DETECTION OF EPISTATIC GENE ACTION IN TWO POPULATIONS OF WINTER WHEAT (*TRITICUM AESTIVUM L.* EM *THELL*)

By

JAMSHID JAFARI-SHABASTARI

Diploma
University of Tehran
Tehran, Iran
1964

Master of Science
University of Tehran
Tehran, Iran
1972

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Thesis Approved:

Edward L. Smith
Thesis Adviser

Dale E. Weibel

Robert L. Westerman

Robert D Morrison

James S. Kirby

Norman N Durham
Dean of the Graduate College

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CHAPTER I

INTRODUCTION

The cereal grain comprise the most important source of carbohydrates for human needs. Wheat is the most important cereal food crop in the world. It is a staple food item in the United States as well as in many other countries around the world. Improvement in the inherent yield potential of wheat cultivars would help greatly to overcome food shortages in those areas of the world that are now faced with production deficits.

Wheat breeders are attempting to develop improved cultivars of wheat by incorporating new germplasm into breeding populations and by devising more effective techniques to handle selection and evaluation systems. A better understanding of the genetic basis of the complex architecture of grain yield formation would be helpful in the breeding and development of improved wheat cultivars. The efficiency of wheat breeding programs would be increased if the plant breeder had a better understanding of the types of gene action controlling yield-related traits.

The total genetic variance of a trait can be partitioned into three types of gene action: additive, dominance, and epistasis. Additive and dominance types of gene action have been studied in some detail but not much is known about epistatic gene action. Most genetic models in plant breeding are designed to examine additive and dominance gene action only. These models assume that there are no epistatic effects. Epistatic gene action may, however, be important.

Evidence from several studies indicates that epistasis can play a significant role in both quantitative and qualitative characters. Although there have been some studies dealing with epistasis in self-pollinated crops, most of the epistatic studies to date have been applied to cross-pollinated crops. Ignoring the presence of epistatic gene action under the assumption of "absence of epistasis" will cause a bias in the estimate of additive and dominance genetic variance if epistasis is operating at a significant magnitude.

The primary objectives of this study were: 1) to determine whether epistatic gene action influences certain yield-related traits in two populations in wheat, 2) evaluate genotype x environment interaction for yield-related characters, and 3) compare 3-way crosses involving different testers.

CHAPTER II

REVIEW OF THE LITERATURE

The plant breeder is interested in using the most efficient breeding procedures in the improvement of economically important quantitative and qualitative traits in the crop under study. Appropriate breeding procedures, as well as the expected rates of progress to be made, are affected by the relative magnitudes of the types of gene action: additive, dominance, and epistasis. In studying gene action, most models have been concerned with the estimation of additive and dominance gene action with the assumption that epistasis is not important. Also, because of the rather complex genetic models and mating systems required for the study of epistasis, this component of genetic variance has been largely ignored in the past. But there are some reports in the past two or three decades which involved genetic studies regarding the detection of epistatic gene action in corn, pearl millet, wheat and flax (4, 6, 7, 13, 16, 21, 24, 25, 31, 33, 37, 38, 41).

The first statistical treatment of epistasis was presented by Fisher (14) in 1918. He developed a statistical model for partitioning the total genetic variance into its three components; additive, dominance, and epistatic effects. He stated that in the cases where more than one locus affected a given character, there may be a deviation from simple additive gene action between loci. In other words, the inter-loci interaction will be shifted from the simple additive effect to a more complicated action. He called this deviation "epistacy" or "dual epistacy".

Epistasis may be defined as inter-allelic or non-allelic interaction. There are three major types of epistatic interactions which are involved in most studies concerning gene action. These types are: additive x additive, additive x dominance, and dominance x dominance epistasis. The types and magnitudes of these epistatic interactions could be better used in breeding schemes if their effects were better understood.

Anderson and Kepthorne (2), Cockerham (8, 9), Hayman and Mather (18), Horner et al. (19), and many others followed Fisher's work in developing models and theories for estimating epistatic effects along with the other components of genetic variance. Comstock and Robinson (10) constructed several models with regard to determination of the effects of epistatic gene action. They indicated that the presence of epistatic gene action would influence the estimation of additive and dominance components of genetic variance and the estimates would be biased upward if models were used that ignored epistasis. They also proposed that genotype x environment interactions may cause an upward bias in the estimation of additive genetic variance.

Many workers have used the models constructed by Comstock and Robinson in many crops (21, 22, 23, 33). Kearsey and Jinks (23) extended these models and described a general test for epistasis. Jinks et al. (22) used a simple extension of the design III of Comstock and Robinson (10) in detecting the epistatic effects in certain quantitative traits on inbred lines of *Nicotiana rustica*.

Much of the research dealing with epistasis has been applied to cross-pollinated crops, probably due to the existence of relationships between hybrid vigor and the epistatic gene action. Bauman (4) conducted a study designed to detect the presence of epistatic gene action in yield, ear height, and kernel row number in corn. He conducted different sets of tests, each set comprised of the two single-crosses (Inbred A x Tester C and Inbred B x Tester C) and the three-way cross (Inbred A x Inbred B F_1 x Tester C). He stated that only the minimum amount of the epistasis present could be detected by this method. He concluded that there are significant interactions between epistasis and year effect which he considered to be a part of genotype x environment interactions.

Sprague et al. (37), in a study dealing with the estimation of epistatic gene action in grain yield of corn, obtained an estimate of epistasis from comparisons of population means over different sets of single and three-way crosses. They found considerable deviations due to epistatic gene effects and concluded that epistatic gene actions may influence yield potential in corn. According to Sprague et al. (37) three main factors must be considered in dealing with genetic studies: The type of gene action, the number of genes involved, and finally, the genotype x environment interactions.

Gorsline (16) noted significant effects of epistasis for yield, grain moisture, plant height, ear diameter, and several other characters in maize. He used five different environments (three environments in one year and two in another) and found that epistasis was present when using one or more testers with a combination of environments. Epistasis x environment interactions were seen mostly in plant height and yield, but were less frequent in the case of grain moisture and ear diameter.

Stuber and Moll (38) examined epistatic gene action in maize hybrids and their progeny and reported that epistasis was present in certain sets of crosses of corn lines for yield, ear number, days to tassel, and plant height. But they noted that the magnitude of epistasis was relatively small. In another experiment which consisted of the crosses among selected lines in maize (39), they found that in some characters, such as ear number, plant height, and ear height, the epistatic values were highly significant, but epistasis did not contribute significantly to yield or lodging. They also concluded that genotype x environment interactions should be conaidered in epistatic studies.

Cockerham (9), in a study of the implications of genetic variances in hybrid breeding schemes, applied mathematical models to compute the relative efficiency of different selection systems with regard to the epistatic gene action. He stated that some kinds of additive types of epistasis would be useful in mass selection and family selection schemes, but would be ineffective in progeny tests and other selection systems. Gamble (15), in a study of gene effects in corn, found that epistatic gene action was of significant influence in eight crosses of his experiment. He noted that, of all kinds of epistatic gene action influencing grain yield in corn, the additive x additive and additive x dominance gene effects were relatively more important than the dominance x dominance effects. He stated that epistatic gene actions were considered to be more effective than additive gene effects in the inheritance of yield in corn.

Burton (6), in a study of epistasis in pearl millet (Pennisetum typhoides Burm.), applied Bauman's method in detecting the presence of epistasis in forage yield. He concluded that although the amount of epistasis detected was not considerable, it is apparent that epistasis for forage yield occurs frequently. Yermanos and Allard (41) noted linear and curvilinear relationships between flax seed-oil content and levels of heterozygosis in flax. They used a genetic model which had been developed by Horner et al. (19) and stated that the curvilinear relationship might be an indication of the existence of epistatic gene action. Ketata et al. (24), in a study of the detection of various types of gene action in wheat, found that heading date, kernels per spikelet, plant height, tiller number, and grain yield were affected by epistatic gene action. They stated that the additive types of epistasis (additive x additive, additive x additive x additive, etc.) could be useful in selection procedures and standard hybridization schemes.

Chapman and McNeal (7) found epistatic gene action for plant height, tiller number, and grain yield in spring wheat. In the case of plant height, the most predominant type of epistasis was dominance x dominance, but in the inheritance of tiller number, the additive x additive type of epistasis played the major role. They stated that the detection of epistatic gene action is dependent on environmental conditions and suggested that genotype x environment interactions must be considered by plant breeders in their studies concerned with epistatic gene action. Sun et al. (40) reported the presence of epistatic gene action in kernel weight in crosses of spring wheat in which the parents were from different kernel weight classes. Apparently, when the parents are genetically diverse, epistasis is more likely to occur. Sandhu and Anand (30), in a study of inheritance of kernel weight in wheat, indicated that this trait was controlled by additive and dominance effects, as well as epistatic gene influences. According to their findings, dominance and epistatic gene actions were more important than additive gene action in contributing to kernel weight. With regard to epistatic gene action, additive x additive and additive x dominance interactions played a more important role than other types of epistatic interactions. Singh and Anand (32), in a study on the inheritance of kernel per spike in wheat, showed the importance of this trait in contributing to the final grian yield. They applied an epistatic model to estimate the effect of epistatic gene action to this trait and found that the dominance x dominance type of epistasis played a major role in the expression of kernels/spike. Complimentary epistatic gene action was found for kernel weight, kernels/spike, and grain yield in wheat by Copp and Wright (11). In contrast, duplicate epistatic gene action was associated mostly with tiller number in wheat in a report by Jasnowski (20). Paroda and Joshi (26) reported that kernel weight is the most reliable yield component contributing to grain yield in wheat. Yield in wheat is the product of three major yield related traits; tiller number, kernels/spike, and kernel weight (12, 17, 34). It is important to determine the types and magnitudes of gene action controlling these traits; it is of particular importance to determine whether epistatic gene action plays an important role. More studies dealing with epistatic gene action in yield components of wheat are needed.

