A GENETIC STUDY OF YIELD COMPONENTS IN THREE POPULATIONS OF WINTER WHEAT (*TRITICUM AESTIVUM* L. EM THELL)

By

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Bachelor of Science

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Stillwater, Oklahoma

1971

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

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THREE POPULATIONS OF WINTER WHEAT
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ACKNOWLEDGMENTS

The author expresses his gratitude to his major adviser, Dr. Edward L. Smith, for his advice, counsel, and on occasion, compassion throughout the course of this study and to the other members of his committee, Dr. Owen G. Merkle and Dr. Donald Holbert for their assistance and constructive criticism. Acknowledgments are also tendered to Dr. Ronald W. McNew for his invaluable assistance and advice in conducting the genetical tests of this study.

Gratitude is also expressed to the Department of Agronomy of Oklahoma State University for the financial support and research facilities that made this study possible.

The author finally gives his sincerest thanks to the entire staff and personnel of the small grains research team for making the day-to-day labors a constant learning experience as well as a source of fulfillment and satisfaction.

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CHAPTER I

INTRODUCTION

The agricultural scientists of the world are being confronted by the challenge of a rapidly rising world population which must be fed on constant, even diminishing resources of land, water, and nutrients. A major part of this effort to meet the world's needs for increased food production is the development of more productive cultivars of basic food crops. Consequently, the plant breeder must acquire with more precision than ever a detailed knowledge of the biology of his crop.

Wheat, a major food crop the world over, will be needed in higher amounts to help feed more and more people, and both the yield and nutritive qualities of this cereal crop must be increased to meet this challenge. The Southern Great Plains of the United States, already an area of intensive wheat production, possesses the potential for even higher yields by the utilization of more efficient, higher producing cultivars. Already the source of much of the bread wheat for the United States and the world, this region has the potential to make even higher contributions to the world food supply if a major breakthrough in yield can be achieved.

A better understanding of the genetic control of yield potential would be useful to the plant breeder in developing improved cultivars.

The objectives of this study were: (1) to determine heritability and genetic advance estimates of yield components in selected populations of winter wheat, and (2) to determine the importance of additive, dominance, and epistatic gene action in the expression of these yield components.

This study has been prepared in a style and form acceptable to the Crop Science Society of America.

Additional index words: Heritability, Plant height, Kernel weight, Tiller number, Kernels per spike, Grain yield, Epistasis, Genetic advance, Gene effects, Additive gene effects, Dominance gene effects

CHAPTER II

REVIEW OF THE LITERATURE

Throughout the Southern Great Plains Region, the predominant hard red winter wheat cultivars are based on the Turkey prototype which is characterized by a small spike size and a very high tillering potential (24). Efforts to increase yield have led to the introduction into breeding programs of germplasm, which has a shorter plant height, a higher kernel weight, a larger spike size and a low tillering potential (24). If yield is to be improved by combining these new attributes into adapted cultivars, a knowledge of the genetic systems involved is essential for an intelligent, realistic estimation of progress to be expected in a breeding program.

An important concept to the plant breeder is the concept of heritability. This is a ratio which measures the extent to which the expression of variance within a character is caused by genetic forces. Heritability, when used in conjunction with the statistics of phenotypic standard deviation and the selection differential, allows the expected gain through selection within a heterogeneous, segregating population to be estimated (1). Heritability has been further refined into narrow- and broad-sense estimates (1). Heritability in the narrow-sense is the ratio of additive genetic variance to the total or phenotypic variance for a character and may be thought of as the "breeding value" for a character. Heritability in the broad-sense is the ratio of the total genotypic variance to the phenotypic variance. Broad-sense heritability, if utilized to estimate gain by selection, would tend to overestimate progress, but it has been utilized when estimates of narrow-sense heritability would have been biased because of invalid assumptions (28).

If heritabilities for yield components are higher than for yield itself, then yield might be increased more rapidly by breeding for these components in lieu of yield _per se_, even if these components were not altogether independent of each other. Fonseca and Patterson (8), Johnson et al. (12), Ketata et al. (14), and Sidwell (22) studying winter wheat crosses have indeed found consistently higher heritabilities for yield components than for yield _per se_, giving credence to this theory.

For the character of plant height, high estimates of narrow-sense heritability were reported by Fonseca and Patterson (8), Johnson et al. (12), Merkle and Atkins (18), Ketata et al. (14), and Reddi et al. (20) in winter wheat crosses, and by Gill et al. (10) studying an Indian by "exotic" wheat cross. Medium to high estimates were reported by Bhatt (5) and medium to low by Anwar and Chowdry (3). Both of these studies involved spring wheat crosses. High broad-sense heritability estimates were reported by Johnson et al. (12) in winter wheat and by Anwar and Chowdry (3) and Bhatt (5) in spring wheats.

For kernel weight, high narrow-sense heritability estimates were reported by Johnson et al. (12), Sidwell (22), and Ketata et al. (14) in winter wheat and by Sharma and Knott (21) and Bhatt (5) in spring wheat. Medium estimates were found by Gill et al. (10) in an Indian by "exotic" wheat cross and by Reddi et al. (20) in a winter wheat cross. High broad-sense heritability estimates were reported by Johnson et al. (12) in hard red winter wheat and by Bhatt (5) and Baker et al. (4) in spring wheat. A medium estimate was reported by Sidwell (22) in a winter wheat cross.

For tiller number, medium estimates of narrow-sense heritability were reported by Sidwell (22) and Ketata et al. (14) both in winter wheat crosses. Medium to high estimates were reported by Fonseca and Patterson (8) in winter wheat. Low estimates were found by Gill et al. (10), Reddi et al. (20), and Johnson et al. (12). Medium estimates of heritability in the broad sense have been reported by Johnson et al. (12) and Sidwell (22), both studying winter wheat crosses.

High narrow-sense heritabilities for kernels per spike were reported by Gill et al. (10) in an Indian by "exotic" wheat cross while medium to high estimates were reported by Fonseca and Patterson (8). Medium estimates were found by Sidwell (22), and low estimates by Ketata et al. (14) in winter wheat crosses. A low estimate of broad-sense heritability was reported by Sidwell (22).

For yield, medium to low narrow-sense heritabilities were reported by Anwar and Chowdry (3) in spring wheat and by Johnson et al. (12), Sidwell (22), Ketata et al. (14) and Fonseca and Patterson (8) in winter wheat crosses. Broad-sense heritability estimates were reported as high by Anwar and Chowdry (3) in four spring wheat crosses, medium by Sidwell (22) in a winter wheat cross and low by Johnson et al. (12) also in a winter wheat cross. Estimates ranging from low to high were reported by Baker et al. (4) in spring wheat crosses.

