GENETIC STUDIES OF AGRONOMIC CHARACTERS IN WINTER WHEAT (*TRITICUM AESTIVUM* L.)

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CHAPTER I

INTRODUCTION

The main task of a wheat breeder in a world faced with food shortages is to increase grain yield potential to help insure an abundant and continuous food supply to meet the growing human requirements.

Genetics has been a major and powerful factor contributing to yield improvement and stability of grain yield in wheat. A better understanding of the mechanisms of inheritance for agronomic characters is essential if further improvements are to be attained. Knowledge of the type of gene action involved in the expression of quantitative characters such as grain yield would be useful in planning efficient breeding programs that could lead to substantial increases in yielding potential of wheat cultivars.

The second chapter of this thesis concerns the detection of various types of gene action but emphasis is placed on epistasis in the genetic control of quantitative characters of agronomic importance. Non-allelic interactions have long been neglected or assumed of minor importance in previous research. Now that advances in genetics have been realized, such simplifying assumptions should be carefully examined and their validity tested by experimental data. Should epistasis be detected for certain important characters, the magnitude of genetic variability arising from epistatic gene effects may need to be examined.

In the third chapter, heritability estimates from a cross involving two winter wheats of diverse origin and plant type are reported. Procedures are discussed that determine not only the type but also the magnitude of gene action in terms of additive, dominance and digenic interaction effects for several agronomic traits.

A somewhat similar procedure of analysis is used in the fourth chapter to evaluate the validity of the conventional additive-dominance model using data from two crosses of winter wheat.

Character association in a cross of winter wheat will be discussed in the fifth chapter to elucidate interrelationships among grain yield and related traits. Characterization of these relationships should provide valuable information on the choice of efficient selection procedures for the concerned characters.

Chapters II, III, IV, and V will be presented in a form acceptable to the Crop Science Society of America.1/ The same format is currently being adopted in most professional journals. Chapter VI is a general summary of the four studies. Additional data pertaining to Chapter II 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

Detection of Epistatic, Additive, and Dominance Variation in Winter Wheat (*Triticum aestivum* L.)[1]

ABSTRACT

Most genetic studies with plants have assumed the absence of epistasis without substantiating this assumption. Our objectives were to determine whether epistasis is a significant part of the genetic systems for selected traits among several winter wheat (*Triticum aestivum* L.) cultivars and to evaluate the importance of additive and dominance gene action for traits not influenced by epistasis. In each of two replicated experiments, two cultivars (referred to as lines L_1 and L_2) and their F_1 (L_3) were crossed to each of 10 cultivars used as testers. The deviations (tester X L_1 + tester X L_2 - 2 tester X L_3) were analyzed to provide a test for epistasis. An additive-dominance model was fitted to the data for those characters not affected by gene interactions.

Results of the two experiments were largely consistent with respect to the detection of epistasis. Non-allelic interactions affected the expression of heading date, kernels/spikelet, and grain yield, but not of plant height, protein content, tiller number, spikelets/

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[1] To be submitted for publication.

spike, and kernels/spike in both experiments. Epistasis was indicated for kernel weight in one experiment but not the other. Expression of epistasis was influenced by the testers used indicating that a limited number may be insufficient to detect non-allelic interactions for a character within a particular species.

Additive gene action was predominant in both experiments for protein content, spikelets/spike, and kernels/spike suggesting that improvement of those characters can be achieved through standard selection procedures. Evidence for dominance gene action was obtained for plant height and kernels/spike in one experiment.

The results of this study indicated that epistasis may be a non-trivial factor in the inheritance of agronomic traits. Genetic models neglecting epistasis may be biased to an unknown extent.

Additional index words: Heading date, Plant height, Protein content, Yield components, Grain yield, Gene action.

Choice of the most efficient breeding procedures depends to a large extent on knowledge of the genetic systems controlling the characters to be selected. Simple genetic models assume additivity of genetic effects over loci. We maintain that more realistic models should be used to account for epistasis in addition to additive and dominance variation. Cockerham (6) suggested that the frequent occurrence of non-allelic interactions in qualitative traits implies their existence in quantitative characters.

Much of the information on epistasis stems from studies in cross-pollinated crops, probably because of the major role of heterosis in those crops and the possible relationship between hybrid vigor and epistasis. Comstock and Robinson (8) indicated that non-allelic interactions might inflate the average degree of dominance by 10 to 25%. The importance of epistasis on the expression of several agronomic traits has been reported in a number of instances. Gorsline (10) found epistasis was a part of the genetic system controlling grain yield and nine other characters in corn (_Zea mays_ L.) populations. Sprague et al. (16) also indicated that epistasis may influence yield in corn. Studies in several other crops tended to indicate that epistatic gene action is a nontrivial factor in the inheritance of agronomically important characters. However, contrasting results have been obtained on several occasions. Burton (3) found that epistatic gene action had very little effect on forage yield in pearl millet (_Pennisetum typhoides_ Burm.). Stuber and Moll (17) detected epistasis in certain combinations of corn lines, but the contribution of epistasis to total genetic variance did not reach 10%.

Lack of information on interallelic interactions in winter wheat

(*Triticum aestivum* L.) warrants a study on the role of epistatic gene action. However, this should not be the sole concern of the plant breeder since additive and dominance variation may have a greater influence on the variation in grain yield and other economic characters. This study was designed to investigate the genetic systems controlling selected traits in a set of winter wheat cultivars with special emphasis on the detection of epistasis.

MATERIALS AND METHODS

The study consisted of two similar experiments conducted at the Agronomy Research Station, Stillwater, Okla. Table 1 lists the cultivars used in the two experiments along with their code numbers and places of origin.

In Experiment 1, cultivars 1 and 2 (hereafter referred to as lines L_1 and L_2) and their F_1 hybrid (designated as L_3) were crossed to cultivars 3 through 12. In Experiment 2, the L_1 and L_2 lines were cultivars 12 and 13, respectively. These, as well as their F_1 (L_3), were crossed to cultivars 2 through 11.

Crosses were made in the greenhouse in 1972 and 1973. Experiment 1 included 12 cultivars (the L_1 and L_2 lines plus 10 testers), 20 single crosses (3 X L_1, 3 X L_2,..., 12 X L_2), and 10 three-way crosses (3 X L_3, 4 X L_3,..., 12 X L_3). Experiment 2 also included 10 cultivars, 20 single crosses, and 10 three-way crosses. Each experiment was arranged in four randomized complete-blocks with 1 plot/entry/replication. The experimental units consisted of single rows 12.2 dm long and spaced 3.0 dm apart. Plantings were made on October 19, 1973, on a Kirkland silt loam soil at a seeding rate of 40 seed/row. The plots received 30 kg/ha of N and 34 kg/ha of P in mid-September, 1973, and were topdressed in early February, 1974, with 56 kg/ha of N. Measurements were recorded for the following characters:

Heading date. Number of days from March 31, 1974, to the date when 50% of the spikes in a plot had completely emerged from the flag-leaf sheath.

Plant height. Mean of two measurements/plot of the distance in centimeters between the ground surface and the tip of the spike on the tallest tiller, awns excluded.

Protein content. Grain from 10 spikes randomly selected from each plot were ground to determine percent grain protein using the Udy method.

Tiller number. Number of seed-bearing tillers along a random section of 3.0 dm of row in each plot.

Number of spikelets/spike. Ten randomly selected spikes from each plot (referred to above for protein content) were used to determine mean number of spikelets/spike.

Number of kernels/spike. The 10 spikes collected to determine the above character were threshed in bulk and the kernels obtained were counted to provide a mean estimate of kernels/spike.

Number of kernels/spikelet. Determined by dividing number of kernels/spike by number of spikelets/spike.

Kernel weight. The number of kernels obtained from the 10 spikes, referred to above, and their weight were used to estimate kernel weight expressed as gm/1000 kernels.

Grain yield. Rows were shortened to eliminate possible border effects and the remaining 9.1 dm was harvested in June, 1974, to determine grain yield expressed as gm/28 dm^2.

Analysis Procedures

The method for detecting epistasis used herein was that described by Kearsey and Jinks (12) which is essentially the same as that of Bauman (1). This method employs a set of testers crossed to each of L_1, L_2, and L_3 where L_3 is the $L_1 \times L_2$ F_1. The following model was used to describe the various phenotypes:

$$L_{ijk} = \mu + G_{ij} + r_k + e_{ijk} \quad \text{where}$$

L_{ijk} denotes the phenotypic value in replication k of the cross between L_i and tester j,

μ denotes the mean of all single and three-way crosses,

G_{ij} is the genotypic value of the cross between L_i and tester j,

r_k represents the effect of replication k, and

e_{ijk} is the error associated with that particular cross in replication k.

It then follows that $L_{1jk} + L_{2jk} - 2L_{3jk} = G_{1j} + G_{2j} - 2G_{3j} + (e_{1jk} + e_{2jk} - 2e_{3jk})$.

Deviations $L_{1jk} + L_{2jk} - 2L_{3jk}$ and their means over replications (denoted as $L_{1j} + L_{2j} - 2L_{3j}$) were computed for each tester. The variation of the deviations $L_{1jk} + L_{2jk} - 2L_{3jk}$ were also computed and pooled over testers to provide an error term. For the jth tester and for any number of loci, the expectation of $G_{1j} + G_{2j} - 2G_{3j}$ depends on epistatic gene effects because of the canceling of additive and dominance effects involved in the expression. It follows that if the mean squares for the deviations $L_{1j} + L_{2j} - 2L_{3j}$ are significantly greater than the pooled error, as evaluated by an F-test with 9 and 30 df, evidence of epistasis is indicated. However if the deviations were all of the same sign and of comparable magnitudes, the F-test would fail to detect epistasis even though present. To cope with this problem, if present, the overall mean of the epistatic deviations $L_{1j} + L_{2j} - 2L_{3j}$ was computed and its significance evaluated by a t-test with 30 df. Thus the F-test indicates whether testers differed in their contribution to the expression of epistasis for a particular trait, whereas the t-test shows the significance of the average epistatic deviation resulting from all testers in the experiment.

For those characters in which epistasis was not detected by either test, an additive-dominance model was fitted to the data as outlined by Jinks et al. (11) and Kearsey and Jinks (12). Direction of dominance was determined by calculating the linear correlation coefficient, $r_{s,d}$, between the sum $(L_{1j} + L_{2j})$ and the corresponding difference $(L_{1j} - L_{2j})$ for all testers. Positive and negative correlations would indicate a predominant direction of dominance towards decreasing and increasing values of the trait, respectively (11). Average degree of dominance was calculated as $(H_1/D)^{\frac{1}{2}}$ where H_1 and D are the dominance and additive variance components, respectively.

RESULTS AND DISCUSSION

Detection of Epistasis

Evidence for the presence of epistasis is indicated in Table 2 by the significance of the tester mean square, the overall epistatic deviation, or both. In Experiment 1, epistasis was detected for heading date, kernels/spikelet, and grain yield. Non-negative values for heading date predominated in the contributions to epistasis, resulting in a positive overall deviation. On the other hand, testers differed significantly in their respective contributions to epistasis in kernels/spikelet and grain yield. For those two traits, individual epistatic deviations are presented in Table 3 to show their directions and relative magnitudes and to identify those testers which interacted with L_1 and L_2 to produce significant deviations. Cultivars 11 and 12 in this experiment played a major but opposite role in influencing non-allelic interactions for kernels/spikelet, while tester 11 accounted for a major positive portion of the observed deviation in grain yield. These results, as well as similar findings by Burton (4), indicate that manifestation of epistasis is determined to some extent by the genotypes of the testers employed. Use of a limited number of testers might fail to detect epistatic gene action when in fact it is part of the genetic system.