CHAPTER III

MATERIALS AND METHODS

Materials and Mating Systems

This study consisted of two spaced-planted populations of winter wheat (*Triticum aestivum* L. em Thell.) which were evaluated at two locations in Oklahoma during the 1977-78 growing season. The two populations were studied at the Agronomy Research Station at Stillwater on a Norge loam soil and at the North Central Research Station at Lahoma on a Pond Creek silt loam soil. The populations were derived from mating systems which were designed to provide for the detection of epistatic genetic variance. Population 1 emphasized kernel weight differences and Population 2 emphasized spike size differences.

Population 1 involved 'TAM W-101', 'Lovrin 6', and their F_1 hybrid in crosses with a set of seven tester lines. Population 2 involved 'TAM W-101', 'F23-71', and their F_1 hybrid in crosses with the same set of testers. Crosses to produce the desired genotypes were made in the greenhouse in 1976 and 1977. For each population, the mating system resulted in 21 F_1's as follows: seven P_1/Tester F_1's, seven P_2/Tester F_1's and seven P_1/P_2/Tester F_1's. These F_1's, along with the parents and tester lines, resulted in 30 entries which comprised each population.

TAM W-101, which was a common parent in both populations is an adapted, semi-dwarf, hard red winter wheat which was released in 1971 by the Texas Agricultural Experiment Station. It has a high tillering potential and a high kernel weight value, but has a relatively low value for number of kernels/spike (29). TAM W-101 was selected from the crosses of 'Norin 16'/3/'Nebraska 60'//'Mediterranean'/'Hope'/4/'Bison'.

Lovrin 6 is a short strawed, early maturing winter wheat unadapted to Oklahoma. This line originated from Romania. Its pedigree is 'Fiorella'/'Bezostaia 1' (35). Of all the types examined in Oklahoma during the past 10 years, Lovrin 6 has had the highest kernel weight values (35).

F23-71 is a winter wheat characterized by large spikes, tall plant height, and relatively late maturity. This germplasm line, also originating from Romania, was selected from the cross 'Neuzucht'/'F362-62' (36). F23-71 is not well adapted for growing in Oklahoma, but it has had the highest value for spike size so far observed in Oklahoma (36).

The seven testers, common to both populations, consisted of six cultivars that originated in the Southern Great Plains and are currently in production in Oklahoma, and one cultivar from Bulgaria. These seven testers, along with their place of origin, plant height and maturity characteristics are listed below:

Tester	Place of Origin	Height	Maturity
'Burgas 2'	Bulgaria	Short	Early
'Centurk'	Nebraska	Mid Tall	Mid Late
'Newton'	Kansas	Short	Mid Late
'Osage'	Oklahoma	Tall	Late
'Payne'	Oklahoma	Short	Mid Early
'Triumph 64'	Oklahoma	Mid Tall	Early
'Vona'	Colorado	Short	Early

Field Layout

Seeds of the 21 F_1's, along with the seven testers and two parents which comprised each population, were planted in flats on October 28, 1977. Sufficient seeds of each entry were planted to provide for enough seedlings for replicated tests at two locations for each population. On November 18, 1977 plants at the 3-leaf stage of the two populations were transplanted on the Agronomy Research Station at Stillwater. Transplanting of the two populations was done on November 22, 1977 at the Agronomy Research Station at Lahoma.

There were two populations grown at each of two locations for a total of four separate experiments. Each experiment consisted of 30 entries arranged in a randomized complete block design with three replications. Each entry was assigned to one plot at random in each replication. Five test plants were grown in each plot with a border (non-test) plant at both ends of the plot. Individual plants were spaced at approximately 30 cm intervals within the row. Rows were 30 cm apart and each row comprised a plot. The two populations in each location were grown adjacent to each other, but were treated as separate experiments. The populations at Stillwater were top-dressed with 135 kg/ha of ammonium nitrate on March 17, 1978. Supplemental irrigation was applied during a brief dry period in early May. The populations at Lahoma were irrigated immediately after transplanting. They were top-dressed with approximately 135 kg/ha of ammonium nitrate in early spring. At maturity, each test plant (5 per plot) was harvested individually with the heads enclosed in a paper bag. The plants were stored for subsequent measurements.

Characters Measured on Individual Plants

Five different characters, consisting of plant height, three yield components, and grain yield, were measured on each individual plant in each population at each location.

Plant Height - This measurement was determined as the distance in centimeters from the crown to the average of the tips of the three tallest spikes, excluding awns.

Tiller Number - The number of fertile tillers in a single plant were counted for this measurement.

Kernels/Spike - This denotes the average number of kernels per spike. The three largest spikes of each plant were selected and threshed separately. The kernels were then counted, and the average number of kernels/spike were determined from these three spikes.

Kernel Weight - The kernels obtained from the three best heads were weighed to the nearest 0.1 gram and divided by the number of kernels comprising the sample. This trait was expressed as g/1000 kernels.

Grain Yield - This measurement was recorded as the total weight in grams of grain from each plant. This value also included the weight of grain from the three heads taken for kernels/spike and kernel weight measurements.

Statistical Analysis

A standard analysis of variance was conducted for each character in each population at each location. Two different analyses were conducted for each character: one consisting of all 30 entries, while the other consisted of the seven testers only. The overall means were computed for the five characters in each population at each location. The means of single-crosses, three-way crosses, and testers were computed so that group comparisons could be made with the overall mean for each character. Cross-products analyses were also conducted for all five characters evaluated in each population at each location and phenotypic correlation coefficients were computed for all possible pairs of characters from the data set of the seven testers.

Detection of Epistasis

Further analyses, which involved the main part of this study, were made for detecting epistatic gene effects in all the characters under study. In genetic studies involving quantitative traits, plant breeders are concerned with the relative magnitudes of the three types of gene action: additive, dominance, and epistasis. Since Fisher (14) first partitioned genetic variance into these three components, most quantitative genetic studies have been concerned with estimates of additive and dominance effects while ignoring epistasis. However, a few attempts have been made to study epistasis.

The model used for detecting epistasis in this study was that described by Bauman (4), and later used by Kearsey and Jinks (23) and by Jinks et al. (22). This model is based on the following relationship: $L_1+L_2-2L_3=0$, where L_1 is Parent_1 x Tester_1, L_2 is Parent_2 x Tester_1, and L_3 is the $F_1(P_1 \text{ x } P_2)$ x Tester 1. Epistasis would be indicated if $L_1+L_2-2L_3$ is significantly different from zero.

The following model was used in describing various phenotypes:

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

L_{ijk} indicates the phenotypic value in the kth replication of the cross

L_{ij} (Parent i and Tester j),

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

G_{ij} is the genotypic value of the cross L_{ij} (Parent i x Tester j),

r_k denotes the effect of replication k, and

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

It then follows that: $L_{1jk}+L_{2jk}-2L_{3jk}=(G_{1j}+G_{2j}-2G_{3j}) + (e_{1jk}+e_{2jk}-2e_{3jk})$ where L_{1jk}=Parent$_1$ x Tester$_j$, L_{2jk}=Parent$_2$ x Tester j, and $2L_{3jk}$= 2 times (P_1 x P_2) x Tester $_j$, all in the <u>kth</u> replication. Deviations $L_{1jk}+L_{2jk}-2L_{3jk}$ were summed over replications (denoted as $L_{1j}+L_{2j}-2L_{3j}$) and computed for each tester. Furthermore, G_{1j}, G_{2j}, and G_{3j} are genotypic values of Parent$_1$ x Tester$_j$, Parent 2 x Tester$_j$, and their F_1 x Tester$_j$, respectively and $(e_{1jk}+e_{2jk}-2e_{3jk})$ are the error values which were derived from the deviations $L_{1jk}+L_{2jk}-2L_{3jk}$ pooled over the testers.

All genotypic values as well as error values shown in the formula are contained in the phenotypic values. All these deviations were computed for each tester used in the study. In using this model to detect epistasis, the assumption was made that all error values are of equal magnitudes, in other words, the environmental effects are assumed to be homogeneous. This means that the expectations are: $e_{1jk}=e_{2jk}=e_{3jk}$. Therefore, the error values can be cancelled out in computation. Consequently, this assumption was made in computing the deviations of $L_1+L_2-2L_3$ and their means over replications for each tester.

An F-test with 6 and 14 df was used to evaluate the value of deviations of $L_{1j}+L_{2j}-2L_{3j}$ for each trait in each population. Epistasis was present if the computed values were significantly different from zero. The use of the F-test indicates whether the testers made different contributions to the epistatic gene action for a particular trait.

However, if the deviations are all of the same sign and of comparable magnitudes, the F-test will fail to detect epistasis even though present. Consequently, in such cases, the use of the T-test is suggested. The T-test provides an accurate measure of the average epistatic deviation resulting from all testers evaluated in the study. Consequently, a T-test with 14df was used to determine whether the overall deviations $L_{1j}+L_{2j}-2L_{3j}$ for epistatic expression of each character was significantly different from zero.

In addition to the detection of epistasis in individual experiments, the general model used in this study also provides for estimation of genotype x environment interaction for the characters measured. To estimate G x E interactions in this study, deviations $L_{1jk}+L_{2jk}-2L_{3jk}$ were computed for each test cross set in each of the two locations. In this case, G x E interaction is the epistatic x location interaction. A special analysis of variance was conducted to determine the different effects of testers in different locations. The corrected total source of variation in this analysis had 41 degrees of freedom associated with it, comprised of the source of variation due to location, replication within location, parental average, testers, location x tester, and error with 1, 4, 1, 6, 6, and 24 degrees of freedom, respectively. Epistasis x environment (location) estimates were indicated if significant mean square values were obtained for location, or location x tester in this analysis.

