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To the Graduate Council:

I am submitting herewith a thesis written by Robert Mack Granger entitled "Estimates of genetic variability in the F4 generation of three populations of common wheat (Triticum aestivum L. Em. Thell.)." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Agronomy.

Vernon H. Reich, Major Professor

We have read this thesis and recommend its acceptance:

Milton J. Constantin, L. M. Josephson

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

August 1, 1969

To the Graduate Council:

I am submitting herewith a thesis written by Robert Mack Granger entitled "Estimates of Genetic Variability in the F_4 Generation of Three Populations of Common Wheat (*Triticum aestivum* L. em. Thell.)." I recommend that it be accepted for nine quarter hours of credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Agronomy.

Vernon H Reich
Major Professor

We have read this thesis
and recommend its acceptance:

Milton J Constantin

L. M. Josephson

Accepted for the Council:

Hilton A. Smith
Vice Chancellor for
Graduate Studies and Research

ESTIMATES OF GENETIC VARIABILITY IN THE F_4 GENERATION OF THREE POPULATIONS OF COMMON WHEAT (*TRITICUM AESTIVUM* L. EM. THELL.)

A Thesis
Presented to
the Graduate Council of
The University of Tennessee

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Robert Mack Granger
August 1969

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To the following, I wish to express my gratitude and appreciation:

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ABSTRACT

Three populations of common bread wheat (Triticum aestivum L. em. Thell.) were studied to gain an estimate of the genetic variability associated with four agronomic characters in each population. The primary objective was to determine if homozygous lines could be isolated from these populations that would be equal to or better than the F_1 of the respective population. Two populations (population 1 and 3) exhibited heterosis for yield in the F_1 generation while the other population (population 2) showed no heterosis for yield in the F_1. Each population consisted of random F_4 lines, each of which could be traced to a single F_2 plant. Population 1 originated from a cross of the cultivars 'Seneca' x 'Knox 62'; population 2 from a cross of 'Monon' x 'Triumph'; and population 3 from a cross of 'Tenn. 9' x 'Knox 62'. The characters studied were: (1) mature plant height (centimeters), (2) heading date (days past March 31), (3) yield (grams per plot), and (4) kernel weight (grams per 1000 kernels). The experimental design was a randomized complete block with two replications and the experiment was grown at three locations.

Estimates of broad sense heritability were obtained via variance component analyses. These heritability estimates were used to calculate expected advance through selection for each character in each population. Phenotypic and genotypic correlation coefficients for all characters in all combinations were calculated. Coefficients of variation and genetic coefficients of variation were also computed.

Analyses of the data revealed that the non-heterotic population (population 2) had significant (P. = .05) variability for all four characters. Population 1 showed significant (P. = .05) variability for heading date and kernel weight only, and population 3, for only heading date and mature plant height. Heading date in population 3, mature plant height and kernel weight in population 2 were the only characters whose expected F_5 means would be better than the best parent. Evidence was found to support a two major gene hypothesis for the inheritance of heading time. From the results of this study, it appears that homozygous lines that equal or better the F_1 could not be found in later generations.

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CHAPTER I

INTRODUCTION

The existence of heterosis in common wheat (Triticum aestivum L. em. Thell.) has been well established (6, 7, 8, 14, 16, 20, 21); however, an economic means of utilizing this heterosis has not been developed. Before the discovery of a male sterility factor by Kihara in 1951 (29) and the subsequent discovery of a nuclear fertility restorer factor by Schmidt in 1962 (38), the main deterrent to the efficient use of wheat hybrids was the expense of hand emasculation and pollination. Even with the use of male sterility and fertility restorer factors there are still many problems associated with the effective use of hybrid wheat. The problems associated with an economic means of utilizing heterosis will not be dealt with directly in this study but will be enumerated briefly for the purposes of establishing some basis for the problem being studied.

In the face of the present problems associated with the use of heterosis in wheat the question arose: "Could homozygous lines of these hybrids be isolated in later generations that would be equal to or better than the respective F_1 hybrid?" The advantage of such lines is obvious. The purpose of this study then was to answer the question stated above with respect to three wheat populations which will be defined later.

CHAPTER II

REVIEW OF LITERATURE

From the time of the first report of heterosis in wheat by Freeman in 1919 (16) much work has been done towards developing a means of utilizing this heterosis and a complete review of the literature on hybrid wheat would be too extensive to cover here. It will be sufficient at this point to state that the existence of heterosis in wheat has been well established. W. L. Briggle (6) made a good review of heterosis in wheat prior to 1963.

This review covers some of the work done since 1963 and also will cover some of the problems that have been encountered in trying to utilize heterosis. A second part of this review will be concerned with that work pertaining to the statistical methods of estimating genetic parameters and the significance of these estimates to the wheat breeding program.

Problems in Utilizing Heterosis

Heyne and Smith (23) summarized the problems encountered in utilizing hybrid wheat as follows:

1. Most of the studies with hybrid wheat have been made using space planted plots which is not entirely comparable to commercial conditions.
2. The percent seed set of the male sterile lines is variable and ranges from 5 to 70 percent which is not sufficient.

3. New techniques will need to be developed which will allow lower seeding rates than those now used for commercial production. At the present commercial sowing rates, the cost of hybrid seed in relation to return would make its use prohibitive.
4. Several hybrids must be made available since hybrids appear to be specifically adapted to specific environments.