In Experiment 2, evidence of epistasis was indicated for heading date, kernels/spikelet, kernel weight, and grain yield (Table 2). Except for grain yield, demonstration of epistasis was influenced by the testers used. Significant contributions were made by testers 6, 8, and 9 for heading date, testers 2, 4, and 11 for kernels/spikelet, and testers 2, 5, and 8 for kernel weight (Table 3). These results reinforce the suggestion that several testers should be used to detect epistasis. On the other hand, consideration of overall deviations obtained from different testers may also be misleading as positive and negative deviations may cancel and result in small, non-significant values. This situation occurred in this experiment for heading date, kernels/spikelet, and kernel weight, and in Experiment 1 for kernels/spikelet and grain yield (Tables 2 and 3).

The two experiments exhibited consistency of results relating to epistasis since in both cases non-allelic interactions were detected for heading date, kernels/spikelet, and grain yield, but not for plant height, protein content, tiller number, spikelets/spike, or kernels/spike. The only apparent discrepancy related to kernel weight. Reported results (9,18) indicate that epistatic gene action may contribute to the expression of kernel weight although no evidence of this was found by Bhatt (2). The discrepancy relating to this trait in our study might have resulted from environmental influences. Such influences have been reported by several workers (1,4,10,19). It must be emphasized that epistasis as measured by this procedure refers only to loci for which the L_1 and L_2 lines differ. Therefore, the discrepancy might be the result of genetic differences among the lines used in the two experiments. If this is the case, two or more pairs of L_1 and L_2 lines should be used for an efficient detection of epistasis.

The procedure described provides an unambiguous test for epistasis that is valid regardless of gene frequencies, degree of inbreeding, or linkage relationships. To our knowledge, this is the first time such a test has been reported in wheat. The importance of using several testers has been pointed out in both experiments and cannot be overemphasized. The presence of epistasis consistently detected for heading date, kernels/spikelet, and grain yield indicates that estimates of additive and dominance variances for those traits will be biased when procedures assuming no epistasis are used. Therefore, breeding techniques based on these estimates may not produce the desired results.

Cockerham (7) stated that the relative merits of current methods of selection with regards to epistatic gene action are not known. However, plant breeders realize that the presence of epistasis usually makes selection more difficult. We cannot determine from our data the most efficient breeding procedures when epistasis is operative. Standard hybridization and selection procedures could take advantage of epistasis if it is of the additive type (additive X additive, additive X additive X additive, etc). Other types of epistasis are not fixable by selection under self-fertilization, therefore would not be favorable for developing pure-line varieties. However, they may be useful in the development of hybrids. The procedure we used to detect epistasis is a first step in determining the importance and potential usefullness of epistasis. More elaborate experiments that include several generations will then provide information pertaining to the magnitudes of the different types of non-allelic interactions. The detection of epistasis followed by the determination of types and magnitudes of these interactions should ultimately lead to the development of more efficient breeding procedures.

Additive-Dominance Model

For those traits not affected by epistasis, a model accounting only for additive and dominance effects should be adequate to explain the genetic variation. Kearsey and Jinks (12) extended the method used by Comstock and Robinson in their design III (8) to estimate additive (D) and dominance (H_1) variance components from populations other than the F_2 of two inbred lines and in which gene frequencies need not necessarily be known. This procedure allows one to estimate D and H_1 from the variances of the sum ($L_{1j} + L_{2j}$) and the difference ($L_{1j} - L_{2j}$), respectively. The components of genetic variance estimated using this design are subject to bias from linkage relationships. However, if L_1 and L_2 are extreme high versus low cultivars for a given trait, both additive and dominance variance components will be affected to the same magnitude for that trait. Therefore, in determining the relative magnitudes of additive and dominance variance, linkage can be ignored.

Estimates of additive and dominance variance components for those traits not affected by epistasis in either or both experiments are shown in Table 4. It is realized that these estimates are confounded with year and location effects since the experiments from which they were derived were conducted at a single location in only one year. Additive gene effects accounted for a major portion of the genetic variation in both experiments for protein content, spikelets/spike, and kernels/spike. Of particular importance to the plant breeder seeking improvement of wheat quality is the absence of non-additive gene action for protein content. Chapman and McNeal (5) also found no evidence for epistatic gene action in grain protein among five spring wheat crosses whereas additive effects were significant in all crosses and consistently greater than dominance effects. Our results showed that additive gene action was more important than dominance gene action for tiller number, but significance was reached in Experiment 2 only. These findings suggest that selection for the yield components spikelets/spike, kernels/spike, and tiller number would be effective in this material.

Data from Experiment 1 showed only additive gene action to be involved in the inheritance of kernel weight, suggesting that improvement of this character could be achieved through standard selection procedures. Although this conclusion is supported by other investigations (13,15), it should be noted that epistatic gene action was detected for the trait in Experiment 2. It is possible that, although present, interallelic interactions for kernel weight were of small magnitude relative to additive and dominance components.

The only significant values for the dominance variance components were obtained in Experiment 2 for plant height and kernels/spike. Incomplete dominance for plant height was in the direction of taller plants $\left[(H_1/D)^{\frac{1}{2}} = 0.86,\ r_{s,d} = -0.88^{**}\right]$ whereas a lower level of partial dominance in the negative direction was found for kernels/spike $\left[(H_1/D)^{\frac{1}{2}} = 0.45,\ r_{s,d} = 0.69^{*}\right]$. The results for plant height agree with those of Romero and Frey (14).

The estimates of variance components herein reported have certain characteristics that should be clarified. Dominance variance, as estimated by this procedure, refers to loci which differ between the two lines. If the number of those loci are less than that of all loci segregating in the population for that trait, the domimance component underestimates total dominance variance. Nevertheless, significance of the variance $(L_{1j} - L_{2j})$ indicates that dominance gene action is involved in the inheritance of the given trait. Under the same conditions, the additive component includes a portion of the dominance variance and thus is biased upwards. Nonsignificance of the variance $(L_{1j} - L_{2j})$ indicates absence of dominance for that character. In this case the variance $(L_{1j} + L_{2j})$ provides an estimate of total additive variance free of dominance contamination regardless of the number of loci differentiating the lines L_1 and L_2. Our data showed no evidence of dominance for protein content, tiller number, and spikelets/spike in either of the experiments. This implies that additive variances for those traits were not biased by dominance contributions.

To derive more reliable estimates of genetic variance components, it has been suggested (12) that the lines L_1 and L_2 be extreme high versus low selections for the character under consideration. However, since this is not easy to achieve, particularly when a number of characters are studied, this type of analysis should be regarded as a means for showing the kinds of gene action involved rather than supplying unbiased estimates for the amounts of additive and dominance variation.

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LIST OF TABLES

Table 1. Wheat cultivars used in Experiments 1 and 2, their code numbers, and places of origin.

Code no.	Cultivar	Place of origin
1	Bezostaia 1	Russia
2	Centurk	Oklahoma
3	Caprock	Texas
4	Danne	Oklahoma
5	Scout 66	Nebraska
6	Palo Duro	Kansas
7	Agent	Oklahoma
8	Nicoma	Oklahoma
9	Osage	Oklahoma
10	Blueboy	N. Carolina
11	Arthur	Indiana
12	Tamwheat 101	Texas
13	Triumph 64	Oklahoma

Table 2. Analyses of epistatic deviations for selected traits in winter wheat.

	Expt.		Heading date	Plant height	Protein content	Tiller number	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight	Grain yield
Mean squares		df									
Testers	1	9	7.058	207.89	4.067	221.93	7.013	195.82	0.323*	94.711	1694.4*
	2	9	12.192**	236.01	13.180	337.51	5.264	94.08	0.238*	84.777*	1174.4
Error	1	30	3.442	129.26	6.612	176.68	6.561	90.78	0.115	46.865	719.5
	2	30	2.908	133.51	6.464	288.03	6.229	58.92	0.090	27.846	1004.2
Overall epistatic deviation †											
	1		0.675*	-0.325	0.110	3.050	0.290	1.045	0.029	0.454	3.900
	2		0.225	0.372	-0.015	1.125	0.625	2.300	0.075	1.625	10.300*

*,**Significant at P = 0.05 and 0.01, respectively.

†Significance of the overall epistatic deviation was evaluated by a t-test with 30 df.

Table 3. Epistatic deviations associated with individual testers for traits exhibiting significant differences among testers for the expression of epistasis as indicated by the mean square analysis in Table 2.

Experiment 1			Experiment 2			
Tester code no.	Kernels/ spikelet	Grain yield	Tester code no.	Heading date	Kernels/ spikelet	Kernel weight
3	-0.194	-24.25	3	-1.75	-0.087	-0.24
4	0.095	15.50	4	-1.00	0.313*	1.11
5	-0.096	20.00	5	1.00	0.087	9.24**
6	0.091	1.00	6	2.00*	0.176	1.14
7	-0.248	6.00	7	0.50	0.014	2.14
8	0.075	-2.75	8	-3.25**	-0.021	7.05*
9	0.052	18.00	9	2.50**	0.056	3.77
10	0.242	20.25	10	1.00	-0.003	-5.04
11	0.640**	41.25*	11	0.75	-0.351*	2.48
12	-0.366*	-16.00	2	0.50	0.566**	-5.40*

*,**Significant at P = 0.05 and 0.01, respectively.

Table 4. Estimates of additive (D) and dominance (H_1) variance components for traits not showing significant epistatic effects in winter wheat.

Traits	Experiment 1		Experiment 2	
	D	H_1	D	H_1
Plant height	10.55	-3.27†	19.98*	14.67*
Protein content	1.71**	0.47	2.81**	0.52
Tiller number	19.97	11.73	68.83**	-17.45†
Spikelets/spike	3.81**	0.05	3.38**	-0.01†
Kernels/spike	45.11**	3.45	38.00**	7.60*
Kernel weight	36.30**	-1.31†	-----‡	-----‡

*,** Significantly different from zero at P = 0.05 and 0.01, respectively.

† Negative values which may be interpreted as zero.

‡ Variance components not estimated because epistasis was detected in this experiment.

CHAPTER III

Inheritance of Eight Agronomic Traits in a Winter Wheat Cross[1]

ABSTRACT

Parents, F_1, F_2, and first generation backcrosses (B_1 and B_2) of a 'Centurk' X 'Bezostaia 1' cross were grown in a space-planted experiment to obtain information pertaining to the genetic systems controlling grain yield and other agronomic characters.

The F_1 deviated significantly from the midparental value for heading date, plant height, and kernels/spikelet, indicating a sizable amount of non-additive gene action for those traits. Narrow-sense heritability estimates were high for heading date, moderately high for kernel weight and plant height, moderate for number of tillers/plant, and low for kernels/spikelet, kernels/spike, grain yield and spikelets/spike. Some of those estimates may be biased upward as epistasis was found to contribute significantly to the genetic variation for heading date, plant height, tiller number, kernels/spikelet, and grain yield. No epistasis was detected for kernel weight, spikelets/spike, or kernels/spike, indicating that estimates of gene effects for those characters were free from linkage bias. Duplicate epistasis was detected for grain yield suggesting difficulty would be encountered

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[1] To be submitted for publication.

in selection for higher yield in this cross. Additive effects were the main source of genetic variation for kernel weight, indicating that early generation selection for higher kernel weight should be effective in this material.

Additional index words: *Triticum aestivum* L., Grain yield, Heading date, Plant height, Tiller number, Spikelets/spike, Kernels/spikelet, Kernel weight, Heritability, Gene effects, Epistasis.