The contemporary plant breeder also needs information on the types and magnitudes of the gene action governing the expression of yield components. This information would be helpful to the plant breeder in deciding on the proper breeding procedure and on the type of cultivar to be developed.

For plant height in a winter wheat cross, Ketata et al. (14) found dominance gene effects to be more important than additive gene effects, using a weighted least squares method. In a study involving two winter wheat crosses over a single growing season, Edwards et al. (7), using an unweighted least squares procedure, reported that additive effects were larger than dominance effects. Chapman and McNeal (6), working with spring wheat found, through an analysis based on generation means and variances, that dominance gene effects were of a greater magnitude than additive in one year but the reverse was true in the second year. Amaya et al. (2), using a weighted least squares technique in a study with durum wheat, involving four crosses over a period of two years at two locations, found additive gene effects more important in two crosses and dominance gene effects more important in the other two.

For tiller number, in studies previously described, Ketata et al. (14) found additive gene effects to have a marginally larger magnitude than dominance gene effects. Chapman and McNeal (6) found contrasting results, depending upon the year studied. In the first year dominance gene effects were more important. In the second year additive gene effects were of a larger magnitude. Edwards et al. (7) found additive gene effects to be more important than dominance gene effects.

For kernels per spike, Ketata et al. (14) found dominance gene effects to be more important than additive gene effects.

For kernel weight, Ketata et al. (14), Sun et al. (28), and Edwards et al. (7) reported additive gene effects to be more important than dominance gene effects.

The question of how epistasis affects the expression of character has been studied relatively little until recently. Types and magnitudes of epistasis present could be of use to the plant breeder in his programs if their effects were better understood. Chapman and McNeal (6) state that although not directly influencing the inheritance of quantitative characters, epistasis, when present in significant amounts will influence the phenotypic expression of these traits, thus influencing the plant breeder's ability to select for favorable expressions of the affected characters. Ketata et al. (13) suggested that standard hybridization and selection procedures could take advantage of epistasis if it was of the additive type (additive x additive, additive x additive x additive, etc.). Other types of epistasis (additive x dominance, dominance x dominance, etc.) are not fixable by selection under self-fertilization and would not be favorable for the development of pure-line cultivars, but may be useful in hybrid cultivar development. Ketata et al. (13) further proposed that selection be delayed when epistasis is present until homozygosity is attained since only additive types of epistasis are present in pure lines. This would avoid bias due to masking effects of epistasis in segregating generations.

For the character of plant height, Amaya et al. (2) found that epistasis was present in two of four durum wheat crosses studied. Decreasing magnitudes of dominance x dominance, additive x dominance, and additive x additive types of epistasis (dominance x dominance the highest, additive x additive the lowest) were present in one cross and the reverse was the case in the other cross. Ketata et al. (13) and Edwards et al. (7) detected no epistasis for this character in a winter wheat cross. In another study, Ketata et al. (14), using a different procedure, detected dominance x dominance epistasis in significant amounts. Chapman and McNeal (6), working with a spring wheat cross, detected epistasis in one of two crosses studied, finding dominance x dominance epistasis present in a much larger magnitude than additive x additive or additive x dominance epistasis.

For kernels per spike, Edwards et al. (7) and Ketata et al. (13, 14) detected no epistasis in significant magnitudes in winter wheat crosses.

Ketata et al. (14) found epistasis present for tiller number in a winter wheat cross. Chapman and McNeal (6) detected epistasis for this trait in one, but not both years of a two-year study. In other studies, epistasis was not detected by either Ketata et al. (13) or Edwards et al. (7) for this character.

For kernel weight, Chapman and McNeal (6) and Bhatt (5) found no epistasis present in spring wheat crosses. Edwards et al. (7) and Ketata et al. (14) found none in winter wheat crosses. However, in another study Ketata et al. (13) found epistasis to be present in one of two populations studied. Sun et al. (28) detected epistasis in three of six spring wheat crosses. However, the detection of epistasis in this study appeared to be influenced largely by different environmental effects since the results were inconsistent from year to year.

CHAPTER III

MATERIALS AND METHODS

Populations and Procedures

The study consisted of three populations. Each population was derived from crosses involving an unadapted cultivar and one that is adapted to the Southern Great Plains Region. Each population consisted of the two parents, F_1, F_2, and backcrosses (B_1 and B_2) of the F_1 to both parents. The unadapted parent, which was common to all three populations, was 'Aurora'. The adapted cultivars 'Sage', 'Tam W 101', and 'Danne', were used in populations one, two, and three respectively. In all cases, Aurora was referred to as P_1 and the adapted cultivars as P_2. The parents, which were selected because of their contrasting characteristics in terms of plant type and yield component expression, are being used extensively in the breeding program of the Oklahoma Agricultural Experiment Station.

Aurora, the unadapted parent used in all three populations, was developed in Krasnodar, U.S.S.R. by the late P. P. Lukyanenko. Aurora is a selection from a cross between 'Lutescens 314h' and 'Bezostaia 1'. Lutescens 314h is a selection from a cross between 'Neuzucht', a German line which contains a rye-wheat chromosome translocation, and 'Bezostaia 4'. 'Bezostaia 1', the other parent of Aurora, is a selection from Bezostaia 4, which in turn is a selection from a cross between

'Lutescens 17' and 'Skorospelka 2.' Lutescens 17 is a selection from a cross between a U.S.S.R. landrace and the cultivar 'Ukranka'. Skorospelka 2 is a selection from a 'Kanred'-'Fulcaster' x 'Klein 33' cross (25). Aurora, when grown in the southern plains, is mid tall with strong stems. It has a rather large spike, large kernels and a somewhat low tillering potential.

Sage (Agent/4*Scout) was released by the Kansas Agricultural Experiment Station in 1973. It is a pure line selection, made in the F4 generation after the last backcross, using Scout as the recurrent parent and Agent as the rust resistant donor parent. Sage is characterized by medium tall plant height, low kernel weight, high tillering potential, and a low number of kernels per spike (15).

Tam W 101 was released in 1971 by the Texas Agricultural Experiment Station. It is a selection from the cross of 'Norin 16'/3/'Nebraska 60'//'Mediterranean'/'Hope'/4/'Bison'. Tam W 101 was developed for irrigated conditions but also performs well under dry land production in the southern plains and is characterized by short plant height, high kernel weight, a high tillering potential, and a low number of kernels per spike (19).