In a study related to the first problem mentioned above, Briggle _et al_. (8) obtained information on hybrid wheat grown at five population levels. Using the F_1 of a cross 'Reed' x 'Gaines' they found that maximum grain yield was reached at a population level of one plant per 2.5 cm (1 inch) or approximately 108 plants per square meter, which is roughly equivalent to 3.25 pecks per acre. This is about half the seeding rate used in most nurseries. Briggle _et al_. (7) reported similar results in a study using a spring wheat hybrid ('Lemhi 53' x 'Henry'). These results somewhat dispell previous inferences that space planting of F_1 hybrids lead to inflated yields. It is evident that the results would not apply to all situations which leaves much work to be done in this area. In both studies, very little heterosis was exhibited for plant height.

In relation to the problem of seed set and separation of hybrid seed from selfed seed in a wheat hybrid program, Watson and McWhorter (43) have proposed the use of a small seeded pollinator line to be planted at "normal" seeding rate, with the male-sterile female parent. After harvesting in bulk the seed could then be separated on seed size by mechanical means. The authors suggested that the small seed size could be obtained from Triticum aestivum ssp. sphaerococcum, which has a small rounded seed. A similar idea was proposed earlier by Sage (36).

One of the more important aspects of hybrid wheat, lies in the area of quality control. McNeal et al. (32) studied four wheat crosses and their reciprocals with respect to milling and baking quality and various agronomic characteristics. They found that quality values of the hybrids were usually intermediate to the parents and in no case did they exceed either of the parents. Reciprocal crosses had very little influence on quality tests as indicated by significant (P. = .05) differences in only two of the 64 quality test comparisons.

Studies by several investigators (10, 14, 30, 33) have shown that the greatest amount of heterosis is exhibited by crosses which represent the greatest amount of genetic diversity in origin of the parents. This led Jensen (25) to postulate that for the most effective utilization of heterosis in wheat a broad base genetically diverse male-sterile line should be used as the seed parent in the cross that produces the F_1 hybrid seed. He proposed that the broad based line could be maintained by backcrossing to a multiparent composite line. His argument is that since previous work has shown to some extent that the degree of genetic diversity determines degree of heterosis, the more diverse gene pool would afford the necessary diversity of relationship and thus permit greater potential in the use of intra-class hybrids such as the hard x hard, soft x soft, etc., crosses. It will be shown later that genetic diversity may not be a prerequisite to the expression of heterosis.

If hybrids are specifically adapted to a given environment, and it appears that they are, then a means by which the outcome of certain crosses could be predicted, even if only to a limited extent, would be a very valuable tool.

In an attempt to develop a method for predicting the response of F_1 hybrids from characteristics of the parents, Shebeski (40) studied five cultivars of wheat by diallel analysis. He found that none of the components of yield were transmitted from parent to hybrid with any consistency, thus indicating that parental components were of no value in predicting hybrid performance. Three of the 14 hybrids studied did yield significantly (P. = .01) more than the higher yielding parent.

Over a three year period, Nettevich (33) studied 48 F_1 spring wheat hybrids and seven F_2's and F_3's which showed heterosis in the F_1. After observing both yield and quality characters, he concluded that: (1) the F_1's consistently outyielded the best parent in separate combinations with a range of 30-45 per cent; (2) the grestest increase in yield was obtained by those crosses which represented high yielding cultivars which differed in agronomic characters and origin but productive under given conditions; (3) the degree of heterosis is determined mostly by specific combining ability and, dependent on the combination, may be governed by one or more components of yield; (4) the heterotic-environmental interaction was large which meant that the same combination might give entirely different results from year to year or location to location; (5) the physical, chemical, and baking qualities of the hybrids were usually intermediate to the parents but sometimes approached one of the parents; and (6) a distinct decrease in yield was observed in the F_2 with only a "few" of the F_2's exceeding the best parent.

In a study by Fonseca and Patterson (14) with a diallel cross of seven cultivars of hard red, soft red, and soft white wheat classes, both the level of hybrid vigor and effect of seeding rate were observed. In studying the F_1 and F_2 it was found that hill planting showed little interaction with seeding rates from 3 to 15 plants per square foot, but the level of hybrid vigor in hill plots was higher than for normal seeding. In 19 of the 21 hybrids studied, the F_1 was significantly (P. = .05) greater than the best parent. Fonseca and Patterson also found, as others have, that the greatest amount of heterosis was exhibited by the more diverse crosses such as the red x white and hard x soft combinations.

Fonseca and Patterson (15) studied yield component heritabilities and inter-relationships of these components in a seven parent diallel cross in winter wheat. Heritability estimates in the narrow sense were calculated by the regression of F_1 or F_2 means on mid-parent values. Narrow sense heritabilities for plant height and earliness were relatively high, being .78 to .87 for F_1's, .80 to .82 for F_2's for earliness and .55 to .78 for F_1's and .87 for F_2's for plant height. Kernel weight heritability was intermediate, being .15 to .51 for F_1's and .44 to .55 for F_2's and grain yield heritability estimates were .17 to .49 for F_1's and .27 to .28 for F_2's.

