104 and .239, respectively). The heritability estimate of this trait based on the single-rep selection method was intermediate in magnitude (.394). For all characters except tiller number, the single-rep selection method resulted in higher heritability estimates than the other two methods of estimation. Fanous, et al. (3) found similar results.

In using the heritability estimates calculated by the different procedures, one should keep in mind the bias associated with each method of calculation and the assumptions under which the estimates were obtained. Heritability estimates based on the narrow-sense method should not be biased by dominance effects as indicated by the heritability expressed in terms of variance components. Since the F_2 and backcross generations were used in calculating the narrow-sense estimates, the assumption of equal environmental influences in these generations was made. Heritability estimates calculated by this method were based on variability between individual space-plants, and if interplant competition was a factor the estimates could be biased as pointed out by Hanson (5).

Heritability estimates based on the single-rep selection method would be biased by dominance effects. Also, the variation within an F_3 family not only includes environmental variation, but also includes additive and dominance variation. Therefore, this method was estimating a different quantity as indicated by the heritability expressed in terms of variance components. Possible biases due to genotype by environment interactions arising from tests conducted at only one location and in one year are pointed out by Comstock and Robinson (2).

Heritability estimates based on the regression method would be biased by one-half the dominance variance as indicated by the heritability expressed in terms of variance components. The assumption of equal environmental influences in the F_2 and F_3 generations was made. However, in the F_3 generation, each character was measured under solid-seeding conditions while measurements in the F_2 generation were based on individual space-plants. By necessity, the two generations were grown in different years and were thus subject to different environmental conditions. However, it should be noted that in a breeding program the F_2 generation is frequently space-planted and selections from this generation are generally grown under solid-seeding conditions. Therefore, heritability estimates based on regression of F_3 families on F_2 plants should be applicable to this type of breeding program.

Realized heritability estimates indicating the effectiveness of selection in the F_2 generation for the various characters, based on their performance in the F_3 generation, are presented in Table 3. As expected, the heritability estimate for kernel weight was the highest followed by seeds/spike, tiller number, and grain yield, respectively, based on selection of the upper 10% of the F_2's for each character. These results are in general agreement with Rasmusson and Cannell (9). When the lower 10% of the F_2 individuals were selected for each character, the realized heritability for grain yield was highest followed by tiller number, kernel weight, and seeds/spike, respectively. These results indicate that in a breeding program direct selection should be applied to kernel weight and seeds/spike if these traits are to be improved. To improve grain yield or tiller number, direct selection for these traits should not be applied in F_2 space-plants. However, if grain yield and tiller number are to be improved by direct selection, advance should be possible by discarding lower yielding and lower tillering types, and retaining a random sample of the remaining plants.

Yield Component Selection

An examination of the mean grain yield of the F_3 families of F_2 plants selected for the upper and lower 10% for each character was made and the results are presented in Table 4. The progeny of F_2 plants selected for the upper 10% on the basis of grain yield, tiller number, and seeds/spike, produced mean grain yields which were less than the mean grain yield of all F_3 families. However, the mean grain yield of progeny of F_2 plants selected for the upper 10% on the basis of kernel weight was higher than the overall mean grain yield (121.30 vs. 116.71). Progeny of F_2 plants selected for the lower 10% on the basis of grain yield, tiller number, and kernel weight, produced mean grain yields which were less than the overall mean; however, the mean grain yield of progeny of F_2 plants selected on the basis of seeds/spike was only slightly larger (117.13 vs. 116.71).

The upper 10% of the F_2 plants selected on the basis of grain yield produced progeny with a mean grain yield slightly larger than progeny of F_2 plants selected for the lower 10% on the basis of grain yield (113.02 vs. 112.13). However, F_2 plants selected for the lower 10% on the basis of tiller number and seeds/spike, produced progeny with mean grain yields slightly larger than progeny of F_2 plants selected for the upper 10% for these characters. The upper 10% of the F_2 plants selected on the basis of kernel weight produced progeny with a mean grain yield much larger than progeny of F_2 plants selected for the lower 10% for this character (121.39 vs. 111.35). These results indicate that an increase in grain yield would be expected if selection were made on the basis of kernel weight rather than on the basis of tiller number or seeds/spike, and that direct selection for grain yield would be ineffective in a breeding program in space-planted F_2's. These conclusions apply to the material studied in this experiment and may not be applicable to other populations; however, these results are in general agreement with McNeal (8).