Most of the wheat (Triticum aestivum L.) cultivars grown in the Great Plains are of the Turkey type characterized by a high tillering capacity, resilient straw, and medium to small spikes. Recently, new germplasm has been introduced for the purpose of changing the architecture of the present-day cultivars in an attempt to raise their yielding potential. An understanding of the genetic factors determining the inheritance of important agronomic characters would serve to guide breeding efforts of which the objective is to improve certain plant characteristics to enhance grain production.

Heritability of a character describes the extent to which it is transmitted from one generation to another and thus is a valuable tool when used in conjunction with other parameters in predicting the magnitude of genetic gain that would follow selection. Heritability estimates reported by several workers tended to indicate that certain morphological traits which influence grain yield in wheat are more heritable than yield itself. Reddi et al. (11) found relatively high heritability estimates for culm length and kernel weight in two wheat crosses. Low heritability values on the other hand were reported for grain yield in a study of hard red winter wheat by Johnson et al. (8).

Estimates of gene effects have a direct bearing on the method of hybridization and selection to be adopted in breeding programs. The magnitude of additive effects is particularly useful to the wheat breeder involved in developing pure-line varieties; whereas, information concerning dominance and epistatic gene effects can be valuable in the development of wheat hybrids. Working with durum wheat, Amaya et al. (2) found that dominance gene effects predominated in the inheritance of grain yield; whereas, mostly additive effects controlled plant height and heading date. Bhatt (3) reported that gene action involved in the inheritance of heading date, plant height, and kernel weight of two spring wheat crosses was primarily of the additive type. Sun et al. (12) found evidence of non-allelic interactions, but pointed out that additive and dominance effects made a major and consistent contribution to the expression of kernel weight in six spring wheat crosses. Chapman and McNeal (4) found that epistasis was involved in the expression of tiller number, grain yield, and plant height in a spring wheat cross.

The present study was initiated in order to estimate heritability and gene effects for grain yield and several other traits in a winter wheat cross involving two parents of diverse origin and plant type.

MATERIALS AND METHODS

Two winter wheat cultivars chosen on the basis of their contrasting characteristics in terms of plant type and yield components, were used as parents in this study which was conducted in 1973 at the Agronomy Research Station, Stillwater, Okla. One of the parents 'Centurk' is an awned wheat characterized by high tillering potential and relatively small kernels. This cultivar was developed by the Nebraska Agricultural Research Station in cooperation with the Agricultural Research Service, USDA. The other parent, 'Bezostaia 1', developed in the Russian Kaban region, is an awnless wheat having relatively few tillers per plant, but large kernels. The two cultivars differ also with respect to other characteristics, although to a lesser extent.

Crosses between the two varieties were made in the greenhouse in 1970 and the F_1 was backcrossed in 1971 to each of the parents (P_1 and P_2) to produce first backcross generations B_1 (P_1 X F_1) and B_2 (P_2 X F_1). Seed produced by self-pollination of F_1 plants was composited for use in the F_2 generation. Parents, F_1, F_2, B_1, and B_2 were planted in flats in the greenhouse, vernalized, and transplanted to the field on December 28, 1972. The layout was a randomized complete-block design with six replications. Plots within a replication were single rows 3 m long with 30 cm between adjacent rows. Plants within a row were 15 cm apart allowing a total of 20 plants/plot. The number of plots per replication was one for each of the non-segregating generations, two for each backcross, and four for the F_2. The terminal plant from each end of a plot was excluded from the analysis to minimize border effects. Due to a few cases of missing plants or very poor growth, data were recorded only on 16 plants in each plot. Where more were available, the 16 plants were chosen at random. The plots received a preplant fertilizer equivalent to 20-22-0 kg/ha of N-P-K applied in mid-September, 1972, and were top-dressed in late February with 56 kg/ha of N. The plots also received a 38 mm supplemental irrigation on May 22, 1973. All measurements for the following characters were made on a per-plant basis:

Heading date. Number of days from March 31 to the date when the first spike on a plant has completely emerged from the flag-leaf sheath.

Plant height. Distance in centimeters between the base of the culm and the tip of the spike on the tallest tiller, awns excluded (if any).

Tiller number. Number of spike-bearing tillers on each plant determined at harvest.

Spikelets/spike. Number of seed-bearing spikelets determined on a random spike taken from each plant.

Kernels/spike. Number of seed obtained by threshing the above spike.

Kernels/spikelet. Calculated as (kernels/spike)/(spikelets/spike).

Kernel weight. Weight in grams of 100 kernels randomly selected from each plant.

Grain yield. Total grain yield expressed in grams per plant. After harvest on June 21, 1973, all spikes of each plant were passed through a belt-thresher thus avoiding any seed breakage or loss.

Analysis Procedures

An analysis of variance including all generations was conducted to determine whether any differences existed among the generations for each character. Separate analyses for each population were also performed on each trait to determine within-plot variances.

Heritability in the narrow sense h^2_{ns} was estimated following Warner's method (13) as:

$$h^2_{ns} = \frac{2V_{F_2} - (V_{B_1} + V_{B_2})}{V_{F_2}}$$

where V_{F_2}, V_{B_1}, and V_{B_2} are the variances of the F_2, B_1, and B_2 generations and were estimated by the corresponding within-plot variances. A standard error for h^2_{ns} was derived as the square root of the following:

$$Vh^2_{ns} = \frac{2}{V_{F_2}^{\,2}} \left(\frac{(V_{B_1} + V_{B_2})^2}{df_{F_2}} + \frac{(V_{B_1})^2}{df_{B_1}} + \frac{(V_{B_2})^2}{df_{B_2}} \right)$$

In this formula df_{F_2}, df_{B_1}, and df_{B_2} refer to the degrees of freedom associated with V_{F_2}, V_{B_1}, and V_{B_2}, respectively. Significance of h^2_{ns} was also evaluated since the ratio $\frac{2V_{F_2}}{V_{B_1} + V_{B_2}}$ approximately follows an F-distribution (5) with n_1 and n_2 degrees of freedom, where $n_1 = df_{F_2}$ and $n_2 = \frac{(V_{B_1} + V_{B_2})^2}{\frac{V^2_{B_1}}{df_{B_1}} + \frac{V^2_{B_2}}{df_{B_2}}}$.

Expected gain from selection (G.S.) was calculated following Allard (1) as G.S. $= k\,\sigma_p\,h^2_{ns}$, where k is the selection differential in standard units, σ_p is the phenotypic standard deviation and was estimated here by the square root of the within plot-variance from the F_2 population, and h^2_{ns} is defined as above.

Scaling tests of Mather (9) with $A = 2\bar{B}_1 - \bar{F}_1 - \bar{P}_1$, $B = 2\bar{B}_2 - \bar{F}_1 -$

$\bar{P}_2$, and $C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$ were performed for all characters. A joint scaling test attributed to Cavelli by Mather and Jinks (10) was also conducted. This test uses data from P_1, P_2, F_1, F_2, B_1, and B_2 to provide estimates for the mean, additive, and dominance effects. These estimates are derived by the procedure of weighted least squares using as weights the inverses of the variances of the generation means. This joint scaling test also evaluates the goodness of fit of the 3-parameter model (mean, additive, and dominance effects) to the observed data by assuming that the sum of squared deviations (observed values - expected values)^2 weighted with the appropriate coefficients follows a X^2 distribution with 3 df. The failure of adequate fit would imply the existence of non-additive gene effects other than dominance.

Generation means for each character were also analyzed by the method of Hayman (7) to fit a six-parameter model. These parameters, using Gamble's designation (6), are the F_2 population mean or mean effect m, the pooled additive effects a, the pooled dominance effects d, the pooled additive X additive epistatic effects aa, the pooled additive X dominance epistatic effects ad, and the pooled dominance X dominance epistatic effects dd. In the estimation procedure presented by Hayman (7) the signs of a and ad depend on the relative values of P_1 and P_2 as well as those of B_1 and B_2. In what follows, P_1 will be the parent with the higher value, P_2 the parent with the lower value, and B_1 and B_2 the corresponding backcrosses. This will usually result in a positive value of a except for the relatively rare case when B_1 had a lower value than B_2. The equations giving the estimates of gene effects in terms of the generation means are (7):

$$\begin{aligned}
m &= \bar{F}_2 \\
a &= \bar{B}_1 - \bar{B}_2 \\
d &= -\tfrac{1}{2}\bar{P}_1 - \tfrac{1}{2}\bar{P}_2 + \bar{F}_1 - 4\bar{F}_2 + 2\bar{B}_1 + 2\bar{B}_2 \\
aa &= - 4\bar{F}_2 + 2\bar{B}_1 + 2\bar{B}_2 \\
ad &= -\tfrac{1}{2}\bar{P}_1 + \tfrac{1}{2}\bar{P}_2 + \bar{B}_1 - \bar{B}_2 \\
dd &= \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\bar{B}_1 - 4\bar{B}_2
\end{aligned}$$

Significance of the various gene effects for this model were determined by computing standard errors from the variances of the corresponding population means.

RESULTS AND DISCUSSION

Means and Variances

The six generations differed significantly with respect to heading date, plant height, tiller number, spikelets/spike, kernels/spikelet, kernel weight, and grain yield (Table 1). The failure to detect significant differences among generations for kernels/spike could be attributed to large sampling errors, but more likely is the result of the nearly equal parental means for this trait (Table 2). The F_1 deviated significantly from the midparental value for heading date, plant height, and kernels/spikelet indicating a sizeable amount of non-additive gene action is involved in the expression of those characters.

Within-plot variances were consistently greater for the segregating generations than for the parents or F_1 (Table 2). This was true even for kernels/spike showing that genetic variability does exist for this trait although no differences were detected among generation means. An excessive within-plot variance with respect to kernel weight was found for Bezostaia 1. This could be attributed to a large sampling error and/or a possible association between mean and variance for this character. No data transformation was made, although this may have removed this kind of association.

Heritability and Genetic Advance

Heritability estimates were high for heading date, moderately high for kernel weight and plant height, moderate for tiller number, and low for the remaining characters (Table 2). The heritability estimate slightly greater than one observed for heading date may be ascribed to several causes. Sampling errors, differential responses of the F_2 and backcrosses to the environment and non-allelic interactions can result in an upward bias of heritability estimates as measured by Warner's method (13). The heritability levels obtained for kernel weight and plant height are corroborated by previous reports (11). Large heritability values were also reported by Johnson et al. (8) for plant height, maturity, and kernel weight in winter wheat. The heritability estimates in our study tended to be high for those characters exhibiting wide differences between the parental means.

The values of genetic advance (G.S.) reported in Table 2 show the possible gain from selection as percent increase over the F_2 mean when the most desirable 5% (k = 2.06) of the F_2 plants are saved for the next generation. Heritability and genetic advance were calculated on an individual plant basis and may not apply to gain from selection based on other units. For most characters, heritability and genetic advance agreed satisfactorily in showing those characters for which selection in the F_2 would lead to substantial improvement. However, a moderate heritability estimate for tiller number was associated with the highest genetic advance. This may be due to a large environmental variation associated with this trait in the F_2 population. Reporting genetic advance along with heritability should be more informative than showing either alone. The ultimate usefulness of these estimates could be evaluated by conducting selection programs and comparing predicted with realized gains.

