HERITABILITY AND INTERRELATIONS OF YIELD, YIELD-RELATED TRAITS, AND POST FLOWERING MORPHOLOGY IN THREE HARD RED WINTER WHEAT CROSSES

(*TRITICUM AESTIVUM* L.)

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May, 1981

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ACKNOWLEDGMENTS

The author wishes to express his sincere and deep appreciation to his major advisor, Dr. Lavoy I. Croy for his invaluable advice, guidance, counsel, and patience throughout the course of this study. Grateful acknowledgments are also extended to Dr. Ronald W. McNew for serving on the author's advisory committee and his invaluable help in the statistical analysis of the data and constructive suggestions in reviewing the manuscript.

The author wishes to express his deep appreciation to Dr. Edward L. Smith for serving on the advisory committee, supplying the basic genetic material for the present study and helpful suggestions in collecting the data and reviewing the manuscript. Thanks are extended also to Dr. Richard R. Frahm for serving on the advisory committee and invaluable suggestions in reviewing the manuscript.

The author wishes also to express his appreciation to the Agronomy Department of Oklahoma State University for providing the facilities which made this study possible, and to fellow graduate students of the crop physiology group for the help in planting and data collection.

Special thanks for the author's late father, Ali M. Alhagi, who passed away before this study was completed for his support and care while he was alive. To the author's wife, Samira; daughter, Wafaa; and sons, Mustafa and Nouraddin, sincere gratitude is expressed for their patience and encouragement they provided throughout my stay in the

United States.

Special thanks are also extended to Mrs. Susan Reinsch for the typing of this manuscript.

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CHAPTER I

INTRODUCTION

The complexity of grain yield in wheat results from the large number of genes involved in its control and also from the fact that it is one of the characters largely affected by environmental factors. In the past, conventional methods of yield improvement have usually resulted in yield increases by exploiting available genetic variability. But, due to the complexity of this trait and the effect of the environmental factors acting on it, maintaining consistently high yields is usually a difficult problem when selection was based on grain yield per se. It seems that the challenge of yield improvement could be met more effectively by manipulating other plant characters such as yield components and certain morphological structures of the wheat plant. The leaves, being major sites of photosynthetic activity, appear to have an obvious relation to the plant's yielding ability. Morphological traits such as the flag leaf, peduncle, and the spike stay photosynthetically active after spike emergence in wheat. From this it appears that manipulation of these plant structures, in conjunction with yield components, offer a good prospect for yield improvement in wheat. Also, if selection for the simultaneous improvement of these plant traits is to be effective in increasing total grain yield, then a knowledge of the heritability and the interrelationships of these traits is necessary. With this in mind, the present study was initiated to investigate the following:

1. The association and interrelationship between the photosynthetic structures above the flag leaf node to grain yield and yield components in three winter wheat crosses.

2. The broad-sense heritability estimates for the above mentioned characters.

Chapters II and III will be presented in a form acceptable to the Crop Science Society of America.[1] Additional data pertaining to the three wheat populations used in this study are presented in a tabular form in the Appendix.

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

CHAPTER II

Heritability and Character Association in Two Winter Wheat Crosses, I[1]

ABSTRACT

The interrelationships among five agronomic and nine morphologic plant traits were investigated in the F_2 and F_3 generations of two winter wheat (Triticum aestivum L.) crosses in order to study the possibility of combining desirable traits from the parents. Broad-sense heritabilities were also estimated for the traits. The plant material of the two-year study was space-planted during the 1977-78 and 1978-79 crop seasons in a randomized complete block design with four replications.

Results of the two populations indicated that the agronomic traits most associated with grain yield per plant were number of tillers per plant followed by kernel weight per spike, kernels per spike, and 1,000-kernel weight, in that order. Plant height produced low magnitude correlations with grain yield. The correlations among the yield-related traits ranged from low to moderately high indicating that simultaneous selection for some of these traits could present the breeder with some difficulties. Tiller morphology indicated that flag leaf blade area, stem area, and peduncle area were the characters most associated with

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[1]To be submitted for publication.

grain yield in that order. The majority of these morphologic traits appeared to contribute to grain yield through kernel weight per spike and, to a lesser extent, kernels per spike. No major negative correlations were obtained among the evaluated traits.

The magnitude of the variances and broad-sense heritability estimates of most of the evaluated traits were found to be affected by the prevailing environmental conditions from one season to the other. Heritability estimates for grain yield ranged from negative to intermediate in population 1. In population 2 the values for this trait ranged from intermediate to moderately high. The range of heritabilities for the other agronomic traits was from negative to positively high depending on the population, season, and the trait; but kernels per spike seemed more consistent than any other agronomic trait. Among the morphologic traits, spike measurements were the most consistent in both populations in having high heritability estimates with flag leaf measurements the most inconsistent in their heritabilities. Selection for larger spike size could be successful under the conditions of this study, but this trait might not lead to improved grain yields. The heritability estimates for the rest of the morphologic traits ranged from negative to high values. Inheritance of plant height was intermediate in both populations.

Additional index words: Triticum aestivum L., Phenotypic correlation, Yield components, Morphologic traits, Plant height.

The emphasis, in recent years, on yield component selection in wheat and other cereal crops was justified due to the fact that grain yield is a multigenic trait and more subject to environmental changes than its components. The importance of such traits as number of plants per unit area, number of spikes per plant, number of kernels per spike, and kernel weight were considered important units of grain yield in cereals (9). When number of plants per unit area was optimum, selection for one or more of the yield components was suggested as a means of yield improvement. However, selection for these traits did not always lead to yield improvements because of interdependence among plant traits and the biological limitation or compensation operating among them (11, 15). In fact negative associations between yield components in wheat are familiar in the literature (17, 25). Watson (36) emphasized that this approach to selection did not provide sound selection criterion, and growth analysis should be used.

Understanding the importance of yield components along with the morphologic traits to grain yield can place in the hands of wheat breeders an additional criterion or means for selecting for high yield. Watson (36) indicated that studies concentrating only on yield components for yield improvement did not include other traits of importance to the breeder. He emphasized the importance of the leaves as yield determinants.

The dependence of grain yield in wheat and other cereals on the photosynthetic parts of the plant was reviewed by Thorne (33). Thorne concluded that grain yield of cereals was most related to photosynthetic structures above the flag leaf node. The importance of the morphologic structures to grain yield was further studied by using radioactive

CO_2. Quinlan and Sagar (23) and Stoy (30) indicated that $^{14}CO_2$ assimilated by the flag leaf of wheat was translocated to the kernels more than any other part of the plant. Thorne (31, 32) reported that CO_2 absorbed after spike emergence by the part of the shoot above the flag leaf node, spike included, accounted for most of the dry weight of grain for wheat and barley. This view was supported also by Austin et al. (5), Rawson and Hofstra (24), and Volding and Simpson (34). Further evidence was also obtained by removing different leaves or shading the stem or ear of wheat (8, 26). The range of contribution of flag leaves and stems of wheat to grain yield was found to be from 20 to 40%, and that of the spike was from 14% (31) to 26% (10).

The importance of the morphologic structures above the flag leaf node arises from the fact that these are the only plant parts to remain photosynthetically active after spike emergence. The contribution of these plant parts to grain yield in wheat could be through one or more of the yield components. Ledent (18) and Ledent and Moss (19) investigated the closeness of association between these morphologic traits and grain yield and its components in winter and spring wheat cultivars. Their findings indicated that flag leaf measurements, peduncle length, spike length, and culm height were most correlated with kernel weight per spike. Other studies indicated that flag leaf area, peduncle area, and spike measurements were significantly associated with tiller number, kernel weight, and grain yield (4, 10, 22, 33).

Although numerous studies reported in the literature were designed to investigate the association of certain morphologic structures with grain yield and its components in wheat, the majority of these studies suffered from one limitation or another. These limitations included the use of the main tiller to represent the plant, the use of a small number of plants to estimate population parameters, some of the studies were greenhouse experiments where the conditions differ from those in the field, and the shortage of more than one year data.

In the present study we sought to investigate the degree of association of above flag leaf node morphology with grain yield and its components in two winter wheat (Triticum aestivum L.) crosses. Broad-sense heritability estimates were also determined for the above mentioned traits. The information gained from this two-year study may give wheat breeders some help in trait selection for improved yields in this worldwide important crop.

MATERIALS AND METHODS

The present study was conducted during the 1977-1978 and 1978-1979 crop seasons at the Agronomy Research Station at Stillwater, Oklahoma. Two populations comprised the plant materials for the study. Each population consisted of two parents, their F_2 and F_3 generations for both crop seasons. The two populations were derived from two crosses each involving two wheat cultivars, one adapted and the other unadapted to the Southern Great Plains Region of the United States. The unadapted cultivars were 'Aurora' and 'Jubilaynia'. In contrast with most hard red winter wheats, these two cultivars were of Eastern European origin and characterized by large spikes, large-size kernels, somewhat low tillering potential, midtall with strong stems, somewhat large leaves, and awnless spikes. The adapted cultivar, which was involved in both populations, was 'Rall'. It is a Scout type wheat developed by the Oklahoma Agricultural Experiment Station and characterized by small-size kernels, medium tall, awned spikes, tolerance to Wheat Streak Mosaic Virus, and narrow leaves.

Initial crosses were made in growth chambers in 1975. The crosses made were 'Aurora' X 'Rall' (designated as population 1) and 'Rall' X 'Jubilaynia' (designated as population 2). The F_1 plants were grown from the cross seed to produce F_2 seed, part of which was planted during the 1976 season to produce the F_3 seed.

The experimental design was a randomized complete block with four replications for both seasons of study. Each of the two populations comprised a separate group within each replication. Randomization for each replication was within a group with the exception of P_2 (Rall), which was always located between the two populations. Each replication consisted of one six-row plot of each of the parents and two six-row plots of the F_2 and F_3 generations for both seasons. The F_2 was a random sample of the F_1 generation and F_3 was also a random sample of F_2 generation. Each row consisted of 34 plants with 15 cm between plants and 30 cm between adjacent rows. Ammonium phosphate in the rate of 250 kg/ha was applied before planting. For the first crop season the seeds were planted in flats in the greenhouse on November 5, 1977, and transplanted by hand to the field on November 22, 1977. Harvesting was completed on June 15, 1978. For the second season, planting was done directly in the field on October 15, 1978, and selected plants were harvested on June 25, 1979. Generally, both growth seasons were favorable for wheat with mild drought periods, supplemented with irrigation during January, February, and March of 1978 combined with heavy weed infestation. The soil type was Kirkland silt loam.

With the exclusion of one border row from each side of each plot and two plants from each end of the row, 45 plants were randomly selected for character evaluation from each of the parental, F_2 and F_3 plots of each replication. This amounted to 180 plants for each of the parents and 360 plants for each of the F_2 and F_3 generations per crop season. Measurements were recorded on the following plant traits:

Grain yield. The yield of hand-threshed and clean grain of each harvested plant.

Tiller number. The number of tillers was determined by counting the spike-bearing tillers of each single plant and recorded as number of tillers per plant.

Number of kernels per spike. After taking other measurements on the three tallest tillers of the plant, three spikes were separately threshed and the number of kernels was determined and reported as number of kernels per spike.