CHAPTER IV

RESULTS AND DISCUSSION

Analysis of Variance

Two spaced-planted populations, each consisting of 30 entries were evaluated at Stillwater, (Location 1) and Lahoma (Location 2) in 1978. Population 1 (TAM W-101/Lovrin 6 crosses) emphasized kernel weight differences, while Population 2 (TAM W-101/F23-71 crosses) emphasized kernels/spike differences. Growth and development of the plants at Lahoma suffered from early drought stress. The mean yield (average of both populations) of the 7 testers at Stillwater was 12.2 g/plant while at Lahoma the yield was 6.7 g/plant. Plant height means also reflected this difference, being 68.6 cm at Stillwater and 62.0 cm at Lahoma.

The mean square values for the five agronomic traits of the two populations at both locations are presented in Table I. For each population in each location two different analyses were conducted. One analysis included all 30 entries, while the other consisted of the testers only. Differences among entries with respect to all five characters in both populations and both locations were highly significant (at probability level 0.01) in both types of analyses with one exception. This exception was with grain yield in Population 2 Location 1, in the analysis of testers only. This mean square was not statistically significant at either the .01 or .05 probability level.

Character Means

Character means for plant height, tiller number, kernels/spike, kernel weight, and grain yield, based on individual plants, are presented in Tables II, III, IV, and V, respectively, for Population 1 Location 1, Population 1 Location 2, Population 2 Location 1, and Population 2 Location 2. The 30 entries shown in the first column of each table were comprised of 14 single-crosses, 7 three-way crosses, 2 parents (selfed), and 7 testers (selfed). In Population 1 at Location 1 (Table II), grain yield ranged from 8.8 g/plant for Osage to 18.0 g for TAM W-101/Payne (single-cross). The average grain yield/plant value of all single-crosses involving TAM W-101 was 15.5 g which exceeded the overall mean of 13.3 g/plant. TAM W-101/Osage was the only single-cross in this category which had a lower value than the overall mean. In contrast, somewhat lower values for grain yield/plant were observed in the single-crosses involving Lovrin 6. These crosses had an average of 11.7 g per plant. The average grain yield of all the three-way crosses was exactly the same as the overall mean (13.3 g/plant). Testers had an average yield/plant of 12.9 g which was slightly below the overall mean value.

In Population 1 Location 1, kernel weight ranged from 25.7 g/1000 kernels for Centurk to 41.3 g/1000 for Lovrin 6/Burgas 2 and Lovrin 6/Triumph 64 (single-crosses). The overall kernel weight mean in this population was 35.0 g/1000 kernels. The Lovrin 6 parent had a value of 34.9, which was below the overall mean. This was unexpected since Lovrin 6 has had high values for kernel weight for the past several years in Oklahoma tests. The particular environmental conditions that were encountered in the 1978 season may have reduced the kernel weight of Lovrin 6 more than expected. The mean kernel weight values of three-way crosses as well as the single-crosses involving Lovrin 6 were higher than the overall mean, but testers with an average of 30 g/1000 kernels were below the overall mean.

In Population 1 at Location 2 (Table III), the overall means for all characters were lower than the corresponding means for Population 1 at Location 1. The differences were seen especially in grain yield and kernels per spike. Grain yield ranged from 3.2 g/plant for both Centurk and Osage to 15.7 g/plant for TAM W-101/Burgas 2. These differences were significant at the .01 probability level. Single-crosses involving TAM W-101 and the three-way crosses, with average grain yield values of 10.3 g and 10.1 g/plant, respectively, were higher than the overall mean (8.6 g). The average value for single-crosses involving Lovrin 6 were 8.1 g/plant which was slightly lower than the overall mean. The testers had an average of 6.3 g/plant. This value was significantly different from the overall mean.

Kernel weight values in Population 1 at Location 2 ranged from 20.0 for Centurk to 40.3 g/1000 kernels for TAM W-101/Burgas 2 with an overall mean of 31.6 g/1000 kernels. These values were significantly different from the overall mean at probability level .01. The lowest mean value was observed for testers with an average of 24.9 g/1000 kernels which was significantly different from the overall mean value. The single-crosses involving each parent as well as all three-way crosses had average kernel weight values which were higher than the overall mean.

In Population 2 at Location 1 (Table IV), the values for grain yield/plant ranged from 5.7 g for F23-71/Osage to 17.9 g/plant for F23-71/Centurk. These values were significantly different from the overall mean value. The single-crosses involving TAM W-101 had a mean yield of 15.3 g/plant while three-way crosses averaged 14.7 g/plant. Both of these values exceeded the overall mean which was 13.6 g/plant. But they were not significantly different from the overall mean at either the .01 or .05 probability level. In contrast, the average value of single-crosses involving F23-71 was 12.8 g/plant which was lower than the overall mean. The mean value for the testers was 11.5 g/plant, which was also below the overall mean.

Kernels/spike ranged from 23.1 for F23-71/Osage to 54.0 for F23-71/Burgas 2. The overall mean of this population was 39.8 kernels/spike. The higher and lower values were both significantly different from the overall mean. The F23-71 parent had a kernels/spike value of 47.1 which was significantly higher than the overall mean value. This was expected since this parent has been the best genotype so far evaluated in Oklahoma with regard to this character. Single-crosses involving TAM W-101 had an average kernels/spike value of 37.8 which was slightly lower than the overall mean value. In contrast, the average value of single-crosses involving the F23-71 parent was 40.3 kernels/spike which was slightly higher than the overall mean. Three-way crosses had an average of 39.8 kernels/spike which was equal to the overall mean value. The mean value of the seven testers was 40.6 kernels/spike which was slightly higher than the overall mean value. However, this value was not significantly different from the overall mean.

For Population 2 at Location 2, the mean values of the five characters are listed in Table V. Grain yield ranged from 4.1 g for Burgas 2 to 12.5 g/plant for TAM W-101/Centurk (single-cross) with an overall mean value of 8.4 g/plant. The higher and lower values were significantly different from the overall mean value. The mean value for the single-crosses involving TAM W-101 was 9.9 g/plant which was higher than the overall mean value. On the other hand, the mean value of the single-crosses involving F23-71 at 7.9 g/plant was slightly below the overall mean. Also, the testers with an average of 7.0 g/plant were below the overall mean value.

The values for kernels/spike for Population 2 at Location 2 ranged from 23.9 for F23-71/Osage tc 41.9 for Newton with an overall mean value of 33.9. There was significant differences between these values and the overall mean value. The average value of single-crosses involving TAM W-101 was equal to the overall mean value. The three-way crosses and the single-crosses involving F23-71 parent had the average values of 33.5 and 32.9, respectively, which were slightly lower than the overall mean value. The average value of testers at 35.3 was slightly higher than the overall mean value.

Kernels/spike and grain yield values for the crosses between the Osage tester and the TAM W-101 parent in Population 1 were considerably lower than the corresponding single-cross value involving the other testers. Similar results were observed also for this tester in Population 2 at both locations. These findings with regard to the Osage crosses are perhaps due to climatic conditions in which this tester did not express its characterstics normally. There may have been a problem with hybrid necrosis. Hybrid necrosis symptoms have been observed in the past with some crosses involving Osage under certain environmental conditions.

Correlation Coefficients

Phenotypic correlation coefficients for all two-way comparisons among the five characters are shown in Tables VI, and VII. In all cases, correlation coefficients were computed from the data set of the seven testers.

Population 1

The phenotypic correlations for Population 1 (seven tester) at Locations 1 and 2 are shown in Table VI. The upper values in the table are the correlation coefficients for Location 1, and the lower values are those for Location 2. Statistically significant correlation coefficients were obtained between plant height and kernels/spike at both locations. These values were intermediate to high in magnitude and positive in sign. Statistically significant positive correlation coefficients were found between plant height and kernel weight in Population 1 which were low to intermediate in magnitude, positive in sign, and statistically significant at the 0.05 probability level at Location 1 and 0.01 probability level at Location 2. Tiller number was positively correlated with grain yield/plant with correlation coefficient of 0.753 at Location 1 and 0.842 at Location 2. Both of these coefficients were relatively high in magnitude and statistically significant at the 0.01 probability level. Kernel weight and kernels/spike were correlated positively at Location 1 but there was no indication of statistical significance for the coefficients among these two characters at Location 2. Positive correlation coefficients were obtained for two-way comparisons between grain yield and kernels/spike and between grain yield and kernel weight at both locations. Correlation coefficients were not statistically significant for two-way comparisons involving plant height and tiller number, tiller number and kernels/spike, tiller number and kernel weight in Population 1 at either Location 1 or Location 2.

Population 2

In Population 2 (seven testers) at Location 1 and 2, the phenotypic correlations for all two-way comparisons among five characters are listed in Table VII. Statistically significant correlation coefficients were obtained between plant height and tiller number at Location 2, but the correlation coefficients between these two traits at Location 1 were not statistically significant. Kernels/spike and plant height were significantly correlated at both locations. Correlations between plant height and kernel weight, and between plant height and grain yield/plant were intermediate in magnitude and significant at the 0.01 probability level at both locations. Statistically significant correlation coefficients were found between tiller number and kernels/spike, and between tiller number and kernel weight at Location 2, while the correlation values of two-way comparisons between these characters were not statistically significant at Location 1. Correlation coefficients of relatively high magnitude were found between tiller number and grain yield, as was the case in Population 1. At Location

1, this correlation coefficient was 0.754, while at Location 2 the value was 0.896. In both cases the coefficients were statistically significant at the 0.01 probability level. Correlations between kernels/spike and kernel weight were highly significant at Location 1 but not at Location 2. Correlation coefficients between kernels/spike and grain yield, and also between kernel weight and grain yield were statistically significant at the 0.01 probability level at both locations and intermediate in magnitude. All of the correlation coefficients in Population 2 at both locations were positive in sign.