Gene Effects

The results showing the significance of the A, B, and C scaling tests are shown in Table 3. Significance of any of those tests indicates epistasis on the scale of measurement used. However, since each has its own expectation in terms of type and magnitude of epistatic effects, no agreement should be expected among those tests. The joint scaling test should be more powerful than any of the other tests in detecting epistasis since it uses information from all six populations. In fact, except for kernels/spike, the joint scaling test detected epistasis whenever it was declared significant by any of the individual scaling tests (Table 3).

Based on the joint scaling test a three-parameter model proved to be satisfactory in explaining the genetic differences for spikelets/spike, kernel weight, and kernels/spike (Table 4), indicating that epistasis is not involved in the inheritance of those characters. Chapman and McNeal (4) also found no significant epistatic gene effects for number of spikelets/spike and kernel weight in a spring wheat cross. Additive gene effects in our study appeared to be the most important factor contributing to the genetic control of kernel weight and spikelets/spike. Dominance effects were positive and smaller than additive effects for kernel weight. This agrees with results reported by Bhatt (3) who found partial dominance for heavier kernels, but a predominance of additive gene action in the control of this trait. A preponderance of additive gene effects coupled with high heritability and genetic advance found in our study for kernel weight indicate that selection for this character should be effective in this material. Dominance gene action played a major role in the inheritance of kernels/spike with a predominant direction towards fewer kernels/spike.

The three-parameter model was not sufficient to explain the genetic variation for heading date, plant height, tiller number, kernels/spikelet, and grain yield (Table 4). Therefore, the six-parameter model was invoked to determine the type and magnitude of gene action involved in the inheritance of those characters. The *aa*, *ad*, and *dd* effects provided by this model are unique; whereas, the *m*, *a*, and *d* effects obtained from the same model are contaminated by epistatic effects. Hayman (7) proposed that an approximation to epistasis-free estimates of *m*, *a*, and *d* would be the estimates obtained from the three-parameter model. Following this suggestion, it appears that dominance effects were at least as important in the expression of heading date as were additive effects (Table 4). Dominance in the direction of early maturity along with a positive dominance X dominance effect would indicate duplicate epistasis (10) which is undesirable in selection. Additive effects contributed significantly to the inheritance of plant height, but dominance effects were more important and favored tallness. Dominance X dominance effects were relatively important for plant height, although statistically nonsignificant. Epistasis was reported to be involved in the expression of plant height in spring wheat (4). Additive, *dd*, and to a lesser extent, *aa* effects contributed to the inheritance of tiller number in this material. The important contributions of epistasis to the genetic differences for heading date, plant height, and tiller number may have inflated the estimates of heritability obtained for those characters. Additive and dominance effects made the major contribution to the inheritance of kernels/spikelet whereas *aa* effects were numerically important. Dominance towards higher yields and significant negative *dd* effects indicated a duplicate type of epistasis for grain yield, suggesting that difficulty would be encountered in selection for higher yield levels.

In general, the important epistatic effects detected by the six-parameter model were of the dd type. The non-significance of the other types in this study, particularly the ad effects, may be due to canceling of positive and negative effects from different loci.

The analysis of generation means proved to be a simple and useful procedure for investigating the gene action involved in the inheritance of eight agronomic characters in this cross. Both the three- and six-parameter models were needed for a complete understanding of the genetic systems for the characters studied. Adequacy of the three-parameter model led to derivation of estimates free from linkage, if present, for additive and dominance effects for kernel weight, spikelets/spike, and kernels/spike. Lack of fit of the three-parameter model provided an irrefutable evidence of gene interactions for five of the eight traits. Information as to kind and magnitude of epistatic effects for those characters were provided by the six-parameter model.

The cross investigated involved two parents with contrasting characteristics, particularly in terms of tiller number and kernel weight. The present study did not provide information as to whether segregates combining the higher tiller number of Centurk and larger kernels of Bezostaia 1 can be obtained. The study did show, however, that selection among F_2 plants of this cross should be effective for kernel weight; whereas, selection for high tiller number would not be as successful.

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Table 1. Analysis of variance of data from parents, F_1, F_2, and backcrosses for eight agronomic characters of a Centurk X Bezostaia 1 cross.

Source	df	Heading date	Plant height	Tiller number	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight	Grain yield
Replications	5	35.76**	62.63	26.36	2.18	148.70	0.41	289.74**	135.21**
Generations	5	173.16**	1358.33**	312.56**	28.96**	177.66	1.18**	1538.44**	116.31**
Error	25	6.06	60.37	21.20	4.78	121.09	0.17	30.88	30.21

** Significantly greater than the error mean square at P = 0.01.

Table 2. Estimates of generation means, within plot variances, F_1-midparent deviation (F_1-MP), heritability in the narrow sense (h^2_{ns}) and expected genetic advance (G.S.) for eight agronomic characters in a winter wheat cross.

Generation or Parameter	Heading date	Plant height	Tiller number	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight	Grain yield
P_1 (Centurk)	40.53†	91.60	12.74	20.02	49.67	2.477	24.60	12.40
	2.90	26.00	8.00	1.48	29.25	0.050	7.33	7.02
P_2 (Bezostaia 1)	37.23	85.60	8.81	21.50	49.18	2.291	34.94	13.22
	2.59	13.58	5.45	1.76	38.94	0.069	21.21	10.16
F_1	37.44	95.27	10.49	21.10	47.20	2.235	30.99	13.96
	1.54	13.86	7.92	1.18	28.39	0.045	9.33	10.63
F_2	38.17	92.17	10.96	20.85	49.80	2.386	30.90	14.46
	11.34	50.93	8.69	2.39	53.85	0.084	14.67	13.06
B_1	38.42	94.93	12.82	20.57	49.76	2.417	28.07	14.98
	6.46	37.18	9.13	1.76	47.74	0.080	9.49	12.37
B_2	37.18	92.80	10.10	21.15	47.98	2.264	33.50	14.60
	4.72	32.18	5.15	2.81	52.05	0.064	10.37	11.69
F_1-MP	-1.44**	6.67**	-0.29	0.34	-2.22	-0.150*	1.22	1.15
h^2_{ns} ±s.e.	1.01**±0.10	0.64**±0.14	0.36*±0.18	0.09±0.20	0.15±0.20	0.28±0.18	0.65**±0.14	0.16±0.19
G.S. (%) ‡	18.4	10.0	19.8	1.3	4.5	7.0	16.5	8.1

*,** Significantly different from zero at P = 0.05 and 0.01, respectively.

† For each generation, the values in the upper and lower lines refer to means and within-plot variances, respectively. ‡Genetic advance (G.S.) represents the percent increase over the F_2 mean when the best 5% of the plants are selected.

Table 3. Significance of the A, B, C, and joint scaling tests evaluated for eight characters in a Centurk X Bezostaia 1 cross.

	Test			
Character	A	B	C	Joint
Heading date	*	ns	ns	**
Plant height	ns	**	**	**
Tiller number	*	ns	ns	*
Spikelets/spike	ns	ns	ns	ns
Kernels/spike	ns	ns	*	ns
Kernels/spikelet	ns	ns	*	**
Kernel weight	ns	ns	ns	ns
Grain yield	*	*	**	**

*,** Significant at P = 0.05 and 0.01, respectively.

ns Non-significant at P = 0.05.

Table 4. Gene effects from the three-parameter (3-PM) and six-parameter (6-PM) models estimated from means of parents, F_1, F_2, and backcrosses of a Centurk X Bezostaia 1 cross.

Model or effect	Heading date	Plant height	Tiller number	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight	Grain yield
3-PM								
m	38.77±0.11	89.77±0.11	10.99±0.17	20.73±0.09	49.64±0.38	2.40±0.02	29.92±0.24	13.19±0.19
a	1.17±0.11	3.01±0.30	2.04±0.16	0.72±0.09	0.28±0.38	0.11±0.02	5.16±0.24	0.45±0.20
d	-1.41±0.17	6.98±0.49	-0.01±0.32	0.33±0.14	-2.02±0.68	-0.14±0.03	1.33±0.40	1.73±0.37
X^2	21.57	23.16	10.99	0.76	6.90	12.56	2.11	21.56
P	<0.001	<0.001	0.010-0.025	>0.80	0.05-0.10	0.005-0.010	>0.50	<0.001
6-PM								
m	38.17±0.17	93.71±0.41	10.96±0.17	20.85±0.15	49.80±0.62	2.39±0.02	30.90±0.34	14.46±0.20
a	1.24±0.26	2.22±0.92	2.72±0.92	0.58±0.28	1.78±1.00	1.15±0.03	4.98±0.58	-0.38±0.61
d	-2.91±0.87	6.70±2.52	1.72±1.07	0.38±0.85	-5.96±3.25	-0.33±0.26	-0.15±1.83	2.49±1.52
aa	-1.47±0.85	0.03±2.47	2.01±1.01	0.03±0.83	-3.74±3.18	-0.18±0.10	-1.37±1.79	1.33±1.47
ad	-0.41±0.29	0.78±0.97	0.76±0.42	-0.16±0.29	1.53±1.08	0.06±0.04	-0.19±0.64	-0.79±0.65
dd	2.90±1.29	-7.15±4.15	-5.33±1.77	0.27±1.21	1.51±4.90	0.05±0.29	0.67±2.82	-6.96±2.70

CHAPTER IV

A Study of Gene Action for Heading Date, Plant Height, and Other Characters in Winter Wheat[1]

ABSTRACT

Two winter wheat (*Triticum aestivum* L.) crosses were used in this study to determine the type of gene action involved in the expression of a number of agronomic characters. An unweighted least squares procedure was adopted to analyze means of parents, F_1, and first generation backcrosses from each cross. Only additive gene effects were significant for plant height, number of tillers/unit of row, and kernel weight, indicating possible improvement of these characters through selection in early generations. Heading date was controlled by genes with additive and dominance effects which indicates that selection for this trait would be more effective if delayed until later generations.

Additional index words: *Triticum aestivum* L., Tiller number, Spikelets/spike, Kernel weight, Gene effects, Epistasis, Unweighted least squares procedure.

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[1] To be submitted for publication.

Knowledge of the type of gene action involved in the expression of a character is helpful in deciding on the breeding procedures to be used for improvement of the character. Whereas dominance gene action would tend to favor the production of hybrids, additive gene action signifies that standard selection procedures would be effective in bringing about advantageous changes in the character. Early maturity in wheat is a desirable attribute especially in the Southern Great Plains areas where it is associated with escape from pests, drought, heat, and other stress injuries that occur late in the growing season. Dwarf or semi-dwarf wheats are preferred to taller ones not only for their resistance to lodging but also because of an intrinsic potential for higher grain yields under favorable conditions. For these reasons, information concerning the nature of gene action for maturity and height in wheat would be a valuable tool for breeding better cultivars. From a diallel study of eight spring wheats, Walton (9) concluded that maturity was controlled by genes with both additive and dominance effects. Amaya et al. (1) found that mostly additive genetic effects governed the inheritance of heading date and plant height in durum wheat, although epistasis was detected in some cases.

Improvement of complex characters such as grain yield may be accomplished through the component approach of breeding (5,6). This method in general assumes strong associations of yield with a number of characters making up yield and simpler inheritance for these component characters. If this procedure is to be fully exploited, the gene action associated with the various yield components should be known. This study is an attempt to obtain information concerning the nature of gene action involved in the inheritance of a number of plant and seed characters in two crosses of winter wheat.