Kernel weight per spike. This variable was determined by weighing the kernels of each of the three spikes used for determining number of kernels per spike after separating the chaff. The average of the three spikes was recorded as kernel weight per spike.

1,000-Kernel weight. This variable was determined as the result of: 1,000-Kernel weight = 1,000 (kernel weight per spike/number of kernels per spike) and was expressed as grams per 1,000-kernels for each sampled plant.

Plant height. The distance in centimeters from the ground surface to the tip of the terminal spike, excluding the awns.

Flag leaf blade area. Flag leaves of the three tallest tillers of the plant were selected for measurement. The length was determined from the base to the tip of the blade. The width of the blade was taken at the widest point perpendicular to the midrib of the leaf. In order to determine actual flag leaf blade area, a factor was calculated using 400 flag leaves selected at random from the field. The areas of these leaves were determined by using a Portable Area Meter (Model LI-3000, Lambda Instruments Corporation) and their length and width were measured as described above. The length X width of the individual leaf was taken as an independent variable and the actual area of the same leaf was considered as the dependent variable. A regression analysis was performed for the first degree fit and after testing for zero intercept, the value of slope, 0.7533, was taken as the factor for determining leaf area using the following equation:

$$FLBA = 0.7533(LW) \quad \text{where,}$$

FLBA = flag leaf blade area in cm^{-2} and

LW = product of length and width of leaf.

Flag leaf blade area for three leaves was calculated and the average was recorded as flag leaf blade area per tiller. Length and width of flag leaves were measured in the field five days after anthesis.

Peduncle area. The length and diameter of the uppermost internode of each of the three tillers mentioned above were measured. The length was determined from the base of the internode to the base of the spike and the diameter was determined from measuring the diameter at the base of the internode. The actual area of the peduncle was calculated using the formula:

$$PA = \pi(LD) \quad \text{where,}$$

PA = peduncle area in cm^{-2} and

LD = product of length and diameter.

The average of the three peduncle areas was taken as peduncle area per tiller.

Stem area. The area in square centimeters of the stem from the surface of the ground to the base of the spike. This variable was determined by measuring the length of the stem from the ground surface to the base of the spike and the diameter of the peduncle as follows:

$$SA = \pi(LD) \quad \text{where,}$$

SA = stem area in cm^{-2} and

LD = product of length and diameter.

Spike area. The length of each of three spikes per plant was measured in centimeters from the base to the tip of the spike. The diameter of each of the three spikes was taken from the average width of the two sides of the spike at the widest point. Spike area was then calculated by the use of the following formula:

$$SPA = \pi(LD) \quad \text{where,}$$

SPA is spike area in cm^{-2} and

LD is the product of the length and diameter of the spike.

The average of the three spike areas was taken as spike area.

Photosynthetic area per tiller. The sum of flag leaf blade area, stem area, and spike area for each tiller in cm^{-2}.

Analysis Procedures

The separate statistical analysis was conducted for each of the two populations and for each crop season. A general analysis of variance was conducted among entries for each of the fourteen plant traits to detect any differences between the entries of each population. When the F-test indicated significant differences the means where compared using the Least Significant Difference (LSD) method (29). Phenotypic coefficients of linear correlation among the variables were determined from the error term of a cross products analysis of variance of the F_2 and F_3 generations.

Heritability in the broad sense was estimated for each trait. The estimates were based on the assumptions: a) total phenotypic variance in the F_2 can be separated into a genetic component (σ_g^2) and a nongenetic component (σ_e^2), and b) the nongenetic component can be estimated by the variances of genotypically uniform parents (35). Heritability in the broad sense was estimated by a formula reported by Allard (2):

$$h^2_{bs} = \sigma_g^2/(\sigma_g^2 + \sigma_e^2) \quad \text{where}$$

σ_g^2 is the genotypic variance and

σ_e^2 is the nongenotypic (environmental) variance for a given trait.

The quantity ($\sigma_g^2 + \sigma_e^2$) was estimated in the present study by the phenotypic variance of the F_2 plants ($\hat{\sigma}_{F_2}$). The nonheritable variance, σ^2_e , was estimated by the average of the two parental variances $\frac{1}{2}(\hat{\sigma}^2_{P_i} + \hat{\sigma}^2_{P_j})$. The estimate of σ^2_g was then obtained by subtraction as follows:

$$\hat{\sigma}^2_g = \hat{\sigma}^2_{F_2} - \tfrac{1}{2}(\hat{\sigma}^2_{P_i} + \hat{\sigma}^2_{P_j}).$$

The standard errors of broad-sense heritability estimates for the variables were calculated by the square root of the following (21):

$$\text{s.e. } h^2_{bs} = \frac{1}{2(\hat{\sigma}_{F_2})^2}\left[(\hat{\sigma}^2_{P_i}/df_{P_i}) + (\hat{\sigma}^2_{P_j}/df_{P_j}) + (\hat{\sigma}^2_{F_2}/df_{F_2})\right]$$

In this formula df_{P_i}, df_{P_j}, and df_{F_2} refer to the degrees of freedom associated with P_i, P_j, and F_2 variances, respectively.

RESULTS AND DISCUSSION

Generation Means

The lack of significant differences among generation means in the 1977-78 crop season for five agronomic and four morphologic traits in population 1 (Tables 1, 2) and three agronomic traits, plant height, and four morphologic traits in population 2 could be attributed to large sampling errors due to the drought period in that season. Also, this could be the result of the nearly equal parental means for some of these traits. This last possibility was supported by the results of the 1978-79 crop season where no significant differences were detected even though the study was conducted under better environmental conditions. For those traits that behaved differently in the 1978-79 season, the dry conditions in the middle of the 1977-78 crop were responsible for the parents not expressing differences.

In general, the means of some of the evaluated traits improved slightly in the 1978-79 season when compared to the 1977-78 season. This could be the result of the more favorable growth conditions for wheat in the second season.

In both seasons Aurora and Jubilaynia seemed to depend on kernels per spike and kernel weight per spike more than tillers per plant for grain yield production. On the other hand, Rall seemed to rely more on tillers per plant for its grain yield. Plant height was consistent in population 1 between the two seasons for the two parents and the F_3, but the F_2 mean increased noticeably in the 1978-79 season in comparison to the 1977-78 season. While flag leaf area means were higher for Aurora compared to Rall, it seems that the later parent compensated for that by having larger peduncle area, and also the fact that Rall was awned could have an important role for grain yield.

The response of spike measurements in population 2 (Table 2) were inconsistent from one crop season to the other which could indicate that spike length and area were subject more to the environmental changes than other factors. Johnson et al. (14) suggested that spike length is either controlled by a large number of genes or a pronounced environmental influence is involved in its genetic expression.

Correlations

The correlation coefficients among five agronomic traits and plant height are presented in Tables 3 (population 1) and 4 (population 2). The results of both populations were consistent with regard to the high association between grain yield and tillers per plant. To justify this result, Adams (1) suggested that reduced competition intensity between neighboring plants allows them full expression of their tillering potential. The results reported herein were similar to other literature reports (7, 12, 13, 15). Grain yield was found to have intermediate to low correlations with the rest of its components with the exception of kernel weight per spike. This last agronomic trait was found to have moderately high correlations with grain yield in both data sets. The absence of significantly negative correlations among four of the agronomic traits of this study was in agreement with Adams' (1) suggestion that such traits would not be expected to show negative associations under space planting conditions. The results of this study, while in agreement with Adams' theory, indicated that 1,000-kernel weight deviated from that by having a negative relationship with kernels per spike. This negative association was expected in this study due to the fact that kernels per spike was the divisor for determining 1,000-kernel weight. The correlations among the yield-related traits differed from comparison to the other, and the magnitude of these correlations also changed from one season to the other, indicating a pronounced environmental effect on these correlations. But there was no indication that these traits were competing for the photosynthate produced by the green parts of the plant under space-planting conditions as it was clear from the absence of large negative correlations between them. It appears from the results of this study that selection for high tiller number, spike weight, and taller plants could result in higher grain yields, but it should be noted that this study was space-planted and the results may not hold true under standard planting conditions. Plant height was found to have intermediate to low correlations with grain yield per plant. This was in agreement with the results obtained by Drake (7) and Ketata et al. (16). Significant intermediate associations between plant height and each of kernels per spike and weight per spike. This could be an indication that taller plants possessed larger photosynthetic area (6).

When the correlations of grain yield and its related traits with the morphologic characters are considered (Tables 5 and 6), the results of the two seasons deviated slightly from each other. Also, the relative importance of the morphologic traits evaluated to one or more of the agronomic traits changed from one generation to the other. Even though the majority of the correlations between grain yield and the evaluated morphologic traits were significant, they were mostly of the intermediate magnitude with the exception of flag leaf blade measurements in population 1 which were slightly higher in their association with grain yield. The results of this study with respect to the importance of the above flag leaf node morphology to grain yield were corroborated by past reports on the subject (12, 24, 28, 33, 34).

Due to the intermediate to low correlations between grain yield and the morphologic traits, the possibility that these traits affect grain yield indirectly does exist, in fact, can be interpreted from the correlations of the morphologic traits with the yield-related traits. The intermediate to high correlations between flag leaf measurements with both kernel number and kernel weight per spike indicates that flag leaf area affect yield through these two agronomic traits. This interpretation was also suggested by other workers on the subject (18, 19, 24, 30). If a cause and effect is assumed in this case, it seems that larger flag leaf blade area would result in heavier and more kernels per spike through its large supply of photosynthate to these agronomic traits (5). This can be true especially when it is coupled with a large size spike and a large capacity of storage by the developing kernel. Two important points need to be considered here. One of these is the size of the spike and its relation to the agronomic traits. From the correlations of spike area with kernels per spike and kernel weight per spike it is clear that the larger the spike the greater the number of kernels per spike and the higher the weight per spike. This could be due to the increased number of fertile florets in the spikelets which was in fact observed in the present study; and also the larger photosynthetic area close to the developing grain in the form of larger size spikes. The other point to be considered is the sink size of the grain. This factor is important in the source-sink relationship (17) because even if the plant possessed large photosynthetic area without having a large sink in the kernel, the photosynthate produced will be converted to more vegetative growth (23) or lost through the other physiologic processes of the plant (10, 33). Therefore, the requirement for a large sink size is a major factor in deciding the utilization of available photosynthate from the leaves and spike of the wheat plant. Hsu and Walton (12) found that spike length was more associated with yield per plant and kernel number than with kernel weight. Reddi et al. (25) found that spike length was negatively correlated with kernel weight in one cross of their study.

The importance of peduncle measurements to grain yield and its related traits was not clear from the results of this study. Even though the correlations of this plant trait was positively significant with all agronomic traits, these correlations were generally low to intermediate in magnitude and, in general, do not differ greatly from one agronomic trait to another. The results obtained by Hsu and Walton (11, 12), also, did not give a clear role of this morphologic trait.

Stem area was found to be closely associated with kernel weight per spike more than any other agronomic trait. The same results were found by Reddi et al. (25) for stem length. This might explain the role of the peduncle. Being a part of the stem, peduncle photosynthate is just a part of the total stem photosynthate which, in the context of this study, goes mainly to the kernel.