The results of the heritability estimates and selection in the F_2 generation indicate that more emphasis should be placed on kernel weight to increase grain yield by indirect selection in the F_2 generation. However, progress in a breeding program may be limited depending on the association between kernel weight and other characters contributing to grain yield.

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Table 1. Character means for the 158 F_2 space-plants represented by progeny in the F_3 generation, and for the 158 F_3 progeny rows.

Character	F_2 space-plants		
	Mean	High	Low
Grain yield (gm/plant)	18.32	33.90	8.30
Tiller number (tillers/plant)	21.67	33.00	11.00
Seeds/spike	41.16	57.00	28.00
Kernel weight (1000 kernels)	26.69	36.50	19.50
Character	F_3 progeny rows		
	Mean	High[a]	Low[a]
Grain yield (gm/row)	116.71	152.82	78.45
Tiller number (tillers/30 cm^2)	68.65	90.33	51.33
Seeds/spike	31.45	40.00	24.23
Kernel weight (1000 kernels)	27.40	32.64	25.12

[a] The high and low value for each character in the F_3 generation is based on means over three replications.

Table 2. Heritability estimates for yield and yield components based on (a) narrow-sense heritability ($\hat{h}^2_{ns}$), (b) heritability for single-rep selection ($\hat{h}^2_{SRS}$), (c) heritability based on regression ($\hat{h}^2_{Reg}$).

Character	$\hat{h}^2_{ns}$	$\hat{h}^2_{SRS}$	$\hat{h}^2_{Reg}$
Grain yield	.285 ± .159	.338 ± .358	.286 ± .249
Tiller number	.316 ± .142	.049 ± .169	.122 ± .139
Seeds/spike	.239 ± .158	.394 ± .213	.104 ± .031
Kernel weight	.511 ± .130	.651 ± .057	.255 ± .044

Table 3. Realized heritability estimates for yield and yield components as a ratio of response in the F_3 generation to the selection differential in the F_2 generation for the upper 10% and lower 10% of F_2 plants selected.

Character	Upper 10%[a]	Lower 10%[b]
Grain yield	-.437 ± .084	.696 ± .090
Tiller number	-.229 ± .014	.456 ± .011
Seeds/spike	.165 ± .002	-.040 ± .001
Kernel weight	.248 ± .001	-.003 ± .001

[a] Negative values indicate that the mean of the progeny of selected individuals was less than the mean of all progeny.

[b] Negative values indicate that the mean of the progeny of selected individuals was greater than the mean of all progeny.

Table 4. Mean grain yield of F_3 families of F_2 plants selected for the upper 10% and lower 10% for yield and yield components.

Character Selected	F_2 plants selected	
	Upper 10%	Lower 10%
Grain yield	113.02 ± 1.76	112.13 ± 2.57
Tiller number	113.11 ± 4.42	115.84 ± 0.33
Seeds/spike	112.15 ± 1.70	117.13 ± 1.77
Kernel weight	121.39 ± 2.39	111.35 ± 0.92
Mean grain yield of all F_3 families	116.71 ± 0.75	

CHAPTER V

SUMMARY

The parental, F_1, BC_1, BC_2, F_2, and F_3 populations, derived from two winter wheat cultivars, were used to study the genetic systems and interrelations of yield and yield-related traits. The parents, F_1, BC_1, BC_2, and F_2 were evaluated in a space-planted experiment at the Agronomy Research Station, Stillwater, Oklahoma, during the 1971-72 crop season. The F_3 generation was studied under solid-seeding conditions at the Stillwater Agronomy Research Station during the 1972-73 crop season.

Grain yield, tiller number, kernel weight, seeds/spike, spikelets/spike, and seeds/spikelet, were the characters studied during the 1971-72 crop season. Estimates of additive and nonadditive gene action for these traits indicated that nonadditive gene action was more pronounced than additive gene action for all traits except kernel weight. Additive and nonadditive gene action were found to be about equally important for kernel weight suggesting that dominance gene action was less than additive gene action for this trait. Narrow-sense and broad-sense heritability estimates indicated that kernel weight was a highly heritable trait and that heritability estimates for the other characters ranged from intermediate to low. In general, narrow-sense heritability estimates were smaller than the broad-sense estimates for the same trait. This was attributed to the unequal environmental influences in the generations used in calculating each of the heritability estimates.