Danne was released by the Oklahoma Agricultural Experiment Station in 1970. Danne is a selection from a cross made by the late Joseph E. Danne between Super Triumph and C66-45-3, a strain of complex pedigree. Joseph Danne was a private plant breeder who bequeathed his wheat germplasm to Oklahoma State University in 1959. Danne is characterized by mid-tall plant height, a rather low kernel weight, a high tillering potential, and a low number of kernels per spike (23).

Initial crosses were made in the greenhouse in 1973. The F_1 plants were grown in the greenhouse to produce the F_2 generation. Other F_1 plants were crossed to each parent to produce the backcross generations. The seeds of all generations were planted in flats in the greenhouse on November 6, 1974. The seedlings were then transplanted from flats to the 2100 field series of the Stillwater Agronomy Station, on a Bethany silt loam soil, on December 5, 1974.

The experimental design of each population consisted of a randomized, complete block with four replications. The three populations were grown adjacent to each other but were treated as separate studies. Within each replication both parents and their F_1 generation were allotted one row each, the F_2 generation was allotted six rows, and each backcross generation was allocated three rows. Rows were 30 cm apart. Each row consisted of ten plants spaced 30 cm apart. The two end plants were border plants and were discarded prior to analysis to preclude border effects. The total numbers of plants analyzed per population were 32 for each parent and the F_1 generation, 96 for each of the backcross generations, and 192 for the F_2 generation. Extra plants of each generation in all populations were grown adjacent to the test. Plants failing to survive before the jointing stage were replaced by their equivalent generation from the extra plants to insure uniformity of competition. Also, plants atypical for any of the characters studied were replaced by normal plants of their equivalent generation prior to statistical analysis.

A preplant treatment of ammonium phosphate was applied on September 9, 1974 at the rate of 224 kg per hectare. A topdressing at the rate of 168 kg per hectare of ammonium nitrate was applied on March 3, 1975.

With the exception of a 12 cm driving rain and hail storm in mid-May, the growing season was very favorable for wheat production. In spite of this storm, no severe damage was sustained and it was felt that meaningful measurements could be made and the study was continued.

The populations were harvested from June 20 to June 26, 1975. At harvest, each plant was pulled, plant height was determined and the spikes of each plant were placed in a Kraft paper bag and stored for later measurements.

During threshing, the three largest spikes for each plant were selected and threshed separately in order to make kernel weight and kernels per spike measurements. The F_1 and F_2 generations were threshed by hand. The remainder were threshed on a belt thresher.

The following measurements were made on a single plant basis.

Plant Height. This was determined as the distance in centimeters from the base of the culm to the average of the tips of the three tallest spikes, excluding awns (if present).

Tiller Number. The number of seed-bearing culms produced by each plant was determined at harvest time.

Kernel Weight. This was determined as the weight in grams of the seed from the three largest spikes, divided by the number of seed of the three heads. Kernel weight was expressed as grams per 1000 kernels.

Kernels Per Spike. The number of kernels contained in the three largest spikes was determined and divided by three.

Grain Yield. The total weight in grams of seed produced by each plant was determined. (Grain yield was not determined for the F_1 generation on a per plant basis because of inadvertent bulking of the entire yield (minus that of the three largest heads for each plant) for each row.)

Genetic Analysis

Generation means were computed for each character in all three populations.

An analysis of variance for each generation and each character was conducted. After removing replication, genotypic, and row effects, the among plants mean square was used as the generation variance for each character in later tests (27).

Heritability in the narrow sense, h^2_{ns}, was estimated for each character by Warner's method (29) as:

$$h^2_{ns} = (2VF_2 - (VB_1 + VB_2)) / VF_2$$

where VF_2, VB_1 and VB_2 are the variances of the F_2, the backcross of the F_1 with Aurora, and the backcross of the F_1 with the adapted parent respectively. The standard error of the narrow-sense heritability estimate, s.e. h^2_{ns}, for each character, was computed after Ketata et al. (14) as:

$$\text{s.e. } h^2_{ns} = ((2/VF_2^2)\ ((VB_1 + VB_2)^2/dfF_2 + VB_1^2/dfB_1 + VB_2^2/dfB_2))^{1/2}$$

where dfF_2, dfB_1, and dfB_2 are the degrees of freedom for the F_2, B_1, and B_2 generations, respectively.

Heritability in the broad sense, H^2_{bs}, was computed by the method outlined in a text by Allard (1) for each character:

$$h^2_{bs} = 1 - ((VP_1 + VP_2 + VF_1)/3)/VF_2$$

where VP_1, VP_2 and VF_1 are the variances of the P_1 generation (Aurora), the P_2 generation (the adapted parent) and the F_1 generation, respectively.

The standard error of the broad-sense heritability estimate, s.e. h^2_{bs}, was computed from a formula derived by McNew (17):

$$\text{s.e. } h^2_{bs} = ((1/9)(2/VF_2^{\,2})((VP_1 + VP_2 + VF_1)^2/dfF_2) + VP_1^{\,2}/dfP_1 + VP_2^{\,2}/dfP_2 + VF_1^{\,2}/dfF_1))^{1/2}$$

For grain yield, the estimate of heritability in the broad sense, due to the missing F_1 variance, was computed by a modification of the method used above:

$$h^2_{bs} = 1 - ((VP_1 + VP_2)/2)/VF_2$$

The standard error of heritability in the broad sense for grain yield was calculated by the following formula which was derived by McNew (17):

$$\text{s.e. } h^2_{bs} = 1.5\ ((1/9)(2/VF_2^{\,2})((VP_1 + VP_2)^2/dfF_2 + VP_1^{\,2}/dfP_1 + VP_2^{\,2}/dfP_2))^{1/2}$$

Expected genetic advance, Gs, based on a five percent selection intensity, was computed following Allard (1) using both broad- and narrow-sense heritability estimates. The formula used was:

$$Gs = (k)(VF_2)^{1/2}(h^2)$$

In this formula, k is the selection differential which is a function of the mean phenotypic value of the selected families, the mean phenotypic value of all the families tested, and the selection intensity.

$VF_2^{1/2}$ is the square root of the F_2 variance, an estimate of the phenotypic standard deviation, while h^2 is the heritability estimate, either in the narrow- or broad-sense. Gs is the expected percent increase of F_3 mean over F_2 mean.