MATERIALS AND METHODS

This study was conducted in the 1973-74 crop season at the Agronomy Research Station, Stillwater, Okla. Two crosses of winter wheat, 'Centurk' X 'Bezostaia 1' and 'Triumph 64' X 'Tamwheat 101' provided the source of the experimental material used in this study. The parents of each cross have contrasting characteristics with respect to maturity, plant height, tillering, and kernel size. Populations for each cross were grown as separate experiments in randomized complete-block designs with four replications/experiment. Each replication included one plot each of P_1, P_2, F_1, B_1 (F_1 X P_1), and B_2 (F_1 X P_2). Experimental units consisted of rows 12.2 dm long and 3.0 dm apart. The plots were solid seeded on October 19, 1973, with a tractor-mounted cone planter at a rate of 40 seed/row. Data were collected from each plot on the following characters:

Heading date. Expressed as days from March 31 to the date when 50% of the spikes in a plot had completely emerged from the flag-leaf sheath.

Plant height. Mean of two measurements/plot of the distance in centimeters between the ground surface and the tip of the spike on the tallest tiller, awns excluded.

Protein content. Determined by the Udy method using grain from 10 spikes randomly selected from each plot.

Tiller number. Number of seed-bearing tillers along a random section of 3.0 dm in each plot.

Number of spikelets/spike. Ten randomly selected spikes from each plot (referred to above for protein content) were used to determine mean number of spikelets/spike.

Number of kernels/spike. The 10 spikes were threshed in bulk and the kernels obtained were counted to provide a mean estimate of kernels/spike.

Number of kernels/spikelet. Determined by dividing number of kernels/spike by number of spikelets/spike.

Kernel weight. The number of kernels obtained from the 10 spikes and their weight were used to estimate kernel weight expressed as gm/1000 kernels.

Grain yield. Rows were shortened to eliminate possible border effects and the remaining 9.1 dm was harvested in June, 1974, to determine grain yield expressed as gm/28 dm^2.

Analyses of variance were conducted for each cross on all characters. Generation means were then subjected to analysis for those characters in which significant genetic variation was detected in order to derive estimates of gene effects. The mean effect m, the pooled additive effects a, and the pooled dominance effects d are related to the generation means by the following equations (7):

$$\begin{aligned}
\bar{P}_1 &= m + a \\
\bar{P}_2 &= m - a \\
\bar{F}_1 &= m + d \\
\bar{B}_1 &= m + \tfrac{1}{2}a + \tfrac{1}{2}d \\
\bar{B}_2 &= m - \tfrac{1}{2}a + \tfrac{1}{2}d
\end{aligned}$$

Estimates of m, a, and d were derived from these equations by an unweighted least squares procedure. Variation among generations were partitioned into variation due to additive and dominance effects and that due to deviations from the additive-dominance model. This permitted a test of the adequacy of the model and an evaluation of the importance of the additive and dominance gene effects in their contribution to the genetic variation. The analysis also allowed removal of replication effect, thus increasing the precision of the experiment.

RESULTS AND DISCUSSION

Analyses of variance indicated significant differences existed among generations for heading date and plant height in both crosses and for tiller number, spikelets/spike, and kernel weight in one cross (Centurk X Bezostaia 1). No significance was observed in either cross for protein content, kernels/spike, kernels/spikelet, or grain yield. Data from the Triumph 64 X Tamwheat 101 cross showed no significance for tiller number, spikelets/spike, or kernel weight. Non-significance in all those cases may be ascribed to large error variances or narrow ranges between parental values for the concerned traits. Means for those characters which showed significance in one or two crosses are presented in Table 1. Centurk was later in heading, taller in height, possessed more tillers/unit of row, fewer spikelets/spike, and lighter kernels than Bezostaia 1. Triumph 64 was earlier and taller than Tamwheat 101. In no case was the F_1 significantly better than the more desirable parent. This indicates that non-additive gene action for most of the characters was of minor importance. However, the means of F_1 for heading date tended to indicate a certain degree of dominance for earliness.

For those cases where significant differences among generations were detected, a genetic analysis of generation means was warranted and consequently conducted. The additive-dominance model accounted for a major portion of the variation among generations (Table 2). Reduction in sums of squares due to fitting additive gene effects was significant or highly so in all cases. Reduction in sums of squares due to fitting dominance gene effects was significant in one cross for heading date and spikelets/spike (Table 2). In no case were the deviations from the additive-dominance model significantly greater than the residual mean square. This indicates that epistasis is not a determining factor in the expression of the characters in question. Therefore, the deviation and residual sums of squares were added to provide a pooled error in order to increase precision in the analysis. The estimates of gene effects obtained (Table 2) are not biased by linkage relationships, if present, since interallelic interactions were not involved. With the exception of heading date in the Centurk X Bezostaia 1 cross, estimates of additive effects were greater than dominance effects. Negative values for additive effects found in three instances (Table 2) were due to the choice as to which parent was designated P_1 or P_2. We adopted the designation of P_1 for Centurk in Cross 1 and Triumph 64 in Cross 2. Our results are consistent with those reported by several workers. Gill et al. (4) found that mainly additive gene action regulated the expression of plant height in wheat. Kernel weight was also reported to be under control of genes with predominantly additive effects (3,8). Contributions from dominance effects to the expression of spikelets/spike are at variance with findings by Walton (10) who reported only additive variation for this trait in spring wheat. This divergence in results can be attributed to differences in the material used in each case.

Dominance effects in our study were significant for heading date in the Centurk X Bezostaia 1 cross and approached significance ($P<.06$) in the other cross. The sign of these effects indicates dominance in the direction of earlier heading which is in agreement with reports by Anwar and Chowdhry (2) and Bhatt (3).

The results of this study indicate that selection in early segregating generations should be effective for plant height (particularly in the Triumph 64 X Tamwheat 101 cross), and for tiller number and kernel weight in the Centurk X Bezostaia 1 cross. On the other hand, conventional selection for early heading in both crosses should be delayed to later generations for a more tangible advance.

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Table 1. Observed means of parents (P_1, P_2), F_1, and backcrosses (B_1, B_2) for agronomic characters in two winter wheat crosses grown at Stillwater, 1974.†

	Heading date		Plant height		Tiller number	Spikelets/spike	Kernel weight
Generation	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 1	Cross 1
P_1	28.25	24.50	86.75	84.75	64.75	15.90	18.95
P_2	27.25	28.00	74.50	74.74	37.73	18.83	27.42
F_1	26.75	25.00	84.25	79.00	49.25	18.60	24.77
B_1	27.75	25.25	87.25	84.25	52.75	17.78	22.27
B_2	27.50	27.50	82.50	80.50	42.50	18.98	25.76
$LSD_{.05}$	.91	1.18	6.88	6.89	11.13	1.59	3.44
CV%	2.15	2.93	5.38	5.55	14.62	5.74	9.36

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† Cross 1 is Centurk X Bezostaia 1 and Cross 2 is Trimph 64 X Tamwheat 101. P_1 is Centurk or Triumph 64 depending on the cross; and P_2 is Bezostaia 1 or Tamwheat 101. $B_1 = F_1 \times P_1$, and $B_2 = F_1 \times P_2$.

Table 2. Analyses of variance, and estimates of gene effects for various agronomic characters in two winter wheat crosses.†

Analyses of variance		Heading date Cross 1	Heading date Cross 2	Plant height Cross 1	Plant height Cross 2	Tiller number Cross 1	Spikelet/ spike Cross 1	Kernel weight Cross 1
Source	df							
Replications	3	.600	.583	102.983*	6.317	138.000	3.247*	.465
Additive-dominance model	2	2.129**	18.614**	197.257**	112.829**	836.200**	12.325**	87.048**
Additive effects	1	2.025*	34.225**	342.225**	225.625**	1651.225**	19.600**	166.919**
Dominance effects	1	2.232*	3.004	52.289	.032	21.175	5.049*	7.177
Deviations from the additive-dominance model	2	.371	1.486	15.093	21.822	24.200	.389	.441
Residual	12	.350	.583	19.942	20.025	52.167	1.068	4.972
Estimates of gene effects								
m		27.86±.19	26.46±.28	81.32±1.44	80.61±1.47	50.50±2.27	17.47±.32	23.19±.68
a		.45±.19	-1.85±.27	5.85±1.39	4.75±1.42	12.85±2.19	-1.40±.31	-4.09±.66
d		-.89±.36	-1.04±.50	4.32±2.62	.11±2.69	-2.75±4.15	1.34±.59	1.60±1.24

*,** Significant at the .05 and .01 levels, respectively when tested against a pooled error with 14 df obtained by combining the deviation and residual mean squares.

† Cross 1 and Cross 2 refer to Centurk X Bezostaia 1, and Triumph 65 X Tamwheat 101, respectively.

CHAPTER V

Character Association in a Winter Wheat Cross[1]

ABSTRACT

Knowledge of the degree of association among agronomic traits is useful in the choice of efficient selection procedures. Correlation coefficients were calculated from parental, F_1, and F_2 data of a cross between two cultivars of winter wheat (*Triticum aestivum* L.) in order to assess the possibility of combining desirable characteristics from the parents. Path coefficient analysis was performed to show the magnitude of cause-and-effect relations among yield and yield components.

The results indicated that earlier heading was associated with fewer spikelets per spike and heavier kernels. Taller stature was correlated with later heading, more spikelets per spike, and larger kernels. A non-negative genotypic correlation was found between tiller number and kernel weight indicating the possibility of deriving from this cross genotypes combining the high tillering capacity of one parent and the heavier kernels of the other. Path coefficient analysis at the genotypic level showed that kernel weight exerted the highest direct and indirect effects upon grain yield. Therefore, more emphasis should be placed on kernel weight in selection for higher grain yield based on morphological characters.

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[1] To be submitted for publication.

Additional index words: *Triticum aestivum* L., Phenotypic correlation, Genotypic correlation, Environmental correlation, Path coefficient, Yield components.

Derivation of selection indices and calculation of correlated response depend upon knowledge of the correlations among the traits under consideration. Since the plant breeder is often faced with the problem of improving a number of characters simultaneously, and that he necessarily uses some sort of selection index, a better understanding of the association among traits of agronomic importance is needed for more efficient selection procedures. In wheat (Triticum aestivum L.), increasing grain yield potential is the major goal in most breeding programs. However, attempts to increase yield have not always met with success, due in part to the susceptibility of this trait to environmental fluctuations. The problem may be alleviated by considering subcharacters of yield that are more heritable. Grafius (6) visualized grain yield in oats (Avena sativa L.) as the volume of a rectangular parallelipiped with the three edges corresponding to three yield components. However, an increase in one edge of the parallelipiped does not necessarily result in a corresponding increase of the volume, because the responses of the components are not biologically independent. In fact negative associations among yield components are commonplace in the literature (1,4,5,9). Adams (1) suggested that correlations of this sort arise primarily as a result of developmental processes regulating the formation and growth of the components.

The objective of this study was to investigate the interrelationships among eight plant and seed characters and to determine the relative importance of the contribution to yield of four yield components in a cross of winter wheat.

MATERIALS AND METHODS

The two parent cultivars used in this study differ in level of expression for several agronomic characteristics. 'Centurk' is a bearded hard red winter wheat developed by the Nebraska Agricultural Experiment Station and the Agricultural Research Service, USDA. It is characterized by medium to early maturity, high tiller number, and relatively small kernels. 'Bezostaia 1' is a beardless winter wheat developed in the USSR. It is earlier in maturity than Centurk, has a smaller number of tillers, but larger kernels. Both parents, the F_1 and F_2 were grown in a randomized complete block design at the Agronomy Research Station, Stillwater, during the 1972-73 crop season. Each of six replications contained one plot for each of the non-segregating generations and four plots for the F_2. Plots within a replication consisted of single rows 3 m long and 30 cm apart. Plants within a row were 15 cm apart making a total of 20 plants/plot. The terminal plant from each end of a plot was excluded from the analysis to minimize border effects. Data were recorded only on 16 plants/plot since in several cases plants were missing or had a poor growth. Where more were available, the 16 plants were chosen at random. Measurements on a per-plant basis were recorded for the following characters:

Heading date. Expressed as days from March 31 to the date when the first spike on a plant had completely emerged from the flag-leaf sheath.