Phenotypic and genetic correlations calculated for all possible two-way combinations of characters, indicated a positive association between grain yield and each of the other characters. Negative correlations between kernel weight and tiller number suggested that simultaneous improvement of these two traits may be difficult. As indicated by path-coefficient analysis at the phenotypic level, tiller number had a large direct effect on grain yield, while the direct effects of kernel weight and seeds/spike on grain yield were intermediate and low, respectively. However, at the genetic level the direct effects of these three traits on grain yield were about equal in magnitude. The results of the path-coefficient analysis and heritability estimates indicated that more emphasis should be placed on kernel weight to increase grain yield by early generation selection.

Grain yield, tiller number, kernel weight, seeds/spike, yield/spike, heading date, and plant height were the characters examined in the F_3 generation during the 1972-73 crop season. Heritability estimates, based on two reference units, were obtained for each of these traits. The two reference units were individual plot values in single replication, and plot means based on three replications. In general, heritability estimates for heading date, plant height, and kernel weight were high, while heritability estimates for the other characters ranged from intermediate to low. For the lower heritable traits, grain yield, tiller number, seeds/spike, and yield/spike, heritability estimates based on plot means were much larger than heritability estimates based on individual plot values. Estimates of genetic advance at two levels of selection intensity indicated that selection based on plot means offers a slight advantage to selection based on individual plot values. However, a greater genetic advance was predicted when selection for shorter plant stature was based on individual plot values as compared to plot means. Estimates of genetic correlation coefficients indicated that earlier genotypes had a greater tiller number and were characterized by greater yields than the later genotypes. Also, taller genotypes had heavier kernels and possessed fewer seeds/spike. Based on estimates of heritability and genetic correlations, kernel weight was the character assumed most likely to bring about an increase in grain yield by indirect selection in early generations.

Heritability estimates were also determined by regressing F_3 family means on their individual F_2 parent plant. In general, heritability estimates based on regression analysis were rather low. However, the heritability estimate for kernel weight was characterized by a small standard error. The relatively small heritability estimate for this character was attributed to a small variance of this character in the F_3 generation compared to the F_2 generation. Realized heritability estimates indicated that if kernel weight and seeds/spike are to be improved, direct selection for these characters should be effective. However, if grain yield and tiller number are to be improved, direct selection for these characters should not be applied in F_2 space-plants. Progeny of F_2 plants selected for grain yield, kernel weight, tiller number, and seeds/spike indicated that individuals selected on the basis of increased kernel weight would produce progeny with greater grain yields than progeny of individuals selected on the basis of the other traits.

In general, the results of these studies indicated that more emphasis should be placed on kernel weight in breeding programs designed to increase grain yield by indirect selection in early generations. However, progress in a breeding program may be somewhat limited depending on the association between kernel weight and other characters contributing to grain yield.

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Table 10. Character values for the upper 10% of the 158 F_3 families selected for kernel weight based on means of three replications.

Table 11. Mean character values for the upper 5% and upper 10% of the F_3 families selected for each character based on means of three replications.

Table 1. Character means for the P_1, P_2, F_1, BC_1, BC_2, and F_2 space-planted populations grown during the 1971-72 crop season, and for the solid-seeded F_3 families grown during the 1972-73 crop season.

Population	Grain Yield	Tiller Number	Seeds/ Spike	Kernel Weight
P_1 (Sturdy)	15.97	20.34	35.15	27.80
P_2 (Centurk)	17.95	23.26	41.18	25.35
F_1	20.35	20.81	42.45	29.23
BC_1	17.83	19.82	39.13	29.48
BC_2	18.60	21.98	42.02	26.70
F_2	18.31	21.66	40.82	26.77
F_3	116.71	68.65	31.45	27.40

Table 2. Character values for the upper 10% and lower 10% of the 158 F_2's represented by offspring in the F_3 generation based on selection for grain yield.