ABC scaling tests as described by Mather and Jinks (16) to determine whether epistatic gene action was present were conducted as follows:

Means

$$A = 2\,\bar{B}_1 - \bar{P}_1 - \bar{F}_1$$

$$B = 2\,\bar{B}_2 - \bar{P}_2 - \bar{F}_1$$

$$C = 4\,\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$$

Variances

$$V_A = 4V_{\bar{B}_1} + V_{\bar{P}_1} + V_{\bar{F}_1}$$

$$V_B = 4V_{\bar{B}_2} + V_{\bar{P}_2} + V_{\bar{F}_1}$$

$$V_C = 16V_{\bar{F}_2} + 4V_{\bar{F}_1} + V_{\bar{P}_1} + V_{\bar{P}_2}$$

where $\bar{P}_1$, $\bar{P}_2$, $\bar{F}_1$, $\bar{F}_2$, $\bar{B}_1$, and $\bar{B}_2$ are generation means and $V_{\bar{P}_1}$, $V_{\bar{P}_2}$, $V_{\bar{F}_1}$, $V_{\bar{F}_2}$, $V_{\bar{B}_1}$, and $V_{\bar{B}_2}$ are variances of the respective generation means.

The ABC scaling tests utilized the values of the respective generation means on the additive-dominance model in three separate tests for epistasis. Each test had an expectation of zero if no epistasis was present. If one or more of the tests for a character failed to equal zero (within the confidence limit of twice its standard deviation), then epistasis was declared present for that character.

A three-parameter joint scaling test attributed to Cavalli by Mather and Jinks (16) was also conducted to estimate the mean, additive, and dominance effects; or m, a, and d, respectively, using Gamble's notation (9). The three-parameter joint scaling test was also used to detect epistatic gene action. The test derived estimates of m, a, and d by a procedure of weighted least squares using as weights the inverses of the variances of the generation means. This joint scaling test also estimated the goodness of fit of the three-parameter model to the observed data on the assumption that the sum of squared deviations, (observed values - expected values)^2, weighted with the appropriate coefficients followed a X^2 distribution with three degrees of freedom. The failure of adequate fit implied the existence of epistasis (14).

In cases where epistasis was detected by either the ABC scaling tests or the three-parameter joint scaling test, Hayman's (11) six-parameter joint scaling test was applied (also using Gamble's notation (9)) to obtain an estimate of the types and magnitudes of epistasis present and unbiased estimates of m, a, and d. Since all six generations were used to estimate the preceding six parameters, no test for goodness of fit could be performed. Therefore, a standard error as derived by McNew (17) was used for each parameter estimate. The equations for the parameter and standard error estimates of the six-parameter test are as follows:

Means

$m = \overline{F}_2$

$a = \overline{B}_1 - \overline{B}_2$

$d = -\frac{1}{2}\overline{P}_1 - \frac{1}{2}\overline{P}_2 + \overline{F}_1 - 4\overline{F}_2 + 2\overline{B}_1 + 2\overline{B}_2$

$aa = -4\overline{F}_2 + 2\overline{B}_1 + 2\overline{B}_2$

$ad = -\frac{1}{2}\overline{P}_1 + \frac{1}{2}\overline{P}_2 + \overline{B}_1 - \overline{B}_2$

$dd = \overline{P}_1 + \overline{P}_2 + 2\overline{F}_1 + 4\overline{F}_2 - 4\overline{B}_1 - 4\overline{B}_2$

Variances

$Vm = V\overline{F}_2$

$Va = V\overline{B}_1 + V\overline{B}_2$

$Vd = \frac{1}{4}V\overline{P}_1 + \frac{1}{4}V\overline{P}_2 + V\overline{F}_1 + 16V\overline{F}_2 + 4V\overline{B}_1 + 4V\overline{B}_2$

$Vaa = 16V\overline{F}_2 + 4V\overline{B}_1 + 4V\overline{B}_2$

$Vad = \frac{1}{4}V\overline{P}_1 + \frac{1}{4}V\overline{P}_2 + V\overline{B}_1 + V\overline{B}_2$

$Vdd = V\overline{P}_1 + V\overline{P}_2 + 4V\overline{F}_1 + 16V\overline{F}_2 + 16V\overline{B}_1 + 16V\overline{B}_2$

The ABC scaling test is a set of three separate but not orthogonal tests. If one or more of the tests detected epistasis, then epistasis was considered present for that character. Since each test had its own expectation in terms of type and magnitude of epistatic effects, agreement was not expected among these tests (14). The ABC scaling tests only detected whether or not epistasis was present. No estimates of types or magnitudes of gene effects could be derived from this procedure.

In addition to detecting epistasis, the three-parameter joint scaling test also provided estimates of the mean, additive, and dominance genetic effects.

Hayman's six-parameter joint scaling test provided estimates of the F_2 population mean or mean effect (m), the pooled additive effects (a), the pooled dominance effects (d), plus the pooled effects of the types of epistasis present, additive x additive (aa), additive x dominance (ad), and dominance x dominance (dd).

Since the three-parameter and six-parameter tests used different procedures to derive parameter estimates, exact agreement was not expected for the estimates of parameter magnitudes between the two tests. The two tests were evaluated separately and then, if appropriate, used in conjunction with each other to obtain more accurate estimates of the actual parameters.

Since Aurora was arbitrarily designated as P_1 in all tests, regardless of whether or not it was the high parent for that trait, the signs of the additive gene effects, a, were indicative of Aurora's position, relative to the adapted parent on the additive-dominance scale. If the sign of the parameter, a, was positive then Aurora was the high parent; if negative then the adapted parent was the high parent. The sign of the dominance gene effects, d, indicated the net direction of dominance. If d was positive then the net direction of dominance gene effects for that character was toward Aurora, if negative the net direction of dominance was toward the adapted parent.

All statistical analyses were conducted by the Oklahoma State University Computer with assistance in programming by the Department of Statistics faculty.

CHAPTER IV

RESULTS AND DISCUSSION

Means and Variances

Of particular note was the failure of Aurora (P_1) to respond similarly in all three populations. Aurora tended to exhibit a general lack of vigor in population three, as evidenced by its shorter plant height, lower kernel weight (resulting from a high percentage of shriveled kernels), and lower grain yield (Table I).

F_1 means were intermediate between their parental means in all populations for the characters of tiller number and kernels per spike (Table I). For the other characters F_1 means were above their high parent. In no instance was the F_1 mean below that of the low parent. Nearly equal parental means were observed in population one for the character of grain yield and in population two for the characters of plant height, kernel weight, and grain yield (Table I). Of the adapted parents, Tam W 101 was shorter, had the highest kernel weight and the highest tiller number and the highest yield but the lowest number of seeds per spike.