The correlation coefficients of the morphologic traits with the agronomic traits of this study suggest that a plant with intermediate to large flag leaf, tall and large diameter stems, and large size spikes will result in higher grain yields. The effect of these morphologic traits appears to be through increased kernel numbers per spike and, to a greater extent, higher kernel weights per spike. But again, it should be cautioned that these conclusions might not apply under more dense stands and at the same time these conclusions are drawn on the assumption that a cause and effect process is involved.

Heritability Estimates

In order for a selection program to be successful, it is important that the trait to be selected for to be heritable. This will reduce the time and effort that the breeder needs to select for that trait. Another factor to be considered, also in this context, is the magnitude of the environmental effect on that trait. Johnson and Frey, reported by Reddi et al. (25), studied the heritabilities of some quantitative traits in oats at varying levels of environmental stress. They found that several attributes, including kernel weight, increased as stress decreased and also under stress conditions the phenotypic variance generally increased more rapidly than the genotypic variance, and heritability was reduced. Under nonstress conditions, genotypic variance increased; thus heritability increased. These conditions may have held true in the present study, especially in population 1, from one crop season to the other in the cases of grain yield, tiller number, stem area, flag leaf blade length and area, and peduncle measurements (Table 7). The same was also true in some cases in population 2; even though to a lesser extent. The above mentioned traits were affected to a large extent by the change in environmental conditions from one season to the other and their heritability estimates were clearly lower in the 1977-78 than in the 1978-79 crop season.

While no negative broad-sense heritability estimates were observed in the evaluated traits of population 2, negative estimates were obtained in population 1 for grain yield, tiller number, stem area, flag leaf length and area, peduncle area, and photosynthetic area per tiller in 1977-78. In 1978-79 the broad-sense heritability estimates were negative for 1,000-kernel weight and flag leaf blade area in the same population. This might be due largely to the effect of the environment on Aurora as indicated by its lower variances in the second crop season (Tables 1, 2). A possible explanation for this is that these traits are influenced by the environmental changes from one season to the other (14, 20).

In population 2 the results indicated that the broad-sense heritability estimates for grain yield ranged from an intermediate value in the first season to a high estimate in the second. Reports of heritability estimates in the literature varied from negative (14), intermediate (27) to high (3, 33). For tiller number, the heritability estimates varied from low in the first season to a medium value in the second. This range of results was also reported in other instances (3, 14). Kernels per spike produced consistently high heritability values in both seasons. This could be due to real differences between the two parents of population 2. Kernel weight per spike seemed to produce higher heritability estimates under stress conditions in the first season compared to the values obtained in the second crop season. The thousand-kernel weight produced intermediate heritability estimates in both seasons in population 2. Intermediate heritability values were also obtained for plant height, stem area, flag leaf length, and peduncle length and area in the first season. Flag leaf blade area produced a low heritability value in the first season and an intermediate value in the second. High heritability values were obtained for stem area (second season), spike length and area, and photosynthetic area per tiller (both seasons). Flag leaf blade measurements were not consistent in their heritability estimates from one season to the other in both populations. In both cases it was clear that the unadapted parent produced an unusually high plant to plant variance (Tables 1, 2). These flag leaf blade characters seem unreliable for selection especially in population 1 of this study. This suggestion agrees with the differences found by Hsu and Walton (12) between greenhouse and field results of flag leaf length and width.

Owing to the large amount of variability in the F_2 generation of both populations with respect to spike length and area, high heritability estimates for these spike traits were obtained. Spike length and area, therefore, seem to be heritable characters affected more by genetic than environmental factors. The results of this study were in contrast to those obtained by Reddi et al. (25) who found low heritability estimates for spike length in two wheat crosses, but in good agreement with those reported by Johnson et al. (14).

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Table 1. Estimates of generation means and among plant variances for five agronomic traits and plant height from population 1 (Aurora X Rall) and population 2 (Rall X Jubilaynia) in 1977-78 (X_1) and 1978-79 (X_2).

Generation	Season	Agronomic Plant Trait					
		Grain Yield (g/plant)	Tillers/ Plant	Kernels/ Spike	Kernel Weight (g/spike)	1,000-Kernel Weight (g)	Plant Height (cm)
				Population 1			
P_1 (Aurora)	X_1†	17.22a*	9.98a	51.83a	2.12 a	41.16a	79.10a
		70.96	21.60	46.49	0.1371	43.78	36.92
	X_2	16.10a	9.12a	53.19b	2.25 c	43.04d	75.81a
		45.88	13.66	55.52	0.1167	46.17	28.05
P_2 (Rall)	X_1	13.92a	12.45a	42.23a	1.53 a	36.33a	87.50ab
		34.47	25.19	17.99	0.0395	28.58	70.22
	X_2	15.24a	13.92b	44.77a	1.60 a	35.75a	87.97b
		31.11	19.02	24.45	0.0638	13.02	56.25
$F_2(P_1$ X $P_2)$	X_1	15.90a	11.18a	44.96a	1.82 a	40.15a	85.75a
		43.06	20.84	66.45	0.1694	37.34	95.60
	X_2	17.37a	12.84b	46.85a	1.81 b	38.98bc	92.54bc
		54.36	33.77	49.72	0.0952	24.88	79.24
$F_3(P_1$ X $P_2)$	X_1	16.39a	12.31a	45.54a	1.67 a	36.73a	95.20b
		70.18	32.09	71.79	0.1568	29.18	144.43
	X_2	16.63a	12.09b	46.09a	1.71 ab	37.12ab	94.87c
		67.29	77.52	82.48	0.1667	21.82	113.48

Table 1. "Continued."

Generation	Season	Grain Yield (g/plant)	Tillers/ Plant	Kernels/ Spike	Kernel Weight (g/spike)	1,000-Kernel Weight (g)	Plant Height (cm)
					Population 2		
P_2 (Rall)	X_1 †	13.92a*	12.45a	42.23a	1.53 a	36.33a	87.50a
		34.47	25.19	17.99	0.0395	29.58	70.22
	X_2	15.24a	13.92b	44.77a	1.60 a	35.75a	87.97ab
		31.11	19.02	24.45	0.0638	13.02	56.25
P_3 (Jubilaynia)	X_1	14.57a	8.58a	53.98c	2.09 c	38.40a	83.57a
		34.15	13.75	35.27	0.1179	11.68	31.85
	X_2	14.26a	8.60a	54.33b	2.06 c	36.63a	80.83a
		42.09	14.29	40.14	0.1208	14.78	44.73
$F_2(P_2 \times P_3)$	X_1	15.93a	11.10a	47.63b	1.81 b	37.94a	92.30a
		51.57	21.46	56.68	0.1326	28.55	92.33
	X_2	19.07a	12.50b	48.29a	1.89 bc	39.28a	94.44b
		79.50	27.60	64.39	0.1151	20.81	87.19
F_3 $(P_2 \times P_3)$	X_1	16.01a	11.15a	47.00b	1.80 b	38.47a	92.96a
		69.65	27.36	55.86	0.1166	23.11	150.07
	X_2	17.32a	11.81b	48.23a	1.86 b	38.95a	93.15b
		83.34	33.76	68.05	0.1241	25.29	121.09

† For each X, the values in the upper and lower lines refer to means and among plant variances, respectively.

* Means from the same crop season followed by different letters are significantly different according to L.S.D. at 0.05 level of probability.

Table 2. Estimates of generation means and among plant variances for eight morphologic plant traits from population 1 (Aurora X Rall) and population 2 (Rall X Jubilaynia) in 1977-78 (X_1) and 1978-79 (X_2).

Generation	Season	Morphologic Plant Trait							
		Stem Area (cm^{-2})	Flag Leaf Blade Length (cm)	Flag Leaf Blade Area (cm^{-2})	Peduncle Length (cm)	Peduncle Area (cm^{-2})	Spike Length (cm)	Spike Area (cm^{-2})	Photosynthetic Area/Tiller (cm^{-2})
					Population 1				
P_1 (Aurora)	X_1†	87.11a*	20.24a	25.96b	30.65a	38.30a	9.20 a	32.46a	145.53a
		287.04	10.76	23.94	11.17	65.63	0.2545	14.29	410.92
	X_2	83.53a	19.67a	25.24b	28.95a	36.58a	9.32 a	34.94a	143.72a
		133.56	6.06	27.75	8.29	34.65	0.2519	31.29	205.71
P_2 (Rall)	X_1	85.34a	18.47a	17.68a	37.99b	41.82a	9.88 b	32.12a	135.14a
		362.93	6.65	15.29	16.30	91.44	0.4320	16.43	481.72
	X_2	86.76a	17.72a	16.65a	38.22b	42.82b	10.08 ab	33.63a	137.04a
		182.47	6.43	14.40	9.99	47.52	0.3644	14.38	266.39
$F_2(P_1 \times P_2)$	X_1	90.41a	18.47a	19.38a	34.93ab	41.92a	10.16 c	35.87b	145.66a
		274.28	6.12	14.64	20.39	62.83	1.7101	45.04	400.41
	X_2	99.91b	18.72a	20.23a	38.67b	47.13b	10.26 b	35.61a	155.75a
		229.71	7.80	18.73	18.44	62.69	1.3339	33.86	388.16
$F_3(P_1 \times P_2)$	X_1	104.76a	18.66a	19.10a	37.41b	46.63a	10.66 c	36.86b	160.73a
		348.01	10.76	29.15	22.51	80.90	2.8263	61.78	598.52
	X_2	103.83b	19.12a	19.78a	37.92b	46.76b	10.39 b	36.13a	159.74a
		347.44	9.75	21.35	17.45	70.88	2.6398	69.58	683.67

Table 2. "Continued."

Generation	Season	Morphologic Plant Trait							
		Stem Area (cm^{-2})	Flag Leaf Blade Length (cm)	Flag Leaf Blade Area (cm^{-2})	Peduncle Length (cm)	Peduncle Area (cm^{-2})	Spike Length (cm)	Spike Area (cm^{-2})	Photosynthetic Area/Tiller (cm^{-2})
					Population 2				
P_2 (Rall)	X_1 †	85.34a*	18.47a	17.68a	37.99a	41.82a	9.88 a	32.12a	135.14a
		362.93	6.65	15.29	16.30	91.44	0.4302	16.43	481.72
	X_2	86.76a	17.72a	16.65a	38.22b	42.82a	10.08 ab	33.63a	137.03a
		182.47	6.43	14.40	9.99	47.52	0.3644	14.38	266.39
P_3 (Jubilaynia)	X_1	101.36b	19.16a	22.94a	35.81a	49.37a	9.90 ab	35.19a	159.49b
		232.76	9.02	27.89	5.55	53.23	0.4137	15.69	291.66
	X_2	98.73a	18.94a	22.44a	34.82a	48.60a	9.76 a	34.04a	155.22a
		220.03	7.56	20.95	8.22	59.65	0.5019	17.45	336.45
$F_2(P_2 \times P_3)$	X_1	95.30ab	18.27a	19.72a	38.54a	45.18a	10.55 bc	37.61c	152.63b
		546.02	11.01	25.47	16.21	120.65	2.4081	77.00	802.09
	X_2	104.02a	16.64a	19.99a	39.46b	49.03a	10.49 b	37.26b	161.28a
		442.14	8.12	23.03	13.70	92.55	2.0058	61.59	693.08
$F_3(P_2 \times P_3)$	X_1	101.23b	19.38a	20.43a	37.77a	46.74a	10.89 c	38.04c	159.71b
		454.21	6.83	21.01	23.86	98.78	2.9138	51.36	718.83
	X_2	102.28a	18.37a	18.94a	38.56b	48.16a	11.04 c	38.99b	160.20a
		444.44	8.43	24.03	17.65	97.82	3.1158	60.40	717.96

† For each X, the values in the upper and lower lines refer to means and among plant variances, respectively.