Observation	Grain Yield				Tiller Number				Seeds/Spike				Kernel Weight			
	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank
1	33.9	(1)	8.3	(158)	33.0	(1)	15.0	(145)	54.0	(5)	35.0	(125)	25.0	(104)	20.0	(155)
2	29.4	(2)	10.3	(156)	27.0	(21)	18.0	(119)	49.0	(15)	35.0	(125)	28.0	(54)	22.0	(145)
3	28.7	(3)	10.3	(156)	28.0	(9)	11.0	(158)	43.0	(55)	42.0	(65)	27.5	(58)	26.5	(73)
4	28.6	(4)	10.9	(155)	27.0	(21)	18.0	(119)	30.0	(93)	28.0	(158)	30.0	(24)	23.0	(131)
5	27.9	(5)	11.0	(154)	28.0	(9)	14.0	(152)	40.0	(82)	38.0	(107)	26.5	(73)	24.0	(117)
6	27.0	(6)	11.2	(153)	28.0	(9)	19.0	(99)	39.0	(93)	34.0	(135)	30.0	(24)	27.5	(58)
7	26.4	(7)	11.7	(152)	23.0	(56)	16.0	(136)	39.0	(93)	33.0	(143)	28.0	(54)	23.5	(122)
8	26.1	(8)	12.2	(151)	30.0	(5)	21.0	(78)	47.0	(27)	33.0	(143)	24.5	(110)	25.5	(96)
9	26.1	(8)	12.3	(150)	28.0	(9)	19.0	(99)	41.0	(72)	44.0	(42)	30.5	(19)	20.5	(154)
10	25.6	(10)	12.5	(148)	26.0	(30)	19.0	(99)	49.0	(15)	35.0	(125)	29.0	(44)	25.5	(96)
11	25.1	(11)	12.5	(148)	24.0	(47)	23.0	(56)	40.0	(82)	36.0	(122)	27.5	(58)	23.0	(131)
12	25.1	(11)	12.8	(146)	32.0	(2)	18.0	(119)	42.0	(65)	34.0	(135)	24.5	(110)	26.5	(73)
13	24.9	(13)	12.8	(146)	27.0	(21)	20.0	(90)	40.0	(82)	34.0	(135)	30.0	(24)	22.5	(138)
14	24.8	(14)	12.9	(145)	28.0	(9)	15.0	(145)	48.0	(22)	30.0	(155)	22.5	(138)	26.5	(73)
15	24.5	(15)	13.0	(143)	31.0	(4)	13.0	(155)	44.0	(42)	35.0	(125)	24.0	(117)	36.5	(1)
16	24.1	(16)	13.0	(143)	30.0	(5)	16.0	(136)	57.0	(1)	31.0	(152)	23.5	(122)	28.5	(50)
Mean	26.8		11.7		28.1		17.2		44.4		34.8		26.9		25.1	
Mean of the 158 F_2's	18.3				21.7				41.2				26.7			

Table 3. Character values for the upper 10% and lower 10% of the 158 F_2's represented by offspring in the F_3 generation based on selection for tiller number.

Observation	Tiller Number				Grain Yield				Seeds/Spike				Kernel Weight			
	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank
1	33.0	(1)	11.0	(158)	33.9	(1)	10.3	(156)	54.0	(5)	42.0	(65)	25.0	(104)	26.5	(73)
2	32.0	(2)	12.0	(157)	25.1	(11)	14.1	(131)	42.0	(65)	34.0	(135)	24.5	(110)	35.0	(2)
3	32.0	(2)	13.0	(155)	19.5	(57)	13.4	(140)	55.0	(4)	35.0	(125)	22.5	(138)	33.0	(4)
4	31.0	(4)	13.0	(155)	24.5	(15)	13.0	(143)	44.0	(42)	35.0	(125)	24.0	(117)	36.5	(1)
5	30.0	(5)	14.0	(152)	24.1	(16)	13.5	(138)	57.0	(1)	33.0	(143)	23.5	(122)	22.5	(138)
6	30.0	(5)	14.0	(152)	26.1	(8)	15.7	(113)	47.0	(27)	39.0	(93)	24.5	(110)	29.5	(31)
7	30.0	(5)	14.0	(152)	16.1	(104)	11.0	(154)	48.0	(22)	38.0	(107)	23.5	(122)	24.0	(117)
8	29.0	(8)	15.0	(145)	16.2	(100)	13.9	(135)	32.0	(149)	44.0	(42)	20.0	(155)	26.0	(82)
9	28.0	(9)	15.0	(145)	28.7	(3)	16.0	(107)	43.0	(55)	47.0	(27)	27.5	(58)	26.0	(82)
10	28.0	(9)	15.0	(145)	27.0	(6)	16.6	(96)	39.0	(93)	33.0	(143)	30.0	(24)	31.5	(15)
11	28.0	(9)	15.0	(145)	24.8	(14)	16.7	(94)	48.0	(22)	40.0	(82)	22.5	(138)	32.0	(9)
12	28.0	(9)	15.0	(145)	26.1	(8)	17.2	(90)	41.0	(72)	49.0	(15)	30.5	(19)	32.0	(9)
13	28.0	(9)	15.0	(145)	27.9	(5)	12.9	(145)	40.0	(82)	30.0	(155)	26.5	(73)	26.5	(73)
14	28.0	(9)	15.0	(145)	24.0	(18)	8.3	(158)	37.0	(112)	35.0	(125)	29.0	(44)	20.0	(155)
15	28.0	(9)	16.0	(136)	21.0	(37)	13.4	(139)	41.0	(72)	39.0	(93)	23.5	(122)	26.5	(73)
16	28.0	(9)	16.0	(136)	20.8	(40)	13.4	(139)	45.0	(37)	39.0	(93)	23.5	(122)	27.5	(58)
Mean	29.4		14.3		24.1		13.7		44.6		38.3		25.0		28.4	
Mean of the 158 F_2's	21.7				18.3				41.2				26.7			