Generation variances in some instances were less for segregating than for the nonsegregating generations. This was noted for certain kernel weight comparisons in populations one and three, for certain tiller number comparisons in all populations, and for certan kernels per spike comparisons in population three (Table II). Also of note

TABLE I

GENERATION MEANS

Character	Popn+	P_1	P_2	F_1	F_2	B_1	B_2
Plant ht. (cm)	1	81.28	89.66	92.50	88.90	83.24	93.12
	2	75.59	75.62	82.12	78.82	78.88	80.07
	3	72.53	86.72	87.75	83.89	83.78	89.36
1000 KWT (g)	1	32.64	28.59	38.47	34.89	36.31	35.00
	2	34.02	34.47	39.62	35.63	34.43	35.48
	3	26.32	29.72	34.31	30.32	30.00	30.79
Tiller no. (per plant)	1	14.34	22.50	19.78	18.58	17.12	19.99
	2	15.97	25.06	18.97	20.70	16.84	21.48
	3	13.47	19.38	16.81	17.70	16.17	20.71
Kernels/spike	1	55.50	46.77	55.17	48.52	52.98	47.72
	2	54.57	44.05	51.30	53.08	57.02	49.94
	3	53.31	48.80	49.95	49.32	52.51	49.96
Grain yield (per plant)	1	16.71	18.15	28.75	20.44	21.72	21.14
	2	19.19	20.82	25.57	24.52	21.23	23.22
	3	12.62	15.95	18.33	15.89	18.25	20.45

+ Popn 1: P_1 = Aurora, P_2 = Sage
Popn 2: P_1 = Aurora, P_2 = Tam W 101
Popn 3: P_1 = Aurora, P_2 = Danne

TABLE II

VARIANCES OF GENERATIONS

Character	Popn[‡]	P_1	P_2	F_1[+]	F_2	B_1	B_2
Plant ht. (cm)	1	21.04	38.35	23.34	82.89	53.64	53.39
	2	09.40	12.79	13.56	88.51	60.37	76.10
	3	17.87	23.97	24.28	90.31	46.26	51.21
1000 KWT (g)	1	15.17	20.26	10.43	20.20	22.84	17.90
	2	12.21	11.95	07.61	24.64	29.76	18.42
	3	11.90	16.53	21.73	25.38	21.89	15.20
Tiller no. (per plant)	1	03.69	16.13	10.14	16.72	09.89	16.61
	2	06.74	27.51	12.88	13.74	08.28	15.58
	3	10.55	16.88	04.95	13.48	06.26	16.56
Kernels/spike	1	40.62	35.40	39.91	73.43	70.80	52.26
	2	31.15	28.82	42.19	64.76	95.99	32.63
	3	76.90	51.68	45.68	66.73	63.57	44.49
Grain yield (g) (per plant)	1	17.74	18.11	-	43.98	46.56	37.24
	2	20.46	20.49	-	35.14	45.75	29.66
	3	18.14	26.10	-	31.13	29.92	35.09

[+] No variances were computed for the F_1 generation for grain yield due to bulking.

[‡] Popn 1: P_1 = Aurora, P_2 = Sage
Popn 2: P_1 = Aurora, P_2 = Tam W 101
Popn 3: P_1 = Aurora, P_2 = Danne

was the fact that backcross generation variances were larger than their corresponding F_2 generation variance in population one for kernel weight and grain yield and in population two for kernel weight, kernels per spike, and grain yield (Table II). These atypical variances could be attributed to the fact that the various generations were not estimated with equal precision due to unequal environmental variances for each generation. Also of note were the disparate variances of Aurora within the characters of plant height, tiller number, and kernels per spike, being highly dissimilar for kernels per spike for population three (Table II). Since these variances were computed with equal precision, either a large sampling error was responsible, or more likely, the disparity was the result of unequal environmental influences on the populations.

Heritability and Genetic Advance

Heritability estimates, after Stansfield's convention (26), were termed high if greater than 0.50, low if less than 0.20, and medium if equal to or between 0.50 and 0.20.

Plant Height

Narrow-sense heritability estimates for plant height were high in populations one (0.71) and three (0.92) and medium in population two (0.46). This is in accordance with most of the reviewed literature (5, 8, 10, 12, 14, 18, 20), although Anwar and Chowdry (3) reported some low heritabilities in their study of spring wheat crosses. The medium heritability in population two may be attributed to the higher backcross variances for this population than in any other (Table II).

Estimates of genetic advance indicated that progress in either direction would be more effective in populations one and three than in population two (Table III), which is in agreement with the narrow-sense heritability estimates. In this case, since the phenotypic standard deviations were of similar magnitudes, because of reasonably uniform phenotypic variances (Table II), the differences in estimates of genetic advance were largely attributed to differential heritabilities.

Broad-sense heritability estimates were uniformly high (Table III) in accordance with all reviewed literature (3, 5, 12), indicating that a rather high degree of genetic diversity was present for this character. In populations one and three, lower estimates of broad-sense heritability than for narrow-sense heritability were obtained, possibly because of possible differential environmental effects on the different generations and the fact that different data sets (P_1, P_2, F_1) were used in this estimate. Sampling error as the cause is unlikely because of the rather large population sizes and the soundness of the experimental design. Based on the expected genetic advance estimates, when computed with broad-sense heritability estimates, selection should be effective in all three populations.

Kernel Weight

For this character, narrow-sense heritabilities were low for populations one (-0.02) and two (0.04) and high for population three (0.54). The negative heritability estimate in population one was interpreted as zero. All reviewed literature reported either high (5, 12, 14, 21, 22) or medium (10, 20) estimates. In population three the rather small mean kernel weight of Aurora, as compared to its means in the other

TABLE III

HERITABILITY ESTIMATES, THEIR STANDARD ERRORS AND ASSOCIATED ESTIMATES OF GENETIC ADVANCE

Character	Popn	h^2ns	Gs (%)+	h^2bs	Gs (%)‡
Plant ht. (cm)	1	0.71±.20	13.29	0.67±.06	12.51
	2	0.46±.24	08.88	0.87±.03	16.77
	3	0.92±.17	18.02	0.76±.05	14.80
1000 KWT (g)	1	-0.02±.31	-00.16	0.24±.15	02.25
	2	0.04±.31	00.45	0.57±.08	05.83
	3	0.54±.23	05.59	0.34±.13	03.54
Tiller no.	1	0.42±.25	03.50	0.40±.12	03.39
	2	0.26±.27	02.02	-0.14±.24	-01.09
	3	0.31±.27	02.32	0.20±.16	01.51
Kernels/spike	1	0.32±.26	05.73	0.47±.10	08.36
	2	0.01±.32	00.23	0.47±.10	07.86
	3	0.38±.25	06.40	0.13±.17	02.18
Grain yield (g) (per plant)	1	0.09±.29	01.29	§0.59±.09	08.09
	2	-0.15±.33	-01.79	§0.42±.13	05.09
	3	-0.09±.32	-01.02	§0.29±.16	03.32