* Means from the same crop season followed by different letters are significantly different according to L.S.D. at 0.05 level of probability.

Table 3. Phenotypic correlation coefficients among five agronomic traits and plant height from F_2 (upper right portion) and F_3 (lower left portion) of population 1 (Aurora X Rall) in 1977-78 (X_1) and 1978-79 (X_2).

Plant Trait	Season	Plant Trait 1	2	3	4	5	6
1. Grain Yield	X_1	1*	0.869	0.447	0.457	0.151	0.398
	X_2		0.922	0.282	0.490	0.304	0.379
2. Tillers/Plant	X_1	0.930	1	0.148	0.096	-0.055	0.204
	X_2	0.622		0.081	0.248	0.223	0.310
3. Kernels/Spike	X_1	0.393	0.243	1	0.767	-0.015	0.491
	X_2	0.463	0.003		0.748	-0.271	0.336
4. Kernel Weight/Spike	X_1	0.605	0.359	0.788	1	0.612	0.377
	X_2	0.582	0.067	0.875		0.415	0.323
5. 1,000-Kernel Weight	X_1	0.492	0.309	-0.003	0.598	1	0.009
	X_2	0.445	0.159	0.108	0.562		-0.022
6. Plant Height	X_1	0.490	0.383	0.320	0.518	0.467	1
	X_2	0.442	0.055	0.494	0.601	0.368	

* Each r value is based on 355 degrees of freedom. Significant r values are 0.106 and 0.139 at the 0.05 and 0.01 levels of probability, respectively.

Table 4. Phenotypic correlation coefficients among five agronomic traits and plant height from F_2 (upper right portion) and F_3 (lower left portion) of population 2 (Rall X Jubilaynia) in 1977-78 (X_1) and 1978-79 (X_2).

Plant Trait	Season	Plant Trait 1	2	3	4	5	6
1. Grain Yield	X_1	1*	0.910	0.327	0.618	0.570	0.449
	X_2		0.873	0.315	0.577	0.463	0.448
2. Tillers/Plant	X_1	0.944	1	0.221	0.405	0.391	0.359
	X_2	0.915		0.169	0.315	0.282	0.353
3. Kernels/Spike	X_1	0.419	0.304	1	0.740	-0.025	0.352
	X_2	0.425	0.348		0.782	-0.183	0.284
4. Kernel Weight/Spike	X_1	0.645	0.497	0.780	1	0.644	0.520
	X_2	0.661	0.481	0.727		0.454	0.471
5. 1,000-Kernel Weight	X_1	0.468	0.400	-0.063	0.564	1	0.380
	X_2	0.415	0.276	-0.202	0.510		0.363
6. Plant Height	X_1	0.522	0.439	0.455	0.589	0.344	1
	X_2	0.478	0.371	0.486	0.577	0.216	

* Each r value is based on 355 degrees of freedom. Significant r values are 0.106 and 0.139 at the 0.05 and 0.01 levels of probability, respectively.

Table 5. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from F_2 and F_3 of population 1 (Aurora X Rall) in 1977-78 (X_1) and 1978-79 (X_2).

Morphologic Plant Trait		Agronomic Plant Trait									
		Grain Yield		Tillers/ Plant		Kernels/ Spike		Kernel Weight/ Spike		1,000-Kernel Weight	
		X_1	X_2	X_1	X_2	X_1	X_2	X_1	X_2	X_1	X_2
Stem Area	F_2	0.408*	0.512	0.204	0.375	0.448	0.387	0.487	0.487	0.239	0.114
	F_3	0.643	0.565	0.521	0.143	0.455	0.643	0.643	0.796	0.523	0.541
Flag Leaf Blade Length	F_2	0.516	0.629	0.319	0.420	0.785	0.790	0.530	0.724	0.582	0.201
	F_3	0.689	0.624	0.380	0.201	0.572	0.700	0.721	0.624	0.490	0.591
Flag Leaf Blade Area	F_2	0.618	0.531	0.311	0.383	0.694	0.699	0.543	0.619	0.520	0.165
	F_3	0.590	0.731	0.321	0.311	0.583	0.786	0.794	0.730	0.536	0.603
Peduncle Length	F_2	0.348	0.439	0.231	0.390	0.281	0.254	0.242	0.320	0.070	0.071
	F_3	0.504	0.346	0.399	0.075	0.284	0.297	0.516	0.483	0.507	0.477
Peduncle Area	F_2	0.387	0.527	0.242	0.407	0.319	0.341	0.390	0.477	0.255	0.160
	F_3	0.560	0.491	0.486	0.148	0.435	0.541	0.612	0.721	0.491	0.569
Spike Length	F_2	0.466	0.286	0.365	0.175	0.423	0.511	0.346	0.426	0.002	-0.068
	F_3	0.321	0.330	0.217	0.024	0.615	0.645	0.605	0.566	0.204	0.046
Spike Area	F_2	0.379	0.400	0.243	0.238	0.475	0.579	0.466	0.678	0.132	0.174
	F_3	0.438	0.405	0.290	0.008	0.738	0.796	0.770	0.796	0.316	0.266
Photosynthetic Area/Tiller	F_2	0.450	0.512	0.421	0.350	0.538	0.448	0.570	0.578	0.256	0.175
	F_3	0.601	0.537	0.463	0.099	0.550	0.714	0.705	0.833	0.489	0.494

* Each r value is based on 355 degrees of freedom. Significant r values are 0.106 and 0.139 at the 0.05 and 0.01 levels of probability, respectively.

Table 6. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from F_2 and F_3 of population 2 (Rall X Jubilaynia) in 1977-78 (X_1) and 1978-79 (X_2).

Morphologic Plant Trait		Agronomic Plant Trait									
		Grain Yield		Tillers/ Plant		Kernels/ Spike		Kernel Weight/ Spike		1,000-Kernel Weight	
		X_1	X_2	X_1	X_2	X_1	X_2	X_1	X_2	X_1	X_2
Stem Area	F_2	0.507*	0.422	0.425	0.370	0.319	0.295	0.550	0.482	0.452	0.359
	F_3	0.440	0.472	0.406	0.351	0.362	0.527	0.417	0.631	0.195	0.252
Flag Leaf Blade Length	F_2	0.405	0.453	0.321	0.282	0.633	0.470	0.632	0.521	0.409	0.590
	F_3	0.410	0.454	0.392	0.203	0.512	0.411	0.533	0.506	0.481	0.440
Flag Leaf Blade Area	F_2	0.486	0.520	0.496	0.391	0.790	0.562	0.560	0.548	0.413	0.601
	F_3	0.520	0.510	0.400	0.334	0.626	0.481	0.618	0.517	0.540	0.489
Peduncle Length	F_2	0.425	0.374	0.331	0.298	0.412	0.147	0.572	0.337	0.400	0.321
	F_3	0.437	0.489	0.349	0.382	0.310	0.392	0.495	0.441	0.406	0.170
Peduncle Area	F_2	0.496	0.370	0.408	0.335	0.362	0.240	0.578	0.422	0.447	0.328
	F_3	0.384	0.463	0.347	0.348	0.286	0.471	0.366	0.543	0.224	0.212
Spike Length	F_2	0.409	0.219	0.303	0.196	0.451	0.409	0.544	0.490	0.282	0.202
	F_3	0.472	0.425	0.392	0.343	0.527	0.529	0.572	0.521	0.204	0.082
Spike Area	F_2	0.241	0.253	0.111	0.166	0.377	0.549	0.491	0.612	0.268	0.194
	F_3	0.489	0.397	0.368	0.272	0.673	0.587	0.721	0.638	0.253	0.154
Photosynthetic Area/Tiller	F_2	0.493	0.401	0.376	0.356	0.366	0.405	0.618	0.562	0.485	0.328
	F_3	0.485	0.477	0.419	0.344	0.492	0.594	0.541	0.683	0.215	0.231

* Each r value is based on 355 degrees of freedom. Significant r values are 0.106 and 0.139 at the 0.05 and 0.01 levels of probability, respectively.

Table 7. Estimates of broad-sense heritabilities (h^2_{bs}) and their standard errors from population 1 (Aurora X Rall) and population 2 (Rall X Jubilaynia) in 1977-78 (X_1) and 1978-79 (X_2).

Plant Trait	Population and Crop Season			
	Population 1		Population 1	
	X_1	X_2	X_1	X_2
Grain Yield	-0.22±0.21†	0.29±0.14	0.33±0.12	0.54±0.08
Tillers/Plant	-0.12±0.26	0.52±0.09	0.09±0.17	0.40±0.11
Kernels/Spike	0.51±0.15	0.20±0.13	0.53±0.12	0.50±0.09
Kernel Weight/ Spike	0.48±0.19	0.05±0.16	0.41±0.11	0.20±0.15
1,000-Kernel Weight	0.03±0.16	-0.19±0.25	0.29±0.12	0.33±0.12
Plant Height	0.44±0.11	0.47±0.12	0.45±0.10	0.42±0.11
Stem Area	-0.18±0.22	0.31±0.14	0.45±0.12	0.54±0.08
Flag Leaf Blade Length	-0.42±0.21	0.20±0.14	0.29±0.13	0.14±0.16
Flag Leaf Blade Area	-0.34±0.24	-0.13±0.23	0.15±0.16	0.23±0.14
Peduncle Length	0.33±0.14	0.50±0.12	0.33±0.13	0.34±0.12
Peduncle Area	-0.25±0.22	0.34±0.13	0.40±0.11	0.40±0.11
Spike Length	0.80±0.03	0.77±0.04	0.82±0.04	0.78±0.04
Spike Area	0.66±0.06	0.33±0.13	0.79±0.04	0.74±0.04
Photosynthetic Area/Tiller	-0.11±0.20	0.39±0.11	0.52±0.08	0.57±0.08

† According to standard practice, best estimate for a negative heritability value is zero.

CHAPTER III

Heritability and Character Association in a Hard Red Winter Wheat Cross, II

ABSTRACT

The plant material for this study included the parents, F_2, F_3, and F_4 generations of a cross involving two parental lines differing in certain morphologic and agronomic plant traits. The entries of this population were part of the study discussed in Chapter III. The objective was to further investigate the interrelationships among five agronomic and eight morphologic traits and plant height. Broad-sense heritabilities were also estimated in order to gain information relative to combining favorable traits from the two parental lines. The plant material was space-planted in a randomized complete block design with four replications in the 1978-79 crop season.