Analysis of Variance for Epistatic Deviations

The results of epistatic deviations for the five characters are shown in Table VIII and IX. Mean square values for testers involving both populations are shown in the upper part of the tables, while the overall epistatic deviations are presented at the lower portion of the tables. Significant values of either the tester mean squares or the overall epistatic deviations, or both indicates the presence of epistatic gene action.

In Population 1 (TAM W-101/Lovrin 6) at Location 1 (Table VIII), epistasis was detected for kernel weight in the overall epistatic deviation analysis. There was no indication of significant epistatic gene action for plant height, tiller number, kernels/spike, or grain yield/plant in this population at Location 1. In Population 2 (TAM W-101/F23-71) at Location 1 (Table VIII) significant epistatic gene effects were observed for tiller number and kernel weight in the overall epistatic deviation analysis, while significant deviations were observed for kernels/spike and kernel weight in the among tester deviation analysis. In this population, epistatic gene action was not detected for plant height or grain yield/plant. For those characters in which there was no significant indication of epistasis, there is still a possibility that epistatic gene action was present but not detected (4). According to Bauman (4), in a theoretical example considering 2 alleles at 2 loci that show epistasis, the testers with AABB, AAbb, and aaBB genotypes will mask the epistatic expressions. Only (P_1 AAbb x P_2 aaBB) x Tester (aabb) would show epistatic deviations.

In Population 1 at Location 2 (Table IX) evidence of epistatic gene action was observed for plant height, tiller number, kernel weight, and grain yield/plant. Kernels/spike was the only character in this population which did not show evidence of epistatic gene influence at this location. In Population 2 at Location 2 (Table IX), there was no indication of significant epistatic effects, neither by the tester mean squares, nor by the overall epistatic deviations in the characters under study.

Considering Population 1 (TAM W-101/Lovrin 6), epistasis was detected for kernel weight at both locations and for plant height, tiller number and grain yield at Location 2 only. In Population 2, epistasis was detected for tiller number, kernels/spike and kernel weight at Location 1 but none of the five characters showed significant epistatic deviations in Location 2. The detection of epistatic gene action for kernel weight in Populations 1 and 2 in this study agrees with the reports by Sun et al. (40), Ketata et al. (24), Paroda and Joshi (26) who found epistasis to be present for kernel weight in studies on wheat. In contrast, Bhatt (5), Chapman and McNeal (7), and Ketata et al. (25), found no indication of the

the presence of epistatic gene action for this character in wheat. For tiller number, the detection of epistasis in Population 2 at Location 1 and Population 1 at Location 2 is in accordance with reports by Paroda and Joshi (26), Ketata et al. (25), and Chapman and McNeal (7). While the failure to indicate the effect of epistatic gene action for tiller number in Population 1 at Location 1 and Population 2 at Location 2 agrees with the finding of Ketata et al. (26).

The indication of epistatic gene action for kernels/spike in Population 2 at Location 2 is in accordance with the findings of Singh and Singh (33), and Paroda and Joshi (26). The failure to detect significant epistatic gene action for kernels/spike in Population 1 at Location 1 and Populations 1 and 2 at Location 2 agrees with the results of work by Ketata et al. (24, 25). Detection of the epistatic gene action for plant height in Population 1 at Location 2 is in accordance with the findings of Ketata et al. (25), Singh and Singh (33), and Amaya et al. (1), who found epistasis to be present for plant height in studies on wheat. For grain yield/plant, the presence of epistatic gene action indicated in Population 1 at Location 2 agrees with the findings of Ketata et al. (24), Chapman and McNeal (7), Singh and Singh (33), and Amaya et al. (1).

In the detection of epistasis in this study, the results tend to be inconsistent. Epistasis was indicated for four of the characters in only one of the four possible population-location combinations. Kernel weight had a significant epistatic deviation in three or four possible population-location combinations.

Epistatic Effects Associated With Individual Testers

The presence of epistatic gene action for kernels/spike and kernel weight in association with testers was indicated in Populations 1 and 2 at one or both locations. This is an indication of a significant epistatic contribution by the testers. In this case, testers differed in contribution of epistatic gene effects to these characters.

To determine the effects of individual testers in contributing to epistasis for each character, special computations were carried out based on the following model:

$$L_{1jk}+L_{2jk}-2L_{3jk}=G_{1j}+G_{2j}-2G_{3j}+(E_{1jk}+E_{2jk}-2E_{3jk})$$

All deviations with respect to the phenotypic expressions $(L_{1j}+L_{2j}-2L_{3j})$, were computed separately for each tester in each population evaluated at each location. The results of these computations for each character are presented in Tables X, through XIV. Plus and minus values presented in these tables indicate the direction and relative magnitudes of epistatic deviations of individual testers based on the $L_1+L_2-2L_3$ model, which are associated with the character in question.

Epistatic deviations associated with individual testers for plant height are presented in Table X. There was only one significant deviation for this character. This deviation was observed with the tester Newton in Population 2 at Location 2. In this case, there was an indication of a significant negative epistatic interaction for plant height involving the tester Newton.

Epistatic deviations associated with individual testers for tiller number are presented in Table XI. There were four significant deviations for this character; two of which involved the tester

Osage. Epistatic gene action for tiller number involving Osage was indicated in Population 2 at Location 1 and also in Population 1 at Location 2. There was a significant deviation for tiller number associated with the tester Payne in Population 1 at Location 2 and with the tester Vona, also in Population 1 at Location 2.

For kernels/spike (Table XII), three significant epistatic deviations were detected. These three significant deviations involved three different testers in Population 1 at Location 2. There was a positive significant deviation associated with Burgas 2, a negative significant epistatic effect associated with Osage, and a negative significant effect associated with Payne.

Individual epistatic deviations for kernel weight are presented in Table (XIII). Seven significant deviations were observed for this character. The tester Centurk in Population 1 at Location 1 contributed a major negative portion of the overall deviation in kernel weight. In contrast, the tester Newton showed a positive significant epistatic deviation for this character in Population 1 at Location 2 and in Population 2 at Location 1. Significant negative deviations for kernel weight were associated with testers Payne, Triumph 64, and Vona in Population 1 at Location 2. Vona also showed a significant positive deviation in Population 2 at Location 1. Newton and Vona contributed positive epistatic effects in Population 2 while Centurk, Payne, Triumph 64, and Vona were associated with significant negative deviations in Population 1 for kernel weight.

The epistatic gene influences associated with individual testers for grain yield are shown in Table XIV. As shown in this table, there was only one case of significant deviation due to epistasis associated with individual testers. This was the significant negative deviation associated with Burgas 2 in Population 2 at Location 2.

The pattern of epistatic deviations associated with individual testers for all five characters studied in the two populations at the two locations, indicate that a relatively large number of testers should be used to detect epistasis gene influence in studies of this type. A small number of testers might not be enough to detect epistatic expression for a character under study. Seven testers were used in this study and several cases of epistasis were detected but a larger number of testers would have been more desirable. The genotypes of the parents and the testers in epistatic studies are also important. In an ideal situation for detecting the epistatic gene action by using the previously mentioned model, one of the parents could be dominant, the other recessive for the character under study, and the testers should be recessive (4).

G x E Interactions for Epistatic Effect

The detection of epistatic gene action for certain characters in one location but not in the other within each population suggests that environmental influences associated with locations plays an important role in determining the influence of epistatic gene action. This suggests a possible non-linear effect of different environments. The importance of genotype x environment interactions in regard to epistasis were indicated in different crops by several workers (3, 4, 6, 21, 27, 28). In the present study, the occurance of significant epistasis x location interactions would be an indication of a differential response among genotypes to the prevailing environmental condition in the two different locations in which the populations were tested.

Tables XV and XVI present the analysis of epistatic deviations for GxE interactions for five characters in Population 1 (TAM W-101/ Lovrin 6) and Population 2 (TAM W-101/F23-71), respectively. The values shown in the tables are deviation mean squares for plant height, tiller number, kernels/spike, kernel weight, and grain yield associated with testers analyzed over the two locations. The model used to detect the epistatic deviations was also applied to compute $L_{1jk}+L_{2jk}-2L_{3jk}$ deviations for each population at each location to determine GxE interactions. Significant mean square values associated either with locations or location x tester sources of variation (Tables XV and XVI) would indicate the presence of significant epistatic x location (GxE) interactions.

In Population 1, as shown in Table (XV), there was no indication of significant GxE interactions with respect to any of the characters since none of the critical mean squares reached statistical significance. In Population 2, as shown in Table XVI, significant epistatic x location (GxE) interactions were indicated for plant height and tiller number. Many workers have indicated the influence of environment affecting epistatic gene action (3, 4, 6, 21, 27, 28,). Burton (6), indicated the importance of the environmental effects in the expression of epistatic gene action in pearl millet forage yields and stated that epistatic gene action may have a larger interaction with the environment than in the case of dominance gene action.

Although the importance of GxE interaction has been shown by several investigators and is generally considered to be an important factor in influencing epistatic gene action, the results of this study involving two populations of winter wheat at two locations showed that epistatic x location interactions were of little importance. However, the possibility exists that the analysis used in this study may not have been sensitive enought to detect epistatic x location interactions for kernels/spike, kernel weight, and grain yield.