+ Gs computed with h^2ns for 5% selection intensity--Gs is % of F_2 mean
‡ Gs computed with h^2bs for 5% selection intensity--Gs is % of F_2 mean
§ h^2bs computed by a modified formula due to missing F_1 variance

populations, seemed to account for the difference between Aurora's mean and that of Danne (Table I). This low mean kernel weight for Aurora in this population was not indicative of its performance in the other populations of this study. The variances of the F_2 generation for this character, however, did indicate a high degree of diversity present in population three, despite the atypical performance of Aurora. The low estimate in population two was attributed to nearly equal parental means (Table I) and the low magnitude of the F_2 generation variance, suggesting that a small amount of genetic diversity might be present (Table II). In population one, in spite of a rather wide spread in parental means (Table I), the low F_2 generation variance (as compared to its backcross generation variances) again indicated a lack of genetic diversity present. In these populations improvement through selection would be at a slow rate as estimated by the estimates of genetic advance.

Broad-sense heritability estimates were high in population two (0.57) and medium in populations one (0.24) and three (0.34). Reviewed literature also reported both high (4, 5, 12) and medium (22) for this character. In population three for this character, the estimate of broad-sense heritability was lower than the estimate of narrow-sense heritability (Table III). Again, this could be attributed to differential environmental effects on the generations, since different generations were used in computing the two heritability estimates.

Tiller Number

For tiller number, the estimates of narrow-sense heritability were medium in all three populations (0.42, 0.26, and 0.31). Estimates reported in the literature were medium or medium to high (8, 14, 22) and low (10, 12, 20). The wide spread of parental means for this character (Table I) and the comparatively high F_2 generation variances (Table II) suggested that a rather high amount of genetic diversity might be present. Success in selection for lower tillering seemed to be promising as evidenced by the estimates of genetic advance (Table III).

Estimates of broad-sense heritability for this character were medium in populations one (0.40) and three (0.20) and low in population two (-0.14). All estimates were lower than their corresponding narrow-sense heritability estimates. The negative estimate in population two was interpreted as zero. Again, differential environmental effects on the different generations were attributed to the smaller broad-sense heritability estimates (Table III). Estimates reported in the literature were medium (12, 22).

Kernels Per Spike

Narrow-sense heritability estimates for this character were medium in populations one (0.32) and three (0.38) and low in population two (0.01). Estimates reported in the literature were high (10), medium to high (8, 14, 22), and low (14). In population two the very high backcross one generation variance (Table II) was noteworthy because of the magnitude of its corresponding backcross two generation variance. Since the F_2 generation variance was similar to those of other populations, the possible biased backcross one generation variance may have caused an unusually low estimate. Parental means in population two were less diverse than in other populations but genetic diversity did exist. In spite of the possible biased narrow-sense heritability estimate in population two, improvement by selection, as estimated by genetic advance, would still be less productive than in the other populations where advance would be expected at a moderate rate. Estimates of broad-sense heritability were medium in populations one (0.47) and two (0.47). The low estimate in population three (0.13) was in agreement with the figure reported by Sidwell (22). Estimates of genetic advance were reflective of the heritability estimates in general. The low estimate of broad-sense heritability could be largely attributed to the higher variances of the nonsegregating generations in this population indicating a high degree of environmental diversity present (Table II). In population three the narrow-sense heritability estimate was greater than the broad-sense heritability estimate (Table III). This could again be attributed to differential environmental effects upon the various generations within this population, especially since the variance of Aurora in population three for this character was much higher than the other populations (Table II).

Grain Yield

For grain yield, uniformly low estimates of narrow-sense heritability were found (Table III), agreeing in general with all literature cited (3, 8, 12, 14, 22). The negative estimates in population two (-0.15) and three (-0.09) were interpreted as being zero. The negative estimates were caused by higher backcross generation variances than the F_2 variance (Table II). This disparity was attributed to differential environmental effects on the generations. Another possible cause of the low heritabilities could have been the lack of genetic diversity among the parents, especially in populations one and two as indicated by parental means (Table I). As reflected by the estimates of genetic advance, selection would be expected to lend the least results for this character than any other studied (Table III).

Estimates of broad-sense heritability were high in population one (0.59) and medium in populations two (0.42) and three (0.29). Estimates of all magnitudes have been reported (3, 4, 12, 22). Estimates of genetic advance calculated with broad-sense heritabilities were reflective of the heritability estimates (Table III).

Gene Action

Scaling tests were conducted on plant height, kernel weight, tiller number and kernels per spike in order to estimate the importance of various types of gene action. Due to the missing F_1 generation variances, no scaling tests of any type were conducted for the character of grain yield.

ABC Scaling Tests

ABC scaling tests of Mather and Jinks (16) were conducted to determine whether epistasis was present. Failure of model fit for any of the tests indicates the presence of epistasis. However, since each test has its own expectations in types and magnitudes of epistatic effects and in scales of measurement, agreement should not be expected among these tests (14).

Epistasis was detected by the ABC scaling test for plant height in populations one and three, for kernel weight in populations one and two, and for tiller number in populations two and three and for kernels per spike in populations one and two (Table IV).

TABLE IV

ABC SCALING TESTS

Character	Popn	A	B	C
Plant ht. (cm)	1	-7.30±1.90+	4.09±2.04+	-0.33±3.42
	2	0.03±1.80	2.40±2.00	-0.18±3.12
	3	-2.53±1.80	4.26±1.91+	0.79±3.44
1000 KWT (g)	1	1.51±1.32	2.93±1.31+	1.37±2.02
	2	-4.77±1.36+	-3.13±1.17+	-5.20±1.94+
	3	-0.62±1.40	-2.45±1.35	-3.37±2.39
Tiller no. (per plant)	1	0.12±0.92	-2.30±1.23	-2.07±1.81
	2	-1.25±0.98	-1.07±1.38	3.84±1.96+
	3	2.05±0.86+	5.23±1.17+	4.34±1.61+
Kernels/spike	1	-0.71±2.34	-2.50±2.13	-10.54±3.67+
	2	8.17±2.51+	4.53±1.89+	11.10±3.54+
	3	1.76±2.55	1.17±2.21	-4.75±3.91

+ Failure of model fit, i.e., epistasis indicated.