Gyawali (21) used a seven-parent diallel cross to study heterosis and combining ability of winter wheat. Five of the seven cultivars used were of the soft red class ('Knox,' 'Knox 62,' 'Monon,' 'Seneca,' and 'Tenn. 9'), one soft white ('Genesee') and one hard red ('Triumph'). Ten of the 21 hybrids yielded significantly (P. = .05) more grain than the best parent with the average yield of all hybrids being 24 percent higher than the best parent. Significant differences were found for all characters in all hybrids and a combining ability analysis showed that the major component of variation was general combining ability. Specific combining ability effects were also significant for six of the eight characters studied. The specific combining ability estimates in this test were greater than obtained in other studies (14, 30). These results will be discussed later. Three of the hybrids observed were selected for study in later generations and are the materials used in this study.

Related Studies

Allard and Harding (1) studied the inheritance of "heading time" in the F_1, F_2, F_3, and the first and second F_2 backcross generations of the hybrid 'Ramona' x 'Baart 46', which exhibit about 15 days difference in heading time. After studying segregating generations they found that the observed distribution corresponded very well with the theoretical distribution for a two gene hypothesis. Transgressive segregation of a few days was observed for late heading but no transgressive segregation was observed for earlier heading.

In a study related to combining ability and heritability estimates, Kronstad and Foote (30) used Griffing's diallel analysis to estimate general and specific combining ability in 10 winter wheat cultivars. They found that specific combining ability effects were significant for grain yield and plant height. They also found that a large portion of the total variation for yield and yield components was associated with a significant amount of general combining ability. Narrow sense heritability estimates were calculated by parent-progeny regression of spaced F_1 plants. The estimates were as follows: plant height .829, kernel weight .472, and grain yield .259. All estimates were significant except grain yield.

Brown et al. (10) in a study at Illinois using a diallel cross of three soft winter cultivars ('Knox,' 'Monon,' and 'Racine') and four hard winter cultivars ('Bison,' 'Crokett,' 'Pawnee,' and 'Triumph') found that considerable heterosis for grain yield could be found in certain crosses but not for others. They also found that most of the variation in yield and other characters in the F_1 was associated with a high general combining ability. The authors stated that although in their study they failed to detect specific combining ability, the possibility of its existence in wheat could not be ruled out since they had used a limited number of cultivars and crosses. In this study, the highest heterotic values were obtained in the crosses of the hard x soft classes. It was pointed out that these crosses might have limited value because of quality problems.

V. A. Johnson et al. (27) studied the genetic variability of seven characters in the progeny of a hard red winter wheat cross of 'Seu Seun 27' x 'Blue Jacket.' The cross represents contrasting characters for plant height, yield, maturity, and kernel weight. They reported that most of the variance associated with plant height was additive and evidence from segregating generations indicated that three major gene pairs control this character. The evidence indicated that only a few genes control kernel weight. Heterosis for yield was exhibited in the

F_1 which exceeded the best parent by 12.9 percent. Broad sense heritability estimates for plant height, heading date, kernel weight, and yield were .608, .805, .612, and -.023, respectively. In this study it was found that plant height, maturity, grain yield, and kernel weight were all significantly correlated.

Schlehuber et al. (37) studying the inheritance of maturity and quality factors in F_4 lines of a hard red winter cross, found that for all 14 quality characters observed the range of the F_4 exceeded the range of the parents, but the progeny mean for these characters equaled the midparent for seven characters and exceeded the midparent for five of the characters.

In studying the genotypic and phenotypic correlations between these quality characters and heading date Schlehuber et al. (37) found the correlations to be small suggesting no strong genetic relation or association. This should allow selection for early maturity without affecting the existing quality characteristics.

Lofgren et al. (31) studied the heritability of certain characters in four wheat crosses between the cultivars 'Atlas 50,' 'Atlas 66,' 'Triumph,' and 'Kaw.' In the 'Triumph' x 'Atlas 66' cross using the regression method the heritability of kernel weight (grams/1000 kernels) for the F_4 on F_3 and F_5 on F_4 generations was 42.7 percent and 42.5 percent, respectively.

Baker et al. (4) studied the inheritance of and the interrelationship among yield and several quality traits in 50 random F_7 and F_8 lines of a wheat cross 'CT423' x 'Prelude.' Seven characters were studied with only two, yield and kernel weight, common to the characters observed in this study. The parameters estimated were heritability, phenotypic correlations, genotypic correlations, and expected genetic advance from selection. First and second order interactions were also observed. In general, the heritability estimates for the quality characters were higher than the estimates for yield. Heritability estimates for yield ranged from .28 to .74 and for kernel weight from .77 to .93. Seven of the 21 possible correlations were significantly (P. = .05) greater than zero. The simple correlation coefficients for yield and kernel weight was .33 and significantly (P. = .05) greater than zero. The genotypic correlations agreed well with the simple correlations.

Other Crops

Direct comparisons of results of studies done with other crops with those of wheat are not possible; however, some of the work on other crops may be useful as far as procedure and technique pertain and certainly some relationships exist as far as results are concerned within the small grains and even more so within the polyploid cereals. The following is a review of that work with other crops which was considered pertinent to the problem at hand.

Johnson *et al*. (26) studied the genetic and environmental variability in two populations of soybeans in the F_4 and F_5 generations. The two populations were grown at two and three locations in one year and both at one location the second year. Variance components, heritability and genetic advance for the average performance over locations and years were calculated for the characters yield, plant height, grams per 100 kernels and oil percentage. The estimates of genotype x environment interactions were higher for yield than for the other characters. The authors stressed the importance of the genotype x environment interaction components with respect to the estimates of heritability and expected advance.