Table 4. Character values for the upper 10% and lower 10% of the 158 F_2's represented by offspring in the F_3 generation based on selection for seeds/spike.

Observation	Seeds/Spike				Grain Yield				Tiller Number				Kernel Weight			
	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank
1	57.0	(1)	28.0	(158)	24.1	(16)	10.9	(155)	30.0	(5)	18.0	(119)	23.5	(122)	23.0	(131)
2	57.0	(1)	29.0	(157)	15.8	(111)	18.6	(72)	18.0	(119)	24.0	(47)	26.0	(82)	26.0	(82)
3	56.0	(3)	30.0	(155)	18.6	(72)	17.4	(88)	25.0	(36)	18.0	(119)	22.0	(145)	27.5	(58)
4	55.0	(4)	30.0	(155)	19.5	(57)	12.9	(145)	32.0	(2)	15.0	(145)	22.5	(138)	26.5	(73)
5	54.0	(5)	31.0	(152)	33.9	(1)	15.4	(118)	33.0	(1)	23.0	(56)	25.0	(104)	26.0	(82)
6	54.0	(5)	31.0	(152)	15.5	(116)	20.1	(45)	23.0	(56)	28.0	(9)	21.0	(153)	26.0	(82)
7	54.0	(5)	31.0	(152)	14.3	(129)	13.0	(143)	19.0	(99)	16.0	(136)	25.5	(96)	28.5	(50)
8	53.0	(8)	32.0	(149)	19.1	(62)	16.2	(100)	26.0	(30)	29.0	(8)	19.5	(158)	20.0	(155)
9	52.0	(9)	32.0	(149)	18.9	(67)	17.2	(90)	27.0	(21)	28.0	(9)	24.5	(110)	25.5	(96)
10	51.0	(10)	32.0	(149)	20.7	(42)	19.9	(50)	19.0	(99)	27.0	(21)	32.0	(9)	21.5	(151)
11	50.0	(11)	33.0	(143)	19.7	(55)	13.5	(138)	22.0	(69)	14.0	(152)	27.0	(66)	22.5	(138)
12	50.0	(11)	33.0	(143)	18.9	(67)	15.9	(109)	19.0	(99)	25.0	(36)	29.5	(31)	20.0	(155)
13	50.0	(11)	33.0	(143)	16.2	(100)	16.6	(96)	18.0	(119)	15.0	(145)	22.0	(145)	31.5	(15)
14	50.0	(11)	33.0	(143)	15.5	(116)	24.1	(16)	16.0	(136)	22.0	(69)	28.0	(54)	35.0	(2)
15	49.0	(15)	33.0	(143)	29.4	(2)	11.7	(152)	27.0	(21)	16.0	(136)	28.0	(54)	23.5	(122)
16	49.0	(15)	33.0	(143)	25.6	(10)	12.2	(151)	26.0	(30)	21.0	(78)	29.0	(44)	25.5	(96)
Mean	52.6		31.5		20.4		16.0		23.8		21.2		25.3		25.5	
Mean of the 158 F_2's	41.2				18.3				21.7				26.7			

Table 5. Character values for the upper 10% and lower 10% of the 158 F_2's represented by offspring in the F_3 generation based on selection for kernel weight.