Three-Parameter Joint Scaling Test

Mather and Jinks (16) three-parameter joint scaling test was also conducted, using Gamble's notation (9), to determine whether epistasis was present for the characters under study and, if epistasis was not detected, to furnish information about magnitudes of gene action (other than epistasis) that were present for that character. In cases where the test for goodness of fit was declared significant by the chi square test, epistasis was declared present and the three-parameter model was proved to be inadequate for illustrating magnitudes of the types of gene action present for that character.

As expected, the three-parameter test detected the presence of epistasis in every case where the ABC scaling tests did so except for kernel weight in population one (Tables IV and V). In both tests, however, the results were "marginal." In the ABC tests the values of B lay slightly outside the range of twice its standard error, and in the three-parameter test, the X^2 value of 6.23 had a probability between 0.25 and 0.10.

The types and magnitudes of gene action indicated by the three-parameter test are discussed in conjunction with the six-parameter joint scaling tests.

The detection of epistasis in populations one and three of this study (Table V) for plant height is in accordance with the findings of Amaya et al. (2), Ketata et al. (14) and in one of the crosses studied by Chapman and McNeal (6). The failure to detect epistasis in population two agrees with the findings of Ketata et al. (13) and the other cross in Chapman's and McNeal's (6) study. The presence of epistasis in this study for kernels per spike in populations one and two disagrees

TABLE V

THREE-PARAMETER ESTIMATES FROM JOINT SCALING TESTS

Character	Popn	m	a	d	X^2(3df)
Plant ht. (cm)	1	85.59±0.58	-5.78±0.57	6.32±1.07	22.53**
	2	75.70±0.39	-0.14±0.39	6.60±0.74	01.53
	3	79.84±0.51	-7.93±0.50	8.13±0.99	08.77*
1000 KWT (g)	1	31.15±0.43	1.65±0.41	7.89±0.77	6.23
	2	33.34±0.37	-0.34±0.37	5.14±0.65	17.80**
	3	27.65±0.42	-1.31±0.37	5.70±0.84	3.66
Tiller no. (per plant)	1	18.00±0.62	-3.58±0.31	1.41±0.62	4.24
	2	20.70±0.40	-4.83±0.35	-1.70±0.75	18.34**
	3	17.70±0.35	-3.57±0.33	-0.02±0.60	22.87**
Kernels/spike	1	50.37±0.67	4.58±0.64	-0.84±1.29	9.37*
	2	50.42±0.61	5.53±0.58	3.98±1.22	15.02**
	3	50.97±0.82	2.25±0.73	-1.14±1.53	5.88

*, ** significant at the .05 and .01 levels respectively

with Ketata et al. (13, 14). For tiller number the detection of epistasis in populations two and three agrees with Ketata et al. (14) and Chapman and McNeal (6) and the failure to detect epistasis in population one agrees with the findings of Ketata et al. (13) and Edwards et al. (7). For kernel weight the detection of epistasis in populations one and two is in accordance with Ketata et al. (13) and Sun et al. (28), while Chapman and McNeal (6), Bhatt (5), Edwards et al. (7) and Ketata et al. (14) found no epistasis present for this character.

Six-Parameter Joint Scaling Test

Hayman's (11) six-parameter joint scaling test was also conducted and was, in cases where the three-parameter model was found to be inadequate, used to detect the types and amounts of gene action present (Table VI). The results of the six-parameter test verified those of the other tests in general, except for kernels per spike in population three, where a significant level of epistasis was indicated by the six-parameter test. Epistasis was not detected for this character in population three by the other tests (Tables IV, V, and VI).

For the character of plant height, nonadditive types of epistasis were present in much larger magnitudes than were additive types (Table VII), in agreement with Amaya et al. (2), Ketata et al. (14), and Chapman and McNeal (6).

For kernel weight, dominance x dominance epistasis was of the largest magnitude in both populations, though additive x additive epistasis was found to be present in a significant amount in population

TABLE VI

PARAMETER ESTIMATES OF 6-PARAMETER JOINT SCALING TEST

Character	Popn	m	a	d	aa	ad	dd
Plant ht. (cm)	1+	88.90±0.66	-9.89±1.06	4.16+3.54	-2.87±3.37	-5.70±1.26	6.08±5.43
	2	78.82±0.68	-1.20±1.19	9.12±3.70	2.60±3.61	-1.18±1.26	-5.03±5.70
	3+	83.89±0.69	-10.49±1.01	9.06±3.56	0.94±3.40	-3.40±1.16	-2.67±5.30
1000 KWT (g)	1+	34.89±0.32	1.31±0.18	10.92±2.00	3.07±1.84	-0.71±0.84	-7.50±3.30
	2+	35.63±0.36	-1.05±0.71	2.68±2.12	-2.69±2.01	-0.82±0.83	10.59±3.43
	3	30.32±0.36	-0.78±0.62	6.59±2.14	0.30±1.91	0.91±0.78	2.77±3.45
Tiller no. (per plant)	1	18.58±0.30	-2.86±0.53	1.26±1.72	-0.10±1.58	1.21±0.66	2.28±2.77
	2+	20.70±0.27	-4.64±0.50	-7.71±1.68	-6.17±1.46	-0.09±0.72	8.49±2.79
	3+	17.70±0.26	-4.54±0.49	3.33±1.56	2.94±1.44	-1.59±0.67	-10.22±2.53
Kernels/spike	1+	48.52±0.62	5.26±1.13	7.36±3.62	7.33±3.35	0.90±1.37	-4.12±5.83
	2+	53.08±0.58	7.08+1.16	3.59±3.54	1.60±3.28	1.82±1.34	-14.30±5.83
	3	49.32±0.59	2.55±1.06	6.57±3.53	7.68±3.17	0.30±1.46	-10.61±5.77

+ Epistasis detected by ABC or 3-Pm tests

TABLE VII

COMBINED ESTIMATES FROM JOINT SCALING TESTS (3-PM AND 6-PM)