The coefficients of linear correlation among the agronomic traits showed that tillers per plant and kernel weight per spike were the most important components in determining yield per plant. Stem area, spike area, photosynthetic area per tiller, and peduncle area influenced yield and its components the most. All other morphologic traits studied were found to be associated with yield and its components. Spike area was the only trait that produced a high heritability estimate. Grain yield, tillers per plant, kernels per spike, kernel weight per spike, spike length, and photosynthetic area per tiller were associated with intermediate heritability estimates. The remaining traits were found to have either negative or low broad-sense heritabilities. Spike size and kernel weight per spike were the traits that could offer higher grain yield in this cross.

Additional index words: Triticum aestivum L., Yield components, Morphologic traits, Plant height, Means and variances.

The need for more and conclusive information about the morphologic structure of the wheat plant arises from the importance of these structures to grain yield itself. As Smith (30) stated, the physiologic processes contributing to grain yield tend to be localized in various morphologic structures of the plant.

Selection and breeding for grain yield or any combination of its components in wheat without regard to the morphologic traits of the plant might not result in increased yields as much as if these traits were considered. Watson (37) pointed out that studies that concentrate only on yield or yield components did not include all the characters of importance to the plant breeder. He stated that leaf size was the main determinant of differences in yield of dry weight and that increased leaf area should be one of the major objectives of plant breeding. Since then, research workers have shown that yield of cereal crops is highly dependent on the morphological structures.

The morphologic structures most important to grain yield seem to be the uppermost photosynthetic area above the flag-leaf node. These include flag-leaf blade area, flag-leaf sheath, peduncle area, spike size, and the awns (34).

Thorne (32, 33) reported that the CO_2 absorbed after spike emergence by the part of the shoot above the flag-leaf node, including the spike, accounted for most of the dry weight of grain for barley and wheat. This suggested that stored sugars did not contribute much to grain yield.

By using radioactive CO_2, many studies indicated that $^{14}CO_2$ assimilated by the flag-leaf of wheat was translocated to the developing grains and that negligible amounts moved into the shoot below the treated leaf. Stoy (31) studied the pattern of C^{14} translocation from wheat leaves to the other parts of the plant. He found that only the uppermost one or two leaves of the plant contributed to grain filling. This indicated that varieties having the ability to maintain a sufficient rate of photosynthesis after spike emergence would be well adapted for producing high grain yields. The same procedure was followed by Quinlan and Sagar (22) to study the C^{14}-labeled assimilates in wheat. It was found that most of the photosynthate of the flag-leaf moved toward the spike, while that of the lower leaves moved toward the root system. This view was supported also by Austin et al. (3), Rawson and Hofstra (23), and Volding and Simpson (35). Further evidence was also obtained by removing different leaves or shading the stem or spike of wheat. Davidson (9) found that reduction of leaf area by removal resulted in 50 to 80 percent reduction in grain yield. He found that yield was correlated with leaf area, and the reduction of leaf area reduced the number of kernels per spike and kernel weight but did not affect tiller number. He concluded that increasing tiller leaf area could result in grain yield increases.

In a study by Saghir et al. (25), leaf area was reduced by hand removal in wheat. The effect was that 1,000-kernel weight was significantly reduced as a result of removing the upper leaves. This reduction effect on 1,000-kernel weight was more pronounced when leaf area was reduced during early bloom or at anthesis.

The amount of photosynthate contributed by flag leaves and the spikes of wheat was measured by Evans and Rawson (10) in three wheat varieties by measuring the rate of photosynthesis and dark respiration throughout the period of grain development. They found that ear photosynthesis alone contributed up to 26 percent of total grain yield requirements and the rest was contributed by the flag leaves. They concluded that flag leaf and spike photosynthesis alone could meet the needs of the grain filling process at all times.

Singh et al. (29), in their study mentioned above, found a positive but non-significant correlation between flag-leaf area and 1,000-kernel weight. The correlation between flag-leaf area and kernel number per spike was negative but also non-significant.

Mohiuddin (19) studied different plant characteristics and their relation to grain yield in five winter wheat varieties for two years. The first year data indicated a positive and significant correlation between flag-leaf area and grain yield, tiller number, and 200-kernel weight (r = 0.387, 0.787, and 0.344, respectively). But flag-leaf area was negatively correlated with number of kernels per spike. Peduncle area and total photosynthetic area per plant followed the same pattern. The second year indicated that flag-leaf area was negatively correlated with 200-kernel weight which was the only difference between the two seasons with regard to photosynthetic structures above the flag-leaf node and their correlation with yield and its components.

In a study by Ledent and Moss (18), 37 morphological traits for four winter and two spring wheat cultivars were investigated in various planting patterns and different environments. Three statistical methods of analysis were also used for the data; namely, simple correlation, stepwise regression analysis, and factor analysis. All three techniques gave similar results in ranking the closeness of association between the morphological traits and grain yield and its components per culm. Flag-leaf width and length and flag-leaf area were correlated with grain yield per culm. Also, spike length, peduncle length, and height were correlated with grain yield per culm. Their conclusion was that the morphologic structures above the flag-leaf node are usually the last photosynthetically active parts of the plant and they should be considered in future yield improvement programs. The same conclusion was stated by Ledent (17) in an earlier study of wheat cultures.

The range of contribution of flag-leaves and stems of wheat to grain yield was discussed by Asana and Mani (1) and Thorne (34) to be in the range of 20 to 42%, and that of the spike ranged from 14% (32) to 26% (10). The close association between grain yield and photosynthetic structures above flag-leaf node was also reported by Borojevic (5), Chowdhry et al. (7), Jain et al. (14), Simpson (28), and Watson (37, 38).

Knowledge and understanding of the nature of the relationship between the morphological and agronomic traits of the wheat plant are very important in order to combine the favorable ones in a single variety. But, in addition to that, the wheat breeder needs to have enough information about the heritability of these favorable traits and the extent of the environmental influence on them.

Drake (8) used a seven-parent diallel cross of winter wheats to study the inheritance of certain morphologic and agronomic traits. He found that flag leaf area was positively correlated with grain yield, tillers per plant, kernels per main tiller, and kernel weight. Narrow-sense heritability for flag leaf area was 0.519 and for plant height was 0.636. The author maintained that selection for large flag leaf area would lead to grain yield increases. A high narrow-sense heritability estimate for flag leaf in barley ($h^2 = 0.73$) was also found by Sharma et al. (26).

In a study by Chowdhry et al. (7), four wheat varieties and their ten crosses, including reciprocals, were used to evaluate the relation between flag leaf, height, grain yield, and yield components. Phenotypic correlations of flag leaf blade length and width with the agronomic traits indicated that when the parent had narrow erect leaves the two traits correlated positively with grain yield and its components. When the parent had droopy broad leaves, the correlations were mixed and sometimes were negative. Broad-sense heritability estimates for flag leaf length ranged from 0.27 to 0.58 and flag leaf width ranged from 0.26 to 0.53.

In a study by Walton (36), a seven-parent diallel analysis in spring wheat was used to study the inheritance of flag leaf area parameters and spike length. Flag leaf size was found to be controlled by a minor gene complex. Spike length and spike extrusion were also found to be controlled by multiple gene systems.

Genetic studies of plant height and other wheat traits prior to 1944 were summarized by Ausemus et al. (2), and it was shown that plant height in wheat is an expression of both polygenic and major gene effects. In subsequent studies, Pao et al. (20) obtained evidence for trigenic control of height. Everson et al. (11) reported results that indicated a two-gene control of plant height in wheat.

The present study, involving a winter wheat cross, was conducted to furnish information on the importance of certain post-flowering morphologic traits to grain yield and its components; and also to furnish information about the heritability of these morphologic traits, grain yield, and yield components.

MATERIALS AND METHODS

The parental, F_2, F_3, and F_4 populations studied in this experiment were derived from two hard red winter cultivars, 'Kavkaz' and 'Centurk'. These cultivars are currently used in the wheat breeding program at the Oklahoma Agricultural Experiment Station. Centurk was developed cooperatively by the Nebraska Agricultural Experiment Station and the Plant Science Research Division of the Agricultural Research Service, U.S.D.A. It has medium height, high tillering potential, small-size kernels, midtall, small leaves, and awned spikes. Kavkaz was of eastern European origin and characterized by large spikes, large-size kernels, somewhat low tillering potential, midtall with strong straw, and somewhat large leaves. These two cultivars were chosen as parents for this study because of their diversity for the characters studied.

Seedlings of the parents, F_2, F_3, and F_4 generations were started in flats and then transplanted to the field on October 15, 1978, and selected plants were harvested on June 25, 1979. Transplanting was made in a randomized complete block design at the Stillwater Agronomy Research Station.

The field layout, sampling procedure, characters evaluated, and statistical analysis are presented in MATERIALS AND METHODS in Chapter II.

RESULTS AND DISCUSSION

Generation Means

Generation means for five agronomic traits and plant height are presented in Table 1. The two parents differed significantly with respect to tillers per plant, kernel weight per spike, and 1,000-kernel weight. Even though the five entries did not differ significantly in grain yield, their means ranged from a low of 14.72 g for F_3 to a high of 17.27 g in the F_4 generation. The F_2 mean exceeded the highest parent with respect to yield per plant (17.05 g vs 16.19 g). It seems that slight yield gains could be obtained from this cross as indicated by the moderate increases of the F_2 and F_4 generation means in comparison to both parental means. Generation means differed significantly in tillers per plant with Centurk producing the highest mean (14.07) and Kavkaz the lowest mean (9.05). The three segregating generation means fell in the range of the two parents. The two parents did not differ significantly in kernels per spike, but Centurk was significantly lower than the three segregating generations. The F_4 produced the largest mean kernels per spike (57.07), followed by F_2 (55.14), Kavkaz (53.24), and Centurk (48.67). Kernel weight per spike entry means ranged from 2.17 g for Kavkaz to a low of 1.51 g for Centurk. The F_2 and F_3 means fell within the range of the two parents with respect to this trait. Kavkaz produced the largest 1,000-kernel weight mean (40.78 g) which was significantly higher than the means of the other four entries.

Entry means for plant height indicated that the F_2 was not significantly different from the two parents, but it was very close to the highest parent. On the other hand, the F_3 and F_4 means fell below the lower parent.

The means of the four entries for eight morphologic traits are summarized in Table 2. With respect to stem area, generation means were not significantly different from each other, but Kavkaz produced the highest stem area mean among the entries, followed by F_3, F_4, F_2 and Centurk. It seems that stem area could be affected more by peduncle diameter than stem length in this cross. Flag leaf blade area and length were found to differ between the parents with Kavkaz, as expected, producing the highest means for these two traits. The F_2 mean fell within the range of the two parents with respect to flag leaf measurements. The two parents produced nearly equal means for peduncle length and area. Spike length means ranged from 8.83 cm for Centurk to 9.93 cm for Kavkaz. The two parents were statistically different with respect to this trait, but the segregating generations and Centurk did not reach the statistical level of significant differences among them. With respect to spike area, the means of the two parents were significantly different from each other and from the three segregating generations. Photosynthetic area per tiller varied from 126.52 cm^{-2} for Centurk to 156.81 cm^{-2} for Kavkaz. The means of the segregating generations were within the range of the two parental lines.