Plant height. Expressed as the distance in centimeters between the base of the culm and the tip of the spike on the tallest tiller, awns excluded.

Tiller number. Number of spike-bearing tillers per plant.

Spikelets/spike. Number of seed-bearing spikelets determined on a random spike taken from each plant.

Kernels/spike. Number of seed obtained by threshing the above spike.

Kernels/spikelet. Calculated as (kernels/spike)/(spikelets/spike).

Kernel weight. Expressed as gm/100 random kernels.

Grain yield. Expressed as gm/plant.

Growing conditions were generally favorable during the 1972-73 crop season and response of the plants was considered normal. Mean yields for P_1 (Centurk), P_2 (Bezostaia 1), the F_1 and F_2 generations were 12.4, 13.2, 14.0, and 14.5 gm/plant, respectively.

Phenotypic correlations on a plant basis (r_p) were calculated as

$$r_p = \frac{\text{cov }(x,y)_{F_2}}{\left[(\text{var }x)_{F_2} \quad (\text{var }y)_{F_2}\right]^{\frac{1}{2}}}$$

where cov $(x,y)_{F_2}$ represents the covariance between the characters x and y, and (var x)$_{F_2}$ and (var y)$_{F_2}$ denote the variances of x and y, respectively. Variances and covariances were based on measurements taken on individual plants of the F_2 generation, and were estimated by the within-plot mean squares and mean products, respectively.

Environmental correlations on a plant basis (r_e) were calculated as:

$$r_e = \frac{\text{cov}(x,y)_e}{\left[(\text{var }x)_e \quad (\text{var }y)_e\right]^{\frac{1}{2}}}$$

where cov $(x,y)_e = \frac{1}{4}$ cov $(x,y)_{P_1} + \frac{1}{2}$ cov $(x,y)_{F_1} + \frac{1}{4}$ cov $(x,y)_{P_2}$;

$$(\text{var } x)_e = \tfrac{1}{4}(\text{var } x)_{P_1} + \tfrac{1}{2}(\text{var } x)_{F_1} + \tfrac{1}{4}(\text{var } x)_{P_2};$$

and a similar formula for $(\text{var } y)_e$. In these expressions, $\text{cov } (x,y)_{P_1}$ is the covariance between characters x and y measured on plants of parent P_1, etc.

Genotypic correlations on an individual plant basis (r_g) were calculated as:

$$r_g = \frac{\text{cov } (x,y)_{F_2} - \text{cov } (x,y)_e}{\left[(\text{var } x)_{F_2} - (\text{var } x)_e\right]^{\frac{1}{2}}\left[(\text{var } y)_{F_2} - (\text{var } y)_e\right]^{\frac{1}{2}}}$$

While significance of the phenotypic and environmental correlation coefficients can be determined in the usual way, no test is as yet available for evaluating the significance of the genotypic correlation coefficient calculated as above. However, the relative magnitude of that coefficient will reflect the degree of genotypic association between two given characters.

To gain more information on the relative contributions of specific traits to grain yield, a path coefficient analysis as described by Dewey and Lu (4) was performed at the phenotypic, environmental and genotypic levels. Grain yield was considered as the resultant variable and tiller number, spikelet/spike, kernels/spikelet, and kernel weight were the causal factors. Path coefficients were derived from the equation $\underline{y} = \underline{R}\ \underline{p}$ where $\underline{y}$ denotes the vector of coefficients of correlation of yield with the four yield components mentioned above, $\underline{R}$ is a symmetric matrix whose elements are the coefficients of correlation among the components, and $\underline{p}$ is the vector of path coefficients. Solving that equation for $\underline{p}$ necessitated the inversion of a 4 X 4 $\underline{R}$ matrix. A path coefficient is a standardized partial regression coefficient and thus can exceed one in absolute value. Correlation coefficients, on the other hand, lie in the range of -1 to +1.

RESULTS

Correlations

Coefficients of linear correlations among the various traits in all combinations are displayed in Table 1. With few exceptions, genotypic correlations were of greater magnitude than phenotypic or environmental correlations. Phenotypic and genotypic correlations in general agreed in sign. Unless otherwise stated, further reference to correlations will indicate genotypic correlations. Heading date was positively correlated with plant height and spikelets/spike indicating that earlier genotypes were shorter and possessed smaller heads. Earlier maturing plants in this material also tended to have heavier kernels. Although statistically significant at the phenotypic level, the negative relationship between heading date and grain yield results more from environmental influences than genotypic association as indicated by the relative magnitude of phenotypic and environmental correlations and the relatively low genotypic correlation. Taller plants in this cross tended to possess more spikelets/spike, larger kernels, and higher yield. Correlation of yield with its components characters will be discussed in the next section in connection with the path coefficient analysis. Although the phenotypic correlation of tiller number with kernel weight was highly significant, the negative association between the two was due to environmental influences (Table 1). Positive correlations were anticipated and indeed obtained between kernels/spike and each of spikelets/spike and kernels/spikelet as these last two traits are the obvious components of the first. However, the values of these correlations indicate that kernels/spikelet may play a greater role in the determination of kernels/spike. The data of Table 1 also show that kernel weight and kernels/spikelet are negatively associated, suggesting that the simultaneous selection for large kernels and greater kernels/spikelet may not be successful in this cross.

Path Coefficient Analysis

Path coefficient analysis was used here to partition the correlations of yield with the contributing components into direct and indirect effects (Table 2). At the phenotypic level, tiller number had the highest direct effect upon grain yield. Kernel weight was the second highest in its direct effect on grain yield. Direct contributions of spikelets/spike and kernels/spikelet seemed of little importance.

The results of path coefficient analysis at the environmental level were similar to those at the phenotypic level except that direct and net effects were smaller in magnitude (Table 2).

At the genotypic level, direct effects and correlation ceofficients (net effects) were largest for kernel weight, relatively smaller for spikelets/spike and kernels/spikelet, and negligible for tiller number. Direct effects in every case were counterbalanced by indirect effects of opposing sign stemming from negative associations among characters contributing to yield. Therefore, correlation coefficients at all levels were smaller in magnitude than the corresponding direct effects.

DISCUSSION

Physiological processes in plants have a direct bearing on the association among yield components (1). Understanding the process of plant and seed growth therefore appears necessary for drawing sound conclusions from correlations. In the development of winter wheat in the Great Plains, two phases can be recognized. The vegetative phase starts upon germination in the fall and extends until early spring. During this period, formation of leaves and tillers takes place. The second or reproductive phase starts in early spring and includes chronologically: initiation of spikes, development of spikelets, development of florets, fertilization, and seed-filling (3). Therefore, it can be assumed that a longer growing period in the vegetative stage should lead to a better green canopy and greater accumulation of reserves in early spring which would be conducive to a higher number of spikelets/spike. Our results are in agreement with this hypothesis. Rawson (8) noted that higher values for spikelets/spike are associated with a longer period in the vegetative stage since it is during this period that potential spikelets begin to form. By the same token, genoytpes that head sooner should have a longer seed-filling period if the ripening process is not correspondingly shortened. This would explain why earlier genotypes tended to possess heavier kernels. Bhatt (2) and Weibel (10) obtained similar results.

The positive correlation of late heading and taller plant stature is corroborated by similar findings of Fonseca and Patterson (5). These results suggest that selection for shorter plants would be beneficial through a correlated response for earliness. No obvious reason besides genetic relationships could be invoked for such an association.

Positive interdependence between plant height and kernel weight cannot be easily explained although Bhatt (3) attributed it to a greater photosynthetic area possessed by taller plants. More likely, this association is due to the correlation of each of these two traits with heading date, the basis of which has been mentioned earlier. In any case, such relationship precludes the extraction from this cross of short-statured segregates with large kernels. This also was found to be the case in a number of instances (3,7,9).

One of the important results of this study was the lack of negative association between tiller number and kernel weight. This could have been expected if genetic relationships were known to be absent, since these two characters develop at different stages of the plant life and, as a consequence, have little probability of competing for environmental resources from a common pool. This result indicates that genotypes endowed with large kernels and high tillering capacity can be derived from this cross. The data however indicate that combining high kernel weight with a large number of kernels/ spikelet would be difficult. It is of course realized that the material in this study was space-planted; therefore, extrapolation of the results to other planting conditions cannot be made without caution.

Correlation coefficients are used to characterize the intensity of association between two traits without regards to causation. Path coefficient analysis on the other hand shows the magnitudes of cause-and-effect relationships and gives an insight into the behavior of the morphological traits as they interact with each other to produce grain yield. Path coefficient analysis does not determine what characters affect yield. It only indicates which of a number of variables postulated or known to affect yield has more or less influence on yield. In this study it was reasoned that yield is completely determined by tiller number, spikelets/spike, kernels/spikelet, and kernel weight. If other factors affect yield, they will do so only indirectly through their effects on these four components. Following this reasoning,it was found that the high direct effect of tiller number obtained at the phenotypic level is the result of environmental influences. On the other hand, the direct effect of kernel weight was highest among all components at the genotypic level. These results do not greatly differ from those that would have been provided by a mere examination of correlations. However, the analysis of path coefficients further revealed that kernel weight exerted the greatest indirect influence on yield through its interaction with other yield components. Therefore, more emphasis should be placed on kernel weight in index selection for yield based on morphological characters. Our results also showed that conclusions from correlations or path coefficient analysis based solely on phenotypic data may be misleading since environmental influences may contribute significantly to the degree of association among characters. Whenever possible, genotypic correlation and path coefficients should be used in analyses of character association.

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Table 1. Coefficients of phenotypic (P), environmental (E), and genotypic (G) correlations among eight agronomic traits in a winter wheat cross.

Trait		Plant height	Tiller number	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight	Grain yield
Heading date	P	0.4724**	-0.1172*	0.3688**	0.1056*	-0.0928	-0.1803**	-0.1999**
	E	-0.1397*	-0.2237**	0.0449	-0.0083	-0.0436	-0.0254	-0.2464**
	G	0.6889	-0.0779	0.6119	0.1858	-0.1413	-0.4277	-0.2333
Plant height	P		0.0285	0.2720**	0.0770	-0.0729	0.1881**	0.1722*
	E		-0.0983	0.0592	0.0239	-0.0036	0.0950	0.0165
	G		0.2476	0.4680	0.1256	-0.1425	0.3842	0.3904
Tiller number	P			-0.0107	-0.0361	-0.0395	-0.2092**	0.7631**
	E			-0.0205	0.0059	0.0239	-0.2972**	0.3742**
	G			0.0248	-0.1563	-0.2341	0.2017	-0.0041
Spikelets/spike	P				0.5773**	0.1028	-0.0747	0.0975
	E				0.5243**	0.0328	-0.0076	0.0942
	G				0.6517	0.2114	-0.2446	0.1077
Kernels/spike	P					0.8668**	-0.1668**	0.1293*
	E					0.8656**	-0.1092	0.0683
	G					0.8767	-0.03217	0.1831
Kernels/spikelet	P						-0.1686**	0.0987
	E						-0.1225*	0.0753
	G						-0.3022	0.1519
Kernel weight	P							0.2175**
	E							0.1862**
	G							0.3268

*,**Significantly different from zero at P = 0.05 and 0.01, respectively. No test of significance is available for genotypic correlations.