Observation	Kernel Weight				Grain Yield				Tiller Number				Seeds/Spike			
	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank	Upper 10%	Rank	Lower 10%	Rank
1	36.5	(1)	19.5	(158)	13.0	(143)	19.1	(62)	13.0	(155)	26.0	(30)	35.0	(125)	53.0	(8)
2	35.0	(2)	20.0	(155)	24.1	(16)	15.9	(109)	22.0	(69)	25.0	(36)	33.0	(143)	33.0	(143)
3	35.0	(2)	20.0	(155)	14.1	(131)	16.2	(100)	12.0	(157)	29.0	(8)	34.0	(135)	32.0	(149)
4	33.0	(4)	20.0	(155)	21.1	(35)	8.3	(158)	18.0	(119)	15.0	(145)	46.0	(34)	35.0	(125)
5	33.0	(4)	20.5	(154)	15.3	(121)	12.3	(150)	16.0	(136)	19.0	(99)	37.0	(112)	44.0	(42)
6	33.0	(4)	21.0	(153)	13.4	(139)	15.5	(116)	13.0	(155)	23.0	(56)	35.0	(125)	54.0	(5)
7	32.5	(7)	21.5	(151)	23.8	(19)	19.9	(50)	25.0	(36)	26.0	(30)	42.0	(65)	39.0	(93)
8	32.5	(7)	21.5	(151)	22.2	(27)	19.9	(50)	25.0	(36)	27.0	(21)	35.0	(125)	32.0	(149)
9	32.0	(9)	22.0	(145)	20.7	(42)	16.2	(100)	19.0	(99)	18.0	(119)	51.0	(10)	50.0	(11)
10	32.0	(9)	22.0	(145)	19.5	(57)	18.5	(75)	18.0	(119)	24.0	(47)	38.0	(107)	39.0	(93)
11	32.0	(9)	22.0	(145)	19.4	(60)	18.6	(72)	19.0	(99)	25.0	(36)	44.0	(42)	56.0	(3)
12	32.0	(9)	22.0	(145)	17.2	(90)	19.0	(64)	15.0	(145)	27.0	(21)	49.0	(15)	44.0	(42)
13	32.0	(9)	22.0	(145)	16.7	(94)	19.1	(62)	15.0	(145)	26.0	(30)	40.0	(82)	47.0	(27)
14	32.0	(9)	22.0	(145)	16.1	(104)	10.3	(156)	16.0	(136)	18.0	(119)	37.0	(112)	35.0	(125)
15	31.5	(15)	22.5	(138)	21.5	(31)	13.5	(138)	20.0	(90)	14.0	(152)	43.0	(55)	33.0	(143)
16	31.5	(15)	22.5	(138)	16.6	(96)	14.0	(133)	15.0	(145)	21.0	(78)	33.0	(143)	45.0	(37)
Mean	32.8		21.3		18.4		16.0		17.6		22.7		39.5		41.9	
Mean of the 158 F_2's	26.7				18.3				21.7				41.2			

Table 6. Mean values of characters in the F_3 generation based on selection of the upper 10% and lower 10% for each character in the 158 F_2's represented in the F_3 generation.

Character Selected		Grain Yield	Tiller Number	Seeds/ Spike	Kernel Weight
Grain Yield	(a)	113.02	67.40	32.08	26.53
	(b)	112.13	65.75	29.96	28.88
Tiller Number		113.11	67.44	32.08	26.76
		115.84	65.10	31.25	28.02
Seeds/Spike		112.14	67.63	33.33	26.81
		117.13	65.50	31.83	27.66
Kernel Weight		121.39	66.81	30.93	28.95
		111.35	68.10	33.33	26.07
Mean of all F_3 families		116.71	68.65	31.45	27.40

(a) The upper value in each cell is the mean value of the character in the F_3 generation based on selection of the upper 10% of the F_2's.

(b) The lower value in each cell is the mean value of the character in the F_3 generation based on selection of the lower 10% of the F_2's.

Table 7. Character values for the upper 10% of the 158 F_3 families selected for grain yield based on means of three replications.