CHAPTER V

SUMMARY AND CONCLUSIONS

Two populations of winter wheat (Triticum aestivum L. em Thell), derived from mating systems which were designed to provide for the detection of epistatic gene action, were evaluated as spaced-plants at the Agronomy Research Stations in Stillwater and Lahoma, Oklahoma, in the 1977-78 crop season.

Population 1 (TAM W-101/Lovrin 6), emphasized kernel weight differences while Population 2 (TAM W-101/F23-71), emphasized kernels/spike differences. Both populations had one parent in common (TAM W-101), which was an adapted, semi-dwarf, hard red winter wheat cultivar. The other two parents, Lovrin 6, a large-seeded genotype, and F23-71, a large-spiked genotype, originated from Romania. Neither of these Romanian germplasm lines is adapted for production in Oklahoma. Seven testers, common to both populations, were crossed with each of the two parents and their F_1 hybrids to produce 21 F_1's (seven P_1/Tester F_1's, seven P_2/Tester F_1's, and seven P_1/P_2//Tester F_1's) for each population. The seven testers consisted of six cultivars adapted to the Southern Great Plains (Centurk, Newton, Osage, Payne, Triumph 64, and Vona) and one unadapted cultivar (Burgas 2) from Bulgaria.

Thirty entries, consisting of 21 F_1's, 2 parents, and 7 testers, for each population were grown in each location. Seeds of the 30 entries of each population were planted in flats on October, 1977. Then in November, 1977, plants at the 3-leaf stage were transplanted to the field (2 populations in each location) utilizing a randomized complete-block design with 3 replications. Each plot consisted of five test plants which were spaced approximately 30 cm from each other within the row. There was a non-test border plant at either end of the row. Rows were 30 cm apart. Data were obtained on five agronomic characters: plant height, tiller number, kernels/spike, kernel weight, and grain yield/plant in each population at each location on an individual plant basis.

Two sets of analyses of variance was used: One analysis included all 30 entries, while the other consisted of the seven testers only. In both sets of analyses, differences among entries with respect to all five characters were highly significant except for grain yield in Population 2 at Location 1 for tester set only, in which no significant value was obtained. Mean values were computed for all characters in each population at each location. Differences in grain yield and kernel weight values in Population 1 (TAM W-101/Lovrin 6), and grain yield and kernels/spike values in Population 2 (TAM W-101/F23-71), based on group comparisons for the average performances of single-crosses, 3-way crosses, and testers (selfed) were examined in each population.

The main part of this study was devoted to the detection of epistatic gene action. An epistatic model of $L_{1jk}+L_{2jk}-2L_{3jk}=(G_{1j}+G_{2j}-2G_{3j})+(E_{1jk}+E_{2jk}-2E_{3jk})$ was used to detect the presence of epistatic genetic variance. Tester mean square values ($L_1+L_2-2L_3$ for each tester) as well as the overall epistatic deviations were used to detect the presence of epistatic gene action affecting the five agronomic characters in each population at each location. The deviations of $L_1+L_2-2L_3$ associated with individual testers were examined to determine whether particular testers made different contributions to epistatic gene action for the characters involved in this study.

With regard to this study, there were eight possible cases for detecting epistasis for each character (two populations, two locations, and two methods of detection). Significant epistasis was detected as follows:

Plant Height - epistasis was detected for this character in one out of eight cases. This indication was found in Population 1 at Location 2 in the overall epistatic deviation analysis.

Tiller Number - epistatic gene action was detected in two out of eight cases. These were found in Population 1 at Location 2, and in Population 2 at Location 1, both in the overall epistatic deviation analysis.

Kernels/Spike - epistatic gene action was detected in one out of eight cases. This indication was found in Population 2 at Location 1 in the among tester deviation analysis.

Kernel Weight - epistasis was detected in five out of eight cases. These deviations were found in Population 1 at Location 1 in the overall epistatic deviation analysis, in Population 1 at Location 2 in both among the tester and the overall epistatic deviation analyses, and in Population 2 at Location 1 in both among the tester and the overall epistatic deviation analyses.

Grain Yield - epistasis was detected for this character in one out of eight cases. This deviation was found in Population 1 at Location 2 in the overall epistatic deviation analysis.

To determine the specific contribution of individual testers to epistatic expression of each character, computations were done utilizing the same epistasis model which was mentioned previously, i.e., $L_{1jk}+L_{2jk}-2L_{3jk}=(G_{1j}+G_{2j}-2G_{3j})+(E_{1jk}+E_{2jk}-2E_{3jk})$. Deviations of $L_{1jk}+L_{2jk}-2L_{3jk}$ were summed over replications (denoted as $L_{1j}+L_{2j}-2L_{3j}$) and computed for each tester.

The results of epistatic effects associated with individual testers in Population 1 (TAM W-101/Lovrin 6) are as follows:

Burgas 2 - did not contribute significant epistatic deviation to any of the five agronomic characters.

Centurk - contributed significant epistatic effects to kernel weight at Location 1.

Newton - contributed significant epistatic deviations to kernel weight at Location 2.

Osage - contributed significant epistatic deviations to tiller number at Location 2.

Payne - contributed significant epistatic deviations to tiller number and kernel weight at Location 2.

Triumph 64 - contributed significant epistatic effects for kernel weight at Location 2.

Vona - contributed significant epistatic deviations to tiller number and kernel weight at Location 2.

The results of epistatic effects associated with individual testers in Population 2 (TAM W-101/F23-71) are as follows:

Burgas 2 - contributed significant epistatic effects to kernels/spike at Location 1 and to grain yield at Location 2.

Centurk - did not contribute significant epistatic deviations to any of the five characters.

Triumph 64 - did not contribute significant epistatic deviations to any of the five characters.

Newton - contributed significant epistatic effects to plant height at Location 2 and to kernel weight at Location 1.

Osage - contributed significant epistatic deviations to tiller number and kernels/spike at Location 1.

Payne - contributed significant epistatic effects to kernels/spike at Location 1.

Vona - contributed significant epistatic deviations to kernel weight at Location 1.

Differences among testers in regard to their contributions to epistatic deviations in the five characters investigated indicate that epistatic gene action played a significant role in influencing these yield-related traits. Therefore, in formulating the breeding schemes to improve wheat populations, attention should be focused on epistatic gene action as well as dominance and additive components of genetic variance. If epistatic gene action is ignored in breeding programs, plant breeders would be denied information about epistatic gene action, and possibly be biased in regard to estimates of the other components of genetic variance.

The number of testers used in studies of this type may play an important role in detecting the presence of epistasis. Seven testers were used in this study and epistasis was detected for each of the five characters in at least one population - location combination. The use of a larger number of testers may have provided a better estimate of the importance of epistasis in affecting these yield related traits in wheat.

An epistatic model was applied also to detect the presence of epistatic x location (G x E) interactions. For this purpose, two different locations were used and effects of the environment were considered as causing a differential influence in the epistatic gene action of the characters under study. The results indicated no significant epistatic x location (G x E) with respect to plant height, tiller number, kernels/spike, kernel weight, and grain yield in Population 1 (TAM W-101/Lovrin 6). In Population 2 (TAM W-101/F23-71), significant epistatic x location (G x E) interactions were obtained for plant height and tiller number.

In contrast to reports in the literature, epistatic x environment (G x E) interactions appeared to be relatively unimportant in this study. Failure to detect a higher frequency of this type of genetic x environment interaction may have been due, at least in part, to limitations of the experimental design. More than two environments (locations) would have been preferable.

TABLE I

MEAN SQUARES FOR FIVE CHARACTERS FOR EACH POPULATION IN EACH LOCATION COMPUTED BOTH FOR 30 ENTRIES AND FOR TESTERS ALONE

Source of Variation	df	Plant Height	Tiller Number	Kernels/ Spike	Kernel Weight	Grain Yield
Popn 1, Loc 1						
All Entries	29	315.54**	80.52**	421.10**	360.82**	93.25**
Error	58	52.32	12.56	68.33	19.63	19.58
Testers only	6	671.47**	120.51**	522.42**	236.94**	108.80**
Error	12	67.53	4.71	70.84	19.92	15.63
Popn 1, Loc 2						
All Entries	29	321.86**	170.52**	220.98**	466.94**	115.32
Error	58	60.84	17.62	41.58	26.48	14.29
Testers only	6	280.63**	255.70**	297.26**	348.96**	114.23**
Error	12	45.23	17.43	38.10	23.90	10.67
Popn 2, Loc 1						
All Entries	29	548.89**	91.83**	501.08**	319.81**	131.61**
Error	58	74.75	20.08	67.29	26.12	30.96
Testers only	6	609.70**	126.65**	374.51**	264.97**	47.81
Error	12	49.20	16.66	46.99	21.80	20.55
Popn 2, Loc 2						
All Entries	29	483.12**	120.66**	260.79**	256.17**	68.50**
Error	58	46.94	20.96	70.39	36.91	15.81
Testers only	6	359.82**	153.63**	405.13**	174.46**	51.93**
Error	12	47.57	16.98	51.15	23.96	7.74

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

TABLE II

MEANS (BASED ON SINGLE PLANTS) OF FIVE CHARACTERS OVER 3 REPLICATIONS FOR 30 ENTRIES IN POPULATION 1 (TAM W-101/LOVRIN 6) AT LOCATION 1