Character	Popn	m	a	d	aa	ad	dd	High Parent	Direction of Dominance
Plant ht. (cm)	1	88.90±0.66	-9.89±1.06	4.16±3.54	-2.87±3.37	-5.70±1.26	6.08±5.43	Sage	Aurora
	2	75.70±0.39	-0.14±0.39	6.60±0.74	-	-	-	Tam W 101	Aurora
	3	83.89±0.69	-10.49±1.01	9.06±3.56	0.94±3.40	-3.40±1.16	-2.67±5.30	Danne	Aurora
1000 KWT (g)	1	34.89±0.32	1.31±0.18	10.92±2.00	3.07±1.84	-0.71±0.84	-7.50±3.30	Aurora	Aurora
	2	35.63±0.36	-1.05±0.71	2.68±2.12	-2.69±2.01	-0.82±0.83	10.59±3.43	Tam W 101	Aurora
	3	27.65±0.42	-1.31±0.37	5.70±0.84	-	-	-	Danne	Aurora
Tiller no. (per plant)	1	18.00±0.62	-3.58±0.31	1.41±0.62	-	-	-	Sage	Aurora
	2	20.70±0.27	-4.64±0.50	-7.71±1.68	-6.17±1.46	-0.09±0.72	8.49±2.79	Tam W 101	Tam W 101
	3	17.70±0.26	-4.54±0.49	3.33±1.56	2.94±1.44	-1.59±0.67	-10.22±2.53	Danne	Aurora
Kernels/spike	1	48.52±0.62	5.26±1.13	7.36±3.62	7.33±3.35	0.90±1.37	-4.12±5.83	Aurora	Aurora
	2	53.08±0.58	7.08±1.16	3.59±3.54	1.60±3.28	1.82±1.34	-14.30±5.83	Aurora	Aurora
	3	50.97±0.82	2.25±0.73	-1.14±1.53	-	-	-	Aurora	Danne

one (Table VII). Also in population one, dominance x dominance epistasis was of a smaller magnitude than the estimate of d.

For tiller number, dominance x dominance type epistasis was of the highest magnitude with additive x additive epistasis being next in both populations (Table VII).

For kernels per spike, additive x additive epistasis had a larger magnitude than dominance x dominance epistasis in population one. However, the reverse was found to be the case in population two (Table VII).

Combined Estimates From Joint Scaling Tests

Estimates of epistasis from the three parameter test (when the three-parameter model was deemed adequate) and the six-parameter test (in cases where epistasis was found to be present by the ABC or three-parameter tests) were combined to form estimates of the types and magnitudes of gene action present for each of the characters in the three populations, except grain yield (Table VII).

For the character of plant height, additive gene effects were more important than dominance gene effects in populations one and three (Table VII), indicating that selection should be effective in these populations. Dominance gene effects were more important in population two, suggesting that a breeding program oriented toward hybrid variety development might be more successful in this population. This is in agreement with the findings of Ketata et al. (14) and Amaya et al. (2).

For kernel weight, dominance gene effects were found to be of a greater magnitude than additive for all populations (Table VII), contrasting the findings of Ketata et al. (14), Sun et al. (28), and

Edwards et al. (7). This infers that a greater degree of success might be achieved by improvement through hybrid variety development than a selection program for this character in these populations.

For tiller number, additive gene effects were found to be more important than dominance gene effects for populations one and three (Table VII) in accordance with Ketata et al. (14), the second year's results of Chapman and McNeal (6), and Edwards et al. (7), suggesting improvement by selection. Dominance gene effects were more important than additive gene effects in population two agreeing with the findings of the first year of Chapman's and McNeal's (6) study.

For kernels per spike, additive gene effects were found to be more important than dominance gene effects in populations two and three (Table VII) in accordance with Ketata et al. (14). Dominance gene effects were of a greater magnitude in population one.

For the character of plant height, the high parents were the adapted cultivars with the net direction of dominance being toward Aurora in all populations (Table VII). For kernel weight, in this study, the adapted cultivars were the high parents in populations two and three, although the poor performance of Aurora in population three renders the results for that population questionable (Table I). The net direction of dominance was again toward Aurora in all populations (Table VII). For tiller number, the adapted cultivars were the high parents with the net direction of dominance toward Aurora only in populations one and three. For kernels per spike, Aurora was the high parent in all three populations, with the net direction of dominance being toward Aurora in populations one and two.

CHAPTER V

CONCLUSIONS

Based on estimates of heritabilities, genetic advance (Table III), and the results from the joint scaling tests (Table VII), all populations seemed to be promising sources for selection toward shorter plant height, especially with the high amounts of additive gene effects present in populations one and three and with the net direction of dominance toward Aurora in all populations. Selection might be hindered by the large amounts of nonadditive epistasis in population one and the high degree of dominance gene effects in both populations.

In this study none of the populations were promising sources for selection for increased kernel weight. The high heritability estimate for this character in population three (Table III) was attributed, in part, to the poor performance of Aurora (Table I) although some degree of genetic diversity appeared to be present (Table II). Here again, selection would have been hampered by relatively large magnitudes of nonadditive types of epistasis in populations one and two and by large magnitudes of dominance gene effects in all populations.

Selection for tiller number appeared to be moderately promising in all populations. In populations one and three, high magnitudes of additive gene effects were present and the net direction of dominance was toward Aurora, which had fewer tillers than any of the adapted parents, but the high magnitudes of dominance x dominance epistasis found in populations one and two would tend to interfere with selection in this character.

For increased number of kernels per spike, progress through selection would be anticipated in populations one and three where the net direction of dominance was toward Aurora and especially in population one where dominance x dominance epistasis was of a lower magnitude than additive by additive, although dominance gene effects were higher than additive in this population.

Based on heritability estimates and rates of expected genetic advance, selection for increased yield per se in all populations would not be productive. The results of this study suggested that yield could be increased at a faster rate by selection for improvement in its components rather than yield as such.

Cases were found where broad-sense heritability estimates were lower than their corresponding narrow-sense estimates. This was attributed to differential environmental effects on the different generations utilized in computing the estimates. These differing environmental effects would have had the effect of biasing the estimates. If the environmental variances for the nonsegregating generations were larger than for the segregating generations the estimate of genetic variance would have been biased downward. If the environmental variances for the backcross generations were larger than the variance of the F_2 generation, then the estimate of additive genetic variance would have been low. Thus, except for the F_2 generation, different generations were used to compute the narrow-sense and broad-sense estimates and the discrepancies could be attributed to unequal environmental variances (22). Estimates of narrow-sense heritability may have been biased upward in cases where appreciable amounts of additive x additive epistasis were present, also biasing upward the estimates of genetic advance for those characters, as was the case for kernel weight and tiller number in population one.

Detection of epistasis and estimates of gene actions may have been influenced by genotype x environment interactions. Since this study was conducted in one year and one location, the effects of these possible interactions could not be ascertained. Since epistasis was detected for each character studied, though not in every population, genotype x environment interactions may have had a rather large effect upon the results of this study.

Aurora seemed to be a promising parent for improvement in plant height, decrease in tiller number, and increase in kernels per spike over the adapted cultivars of this study.

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