Correlations

Table 4 contains the coefficients of linear correlation among five agronomic traits and plant height from the F_2 and F_3 data sets. Grain yield was found to be positively correlated with all the evaluated agronomic traits in both generations. In both generations, the highest correlation involving grain yield was with tiller number. In the absence of intensive competition between neighboring plants under space-planting conditions the potential of the plant for producing more spikes could be expressed fully. This might explain the high association between tiller number and grain yield in the material of this study. High correlation coefficients between these two agronomic traits were also reported in several other instances (8, 12, 13, 14).

Kernel weight per spike was found to have intermediate association with grain yield in both generations. This association was second in magnitude to the association between tiller number and grain yield. In the F_2 1,000-kernel weight was found to have intermediate correlations with grain yield but in the F_3 these two traits were found to have a low positive correlation. Number of kernels per spike had low correlation with grain yield per plant. The positive and significant correlations between grain yield and the components of yield of this cross indicate that selection for these traits simultaneously for grain yield improvement can be successful especially since no high negative correlations were observed in this material. The results reported herein agree with those reported by Drake (8). Higher correlations between weight per spike and grain yield than that between grain yield and kernels per spike were also reported by Sidwell (27), but the ones reported here are higher than those reported by Sidwell and lower than those reported by Hsu and Walton (13).

The correlation between grain yield and plant height was intermediate in F_2 and low in the F_3 generation. This positively significant association can not be easily explained although the possibility of a greater photosynthetic area possessed by taller plants (4) does exist. More likely, this association could be reasoned on the basis of the correlation of both these two traits with kernel weight per spike.

The absence of negative associations between tillers per plant and each of kernel weight per spike and 1,000-kernel weight could be the result of the different stages at which these traits develop and so no competition exists between them. Similar results were reported by Ketata (16).

High correlation coefficients between kernels per spike and weight per spike were anticipated and indeed obtained as the first is the obvious component of the latter. Positive but low magnitude correlations were observed between kernels per spike and each of 1,000-kernel weight and plant height.

Taller plants were associated with heavier kernel weights per spike and 1,000-kernel weights as was indicated by the high to intermediate correlations observed between these traits in the F_3 data set. These correlations were lower in magnitude in the F_2 generation suggesting that these associations can be affected by the differential effects of the environment on the two generations.

The coefficients of correlation between five agronomic and eight morphologic plant traits are recorded in Table 4. The association between grain yield and each of stem area, peduncle area, spike length and area, and photosynthetic area per tiller were intermediate in magnitude with the latter trait producing the highest correlations with grain yield per plant ($r = 0.579$) in F_2. The other morphologic traits were found to have low but significant correlations with grain yield. On the other hand, the F_3 data set indicated that the highest association was between grain yield and stem area among all per tiller morphology. This may explain the association of taller plants with higher grain yield and the other yield components suggested by Bhatt (4). From these results it seems that increasing the size of any of the morphologic traits studied, with the exception of flag leaf, could result in grain yield increases in this cross. An important note here is the lower magnitude of importance of flag leaf area in comparison to the other morphologic traits. The reason behind that could be because flag leaf area exerts its effect on grain yield indirectly through yield components. The results of this study were comparable to those reported in the literature (10, 13).

Number of kernels per spike appeared to be more associated with spike size than any of the other morphologic traits in the F_2 of this study. In the F_3 it was spike area and photosynthetic area per tiller that were found to have the closest association with kernels per spike. The close association between spike measurements and number of kernels per spike agrees well with the suggestion by Hsu and Walton (13) that larger spikes provide more space for more kernels to develop through more spikelets per spike, and also agrees with Thorne's (33) theory that larger spikes offer more photosynthetic area close to the sink site to develop its potential. Ledent (17) and Ledent and Moss (18) reported similar results concerning the association of spike size and kernels per spike. The results of this study suggest that increased spike area and total photosynthetic area per tiller should lead to greater number of kernels per spike and, as a consequence, higher grain yield per plant in the material of this cross.

Kernel weight per spike and 1,000-kernel weight were closely associated with spike area, photosynthetic area per tiller, spike length, peduncle area, and stem area. These two agronomic traits were also intermediately associated with flag leaf measurements. This could suggest that kernel size could be an important factor in determining yield when photosynthate supply is ample. Selection for any of these mentioned morphologic traits could lead to increased kernel weights if kernel size was not a limiting factor.

Variances and Heritability Estimates

The variances and broad-sense heritability estimates for the five agronomic traits and plant height are presented in Table 1 and those of the morphologic traits are in Table 2. The variances in the F_2 generation exceeded those of the parents in grain yield, kernels per spike, kernel weight per spike, 1,000-kernel weight, and spike measurements. This indicates that sizeable amounts of variability existed for these traits in the F_2 data set. The F_2 variances fell within the range of the two parents in the cases of tiller number, plant height, stem area, flag leaf blade area, peduncle area and length, and photosynthetic area per tiller. For the remaining traits, the F_2 variances fell short from both parents which could be due to either large sampling error or a differential effect of the prevailing environmental conditions on the parents and the F_2 generation. However, the variances in the F_3 and F_4 generations showed mixed responses. The variability in F_3 was lower than that in the F_2 generation in the cases of three agronomic traits, plant height, and five morphologic traits (Tables 1, 2), and exceeded those in the F_2 for kernels per spike, 1,000-kernel weight, flag leaf blade measurements, and peduncle length; indicating that selection for these traits could be more successful in the F_3 than F_2 due to the larger size variability existing in the F_3 generation. On the other hand, the variances in the F_4 generation were higher than both of those in the F_2 and F_3 with respect to 1,000-kernel weight, and flag leaf blade area. This suggests that selection for these traits could afford more success if practiced in the F_4 or later generations.

Broad-sense heritability estimates for the evaluated traits ranged from high to negatively low. Negative heritability estimates were found for flag leaf measurements and peduncle length (Table 2). The reason for these negative values seems to be the large variance of Kavkaz in the case of flag leaf, and the large variance of Centurk in the case of peduncle length. Intermediate estimates were recorded for grain yield, tillers per plant, kernels and kernel weight per spike, spike length, and photosynthetic area per tiller. The only high heritability value observed in this population was for spike area (0.51 0.09). An important note here is the low heritability estimate obtained for plant height. This could be due to closeness of the parental means and the lack of large differences between them with respect to this trait. Another important result of this cross was the higher heritability value of kernels per spike than that of kernel weight per spike. This suggests that kernels per spike may afford a consistent factor in selection for higher grain yield per plant, but a look to the correlation between each of these two traits (kernels per spike and kernel weight per spike) with grain yield indicates that kernel weight per spike is a higher contributor to grain yield. A safe conclusion from these data would be that selection for increased values of these agronomic traits could be successful and would result in yield increases. Bhatt (4) reported high broad-sense heritability values for plant height and kernel weight in two crosses of spring wheat. Reddi et al. (24) observed negative heritability estimates for number of tillers in one wheat cross and a low value in another. They reported high heritability values for culm length in both crosses, low values for spike length, and intermediate to low heritability values for kernel weight. Johnson et al. (15) found that plant height as well as spike length and kernel weight were highly heritable, but grain yield was found to have a negative heritability value and the heritability value for tillers per plant was intermediate in magnitude. Paroda and Joshi (21) reported narrow-sense heritability values of a two-year study. These values were low for grain yield, low to intermediate for number of tillers, kernels per spike, and kernel weight per spike. The heritability values for 1,000-kernel weight were found to be high for the two seasons. For flag leaf area, Drake (8) reported narrow-sense heritability estimate of 0.519 and that of plant height was 0.636. Chowdhry et al. (7) reported that broad-sense heritability estimates ranged from 0.27 to 0.58 for flag leaf length.

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LIST OF TABLES

Table 1. Estimates of generation means, among plant variances, and broad-sense heritabilities (h^2_{bs}) with their standard errors for six agronomic traits and plant height in a hard red winter wheat cross.

Generation or Parameter	Plant Trait					
	Grain Yield (g/plant)	Tillers/ Plant	Kernels/ Spike	Kernel Weight (g/spike)	1,000-Kernel Weight (g)	Plant Height (cm)
Kavkaz	15.79†a* 35.79	9.05a 12.99	53.24ab 48.45	2.17 d 0.1292	40.78b 16.38	85.63ab 42.24
Centurk	16.19a 50.06	14.07e 33.82	48.67a 32.89	1.51 a 0.0816	30.82a 15.01	92.91b 62.84
F_2	17.05a 61.06	12.91d 29.84	55.15b 77.00	1.70 b 0.1515	30.76a 19.42	91.30b 59.86
F_3	14.72a 47.56	10.62b 18.76	54.14b 97.77	1.75 bc 0.1299	32.32a 20.30	84.54a 52.57
F_4	17.27a 59.53	12.06c 22.66	57.07b 85.06	1.84 c 0.1172	32.42a 25.87	82.61a 48.90
h^2_{bs} ±s.e.	0.30±0.13	0.22±0.15	0.47±0.10	0.30±0.13	0.19±0.15	0.12±0.16

† The upper value in each cell is the mean and lower value is the variance of the trait.

* Means followed by different letters are significantly different according to L.S.D. at 0.05 level of probability.

Table 2. Estimates of generation means, among plant variances, and broad-sense heritabilities (h^2_{bs}) with their standard errors for eight morphologic traits in a hard red winter wheat cross.

Generation or Parameter	Stem Area (cm^{-2})	Flag Leaf Blade Length (cm)	Flag Leaf Blade Area (cm^{-2})	Peduncle Length (cm)	Peduncle Area (cm^{-2})	Spike Length (cm)	Spike Area (cm^{-2})	Photosynthetic Area/Tiller (cm^{-2})
Kavkaz	94.87†a* 280.08	21.62d 8.50	27.89e 35.92	31.24a 12.80	39.40d 60.03	9.93 b 0.4158	34.65c 18.60	156.81c 395.02
Centurk	82.88a 379.91	16.67a 6.57	16.16a 14.46	33.48ab 21.78	33.36a 80.15	8.83 a 0.9126	27.48a 15.90	126.52a 1041.92
F_2	87.94a 341.32	17.71ab 6.23	18.86b 17.48	34.70b 16.54	37.44a 76.23	9.12 a 1.1630	31.82b 35.32	138.62ab 969.05
F_3	94.21a 211.18	18.91bc 9.42	21.80c 27.61	31.55a 19.63	39.69a 64.91	9.13 a 1.0559	31.28b 28.84	147.29bc 640.07
F_4	93.63a 200.87	19.84c 5.65	23.86d 36.92	31.63a 18.14	40.51a 58.98	9.14 a 0.5997	31.90b 20.54	149.40c 596.99
h^2_{bs}±s.e.	0.03±0.18	-0.21±0.22‡	-0.44±0.28	-0.05±0.20	0.08±0.17	0.43±0.11	0.51±0.09	0.30±0.14

† The upper value in each cell is the mean and lower value is the variance of the trait.

* Means followed by different letters are significantly different according to L.S.D. at 0.05 level of probability.