Working with barley, Rasmusson and Glass (35) studied two populations of F_3 derived lines in the F_5, F_6, and F_7 generations to gain estimates of genetic and environmental variability associated with these lines. Their primary objective was to estimate and observe the magnitude of the genotype, genotype x environment, and error components of variance. They found that, with one exception, the genotype x environment interaction components of variance were smaller than the genotype and plot error components and second order interactions were generally larger than first order interactions. Their data indicated that one test in one year would have been sufficient to give favorable odds for including the elite lines if the top 25 percent were selected. In the authors' opinion, the need to test under several environments in a selection program should not be taken for granted but should be evaluated carefully.

Frey and Horner (18) studied the relationship of the actual gains and predicted gains in a barley selection experiment. Two populations of F_2 derived lines were studied in the F_4 and F_5 generation. Two methods of calculating heritability were used, the components of variance method and the parent-progeny regression method. In comparing the predicted gains by the two methods with actual gains in the F_5 it was found that the parent-progeny regression method of predicting gains tended to underestimate heritability while the components of variance method gave values which closely approximated the actual gains made from selection. These results tend to dispell the idea that the components of variance method would contain discrepancies due to the year and interaction components.

Wallace et al. (42) studied genotypic variances and covariances of six quantitative characters in oats. One population resulting from a cross of the cultivars 'Letoria' x 'Fulwin' were studied in the F_3 and F_4 generation. Each line was a descendant of a randomly chosen F_2 plant. Those characters studied were yield, kernel weight, kernels per panicle, culms per plant, kernels per plant, and plant height. In general, the statistical analysis followed that outlined by Comstock and Robinson (12). Those parameters estimated were variance components, heritability estimates, genetic advance from selection, and phenotypic and genotypic correlations. All direct estimates of the genotypic variance were biased upward by one or more interaction components of variance but later evidence allowed for correction of this factor. The variance components for three of the characters (kernel weight, kernels per panicle, and plant height) studied were of similar magnitude for both generations while the other three characters had higher variance components and means in the F_4 than in the F_3 generation. The data indicated that within the cross, selection of the top 5 percent would yield lines 15 to 18 percent superior in yield to the population mean. It was the authors' opinion that selection based on indices other than for yield alone, would be of little value.

From this review it is evident that studies related directly to this author's study have not been reported. The review, however, gives enough background in ancillary studies for basic techniques and pertinent relationships for a good understanding of the problem at hand.

CHAPTER III

MATERIALS AND METHODS

Populations

Three populations of wheat (Triticum aestivum L. em. Thell.) were studied each consisting of randomly derived F_4 lines which could be traced to a different F_2 plant. Population 1 resulted from a cross of the cultivars 'Seneca' (C.I. 12529) x 'Knox 62' (C.I. 13701). Population 2 was derived from a cross of the cultivars 'Monon' (C.I. 13278) x 'Triumph' (C.I. 12132) and Population 3 originated from a cross of 'Knox 62' (C.I. 13701) x 'Tenn. 9.'

The five parental cultivars all belong to the winter wheat class. The parents used to develop each population show diversity in at least one character. 'Seneca' is a tall, late maturing soft red wheat developed at Ohio and 'Knox 62' is a short, early maturing, soft red wheat originating in Indiana. The short-tall and early-late designations given here are relative terms indicating plant height and days to maturity, respectively. Both 'Monon' and 'Triumph' are classified as short and early but differ in their kernel hardness index, 'Monon' being a soft red wheat and 'Triumph,' a hard red wheat. 'Monon' originated in Indiana and 'Triumph,' in Oklahoma. In population 3, 'Tenn. 9' contrasts 'Knox 62' (described previously) in that it is tall and late maturing. The parentage of the cultivars in each cross are quite diverse in origin and offer no apparent relationship with the possible exception of 'Tenn. 9,' of which the parentage is unknown. 'Tenn. 9' is an experimental line developed at The University of Tennessee by C. D. Sherbakoff. It is classified as a soft wheat although its kernel is somewhat intermediate to the hard and soft types. For further information on parental cultivars used in this study (except 'Tenn. 9') see Briggle and Reitz (9). Of the three hybrids, the most diverse as far as origin and "type" is concerned is probably the 'Monon' x 'Triumph' cross. The discussion on parental differences is summarized in Table I.

Experimental Methods

The original crosses were made in the greenhouse at The University of Tennessee Agricultural Experiment Station in 1964. In 1965 the F_1 seeds were planted in 10 foot rows with one foot between plants and rows. F_2 seeds were planted in 1966 in 10 foot rows with six inches between plants within rows and one foot between rows. From this F_2 generation each plant was harvested individually and planted as one row in the F_3. The F_3 seeds were planted with a tractor mounted cone planter at approximately normal planting rates (1 gram/foot) in 10 foot rows with one foot between rows. Each row was harvested individually to comprise a single F_4 line. The same procedure was followed for each population.

Lines to be studied in the F_4 generation were chosen at random from the group of F_3 lines. A hail storm caused considerable damage to the F_3's and a subsequent reduction in yield of F_4 seed and therefore only those F_4 lines with a sufficient quantity of seed (60 grams) were used in the study.