Observation	Grain Yield	Rank	Tiller Number	Rank	Seeds/Spike	Rank	Kernel Weight	Rank
1	152.82	(1)	68.33	(89)	31.43	(82)	28.07	(60)
2	146.70	(2)	82.67	(8)	34.67	(12)	28.01	(63)
3	143.45	(3)	66.33	(96)	31.50	(77)	32.10	(4)
4	143.37	(4)	56.00	(150)	34.43	(15)	28.18	(54)
5	141.63	(5)	78.67	(17)	29.77	(119)	28.95	(36)
6	140.93	(6)	54.67	(152)	32.30	(54)	28.59	(48)
7	140.23	(7)	82.67	(8)	27.97	(146)	30.60	(1)
8	140.10	(8)	78.33	(18)	26.20	(156)	32.25	(2)
9	139.92	(9)	90.33	(1)	28.97	(135)	26.19	(112)
10	138.35	(10)	72.00	(52)	32.93	(39)	25.35	(133)
11	137.47	(11)	77.33	(25)	31.37	(85)	24.86	(145)
12	135.95	(12)	71.33	(58)	32.50	(51)	29.57	(24)
13	135.57	(13)	79.00	(16)	30.07	(114)	26.31	(110)
14	135.40	(14)	70.67	(63)	34.20	(17)	27.47	(76)
15	134.72	(15)	64.00	(112)	31.00	(90)	28.11	(57)
16	134.35	(16)	63.00	(119)	29.77	(119)	29.20	(29)
Mean	140.06		72.21		31.19		28.36	
Mean of all F_3 families	116.71		68.65		31.45		27.40	

Table 8. Character values for the upper 10% of the 158 F_3 families selected for tiller number based on means of three replications.

Observation	Tiller Number	Rank	Grain Yield	Rank	Seeds/Spike	Rank	Kernel Weight	Rank
1	90.33	(1)	139.92	(9)	28.97	(135)	26.19	(112)
2	84.00	(2)	132.43	(20)	28.03	(145)	28.87	(39)
3	84.00	(2)	112.73	(97)	27.83	(148)	26.55	(102)
4	83.33	(4)	94.30	(150)	34.93	(9)	20.88	(158)
5	83.33	(4)	118.00	(77)	28.47	(142)	28.08	(59)
6	83.00	(6)	123.13	(52)	30.17	(110)	29.18	(30)
7	83.00	(6)	113.77	(94)	31.77	(71)	23.31	(156)
8	82.67	(8)	140.23	(7)	27.97	(146)	30.60	(10)
9	82.67	(8)	146.70	(2)	34.67	(12)	28.01	(63)
10	82.33	(10)	121.85	(58)	31.60	(72)	24.84	(146)
11	81.67	(11)	103.10	(134)	28.83	(140)	25.66	(126)
12	81.33	(12)	125.85	(40)	33.17	(35)	26.70	(94)
13	81.00	(13)	105.83	(123)	32.03	(62)	27.73	(72)
14	80.33	(14)	128.67	(29)	33.43	(32)	26.88	(89)
15	80.33	(14)	133.10	(18)	29.20	(131)	27.78	(70)
16	79.00	(16)	135.57	(13)	30.07	(114)	26.31	(110)
Mean	82.65		123.45		30.70		26.72	
Mean of all F_3 families	68.65		116.71		31.45		27.40	

Table 9. Character values for the upper 10% of the 158 F_3 families selected for seeds/spike based on means of three replications.

Observation	Seeds/Spike	Rank	Grain Yield	Rank	Tiller Number	Rank	Kernel Weight	Rank
1	40.00	(1)	101.58	(139)	60.67	(134)	25.64	(128)
2	38.93	(2)	107.37	(120)	62.33	(122)	25.78	(123)
3	38.67	(3)	121.12	(64)	74.00	(39)	26.15	(113)
4	36.90	(4)	120.13	(68)	78.33	(18)	24.76	(147)
5	36.90	(4)	110.80	(109)	65.00	(104)	22.86	(157)
6	36.23	(6)	124.73	(43)	72.00	(52)	23.91	(150)
7	35.87	(7)	126.43	(36)	69.67	(69)	26.31	(110)
8	35.77	(8)	99.72	(142)	69.67	(69)	23.33	(155)
9	34.93	(9)	94.30	(150)	83.33	(4)	20.88	(158)
10	34.77	(10)	116.98	(78)	61.33	(129)	26.82	(92)
11	34.77	(10)	104.97	(127)	76.00	(28)	23.82	(151)
12	34.67	(12)	146.70	(2)	82.67	(8)	28.01	(63)
13	34.60	(13)	94.50	(147)	58.33	(144)	24.57	(148)
14	34.47	(14)	111.77	(102)	78.00	(21)	26.43	(106)
15	34.43	(15)	143.37	(4)	56.00	(150)	28.18	(54)
16	34.23	(16)	123.13	(52)	61.00	(131)	29.64	(22)
Mean	36.01		115.48		69.27		25.44	
Mean of all F_3 families	31.45		116.71		68.65		27.40	