‡ According to standard practice, best estimate for a negative heritability value is zero.

Table 3. Phenotypic correlation coefficients among five agronomic traits and plant height from F_2 (upper right portion) and F_3 (lower left portion) of a hard red winter wheat cross.

Plant Trait	Plant Trait					
	1	2	3	4	5	6
1. Grain Yield	1*	0.859	0.386	0.534	0.445	0.553
2. Tillers/Plant	0.921	1	0.109	0.153	0.159	0.476
3. Kernels/Spike	0.391	0.183	1	0.808	0.177	0.234
4. Kernel Weight/Spike	0.593	0.354	0.774	1	0.709	0.386
5. 1,000-Kernel Weight	0.386	0.317	-0.156	0.493	1	0.349
6. Plant Height	0.476	0.351	0.296	0.601	0.540	1

* Each r value is based on 355 degrees of freedom. Significant r values are 0.106 and 0.139 at the 0.05 and 0.01 levels of probability, respectively.

Table 4. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from F_2 and F_3 of a hard red winter wheat cross.

Morphologic Plant Trait	Generation	Agronomic Plant Trait				
		Grain Yield	Tillers/ Plant	Kernels/ Spike	Kernel Weight/ Spike	1,000-Kernel Weight
Stem Area	F_2	0.556*	0.287	0.395	0.646	0.595
	F_3	0.500	0.324	0.463	0.769	0.554
Flag Leaf Blade Length	F_2	0.422	0.275	0.439	0.518	0.301
	F_3	0.401	0.351	0.448	0.511	0.316
Flag Leaf Blade Area	F_2	0.465	0.370	0.482	0.537	0.326
	F_3	0.425	0.360	0.456	0.525	0.337
Peduncle Length	F_2	0.417	0.392	0.222	0.386	0.350
	F_3	0.245	0.195	0.089	0.432	0.554
Peduncle Area	F_2	0.504	0.267	0.415	0.661	0.588
	F_3	0.349	0.235	0.305	0.625	0.546
Spike Length	F_2	0.531	0.314	0.615	0.671	0.391
	F_3	0.319	0.225	0.445	0.499	0.178
Spike Area	F_2	0.553	0.254	0.605	0.763	0.561
	F_3	0.495	0.340	0.568	0.743	0.402
Photosynthetic Area/Tiller	F_2	0.579	0.287	0.470	0.704	0.603
	F_3	0.498	0.320	0.511	0.783	0.518

* Each r value is based on 355 degrees of freedom. Significant r values are 0.106 and 0.139 at the 0.05 and 0.01 levels of probability, respectively.

CHAPTER IV

SUMMARY AND CONCLUSIONS

The parental, F_2, and F_3 generations, derived from two crosses each involving two winter wheat cultivars, were used to study the heritability and interrelations of yield, yield-related traits, plant height, and eight post-flowering morphologic characters. The populations of this study were evaluated in a space-planted experiment at the Agronomy Research Station, Stillwater, Oklahoma, during the 1977-78 and 1978-79 crop seasons. During the 1978-79 crop season, parental, F_2, F_3, and F_4 generations of a third cross involving two winter wheat cultivars were added to the experiment to study the same traits mentioned above.

Grain yield, tiller number, kernels per spike, kernel weight per spike, 1,000-kernel weight, plant height, stem area, flag-leaf blade length and area, peduncle length and area, spike length and area, and photosynthetic area per tiller, were the characters evaluated. Coefficients of phenotypic correlation among these traits indicated that the three populations were consistent with regard to the magnitude of association between yield per plant and tiller number per plant. Of all five agronomic traits studied, tiller number had the highest correlation coefficients with grain yield per plant. The high associations between these two traits were attributed to the space-planting conditions of this study. The three populations were consistent also in indicating that the association between kernel weight per spike and grain yield was higher than the association between kernels per spike and grain yield. The correlations between grain yield and kernel weight per spike ranged from low to intermediate in magnitude, and those between kernels per spike and grain yield were all low in magnitude. Plant height was associated with grain yield in populations 2 and 3 more than population 1. In general, plant height seemed to have low magnitude correlations with grain yield.

With the exception of number of kernels per plant, simultaneous selection for tiller number and any of the yield-related traits in population 1 would not be successful due to the low magnitude and some instances negative correlations between tillers per plant and these traits. In populations 2 and 3 the success would be limited also but not to the extent as that in population 1. If a cause and effect is to be assumed here, combining higher kernel weight and larger number of kernels per spike will not be successful in these three populations. Plant height seemed to contribute to yield per plant either directly or through increased kernel weight per spike. This was indicated by the low to intermediate correlations between this plant trait and both grain yield per plant and kernel weight per spike. The indication from the signs and magnitudes of the correlation coefficients among the five agronomic traits was that more emphasis should be directed towards selection for higher tiller number per plant and higher kernel weight per spike for higher grain yield based on yield components. But, a word of caution here, that the material of this study was space-planted and the effect of tiller number on grain yield might change under conditions of more dense stands.

The morphologic traits differed in their magnitude of association with grain yield per plant and the other four agronomic traits. Stem area was found to have low magnitude correlations with grain yield and seemed to contribute to yield through kernel weight per spike in all three populations. The magnitude of association between stem area and both kernels per spike and kernel weight per spike could be affected by the prevailing environmental conditions. In population 1, flag leaf blade area measurements were found to have intermediate magnitude association with grain yield per plant and seem to affect yield through both kernels per spike and kernel weight per spike. In populations 2 and 3 the correlations between grain yield and both flag leaf blade measurements were of low magnitude and, here again, the contribution of these two traits to grain yield seems to be through kernels per spike and kernel weight per spike. Peduncle and spike measurements both had low magnitude correlations with grain yield, tiller number, kernels per spike, kernel weight per spike, and 1,000-kernel weight in populations 1 and 2 for the 1977-1978 data. But these correlations were mostly of intermediate magnitude in the 1978-1979 for the three populations. In all three populations, peduncle area and spike area seem to affect grain yield indirectly through kernel number per spike and kernel weight per spike. The correlations between grain yield per plant and total photosynthetic area per tiller ranged from low to intermediate. If a cause and effect is to be postulated here, then photosynthetic area per tiller could be most important to kernel filling and, to a lesser extent, number of kernels per spike. The per tiller morphologic traits could be ranked according to their contribution to grain yield from high to low as follows: flag leaf blade area, stem area, peduncle area, and spike area.

Negative broad-sense heritability values were obtained in the first season of population 1 for grain yield per plant, tiller number, stem area, flag-leaf blade measurements, peduncle area, and photosynthetic area per tiller. These negative values were attributed either to high plant to plant variability in the parental lines or low variation among the F_2 plants due to the low differences between the parental means for these traits due to environmental effects. Low heritability estimates were found in the same population and season for 1,000-kernel weight. Intermediate heritability estimates were obtained for kernel weight per spike, plant height, and peduncle length. Moderately high heritability estimates were observed for number of kernels per spike, and spike area. The highest broad-sense heritability estimate was that of spike length.

In the second season of population 1, a more favorable growth season for wheat, the values of broad-sense heritability were improved for almost all evaluated traits. But some of the evaluated traits still produced negative heritability values. These traits included 1,000-kernel weight, and flag leaf blade area. The plant traits that produced low magnitude heritability estimates in the second season included number of kernels per spike, kernel weight per spike, and flag leaf length. Grain yield, plant height, stem area, peduncle area, spike area, and photosynthetic area per tiller, all produced intermediate heritability estimates. The rest of the studied traits fell in the high range of broad-sense heritability estimates for this season.

In population 2 low magnitude heritability estimates in the first season were obtained for tillers per plant and flag-leaf blade area. Intermediate heritability values were obtained for grain yield per plant, kernel weight per spike, 1,000-kernel weight, plant height, stem area, flag-leaf blade length, and peduncle length and area. The rest of the evaluated traits were in the high range of the heritability values. In the second season, improvements in the heritability values for most traits were indicated. The plant characters exhibiting high broad-sense heritability estimates were arranged from high to low in the following order: spike length and area, photosynthetic area per tiller, grain yield, and stem area. The remaining traits ranged from low to intermediate in their heritability estimates.

In population 3, a one-year data, broad-sense heritability values ranged from negatively low to intermediate. The plant characters exhibiting negative heritability estimates were three of the morphologic traits. The only high heritability estimate observed was that of spike area.

The general conclusions that could be drawn from the three populations of this study are the following: 1) spike length and area are highly heritable traits and selection for larger size spikes could result in higher kernel weight and, to a lesser extent, kernel number per spike; 2) flag-leaf length and area are low heritability traits and, even though they were associated with grain yield and yield-related traits, these traits will be difficult to select for in early generations; 3) peduncle length and area were intermediate in their heritabilities but their role with respect to grain yield was not clear; 4) plant height and stem area were also intermediately inherited and larger stem areas could result in improved grain yields; 5) tillers per plant and kernel weight per spike were the most associated with grain yield among the yield components and selection for higher tillers per plant and kernel weight per spike could result in higher yields even though their heritabilities were of intermediate magnitudes; 6) of course, the other interrelationships among the other agronomic and morphologic plant traits and a good balance among them should be considered as well.

APPENDIX

LIST OF APPENDIX TABLES

Table 10. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from Centurk in 1978-79.

Table 11. Phenotypic correlation coefficients among five agronomic traits and plant height from F_4 (Kavkaz X Centurk) in 1978-79.

Table 12. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from F_4 (Kavkaz X Centurk) in 1978-79.

Table 1. Phenotypic correlation coefficients among five agronomic traits and plant height from Aurora in 1977-78 (upper right portion) and 1978-79 (lower left portion).

Plant Trait	Plant Trait					
	1	2	3	4	5	6
1. Grain Yield	1*	0.952	0.335	0.364	0.139	0.548
2. Tillers/Plant	0.885	1	0.222	0.188	0.027	0.453
3. Kernels/Spike	0.312	0.149	1	0.609	-0.148	0.299
4. Kernel Weight/Spike	0.452	0.193	0.557	1	0.690	0.200
5. 1,000-Kernel Weight	0.149	0.037	-0.420	0.512	1	-0.052
6. Plant Height	0.484	0.365	0.511	0.505	-0.040	1

* Each r value is based on 175 degrees of freedom. Significant r values are 0.149 and 0.195 at the 0.05 and 0.01 levels of probability, respectively.

Table 2. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from Aurora in 1977-78 (X_1) and 1978-79 (X_2).