Table 2. Path coefficient analysis of the direct and indirect effects of tiller number, spikelets/spike, kernels/spikelet, and kernel weight in a cross of winter wheat.

Pathways of association	Phenotypic	Environmental	Genotypic
Effect of tiller number on grain yield			
Direct effect	.8641	.4751	-.0403
Indirect effect via spikelets/spike	-.0013	-.0021	.0025
Indirect effect via kernels/spikelet	-.0077	.0024	0.0569
Indirect effect via kernel weight	-.0920	-.1013	.0906
Net effect (total correlation)	.7631	.3742	-.0041
Effect of spikelets/spike on grain yield			
Direct effect	.1196	.1032	.1668
Indirect effect via tiller number	-.0092	-.0097	-.0006
Indirect effect via kernels/spikelet	.0200	.0034	.0513
Indirect effect via kernel weight	-.0329	-.0026	-.1098
Net effect (total correlation)	.0975	.0942	.1077
Effect of kernels/spikelet on grain yield			
Direct effect	.1947	.1023	.2429
Indirect effect via tiller number	-.0341	.0114	.0094
Indirect effect via spikelets/spike	.0123	.0034	.0353
Indirect effect via kernel weight	-.0742	-.0417	-.1357
Net effect (total correlation)	.0987	.0753	.1519
Effect of kernel weight on grain yield			
Direct effect	.4400	.3407	.4491
Indirect effect via tiller number	-.1808	-.1412	-.0081
Indirect effect via spikelets/spike	-.0089	-.0008	-.0408
Indirect effect via kernels/spikelet	-.0328	-.0125	0.0734
Net effect (total correlation)	.2175	.1862	.3268

CHAPTER VI

SUMMARY

Several studies were conducted in order to investigate the nature of inheritance of a number of agronomic characters in winter wheat.

A major part of this work was devoted to detecting epistasis as it affects the expression of certain agronomic traits in a set of winter wheat cultivars. In each of two experiments conducted in 1974 at one location, two cultivars (L_1 and L_2) and their F_1 hybrid (L_3) were crossed to each of 10 cultivars used as testers. The L_1 and L_2 cultivars were different in each experiment but nine of the 10 testers were common to both. The deviations (tester X L_1 + tester X L_2 - 2 tester X L_3) were analyzed to provide a test for epistasis. Additive and dominance variation was estimated for those characters not affected by epistasis. Results of the two experiments were largely consistent regarding the detection of epistasis. Non-allelic interactions affected the expression of heading date, grain yield, and kernels/spikelet, but not of plant height, tiller number, protein content, spikelets/spike, and kernels/spike. Epistasis was indicated for kernel weight in one experiment but not the other. Expression of epistasis was influenced by the testers indicating that a limited number may be insufficient to detect non-allelic interactions for a character within a particular species. The presence of epistasis consistently detected for heading date, kernels/spikelet, and grain yield indicates that estimates of additive and dominance variances for those traits will be biased when procedures assuming no epistasis are used. Therefore, breeding techniques based on these estimates may not produce the desired results. Additive gene action was predominant in both experiments for protein content, spikelets/spike, and kernels/spike, suggesting that improvement of those traits can be achieved through standard selection procedures. Evidence for dominance gene action was found for plant height and kernels/spike in one experiment. Incomplete dominance towards taller plants and partial dominance in the negative direction for kernels/spike were observed.

In another study, F_1, F_2, B_1, and B_2 generations were derived from a Centurk X Bezostaia 1 cross and utilized in a space-planted experiment to obtain information concerning the genetic systems controlling grain yield and related traits. The results indicated high values for narrow sense heritability and genetic advance for heading date, kernel weight, and tiller number. Some of those estimates may be biased by genotypic X environment and non-allelic interactions. In effect, epistasis was found to contribute significantly to the genetic variation for heading date, plant height, tiller number, kernels/spikelet, and grain yield. Additive effects were the main source of genetic variation for kernel weight suggesting that selection for higher kernel weight among F_2 plants of this cross should be effective.

In a similar study involving two winter wheat crosses, parents, F_1, B_1, and B_2 were grown in a solid-seeded experiment to determine the gene action involved in the expression of various traits. Only additive gene effects were significant for plant height, number of tillers/unit row, and kernel weight indicating possible improvement of these characters through selection in early generations. Heading date, on the other hand, was controlled by genes with additive and dominance effects which indicates that selection for this trait would be more effective if delayed until later generations.

Correlation coefficients were calculated from parental, F_1, and F_2 data of the previously described Centurk X Bezostaia 1 cross in order to assess the possibility of combining desirable characters from the parents. Path coefficient analysis was also performed on the data in an attempt to show cause-and-effect relationships among yield and its components. The results from this study indicated that earlier heading was associated with fewer spikelets/spike and heavier kernels. Taller stature was correlated with later heading, more spikelets/spike, and larger kernels. A non-negative genotypic correlation was found between tiller number, plant height and, kernel weight indicating the possibility of deriving from this cross genotypes combining the high tillering capacity of Centurk and the heavier kernels of Bezostaia 1. Path coefficient analysis at the genotypic level showed that kernel weight exerted the highest direct and indirect effects upon grain yield. It was concluded that more emphasis should be placed on kernel weight in selection for higher grain yield based on yield components.

APPENDIXES

LIST OF APPENDIX TABLES

kernel weight as determined on a cultivar or cross mean basis from parents and F_1's grown at Stillwater, 1974.

Appendix Table 1. Mean epistatic deviations ($L_{1j} + L_{2j} - 2L_{3j}$) associated with individual testers for all characters in Experiment 1.

Tester	Code number	Heading date	Plant height	Protein content	Tiller number	Spikelets/ spike	Kernels/ spike	Kernel weight	Kernels/ spikelet	Grain yield
Caprock	3	0.00	3.25	1.15	12.75	-1.20	-6.13	3.65	-0.194	-24.25
Danne	4	-0.25	7.00	1.10	-0.75	0.35	2.28	1.76	0.095	15.50
Scout 66	5	1.50	-11.75	0.58	-0.25	-1.98	-5.55	-2.46	-0.096	-20.00
Palo Duro	6	2.50	-1.25	1.10	7.50	0.70	2.88	-2.30	0.091	1.00
Agent	7	1.25	-3.00	-0.38	8.50	0.90	-2.88	4.25	-0.248	6.00
Nicoma	8	2.50	0.500	1.10	7.75	0.98	2.98	-5.12	0.075	-2.75
Osage	9	1.00	-5.00	0.80	-6.50	-0.63	-0.33	10.35	0.052	18.00
Blueboy	10	-0.75	8.50	-1.58	13.25	2.00	8.98	-0.83	0.242	20.25
Arthur	11	0.50	8.25	-0.73	0.50	2.10	15.03	-2.75	0.640	41.25
Tamwheat 101	12	-1.50	-9.97	-0.45	4.75	-0.33	-6.80	5.29	-0.366	-16.00

Appendix Table 2. Mean epistatic deviations ($L_{1j} + L_{2j} - 2L_{3J}$) associated with individual testers for all characters in Experiment 2

Tester	Code number	Heading date	Plant height	Protein content	Tiller number	Spikelets/ spike	Kernels/ spike	Kernel weight	Kernels/ spikelet	Grain yield
Centurk	2	0.500	4.00	-2.23	-9.00	1.35	11.70	-5.40	0.566	7.25
Caprock	3	-1.75	-2.75	0.55	9.25	0.08	-1.05	-0.24	-0.087	28.00
Danne	4	-1.00	2.25	-2.50	21.00	-0.93	3.40	1.11	0.313	20.50
Scout 66	5	1.00	4.50	0.18	-1.25	1.83	4.23	9.24	0.087	32.00
Palo Duro	6	2.00	-5.25	0.65	-1.25	0.33	3.40	1.14	0.176	0.25
Agent	7	0.500	-14.50	-0.50	-5.00	1.08	2.03	2.14	0.014	-14.50
Nicoma	8	-3.25	12.25	-1.28	5.00	2.13	3.15	7.05	-0.021	20.75
Osage	9	2.50	0.25	0.400	-7.50	0.23	0.55	3.77	0.056	-0.25
Blueboy	10	1.00	-5.25	0.68	5.25	1.68	3.35	-5.04	-0.003	-14.75
Arthur	11	0.75	8.25	3.90	-5.25	-1.05	-7.75	2.48	-0.351	23.75

Appendix Table 3. Plot means for nine characters recorded for the 12 cultivars grown in Experiment 1 at Stillwater, 1974

Cultivar	Heading date (days)	Plant height (cm)	Protein content (%)	Tillers/ 3 dm	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight (gm/1000 Ker.)	Grain yield (gm/28 dm^2)
Centurk	28.25	86.75	15.03	64.75	15.90	33.35	2.09	18.95	79.25
Bezostaia 1	27.25	74.50	15.50	37.73	18.83	35.03	1.86	27.42	65.25
Caprock	25.00	73.50	13.88	48.75	15.28	34.88	2.28	24.21	71.50
Danne	26.00	89.25	11.48	55.50	16.00	30.93	1.93	24.38	71.50
Scout 66	30.00	94.75	14.60	62.75	15.25	28.43	1.86	24.41	69.25
Palo Duro	30.75	79.25	16.83	71.25	14.60	23.25	1.60	20.72	49.00
Tamwheat 101	28.00	74.50	13.15	79.25	14.05	25.15	1.79	30.04	83.75
Agent	30.75	94.75	16.73	51.75	15.00	28.55	1.90	20.73	58.50
Nicoma	24.00	92.75	12.60	45.50	16.80	31.58	1.88	30.07	80.00
Osage	30.50	90.75	14.35	55.75	15.33	27.80	1.81	22.24	76.75
Blueboy	29.25	86.00	14.93	41.00	20.08	40.93	2.02	23.30	69.25
Arthur	23.00	78.00	14.43	45.25	17.18	30.33	1.76	27.40	82.75
LSD$_{.05}$	1.21	7.92	1.14	10.77	1.73	5.58	0.19	3.41	16.45

Appendix Table 4. Plot means for nine characters recorded for the 12 cultivars grown in Experiment 2 at Stillwater, 1974.

Cultivar	Heading date (days)	Plant height (cms)	Protein content (%)	Tillers/ 3 dm	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight (gm/1000 ker.)	Grain yield ($gm/28\ dm^2$)
Centurk	28.00	91.25	14.43	62.75	15.33	32.05	2.08	18.68	89.00
Triumph 64	24.50	84.75	14.30	53.75	15.03	26.65	1.77	25.91	79.50
Caprock	25.00	69.75	14.53	49.50	14.60	31.98	2.18	22.71	64.75
Danne	26.75	81.25	12.73	56.00	13.95	25.30	1.81	22.33	53.50
Scout 66	30.75	88.25	15.08	65.00	13.53	23.98	1.77	20.19	54.75
Palo Duro	30.00	79.25	16.68	67.00	14.88	25.63	1.72	16.78	53.50
Tamwheat 101	28.00	74.75	13.40	62.75	13.93	24.23	1.73	29.32	76.75
Agent	31.50	95.50	17.35	55.00	15.00	27.88	1.86	18.71	52.50
Nicoma	24.75	85.50	13.58	58.50	16.28	30.35	1.87	23.92	70.00
Osage	31.00	91.75	14.88	62.75	15.63	30.15	1.92	24.18	83.25
Blueboy	28.75	79.95	15.63	39.75	18.78	35.93	1.91	20.85	61.75
Arthur	23.50	74.50	15.40	52.50	16.95	29.85	1.76	26.84	86.25
$LSD_{.05}$	0.91	5.11	1.51	11.95	1.17	5.22	0.22	3.48	15.41

Appendix Table 5. Plot means for nine characters recorded for 20 single crosses involving the 10 testers and two lines grown in Experiment 1 at Stillwater, 1974.