Entry	Plant Height (cm)	Tiller Number (number)	Kernels/ Spike (number)	Kernel Weight (g/1000)	Grain Yield (g)
TAM W-101/Burgas 2	70.7	17.0	41.2	41.0	16.7
TAM W-101/Centurk	75.0	16.9	45.6	33.0	16.8
TAM W-101/Newton	70.5	14.7	49.3	34.1	15.6
TAM W-101/Osage	70.1	13.1	31.1	34.5	9.7
TAM W-101/Payne	69.3	17.1	44.7	35.3	18.0
TAM W-101/Triumph 64	76.7	17.9	38.1	39.5	17.2
TAM W-101/Vona	64.9	17.5	38.6	33.8	14.3
TAM W-101/Tester $\bar{X}$	71.0	16.3	41.2	35.9	15.5
TAM W-101/Lovrin 6//Burgas 2	67.4	12.5	36.8	40.9	12.7
TAM W-101/Lovrin 6//Centurk	74.1	14.8	39.7	35.6	13.1
TAM W-101/Lovrin 6//Newton	72.1	16.5	46.1	37.1	16.3
TAM W-101/Lovrin 6//Osage	69.5	15.3	33.2	37.6	12.7
TAM W-101/Lovrin 6//Payne	71.9	13.7	41.5	37.4	14.1
TAM W-101/Lovrin 6//Triumph 64	73.5	15.1	33.4	38.6	12.4
TAM W-101/Lovrin 6//Vona	65.9	14.3	40.5	33.5	12.0
F_1 x Tester $\bar{X}$	70.6	14.6	38.7	37.2	13.3
Lovrin 6/Burgas 2	66.9	13.1	37.6	41.3	13.0
Lovrin 6/Centurk	68.9	14.5	39.0	30.4	12.6
Lovrin 6/Newton	61.9	11.4	35.2	35.3	9.7
Lovrin 6/Osage	70.8	13.8	33.5	36.6	11.3
Lovrin 6/Payne	68.7	11.7	38.0	36.4	12.6
Lovrin 6/Triumph 64	72.9	12.1	36.3	41.3	12.1
Lovrin 6/Vona	66.3	14.7	37.6	33.5	10.8
Lovrin 6/Tester $\bar{X}$	68.1	13.0	36.7	36.4	11.7
Burgas 2	60.0	10.7	47.1	32.4	11.8
Centurk	72.7	16.8	48.5	25.7	13.3
Newton	67.2	15.0	48.6	28.8	13.7
Osage	71.3	14.3	35.5	28.6	8.8
Payne	69.5	19.0	47.5	31.1	17.7
Triumph 64	80.6	16.7	35.5	37.3	13.2
Vona	63.5	18.4	42.9	26.4	11.7
Tester $\bar{X}$	69.3	15.8	43.7	30.0	12.9
TAM W-101 (P_1)	66.3	17.2	40.1	36.6	14.9
Lovrin 6 (P_2)	61.1	10.6	32.9	34.9	9.5
Overall Mean	69.3	14.9	39.9	35.0	13.3
LSD .05	3.4	2.3	4.3	3.1	2.5
LSD .01	4.4	3.1	5.6	4.1	3.3

TABLE III

MEANS (BASED ON SINGLE PLANTS) OF FIVE CHARACTERS OVER 3 REPLICATIONS FOR 30 ENTRIES IN POPULATION 1 (TAM W-101/LOVRIN 6) AT LOCATION 2

Entry	Plant Height (cm)	Tiller Number (number)	Kernels/ Spike (number)	Kernel Weight (g/1000)	Grain Yield (g)
TAM W-101/Burgas 2	70.2	18.1	36.2	40.3	15.7
TAM W-101/Centurk	73.6	18.5	35.6	31.7	11.5
TAM W-101/Newton	65.9	13.8	32.9	29.5	8.9
TAM W-101/Osage	65.9	14.2	21.5	28.3	5.6
TAM W-101/Payne	69.2	17.9	33.8	33.1	12.0
TAM W-101/Triumph 64	74.8	15.9	29.7	35.3	10.1
TAM W-101/Vona	59.4	14.5	33.0	31.6	8.6
TAM W-101/Tester $\bar{X}$	68.4	16.1	31.8	32.8	10.3
TAM W-101/Lovrin 6//Burgas 2	68.0	14.9	29.6	39.8	10.3
TAM W-101/Lovrin 6//Centurk	72.4	17.4	32.9	32.0	11.0
TAM W-101/Lovrin 6//Newton	65.4	12.6	33.8	28.9	8.1
TAM W-101/Lovrin 6//Osage	70.1	17.2	26.2	34.2	9.6
TAM W-101/Lovrin 6//Payne	70.1	16.7	31.9	35.4	12.4
TAM W-101/Lovrin 6//Triumph 64	72.5	15.5	26.7	39.9	9.7
TAM W-101/Lovrin 6//Vona	65.8	15.1	34.5	32.7	9.4
F_1 x Tester $\bar{X}$	69.2	15.6	30.8	34.7	10.1
Lovrin 6/Burgas 2	63.6	11.8	31.9	39.5	9.0
Lovrin 6/Centurk	70.4	12.9	33.3	30.0	8.7
Lovrin 6/Newton	61.5	12.5	33.6	34.4	9.0
Lovrin 6/Osage	72.3	13.1	27.9	38.5	9.4
Lovrin 6/Payne	69.9	10.1	33.6	31.0	8.0
Lovrin 6/Triumph 64	67.3	11.2	28.8	37.4	7.4
Lovrin 6/Vona	61.7	10.3	29.1	27.5	5.5
Lovrin 6/Tester $\bar{X}$	66.7	11.7	31.2	34.0	8.1
Burgas 2	58.4	8.9	33.8	24.6	5.0
Centurk	64.2	6.7	30.3	20.0	3.2
Newton	66.0	12.1	36.6	22.3	6.9
Osage	61.1	9.0	23.6	22.4	3.2
Payne	65.2	17.4	35.1	28.0	10.4
Triumph 64	69.5	16.4	29.3	34.3	8.9
Vona	57.4	14.8	34.3	22.8	6.5
Tester $\bar{X}$	63.1	12.2	31.8	24.9	6.3
TAM W-101 (P_1)	64.5	18.1	27.9	31.3	8.9
Lovrin 6 (P_2)	61.7	6.7	25.3	30.0	4.2
Overall Mean	66.5	13.8	31.1	31.6	8.6
LSD .05	3.3	2.5	3.5	2.7	1.9
LSD .01	4.4	3.2	4.6	3.6	2.5

TABLE IV

MEANS (BASED ON SINGLE PLANTS) OF FIVE CHARACTERS OVER 3 REPLICATIONS FOR 30 ENTRIES IN POPULATION 2 (TAM W-101/F23-71) AT LOCATION 1

Entry	Plant Height (cm)	Tiller Number (number)	Kernels/ Spike (number)	Kernel Weight (g/1000)	Grain Yield (g)
TAM W-101/Burgas 2	71.4	16.5	35.7	42.1	17.3
TAM W-101/Centurk	72.0	15.3	39.8	34.9	14.1
TAM W-101/Newton	70.2	14.7	43.6	38.1	17.2
TAM W-101/Osage	75.7	13.9	33.0	36.6	11.7
TAM W-101/Payne	70.9	16.6	37.5	35.4	16.4
TAM W-101/Triumph 64	73.0	15.9	37.9	43.2	16.4
TAM W-101/Vona	61.8	16.1	37.2	35.2	13.8
TAM W-101/Tester $\bar{X}$	70.7	15.6	37.8	37.9	15.3
TAM W-101/F23-71//Burgas 2	72.9	14.5	36.9	39.2	15.6
TAM W-101/F23-71//Centurk	73.3	17.4	41.4	36.2	16.6
TAM W-101/F23-71//Newton	72.4	17.0	41.4	33.2	14.2
TAM W-101/F23-71//Osage	75.1	16.2	37.5	35.2	13.1
TAM W-101/F23-71//Payne	76.0	14.1	40.9	38.4	15.5
TAM W-101/F23-71//Triumph 64	79.3	13.9	40.2	40.0	15.0
TAM W-101/F23-71//Vona	67.3	14.5	40.7	33.6	12.7
F_1/Tester $\bar{X}$	73.7	15.4	39.8	36.5	14.7
F23-71/Burgas 2	72.1	10.8	54.0	34.6	12.8
F23-71/Centurk	83.9	14.5	48.5	37.9	17.9
F23-71/Newton	77.3	12.5	42.7	39.8	13.8
F23-71/Osage	78.7	8.8	23.1	37.5	5.7
F23-71/Payne	72.1	8.6	33.3	35.2	7.4
F23-71/Triumph 64	83.5	13.5	36.2	42.1	14.9
F23-71/Vona	77.7	15.0	44.7	40.2	17.4
F23-71/Tester $\bar{X}$	77.9	11.9	40.3	38.2	12.8
Burgas 2	59.7	9.7	46.1	31.6	10.1
Centurk	67.7	13.8	42.0	25.2	9.6
Newton	66.5	14.7	45.3	28.2	12.2
Osage	71.8	14.5	33.3	28.5	9.7
Payne	66.9	14.9	43.6	31.6	14.1
Triumph 64	79.7	16.0	35.2	36.8	13.3
Vona	63.7	19.5	38.5	24.7	11.8
Tester $\bar{X}$	68.0	14.7	40.6	29.5	11.5
TAM W-101 (P_1)	65.8	16.7	37.4	36.5	14.9
F23-71 (P_2)	80.5	12.7	47.1	33.6	12.4
Overall Mean	72.6	14.4	39.8	35.5	13.6
LSD .05	3.2	2.2	4.5	3.3	2.8
LSD .01	4.3	2.9	5.9	4.3	3.7