TABLE I

PARENTAGE, ORIGIN, MARKET CLASS, PLANT HEIGHT, AND MATURITY FOR PARENTS USED TO DEVELOP THE THREE POPULATIONS[a]

Cultivar	Maturity	Height	Market class[b]	Origin	Parentage
Seneca - C.I. 12529[c]	Late	Tall	SRW	Ohio	Portage, Fulcaster
Knox 62 - C.I. 13701	Early	Short	SRW	Indiana	Knox, P.I. 94587, Hope, Hussar, Kawvale, Hungarian, Fairfield, W38
Monon - C.I. 13278	Early	Short	SRW	Indiana	Trumbull, Fultz Sel., Minhardi, Wabash, Purplestraw, Chinese, Michigan Amber, Kawvale, Hungarian, W38, Fairfield, Hope Hussar
Triumph - C.I. 12132	Early	Short	HRW	Oklahoma	Blackhull, Kanred, Florence
Tenn. 9	Late	Tall	SRW	Tennessee	Unknown

[a] Taken in part from Gyawali (20).

[b] SRW - Soft red winter; SWW - Soft white winter; and HRW - Hard red winter.

[c] Accession number of the Crops Research Division, U.S.D.A.

Lack of sufficient amount of seed and inflexibility of planting procedures necessitated the use of one row plots. Two row plots were considered, but it was felt that the gain in information by using three locations instead of two, outweighed the gain in precision expected from the use of two row plots. The cultivar 'Monon' was used as border rows on the outside parameters of the field experiment at all locations. The three locations were: Plant Science Farm, Knoxville, Tennessee (L1), Highland Rim Experiment Station, Springfield, Tennessee (L2), and the West Tennessee Experiment Station, Jackson, Tennessee (L3). At Knoxville the experiment was grown on Etowah silt loam, at Springfield on Dickson silt loam, and at Jackson on Calloway silt loam. Each population was handled as a separate experiment, in that all lines comprising one cross were randomized and kept together in one block. The parents of each population were included in the experiments and replicated four times. Population 1 consisted of 90 individual lines; population 2, 102 lines; and population 3, 100 lines. The three populations of F_4 lines were planted at a rate of one gram per foot in plots nine feet in length with plots spaced one foot apart. The experimental design was a randomized complete block with two replications.

Characters Studied

The characters studied were: mature plant height (centimeters) recorded at harvest at all locations; heading date recorded as days past March 31, recorded at locations 1 and 3; yield (grams/plot) recorded at all locations; and, kernel weight (grams/1000 kernels) recorded at all locations. The above mentioned characters are considered to be quantitatively inherited. Lodging and disease were severe problems at all locations. Because of complications caused by the use of one row plots no attempt was made to record lodging or disease reactions.

Statistical Methods

Data for yield and kernel weight missing in one plot in population 3 at Knoxville (L1) were estimated by covariance analysis as described by Steel and Torrie (41).

All data were then subjected to an analysis of variance to gain an estimate of the different components of variance. The mathematical model assumed for this analysis for all characters was as follows:

$$Y_{ijk} = \mu + A_i + B_{j(i)} + C_k + AC_{ik} + \epsilon_{jk(i)}$$

Where Y_{ijk} = i, j, kth observation

μ = population mean

A_i = ith location effect

$B_{j(i)}$ = jth replication effect within the ith location

C_k = kth genotype effect

AC_{ik} = i, kth location x genotype effect

$\epsilon_{jk(i)}$ = experimental error

The expected mean squares were calculated as described by Hicks (24). All effects were assumed to be random and the expected mean squares are given in Table II.

TABLE II

GENERAL MODEL OF THE ANALYSIS OF VARIANCE TABLE AND EXPECTED MEAN SQUARES USED TO STUDY THE RANDOM F_4 LINES OF THREE WHEAT POPULATIONS

Source	d f	Expected Mean Square
A - Location	$(\ell-1)$	$\sigma_e^2 + r\sigma_{AC}^2 + g\sigma_B^2 + rg\sigma_A^2$
B - Reps within Locations	$\ell(r-1)$	$\sigma_e^2 + g\sigma_B^2$
C - Genotypes	$(g-1)$	$\sigma_e^2 + r\sigma_{AC}^2 + rl\sigma_C^2$
AC - Location x Genotype	$(\ell-1)(g-1)$	$\sigma_e^2 + r\sigma_{AC}^2$
E - Residual	$\ell(r-1)(g-1)$	σ_e^2

Since the experiment was conducted only for one year, no estimate was available for year effects. The year and year interaction components of variance are not shown in the expected M.S. table although these components are contained in each effect.

From these mean square estimates the genetic components of variance were calculated for each character and for each source, following the procedure as described by Comstock and Robinson (12). Broad sense heritability estimates were then calculated using the procedure given by Burton (11). Heritability in the broad sense (H) is calculated by the formula ($\sigma^2_g / \sigma^2_{ph}$ x 100) where σ^2_{ph} is the phenotypic variance associated with a particular character and σ^2_g is the genetic component associated with the same character. Heritability in the narrow sense, $\sigma^2_a / \sigma^2_{ph}$, the ratio of the additive variance to the phenotypic variance was not calculated since no estimate of the additive variance was available. However, in the F_4 the portion of genetic variance attributable to non-additive effects would be small.

The phenotypic variance (σ^2_{ph}) was calculated by the formula: $\sigma^2_{ph} = \sigma^2_g + \sigma^2_{ac}/l + \sigma^2_e / rl$ where σ^2_g represents the genetic component of variance, σ^2_{ac} the location x genetic component, σ^2_e the residual component, l the locations, and rl, replication x locations.