Plant Trait	Season	Plant Trait				
		Grain Yield/ Plant	Tillers/ Plant	Kernels/ Spike	Kernel Weight/ Spike	1,000-Kernel Weight
Stem Area	X_1	0.406*	0.362	0.376	0.195	-0.095
	X_2	0.603	0.233	0.602	0.542	-0.046
Flag Leaf Blade Length	X_1	0.420	0.301	0.301	0.421	-0.110
	X_2	0.530	0.431	0.656	0.421	0.011
Flag Leaf Blade Area	X_1	0.441	0.381	0.438	0.580	-0.036
	X_2	0.550	0.402	0.601	0.582	0.021
Peduncle Length	X_1	0.507	0.467	0.305	0.181	-0.079
	X_2	0.516	0.450	0.410	0.377	-0.028
Peduncle Area	X_1	0.423	0.402	0.388	0.204	-0.097
	X_2	0.507	0.299	0.508	0.438	-0.041
Spike Length	X_1	0.202	0.130	0.335	0.467	0.252
	X_2	0.321	0.357	0.233	0.229	-0.027
Spike Area	X_1	0.327	0.294	0.299	0.335	0.140
	X_2	0.164	0.242	0.061	0.106	0.052
Photosynthetic Area/Tiller	X_1	0.408	0.367	0.350	0.204	-0.062
	X_2	0.491	0.266	0.512	0.689	-0.009

* Each r value is based on 175 degrees of freedom. Significant r values are 0.149 and 0.195 at the 0.05 and 0.01 levels of probability, respectively.

Table 3. Phenotypic correlation coefficients among five agronomic traits and plant height from Rall in 1977-78 (upper right portion) and 1978-79 (lower left portion).

Plant Trait	Plant Trait					
	1	2	3	4	5	6
1. Grain Yield	1*	0.957	0.300	0.430	0.152	0.352
2. Tillers/Plant	0.911	1	0.272	0.367	0.096	0.262
3. Kernels/Spike	0.461	0.285	1	0.568	-0.389	0.552
4. Kernel Weight/Spike	0.642	0.476	0.805	1	0.516	0.489
5. 1,000-Kernel Weight	0.530	0.456	0.202	0.739	1	-0.039
6. Plant Height	0.592	0.479	0.564	0.716	0.545	1

* Each r value is based on 175 degrees of freedom. Significant r values are 0.149 and 0.195 at the 0.05 and 0.01 levels of probability, respectively.

Table 4. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from Rall in 1977-78 (X_1) and 1978-79 (X_2).

Plant Trait	Season	Plant Trait: Grain Yield/ Plant	Tillers/ Plant	Kernels/ Spike	Kernel Weight/ Spike	1,000-Kernel Weight
Stem Area	X_1	0.355*	0.273	0.614	0.519	-0.075
	X_2	0.699	0.635	0.507	0.723	0.615
Flag Leaf Blade Length	X_1	0.525	0.234	0.690	0.703	-0.003
	X_2	0.470	0.431	0.701	0.691	0.728
Flag Leaf Blade Area	X_1	0.431	0.185	0.511	0.692	-0.055
	X_2	0.567	0.360	0.692	0.682	0.531
Peduncle Length	X_1	0.569	0.487	0.651	0.538	-0.094
	X_2	0.643	0.515	0.510	0.747	0.650
Peduncle Area	X_1	0.457	0.380	0.652	0.548	-0.087
	X_2	0.655	0.588	0.450	0.677	0.602
Spike Length	X_1	0.494	0.489	0.442	0.416	-0.045
	X_2	0.345	0.274	0.580	0.504	0.166
Spike Area	X_1	0.339	0.290	0.666	0.717	0.078
	X_2	0.468	0.418	0.589	0.716	0.493
Photosynthetic Area/Tiller	X_1	0.402	0.323	0.676	0.605	-0.060
	X_2	0.685	0.631	0.551	0.721	0.550

* Each r value is based on 175 degrees of freedom. Significant r values are 0.149 and 0.195 at the 0.05 and 0.01 levels of probability, respectively.

Table 5. Phenotypic correlation coefficients among five agronomic traits and plant height from Jubilaynia in 1977-78 (upper right portion) and 1978-79 (lower left portion).

Plant Trait	Plant Trait					
	1	2	3	4	5	6
1. Grain Yield	1*	0.916	0.340	0.469	0.477	0.411
2. Tillers/Plant	0.923	1	0.116	0.210	0.267	0.276
3. Kernels/Spike	0.624	0.568	1	0.891	0.450	0.300
4. Kernel Weight/Spike	0.698	0.568	0.829	1	0.801	0.526
5. 1,000-Kernel Weight	0.507	0.352	0.309	0.780	1	0.713
6. Plant Height	0.459	0.360	0.340	0.495	0.555	1

* Each r value is based on 175 degrees of freedom. Significant r values are 0.149 and 0.195 at the 0.05 and 0.01 levels of probability, respectively.

Table 6. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from Jubilaynia in 1977-78 (X_1) and 1978-79 (X_2).

Plant Trait	Season	Plant Trait: Grain Yield/ Plant	Tillers/ Plant	Kernels/ Spike	Kernel Weight/ Spike	1,000-Kernel Weight
Stem Area	X_1	0.265*	0.161	0.374	0.471	0.477
	X_2	0.523	0.435	0.553	0.694	0.625
Flag Leaf Blade Length	X_1	0.471	0.290	0.460	0.687	0.446
	X_2	0.483	0.170	0.492	0.728	0.688
Flag Leaf Blade Area	X_1	0.512	0.301	0.540	0.734	0.493
	X_2	0.518	0.212	0.683	0.700	0.724
Peduncle Length	X_1	0.189	0.116	0.195	0.397	0.589
	X_2	0.412	0.361	0.343	0.569	0.647
Peduncle Area	X_1	0.149	0.081	0.322	0.401	0.404
	X_2	0.462	0.410	0.532	0.685	0.612
Spike Length	X_1	0.409	0.343	0.365	0.466	0.451
	X_2	0.440	0.488	0.582	0.425	0.109
Spike Area	X_1	0.452	0.333	0.609	0.744	0.677
	X_2	0.493	0.476	0.573	0.700	0.559
Photosynthetic Area/Tiller	X_1	0.304	0.222	0.461	0.540	0.496
	X_2	0.548	0.460	0.621	0.780	0.691

* Each r value is based on 175 degrees of freedom. Significant r values are 0.149 and 0.195 at the 0.05 and 0.01 levels of probability, respectively.

Table 7. Phenotypic correlation coefficients among five agronomic traits and plant height from Kavkaz in 1978-79.

Plant Trait	Plant Trait					
	1	2	3	4	5	6
1. Grain Yield/Plant	1*	0.909	0.290	0.471	0.448	0.581
2. Tillers/Plant		1	0.063	0.206	0.290	0.554
3. Kernels/Spike			1	0.855	0.155	0.250
4. Kernel Weight/Spike				1	0.638	0.364
5. 1,000-Kernel Weight					1	0.355
6. Plant Height						1

* Each r value is based on 175 degrees of freedom. Significant r values are 0.149 and 0.195 at the 0.05 and 0.01 levels of probability, respectively.

Table 8. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from Kavkaz in 1978-79.

Plant Trait	Plant Trait				
	Grain Yield/ Plant	Tillers/ Plant	Kernels/ Spike	Kernel Weight/ Spike	1,000-Kernel Weight
Stem Area	0.048*	-0.072	0.286	0.378	0.285
Flag Leaf Blade Length	0.372	0.408	-0.060	0.037	0.169
Flag Leaf Blade Area	0.373	0.401	-0.010	0.071	0.152
Peduncle Length	0.385	0.321	0.202	0.286	0.280
Peduncle Area	0.016	-0.124	0.300	0.376	0.265
Spike Length	0.223	0.208	0.459	0.307	-0.072
Spike Area	0.224	0.047	0.695	0.591	0.100
Photosynthetic Area/Tiller	0.201	0.071	0.389	0.468	0.307

* Each r value is based on 175 degrees of freedom. Significant r values are 0.149 and 0.195 at the 0.05 and 0.01 levels of probability, respectively.

Table 9. Phenotypic correlation coefficients among five agronomic traits and plant height from Centurk in 1978-79.

Plant Trait	Plant Trait					
	1	2	3	4	5	6
1. Grain Yield/Plant	1*	0.947	0.455	0.613	0.535	0.708
2. Tillers/Plant		1	0.327	0.498	0.484	0.648
3. Kernels/Spike			1	0.790	0.276	0.557
4. Kernel Weight/Spike				1	0.801	0.704
5. 1,000-Kernel Weight					1	0.585
6. Plant Height						1

* Each r value is based on 175 degrees of freedom. Significant r values are 0.149 and 0.195 at the 0.05 and 0.01 levels of probability, respectively.

Table 10. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from Centurk in 1978-79.

Plant Trait	Plant Trait				
	Grain Yield/ Plant	Tillers/ Plant	Kernels/ Spike	Kernel Weight/ Spike	1,000-Kernel Weight
Stem Area	0.484*	0.410	0.372	0.608	0.574
Flag Leaf Blade Length	0.591	0.323	0.680	0.521	0.531
Flag Leaf Blade Area	0.620	0.422	0.704	0.593	0.619
Peduncle Length	0.646	0.649	0.441	0.630	0.580
Peduncle Area	0.508	0.470	0.352	0.607	0.599
Spike Length	0.600	0.550	0.388	0.719	0.755
Spike Area	0.548	0.433	0.599	0.831	0.719
Photosynthetic Area/Tiller	0.520	0.441	0.419	0.675	0.634

* Each r value is based on 175 degrees of freedom. Significant r values are 0.149 and 0.195 at the 0.05 and 0.01 levels of probability, respectively.

Table 11. Phenotypic correlation coefficients among five agronomic traits and plant height from F_4 (Kavkaz X Centurk) in 1978-79.

Plant Trait	1	2	3	4	5	6
1. Grain Yield/Plant	1*	0.889	0.289	0.615	0.424	0.553
2. Tillers/Plant		1	0.155	0.328	0.249	0.380
3. Kernels/Spike			1	0.611	-0.327	0.395
4. Kernel Weight/Spike				1	0.538	0.559
5. 1,000-Kernel Weight					1	0.253
6. Plant Height						1

* Each r value is based on 595 degrees of freedom. Significant r values are 0.057 and 0.075 at the 0.05 and 0.01 levels of probability, respectively.

Table 12. Phenotypic correlation coefficients among five agronomic and eight morphologic traits from F_4 (Kavkaz X Centurk) in 1978-79.

Plant Trait	Plant Trait				
	Grain Yield/ Plant	Tillers/ Plant	Kernels/ Spike	Kernel Weight/ Spike	1,000-Kernel Weight
Stem Area	0.553*	0.324	0.298	0.715	0.537
Flag Leaf Blade Length	0.510	0.438	0.655	0.591	0.476
Flag Leaf Blade Area	0.416	0.413	0.659	0.468	0.391
Peduncle Length	0.364	0.202	0.227	0.540	0.406
Peduncle Area	0.435	0.220	0.239	0.689	0.569
Spike Length	0.279	0.123	0.634	0.487	-0.097
Spike Area	0.424	0.226	0.586	0.698	0.206
Photosynthetic Area/Tiller	0.505	0.288	0.352	0.691	0.448

* Each r value is based on 595 degrees of freedom. Significant r values are 0.057 and 0.075 at the 0.05 and 0.01 levels of probability, respectively.

VITA

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Candidate for the Degree of

Doctor of Philosophy

Thesis: HERITABILITY AND INTERRELATIONS OF YIELD, YIELD-RELATED TRAITS, AND POST FLOWERING MORPHOLOGY IN THREE HARD RED WINTER WHEAT CROSSES (TRITICUM AESTIVUM L.)

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