TABLE V

MEANS (BASED ON SINGLE PLANTS) OF FIVE CHARACTERS OVER 3 REPLICATIONS FOR 30 ENTRIES IN POPULATION 2 (TAM W-101/F23-71) AT LOCATION 2

Entry	Plant Height (cm)	Tiller Number (number)	Kernels/ Spike (number)	Kernel Weight (g/1000)	Grain Yield (g)
TAM W-101/Burgas 2	63.2	13.7	33.3	33.4	8.8
TAM W-101/Centurk	72.0	19.6	36.1	31.7	12.5
TAM W-101/Newton	64.4	16.7	39.9	28.2	11.5
TAM W-101/Osage	66.2	15.1	26.7	27.6	7.0
TAM W-101/Payne	61.9	14.5	33.9	29.3	8.8
TAM W-101/Triumph 64	69.8	17.9	33.3	35.2	10.3
TAM W-101/Vona	61.0	17.7	34.5	30.6	10.8
TAM W-101/Tester $\bar{X}$	65.5	16.4	33.9	30.8	9.9
TAM W-101/F23-71//Burgas 2	67.9	14.4	35.9	33.7	10.5
TAM W-101/F23-71//Centurk	72.4	16.6	33.1	29.0	10.9
TAM W-101/F23-71//Newton	73.3	17.5	34.2	32.1	11.0
TAM W-101/F23-71//Osage	69.5	14.2	28.9	27.8	7.0
TAM W-101/F23-71//Payne	67.9	13.3	36.5	32.6	10.0
TAM W-101/F23-71//Triumph 64	73.5	14.8	32.4	32.2	8.6
TAM W-101/F23-71//Vona	59.4	12.7	33.7	28.1	7.7
F_1/Tester $\bar{X}$	69.1	14.8	33.5	30.8	9.4
F23-71/Burgas 2	65.3	7.9	35.9	26.3	5.1
F23-71/Centurk	71.5	14.2	34.4	29.0	9.0
F23-71/Newton	69.9	12.1	28.8	35.2	7.9
F23-71/Osage	73.1	13.4	23.9	31.7	5.9
F23-71/Payne	72.3	13.7	33.9	30.3	8.2
F23-71/Triumph 64	74.8	14.1	32.4	36.0	9.3
F23-71/Vona	68.7	14.5	41.3	31.4	10.1
F23-71/Tester $\bar{X}$	70.8	12.8	32.9	31.4	7.9
Burgas 2	53.5	6.8	34.9	24.0	4.1
Centurk	66.5	14.8	34.7	20.4	6.6
Newton	63.5	14.0	41.9	23.0	8.9
Osage	62.7	13.1	29.0	23.2	5.1
Payne	60.5	16.2	35.9	23.3	9.0
Triumph 64	64.7	14.1	29.1	31.1	7.5
Vona	55.1	16.1	41.7	21.9	7.9
Tester $\bar{X}$	60.9	13.6	35.3	23.8	7.0
TAM W-101 (P_1)	61.5	17.7	31.4	28.7	8.4
F23-71 (P_2)	74.0	8.7	33.7	26.8	4.3
Overall Mean	66.7	14.3	33.9	29.1	8.4
LSD .05	3.6	2.6	4.2	2.9	2.1
LSD .01	4.7	3.4	5.5	3.8	2.7

TABLE VI

PHENOTYPIC CORRELATION COEFFICIENTS AMONG FIVE CHARACTERS IN POPULATION 1 (SEVEN TESTERS) AT LOCATIONS 1 AND 2

Character	Plant Height	Tiller Number	Kernels/ Spike	Kernel Weight
Tiller	0.051[1]			
Number	0.147			
Kernels/	0.469**	-0.066		
Spike	0.507**	0.211		
Kernel	0.312**	0.147	0.420**	
Weight	0.361**	-0.018	0.098	
Grain	0.276*	0.753**	0.279*	0.450**
Yield	0.391**	0.842**	0.428**	0.247*

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

[1]The upper value is the phenotypic correlation coefficient at Location 1 and the lower is the phenotypic correlation coefficient at Location 2.

The values are based on 84 d.f. from among plants source of variation involving the testers.

TABLE VII

PHENOTYPIC CORRELATION COEFFICIENTS AMONG FIVE CHARACTERS
IN POPULATION 2 (SEVEN TESTERS)
AT LOCATIONS 1 AND 2

Character	Plant Height	Tiller Number	Kernels/ Spike	Kernel Weight
Tiller Number	0.204[1]			
Number	0.377**			
Kernels/	0.399**	0.198		
Spike	0.364**	0.335**		
Kernel	0.455**	0.129	0.308**	
Weight	0.343**	0.391**	0.150	
Grain	0.428**	0.754**	0.494*	0.455**
Yield	0.516**	0.896**	0.454**	0.472**

*, ** Significant at $p \doteq 0.05$ and 0.01, respectively

[1] The upper value is the phenotypic correlation coefficient at Location 1 and the lower is the phenotypic correlation coefficient at Location 2.

The values are based on 84 d.f. from among plants source of variation involving the testers.

TABLE VIII

ANALYSES OF EPISTATIC DEVIATIONS FOR FIVE CHARACTERS FOR TWO POPULATIONS AT LOCATION 1

Source of Variation	df	Plant Height	Tiller Number	Kernels/ Spike	Kernel Weight	Grain Yield
		Mean Squares				
Popn 1						
Testers	6	89.40	51.84	98.21	42.69	61.94
Error	14	83.69	34.20	63.11	38.12	45.64
Popn 2						
Testers	6	109.45	55.57	397.03**	110.35*	80.99
Error	14	96.81	42.13	42.87	33.61	44.94
Overall Epistatic deviation †						
Popn 1	1	99.89	0.15	5.89	93.89*	6.69
Popn 2	1	24.97	213.76**	52.70	178.38**	32.81

*, ** Significant at $p \doteq 0.05$ and 0.01, respectively.

† Significance of overall epistatic deviation (parental average) was evaluated by a t-test with 14 d.f.

TABLE IX

ANALYSIS OF EPISTATIC DEVIATIONS FOR FIVE CHARACTERS FOR TWO POPULATIONS AT LOCATION 2

Source of Variation	df	Plant Height	Tiller Number	Kernels/ Spike	Kernel Weight	Grain Yield
			Mean Squares			
Popn 1						
Testers	6	30.31	27.71	86.10	66.35*	35.10
Error	14	110.81	13.69	94.12	20.33	22.10
Popn 2						
Testers	6	153.34	71.45	87.21	92.65	49.40
Error	14	71.25	37.04	105.74	44.56	26.43
Overall Epistatic deviation †						
Popn 1	1	263.59*	245.49**	39.68	136.84**	59.27**
Popn 2	1	84.00	1.60	0.49	10.96	15.02

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

† Significance of overall epistatic deviation (parental average) was evaluated by a t-test with 14 df.

TABLE X

EPISTATIC DEVIATIONS ASSOCIATED WITH INDIVIDUAL TESTERS FOR PLANT HEIGHT

Tester	Loc 1		Loc 2	
	Popn 1	Popn 2	Popn 1	Popn 2
Burgas 2	2.8	-2.33	-2.27	-7.33
Centurk	-4.2	9.4	-0.8	-1.33
Newton	-11.87	2.73	3.33	-12.33**
Osage	1.93	4.2	-1.87	0.27
Payne	-5.87	-9.0	-3.07	-1.67
Triumph 64	2.67	-2.2	-3.0	-2.47
Vona	-0.73	4.93	-10.47	10.87

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

TABLE XI

EPISTATIC DEVIATIONS ASSOCIATED WITH INDIVIDUAL TESTERS FOR TILLER NUMBER

Testers	Loc 1		Loc 2	
	Popn 1	Popn 2	Popn 1	Popn 2
Burgas 2	5.00	-1.80	0.13	-7.27
Centurk	1.80	-4.93	-3.4	0.60
Newton	-6.87	-6.80	1.13	-6.07
Osage	-3.80	-9.73*	-7.13**	0.13
Payne	1.33	-3.07	-5.53*	1.53
Triumph 64	-0.33	1.73	-3.80	2.40
Vona	3.47	2.00	-5.3*	6.73

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

TABLE XII

EPISTATIC DEVIATIONS ASSOCIATED WITH INDIVIDUAL TESTERS FOR KERNELS/SPIKE

Testers	Loc 1 Popn 1	Loc 1 Popn 2	Loc 2 Popn 1	Loc 2 Popn 2
Burgas 2	5.29	15.87**	8.94	-2.49
Centurk	5.24	5.44	3.04	4.28
Newton	-7.53	3.48	-1.14	0.27
Osage	-1.86	-18.88**	-2.87	-7.22
Payne	-0.27	-11.11*	3.6	-5.18
Triumph 64	7.69	-6.24	5.02	0.84
Vona	-4.85	0.49	-6.98	8.39

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

TABLE XIII

EPISTATIC DEVIATIONS ASSOCIATED WITH INDIVIDUAL TESTERS FOR KERNEL WEIGHT

Testers	Loc 1		Loc 2	
	Popn 1	Popn 2	Popn 1	Popn 2
Burgas 2	0.57	-1.75	0.14	-7.63
Centurk	-7.47*	0.39	-2.33	2.61
Newton	-4.72	11.53**	5.95*	0.68
Osage	-4.02	3.65	-1.52	3.73
Payne	-3.06	-6.14	-6.75*	-5.51
Triumph 64	3.54	5.28	-7.06*	6.74
Vona	0.36	8.04*	-6.3*	5.78