The theoretical advance that could be expected from selection at a given intensity was then calculated. The procedure for calculating genetic advance (Gs) is given by Hanson et al. (22) and is defined by the following formula: $Gs = K\sigma_{ph}H$ were K is the selection differential expressed in phenotypic standard deviations and H is recognized as the heritability for that particular character. These estimates of advance from selection may be expressed in two ways, either as a percent of the population mean or in terms of the unit measurement.

Simple correlation coefficients were calculated for all characters in all combinations. The correlation coefficients were calculated by location since the large number of degrees of freedom made possible a very good estimate of this parameter.

To obtain a clearer picture of the relationships of these characters, the genotypic correlations among these characters were calculated from the formula:

$$rg = \frac{\sigma^2_{ph_1 \quad ph_2}}{\sigma^2_{ph_1} \times \sigma^2_{ph_2}}$$

Where $\sigma^2_{ph_1\, ph_2}$ is the genotypic covariance component for two characters and $\sigma^2_{ph_1}$ and $\sigma^2_{ph_2}$ are the respective genetic variance components.

The genetic coefficient of variability (G.C.V.) used by Burton (11) was calculated for each character over the three locations. The computations for this value were calculated by the following formula:

$$\text{G.C.V.} = \sigma^2_g \ / \ \bar{x} \times (100)$$

This value then gives the estimate of genetic variance in relation to the mean.

No attempt was made to test for differences among populations although such a comparison was possible but with certain limitations.

CHAPTER IV

RESULTS

The Analysis of Variance

Parent and population means for all characters and all populations are given in Table III. These data will be discussed in more detail in later discussion.

Analyses of variance were applied to all data by the format described in Table II, page 19. The results of these analyses are given in Tables IV, V, and VI, for populations 1, 2, and 3, respectively. In general, for all characters, the location source had a very large mean square compared to other sources and thus accentuates the necessity for conducting experiments of this type under more than one environment. This point was emphasized by Johnson *et al*. (26).

The residual mean square calculated for heading date was larger than the location x genotype mean square in all three populations. The same is true for mature plant height in population 3. There was very little difference in the expression of these characters relative to location.

The location x genotype mean square estimate for yield was significant (P. = .05) for all populations indicating that the random lines within each population yielded differently in each location. Again, the need is shown for conducting this type of experiment under more than one environment.

TABLE III

POPULATION AND PARENT MEANS FOR ALL CHARACTERS IN ALL POPULATIONS

Parents and Populations	Characters			
	Mature Plant Height (Cm.)	Heading Date Days past March 31	Yield g./plot	Kernel Weight g./kernels
Seneca	120.3	38.8	176.9	35.7
Pop. 1	117.4	30.8	187.9	33.5
Knox 62	115.8	28.6	110.9	30.4
Monon	110.1	28.3	244.4	31.1
Pop. 2	111.1	28.6	194.2	30.6
Triumph	109.7	28.8	162.8	29.6
Knox 62	109.5	29.0	188.7	30.0
Pop. 3	115.6	30.5	169.0	32.3
Tenn. 9	119.1	38.3	173.3	35.0

TABLE IV

MEAN SQUARE ESTIMATES FROM THE ANALYSIS OF VARIANCE FOR FOUR CHARACTERS IN POPULATION 1

Source	Expected Mean Square Subscript	df	Mean Square Estimates			
			Mature Plant Height	Heading Date	Yield	Kernel Weight
Locations	(A)	2	23104.94	68.47	156344.05	872.12
Reps/Loc	(B)	3	593.80**	5.25 N.S.	13309.20**	89.47**
Genotypes	(C)	89	77.92 N.S.	10.97**	3958.10 N.S.	19.33**
Loc. x Genotype	(AC)	178	67.71*	6.08 N.S.	3420.96**	5.81**
Residual	(E)	267	55.56	8.79	2493.85	4.20

NOTE: * = Significantly greater than zero at the .05 level of probability.
** = Significantly greater than zero at the .01 level of probability.
N.S. = Not significantly greater than zero at the .05 level of probability.

TABLE V

MEAN SQUARE ESTIMATES FROM THE ANALYSIS OF VARIANCE FOR FOUR CHARACTERS IN POPULATION 2

Source	Expected Mean Square Subscript	df	Mean Square Estimates			
			Mature Plant Height	Heading Date	Yield	Kernel Weight
Locations	(A)	2	31754.57	32.19	170228.09	503.33
Reps/Loc	(B)	3	216.48**	0.31 N.S.	763.04 N.S.	33.41**
Genotypes	(C)	101	59.81**	10.34**	4924.86**	21.88**
Loc. x Genotype	(AC)	202	45.78 N.S.	6.99 N.S.	2908.51**	6.43**
Residual	(E)	303	40.15	7.78	2017.12	4.64

NOTE: ** = Significantly greater than zero at the .01 level of probability.
N.S. = Not significantly greater than zero at the .05 level of probability.