Cross (Texter X line)	Heading date (days)	Plant height (cm)	Protein content (%)	Tillers/ 3 dm	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight (gm/1000 Ker.)	Grain yield (gm/28 dm^2)
3 X 1	26.00	83.50	14.45	43.00	17.65	35.60	2.01	24.37	67.25
4 X 1	25.50	83.50	12.73	38.75	18.38	33.88	1.84	29.44	73.50
5 X 1	27.00	89.75	15.63	39.50	17.35	29.85	1.72	25.64	61.50
6 X 1	25.50	85.15	14.38	44.25	18.95	39.18	2.06	23.87	73.50
7 X 1	26.50	92.25	14.83	41.25	19.08	35.30	1.85	26.28	80.50
8 X 1	25.50	87.75	14.15	39.50	19.60	35.23	1.80	27.97	73.50
9 X 1	26.00	88.00	13.93	41.25	19.20	34.53	1.79	33.56	89.75
10 X 1	27.75	89.50	14.40	39.00	20.10	40.15	1.99	25.18	81.50
11 X 1	25.00	86.75	15.55	39.00	18.73	31.90	1.70	30.82	77.25
12 X 1	24.75	83.25	13.45	38.25	17.50	33.30	1.90	31.46	72.50
3 X 2	25.50	86.75	13.60	46.75	16.85	39.13	2.32	25.47	82.50
4 X 2	26.25	90.00	13.73	40.00	17.93	37.20	2.07	24.72	81.50
5 X 2	28.00	85.50	13.90	54.75	15.88	30.45	1.92	23.82	78.00
6 X 2	29.00	91.00	15.03	56.75	17.55	34.05	1.94	20.44	81.00
7 X 2	29.25	93.25	14.70	54.25	17.43	32.28	1.85	23.20	86.00
8 X 2	25.50	87.75	12.85	55.75	17.93	36.05	2.01	25.15	87.75
9 X 2	28.00	91.00	13.98	52.25	17.43	34.00	1.95	28.71	109.75
10 X 2	27.50	93.00	13.73	44.75	20.35	43.03	2.11	23.13	84.75
11 X 2	26.50	86.00	16.03	56.50	18.13	27.53	1.51	29.70	84.50
12 X 2	27.75	87.50	14.55	56.00	16.38	28.70	1.74	31.38	85.50
$\text{LSD}_{.05}$	0.96	ns	1.39	9.28	1.24	5.73	0.24	4.45	15.58

Appendix Table 6. Plot means for nine characters recorded for 20 single crosses involving the 10 testers and two lines grown in Experiment 2 at Stillwater, 1974.

Cross (Texter X line)	Heading date (days)	Plant height (cm)	Protein content (%)	Tillers/ 3 dm	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight (gm/1000 ker.)	Grain yield (gm/28 dm^2)
2 X 12	27.25	86.25	14.33	51.50	15.28	28.88	1.90	26.20	95.00
3 X 12	24.75	74.50	13.34	46.75	13.73	28.83	2.10	26.79	73.00
4 X 12	25.75	80.00	12.43	57.50	13.68	23.68	1.71	28.32	71.75
5 X 12	28.75	91.00	15.20	55.00	14.38	26.15	1.82	24.03	66.25
6 X 12	28.75	79.50	15.18	64.00	14.45	25.33	1.74	22.14	65.75
7 X 12	29.50	90.50	15.18	48.50	15.85	27.43	1.73	25.06	69.25
8 X 12	24.75	83.25	13.00	47.25	13.98	25.63	1.83	30.20	66.25
9 X 12	28.75	87.00	14.10	59.50	13.55	23.50	1.73	26.30	66.00
10 X 12	27.75	80.50	14.25	45.00	16.65	31.23	1.88	23.09	64.75
11 X 12	25.75	82.25	14.78	48.75	15.35	26.13	1.71	28.70	98.25
2 X 13	25.75	85.75	13.65	53.00	17.33	35.83	2.07	24.06	90.25
3 X 13	24.50	83.25	13.65	45.00	15.35	32.88	2.14	27.10	81.50
4 X 13	25.25	83.25	12.78	57.50	15.00	27.08	1.80	25.34	69.75
5 X 13	26.25	85.00	13.98	57.75	14.75	22.48	1.52	30.88	74.75
6 X 13	25.75	83.75	13.73	55.25	15.98	28.73	1.90	24.99	85.00
7 X 13	27.50	84.50	14.33	53.00	15.48	26.90	1.73	23.97	62.75
8 X 13	23.50	86.00	13.08	56.75	15.35	27.63	1.80	27.71	79.00
9 X 13	27.25	82.75	14.60	60.60	14.38	24.50	1.69	26.64	77.25
10 X 13	26.75	96.75	14.83	47.74	17.18	32.73	1.91	24.17	68.50
11 X 13	24.50	85.00	16.98	49.00	16.85	21.03	1.25	32.60	71.50
$\text{LSD}_{.05}$	1.15	6.84	1.59	ns	1.46	4.70	0.19	3.81	18.71

Appendix Table 7. Mid-parent heterosis (MP), better parent heterosis (BP), and average direction of dominance (DD) determined from 40 single crosses for nine characters measured in two experiments at Stillwater, 1974.

	Experiment 1			Experiment 2		
Character	MP	BP	DD	MP	BP	DD
Heading date	10	3	-1.075**	6	0	-0.688**
Plant height	10	3	5.063**	6	1	2.825**
Protein content	1	0	-0.476**	1	0	-0.265
Tiller number	0	0	-6.338**	0	0	-4.600**
Spikelets/spike	12	3	1.459**	2	1	0.198
Kernels/spike	5	0	2.381**	1	0	-0.048
Kernels/spikelet	1	0	-0.026	0	0	-0.023
Kernel weight	7	3	2.747**	4	2	1.849**
Grain yield	7	2	8.838	2	0	2.300

** Significant at P = 0.01.

The columns for MP and BP show the number of crosses (from a total of 20) exhibiting significant heterosis at P = 0.05. Average direction of dominance (DD) was calculated as $\bar{F}_1 - \frac{1}{2}(\bar{T} + \bar{L})$, where $\bar{F}_1$, $\bar{T}$, and $\bar{L}$ represent the overall means for the single crosses, testers, and lines, respectively.

Appendix Table 8. Coefficients of phenotypic correlations among nine characters calculated on a variety or cross mean basis for parents and F_1 hybrids grown in Experiment 1 at Stillwater, 1974.

Character	Plant height	Protein content	Tiller number	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight	Grain yield
Heading date	.336	.606*	.496	-.249	-.295	-.266	-.625*	-.574
	.650**	.280	.574**	-.228	-.146	-.037	-.474*	.365
	.295	.500**	.563**	-.342	-.308	-.150	-.567**	-.240
Plant height		-.040	.167	-.067	-.061	-.045	-.314	-.056
		.224	.186	.253	.223	.083	-.393	.440
		.006	.028	.191	.151	.011	-.194	.232
Protein Content			.168	.012	-.117	-.245	-.570	-.674*
			.123	-.004	-.477*	-.597**	-.020	-.179
			.165	-.036	-.277	-.401*	-.303	-.412*
Tiller number				-.767**	-.705*	-.299	-.484	-.229
				-.544*	-.359	-.063	-.265	.491*
				-.726**	-.603**	-.159	-.435	-.029
Spikelets/ spike					.803**	.191	.168	.057
					.596**	.006	.037	-.016
					.765**	.084	.246	.247
Kernels/ spike						.702	.002	.169
						.805**	-.415	.071
						.703**	-.087	.260

Appendix Table 8 "Continued".

Character	Plant height	Protein content	Tiller number	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight	Grain yield
Kernels/ spikelet							-.172 -.533* -.374	.247 .099 .148
Kernel weight								.517 .153 .380*

*,** Significant at $P = 0.05$ and 0.01, respectively.

For each comparison, the numbers in the top, middle, and bottom lines are correlation coefficients derived from parents (10 df), F_1 hybrids (18 df), and parents and F_1 combined (30 df), respectively.

Appendix Table 9. Coefficients of phenotypic correlations among nine characters calculated on a variety or cross mean basis for parents and F_1 hybrids grown in Experiment 2 at Stillwater, 1974.

Character	Plant height	Protein content	Tiller number	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight	Grain yield
Heading date	.602*	.511	.380	-.199	-.189	-.102	-.557	-.416
	.370	.405	.270	-.075	-.099	-.100	-.586**	-.343
	.444*	.500**	.389*	-.121	-.080	-.035	-.611**	-.425*
Plant height		.322	.264	-.074	-.168	-.201	-.319	-.193
		.337	.048	.303	.006	-.210	-.059	-.006
		.258	.115	.066	-.109	-.208	-.090	-.070
Protein content			-.062	.266	.145	-.079	-.571	-.303
			-.104	.407	-.245	-.527*	.024	-.085
			.008	.340	-.028	-.288	-.368*	-.247
Tiller number				-.662*	-.663*	-.300	-.135	.058
				-.444*	-.464*	-.311	-.151	-.114
				-.510**	-.455**	-.216	-.277	-.099
Spikelets/ spike					.814**	.126	.012	.255
					.538*	-.013	-.162	.196
					.648**	.044	-.092	.204
Kernels/ spike						.678*	.130	.301
						.833*	-.557*	.298
						.787**	-.399*	.238

Appendix Table 9 "Continued".

Character	Plant height	Protein content	Tiller number	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet	Kernel weight	Grain yield
Kernels/ spikelet							-.228	.198
							-.531*	.227
							-.434*	.151
Kernel weight								.550
								.168
								.438*

*,** Significant at P = 0.05 and 0.01, respectively.

For each comparison, the numbers in the top, middle, and bottom lines are correlation coefficients derived from parents (10 df), F_1 hybrids (18 df), and parents and F_1 combined (30 df), respectively.

Appendix Table 10. Path coefficient analysis of the direct and indirect effects of tiller number, spikelets/spike, kernels/spikelet, and kernel weight as determined on a cultivar or cross mean basis from parents and F_1's grown at Stillwater, 1974.

Pathways of association	Experiment 1	Experiment 2
Effects of tiller number on grain yield		
Direct effect	.8611	.5930
Indirect effect via spikelets/spike	-.4594	-.2874
Indirect effect via kernels/spikelet	-.0841	-.1437
Indirect effect via kernel weight	-.3466	-.2612
Net effect	-.0290	-.0993
Effect of spikelets/spike on grain yield		
Direct effect	.6325	.5639
Indirect effect via tiller number	-.6255	-.3023
Indirect effect via kernels/spikelet	.0443	.0293
Indirect effect via kernel weight	.1959	-.0870
Net effect	.2472	.2039
Effect of kernels/spikelet on grain yield		
Direct effect	.5295	.6640
Indirect effect via tiller number	-.1367	-.1283
Indirect effect via spikelets/spike	.0529	.0249
Indirect effect via kernel weight	-.2980	-.4092
Net effect	.1477	.1514
Effect of kernel weight on grain yield		
Direct effect	.7969	.9427
Indirect effect via tiller number	-.3745	-.1643
Indirect effect via spikelets/spike	.1555	-.0520
Indirect effect via kernels/spikelet	-.1980	-.2882
Net effect	.3799	.4382

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