Table 10. Character values for the upper 10% of the 158 F_3 families selected for kernel weight based on means of three replications.

Observation	Kernel Weight	Rank	Grain Yield	Rank	Tiller Number	Rank	Seeds/Spike	Rank
1	32.64	(1)	115.87	(84)	59.33	(141)	28.17	(144)
2	32.25	(2)	140.10	(8)	78.33	(18)	26.20	(156)
3	32.12	(3)	92.00	(154)	57.33	(145)	25.93	(157)
4	32.10	(4)	143.45	(3)	66.33	(96)	31.50	(77)
5	31.50	(5)	116.48	(81)	70.67	(63)	28.93	(137)
6	31.26	(6)	104.13	(130)	68.33	(82)	30.30	(105)
7	31.03	(7)	132.77	(19)	75.00	(34)	27.17	(154)
8	30.70	(8)	93.07	(151)	52.00	(156)	31.57	(73)
9	30.65	(9)	94.37	(149)	51.33	(157)	30.57	(102)
10	30.60	(10)	140.23	(7)	82.67	(8)	27.97	(146)
11	30.35	(11)	108.23	(118)	60.00	(138)	31.50	(77)
12	30.28	(12)	101.60	(138)	68.00	(85)	29.50	(124)
13	30.28	(12)	94.67	(146)	68.67	(78)	24.23	(158)
14	30.25	(14)	127.03	(34)	74.67	(36)	29.87	(118)
15	30.24	(15)	100.13	(141)	66.67	(91)	30.10	(111)
16	30.18	(16)	122.58	(56)	62.33	(122)	28.40	(143)
Mean	31.03		114.17		66.35		28.87	
Mean of all F_3 families	27.40		116.71		68.65		31.45	

Table 11. Mean character values for the upper 5% and upper 10% of the F_3 families selected for each character based on means of three replications.

Character Selected		Grain Yield	Tiller Number	Seeds/ Spike	Kernel Weight
Grain Yield	(a)	143.65	70.96	31.03	29.59
	(b)	140.06	72.21	31.19	28.36
Tiller Number		121.81	84.21	29.77	26.71
		123.45	82.65	30.70	26.72
Seeds/Spike		113.99	68.96	37.41	24.84
		115.48	69.27	36.01	25.44
Kernel Weight		117.23	65.92	28.72	31.70
		114.17	66.35	28.87	31.03
Mean of all F_3 families		116.71	68.65	31.45	27.40

(a) The upper value in each cell is the mean value of the character based on selection of the upper 5%.

(b) The lower value in each cell is the mean value of the character based on selection of the upper 10%.

VITA

Raymond Joseph Sidwell

Candidate for the Degree of

Doctor of Philosophy

Thesis: HERITABILITY AND INTERRELATIONS OF YIELD AND YIELD-RELATED TRAITS IN A HARD RED WINTER WHEAT CROSS (*TRITICUM AESTIVUM* L.)

Major Field: Crop Science

Biographical:

Personal Data: Born in Enid, Oklahoma, June 5, 1947, the son of Jess and Marie Sidwell.

Education: Attended Pond Creek Elementary School and graduated from Pond Creek High School in Pond Creek, Oklahoma, in 1965. Attended Northwestern Oklahoma State University and graduated from Oklahoma State University, Stillwater, Oklahoma, with a Bachelor of Science degree in Agronomy in May, 1969; received the Master of Science degree in Agronomy from Oklahoma State University, in July, 1971; completed the requirements for the Doctor of Philosophy degree at Oklahoma State University, in May, 1975.

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