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

TABLE XIV

EPISTATIC DEVIATIONS ASSOCIATED WITH INDIVIDUAL TESTERS FOR GRAIN YIELD

Testers	Loc 1		Loc 2	
	Popn 1	Popn 2	Popn 1	Popn 2
Burgas 2	4.24	-1.16	4.08	-7.06*
Centurk	3.33	-1.24	-1.82	-0.31
Newton	-7.27	2.64	1.68	-2.52
Osage	-4.25	-8.71	-4.24	-1.09
Payne	2.32	-7.16	-4.78	-2.96
Triumph 64	4.37	1.17	-1.94	2.39
Vona	1.20	5.84	-4.73	5.39

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

TABLE XV

ANALYSIS OF EPISTATIC DEVIATIONS FOR G x E INTERACTIONS
FOR FIVE CHARACTERS IN POPULATION 1
(TAM W-101/LOVRIN 6)

Source	df	Plant Height	Tiller Number	Kernels/ Spike	Kernel Weight	Grain Yield
Loc	1	19.47	128.97	7.49	2.02	52.91
Rep (Loc)	4	120.77	20.24	74.81	54.99	30.82
Parental Average	1	344.01	113.89	38.32	228.72	13.05
Among Testers	6	58.61	35.44	163.88	30.10	47.23
Loc x Tester	6	61.09	44.11	20.42	78.94	49.28
Error	24	93.37	24.55	79.25	24.92	34.07

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

TABLE XVI

ANALYSIS OF EPISTATIC DEVIATIONS FOR G x E INTERACTIONS FOR FIVE CHARACTERS IN POPULATION 2 (TAM W-101/F23-71)

Source	df	Plant Height	Tiller Number	Kernels/ Spike	Kernel Weight	Grain Yield
Loc	1	100.29*	89.18*	21.52	50.44	1.72
Rep (Loc)	4	6.51	3.16	29.38	27.82	5.39
Parental Average	1	8.68	126.19	31.67	138.91	46.12
Among Testers	6	162.11	92.01	329.56	161.45	95.70
Loc x Tester	6	100.68	35.01	154.67	41.55	34.69
Error	24	96.94	45.66	81.79	40.96	40.73

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

LITERATURE CITED

1. Amaya, A. A., R. H. Busch, and K. L. Lebsock. 1972. Estimates of genetic effects of heading date, plant height, and grain yield in durum wheat. Crop Sci. 12:478-481.

2. Anderson, V. L., and O. A. Kempthorne. 1954. A model for the study of quantitative inheritance. Genetics 39:883-898.

3. Bains, K. S. 1976. Parent dependent genotype x environment interaction in crosses of spring wheat. Heredity 36:163-171.

4. Bauman, L. F. 1959. Evidence of non-allelic gene interaction in determining yield, ear height, and kernel row number in corn. Agron. J. 51:531-534.

5. Bhatt, G. M. 1972. Inheritance of heading date, plant height, and kernel weight in two spring wheat crosses. Crop Sci. 12:95-98.

6. Burton, G. W. 1968. Epistasis in pearl millet forage yields. Crop Sci. 8:365-368.

7. Chapman, S. R., and F. H. McNeal. 1971. Gene action for yield components and plant height in a spring wheat cross. Crop Sci. 11:384-386.

8. Cockerham, C. C. 1959. Partitions of hereditary variance for various genetic models. Genetics 44:1141-1148.

9. Cockerham, C. C. 1961. Implications of genetic variances in a hybrid breeding program. Crop Sci. 1:47-52.

10. Comstock, R. E. and H. F. Robinson. 1952. Genetic parameters, their estimation and significance. Proc. VIth Int. Grassland Cong. 1:284-291.

11. Copp, L. G. L., and G. M. Wright. 1952. The inheritance of kernel weight in a Triticum vulgare cross. Heredity 6:187-199.

12. Donald, C. M. 1968. The breeding of crop ideotypes. Euphytica 17:385-403.

13. Edwards, L. H., H. Ketata, and E. L. Smith. 1976. Gene action of heading date, plant height, and other characters in two winter wheat crosses. Crop Sci. 16:275-277.

14. Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. Trans. Roy. Soc. of Edinburgh 52, Part 2:399-433.

15. Gamble, E. E. 1962. Gene effects in corn (Zea mays L.). Can. J. Plt. Sci. 42:339-348.

16. Gorsline, G. W. 1961. Phenotypic epistasis for ten quantitative characters in maize. Crop Sci. 1:55-58.

17. Grafius, J. E. 1964. A geometry in plant breeding. Crop Sci. 4:241-246.

18. Hayman, B. I., and K. Mather. 1955. The description of genic interactions in continuous variation. Biometrics 11:69-82.

19. Horner, T. W., R. E. Comstock, and H. F. Robinson. 1955. Non-allelic gene interactions and the interpretation of quantitative genetic data. North Carolina Agr. Exp. Sta. Tech. Bull. 118. 117pp.

20. Jasnowski, S. 1953. On the inheritance of some characters of the ear of wheat (in polish). Polon. Acad. Bull. Sci. cracovie 199-218. Plant Breed. Abstr. 5:217 (#654).

21. Jinks, J. L., J. M. Perkins, and H. S. Pooni. 1973. The incidence of epistasis in normal and extreme environments. Heredity 31:263-269.

22. Jinks, J. L., J. M. Perkins, and E. L. Breese. 1969. A general method of detecting additive, dominance and epistatic variation for metrical traits. II. Application to inbred lines. Heredity 24:45-57.

23. Kearsey, M. J., and J. L. Jinks. 1968. A general method of detecting additive, dominance and epistatic variation for metrical traits. I. Theory. Heredity 23:403-409.

24. Ketata, H., E. L. Smith, L. H. Edwards, and R. W. McNew. 1976. Detection of epistatic, additive, and dominance variation in winter wheat (Triticum aestivum L. em Thell.). Crop Sci. 16:1-4.

25. Ketata, H., L. H. Edwards, and E. L. Smith. 1976. Inheritance of eight agronomic characters in a winter wheat cross. Crop Sci. 16:19-22.

26. Paroda, R. S., and A. B. Joshi. 1970. Genetic architecture of yield and components of yield in wheat. Indian J. Genet. 30:298-314.

27. Perkins, J. M., and J. L. Jinks. 1973. The assessment and specificity of environmental and genotypic-environmental components of variability. Heredity 30:111-126.

28. Pooni, H. S., J. L. Jinks, and N. E. M. Jayasekara. 1978. An investigation of gene action and genotype x environment interaction in two crosses of Nicotiana rustica by triple test cross and inbred line analysis. Heredity 41:83-92.

29. Porter, K. B. 1974. Registration of TAM W-101 wheat. Crop Sci. 14:608.

30. Sandhu, J. S., and S. C. Anand. 1972. Inheritance of kernel weight in wheat. Indian Journal of Genetics and Plant Breeding. 32:299-302.

31. Sharma, D., and D. R. Knott. 1964. The inheritance of seed weight in a wheat cross. Can. J. Genet. Cytol. 6:419-425.

32. Singh, J., and S. C. Anand. 1971. Inheritance of grain number in wheat. Indian Journal of Genetics and Plant Breeding. 31:177-183.

33. Singh, S., and R. B. Singh. 1976. Triple test cross analysis in two wheat crosses. Heredity. 37:173-177.

34. Smith, E. L. 1976. The genetics of wheat architecture. Oklahoma Academy of Science. 6:117-132.

35. Smith, E. L. 1978. Personal Communication. Oklahoma State University, Stillwater, Oklahoma.

36. Smith, E. L. 1979. Personal Communication. Oklahoma State University, Stillwater, Oklahoma.

37. Sprague, G. F., W. A. Russell, L. H. Penny, T. W. Horner, and W. D. Hanson. 1962. Effect of epistasis on grain yield in maize. Crop Sci. 2:205-208.

38. Stuber, C. W., and R. H. Moll. 1969. Epistasis in maize (Zea mays L.). I. F_1 hybrids and their S_1 progeny. Crop Sci. 9:124-127.

39. Stuber, C. W., and R. H. Moll. 1974. Epistatic in maize (Zea mays L.). IV. Crosses among lines selected for superior intervariety single cross performances. Crop Sci. 14:314-317.

40. Sun, P. L. F., H. L. Shands, and R. A. Forsberg. 1972. Inheritance of kernel weight in six spring wheat crosses. Crop Sci. 12:1-5.

41. Yermanos, D. M., and R. W. Allard. 1961. The detection of epistatic gene action in flax. Crop Sci. 1:307-310.

VITA 2

Jamshid Jafari-Shabastari

Candidate for the Degree of

Doctor of Philosophy

Thesis: DETECTION OF EPISTATIC GENE ACTION IN TWO POPULATIONS OF WINTER WHEAT (TRITICUM AESTIVUM L. EM THELL).

Major Field: Crop Science

Biographical:

Personal Data: Born in Shalbastar, Iran, August 15, 1941, the son of Mr. and Mrs. Abdollah Jafari-Shabastari.

Education: Graduated from Hekmat High School, Tabriz, Iran, in June, 1960; received Diploma in Agronomy from the University of Tehran in June, 1964; received Master of Science degree in Plant Breeding from the University of Tehran in June, 1972; completed the requirements for the Doctor of Philosophy degree at Oklahoma State University in May, 1980.

Professional Experience: Plant breeder, Agronomy Department, University of Tehran, Iran, from 1964 to 1973; Instructor and Faculty Member, Agronomy Department, University of Tehran, Iran, 1973-1976; part-time graduate training, Department of Agronomy, Oklahoma State University, Stillwater, Oklahoma, May, 1976 to May 1980.

Professional Organizations: Student Member, American Society of Agronomy.