TABLE VI

MEAN SQUARE ESTIMATES FROM THE ANALYSIS OF VARIANCE FOR FOUR CHARACTERS IN POPULATION 3

Source	Expected Mean Square Subscript	df	Mean Square Estimates			
			Mature Plant Height	Heading Date	Yield	Kernel Weight
Locations	(A)	2	32089.62	90.25	274812.92	461.91
Reps/Loc	(B)	3	1670.64**	21.13*	78979.15**	107.19**
Genotypes	(C)	99	85.92**	13.91**	3536.88 N.S.	12.71 N.S.
Loc. x Genotype	(AC)	198	64.72 N.S.	4.53 N.S.	3331.58*	10.55*
Residual	(E)	297	72.14	6.43	2742.65	8.28

NOTE: * = Significantly greater than zero at the .05 level of probability.
** = Significantly greater than zero at the .01 level of probability.
N.S. = Not significantly greater than zero at the .05 level of probability.

The coefficients of variation and genetic coefficients of variation are given in Table VII. In general, the coefficients of variation are within the limits acceptable for small grain except for yield which is relatively high. More will be said about these high coefficients of variation for yield in later discussion. The coefficients of variation are similar in all populations. They were expected to be similar since they grew adjacent in the field and all measurements and observations were made at the same time. The genetic coefficient of variation (G.C.V.) was calculated only for those characters which had a significant genetic component of variance. The G.C.V. for all characters presented was consistently smaller than the C.V. and the values compare well over populations except in the case of yield where no comparison was possible.

Components of Variance

Table VIII gives the components of variance that were calculated for each of the three populations. In all cases, the location x genotype component of variance (σ^2_{ac}) was considerably smaller than the residual component (σ^2_e). The location x genotype interaction component was significant (P. = .05) in all populations for yield and kernel weight and significant (P. = .05) in population 1 for mature plant height. For heading date, the location x genotype component of variance was non-significant (P. = .05) for all three populations. This would tend to indicate that the lines within each population headed at the same time, relative to each other, regardless of the environment. The location x genotype interaction component for yield, although much smaller than the

TABLE VII

COEFFICIENTS OF VARIATION (C.V.) AND GENETIC COEFFICIENTS OF VARIATION (G.C.V.) FOR ALL CHARACTERS IN ALL POPULATIONS

Characters	Population 1	Population 2	Population 3
Mature Plant Height			
C.V.	6.35	5.70	7.40
G.C.V.	——[a]	1.62	1.62
Heading Date			
C.V.	9.62	9.74	8.32
G.C.V.	3.59	3.19	5.02
Yield			
C.V.	26.57	23.13	29.14
G.C.V.	——[a]	9.44	——[a]
Kernel Weight			
C.V.	6.12	7.03	7.41
G.C.V.	4.47	5.23	——[a]

[a] Not calculated since σ_c^2 was not significantly (P. = .05) greater than zero.

TABLE VIII

INDIVIDUAL COMPONENTS OF VARIANCE CALCULATED FROM EXPECTED MEAN SQUARE ESTIMATES FOR FOUR CHARACTERS AND ALL POPULATIONS

Character	Population	σ^2_{AC}	σ^2_{C}	σ^2_{ph} [a]	σ^2_{C} [a]
Mature Plant Height	1	6.08*	1.70 N.S.	11.29	55.56
	2	2.82 N.S.	3.28**	9.97	40.15
	3	-3.71 N.S.	3.53*	15.56	72.15
Heading Date	1	-1.36 N.S.	1.22**	3.42	8.79
	2	- .40 N.S.	0.84**	2.78	7.78
	3	- .95 N.S.	2.34**	3.95	6.43
Yield	1	463.55**	89.53 N.S.	570.16	2493.85
	2	445.69**	336.06**	820.81	2017.12
	3	294.47*	34.22 N.S.	555.26	2742.65
Kernel Weight	1	0.80**	2.25**	3.22	4.20
	2	0.89**	2.57**	3.65	4.64
	3	1.13*	.36 N.S.	1.76	8.28

[a] A Statistical test of significance is not indicated for these components.

NOTE: * = Significantly greater than zero at the .05 level of probability.
** = Significantly greater than zero at the .01 level of probability.
N.S. = Not significantly greater than zero at the .05 level of probability.

residual component for that character, is still significant (P. = .05) indicating that the lines in each population yielded differently in relation to each other over the three locations. The location x genotype interaction components for kernel weight, even though small, were significant (P. = .05) for all three populations and highly significant (P. = .01) for two of the populations. This evidence indicates that the kernel weight of the lines within a cross vary relative to each other from location to location or it can be said that the kernel weight in wheat is influenced a great deal by the environment.

The residual component of variance (σ_e^2) was relatively small for all three populations for heading date and kernel weight, somewhat larger for mature plant height, and very large for yield. The pattern in the relative magnitude of the residual components over the four characters seems logical if one considers the amount of variation associated with the measurement of each of these characters. The large residual variance for yield cannot be attributed to poor methodology along; some of it was undoubtedly caused by the severe lodging and disease which was prevalent in all populations and at all locations. The use of one row plots made it impractical to record lodging or disease reactions. Further discussion of this point will follow.

The genetic component of variance (σ_c^2) for mature plant height was significant (P. = .05) for populations 2 and 3, but non-significant (P. = .05) for population 1. The parents of population 1 contrast with respect to this character (Table I, page 16) and the random F_4 lines are expected to show some genetic diversity. The parents of population 2, however, are both considered short and thus no genetic diversity was expected in the F_4 generation. The exact nature of the inheritance of plant height is not known (2) and any attempt to explain these results would only be speculation. The precision of the experiment was probably too low to detect small differences.

The genetic component of variance (σ_c^2) for heading date was highly significant (P. = .01) for all populations. Some degree of genetic diversity among F_4 lines is expected for population 1 and 3 since the parents of each of these two populations contrast with respect to heading date. The parents of population 2, however, are both considered early maturing and thus no genetic variation among random F_4 lines of this cross is expected. Ayad (3) and Allard and Harding (1) presented evidence to support a hypothesis for a two major gene system controlling heading date with a large number of genes with lesser effect modifying the major gene effects. The distribution of days to heading for population 2 is shown in Figure 1 and closely resembles the distribution found by Allard for his F_2 generation. The bimodal distribution shown in Figure 1 suggests the possibility that the parents of population 2 had different major genes for heading date with modifiers that caused each to react similarly.

The genetic component of variance (σ_c^2) for yield was highly significant (P. = .01) for population 2 but non-significant (P. = .05) for populations 1 and 3. Means of the parents (Table III, page 23) for all populations suggest that each parent differs in their yield potential and thus some genetic variation is expected in the F_4 generation of each cross. The inheritance of yield is considered very complex and no attempt will be made to explain these results. Again there is the

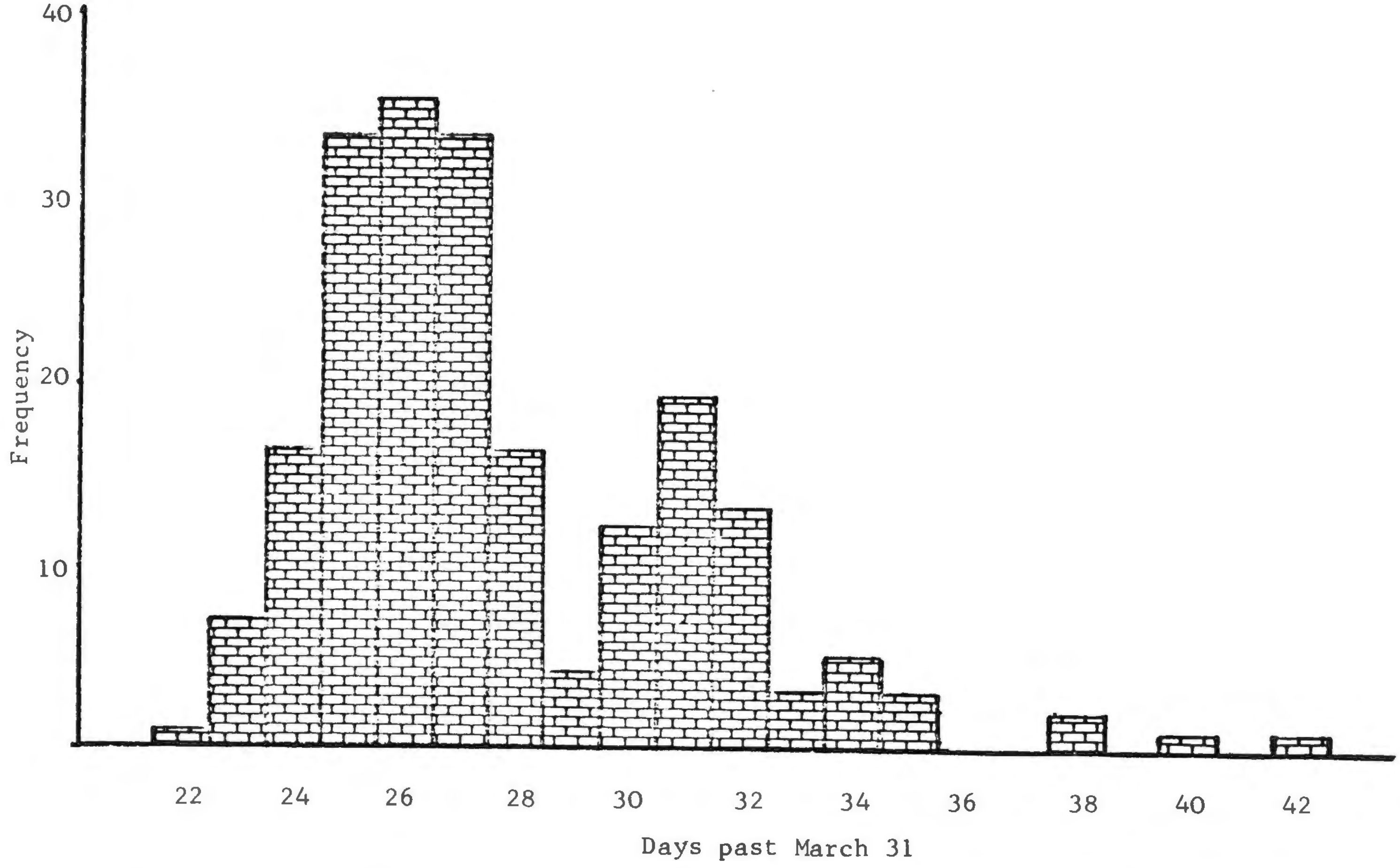

Figure 1. Frequency distribution for heading date for population 2, location 1.

possibility that the precision of the experiment did not allow detection of small differences.

The genetic component of variance (σ_c^2) for kernel weight was highly significant (P. = .01) for populations 1 and 2 and very similar in magnitude. Parental means for kernel weight (Table III, page 23) show about a five gram difference between the parents of population 1 and a 1.4 gram difference between the parents of population 2. It is not known definitely how kernel weight is inherited (2) but more recent results by Sharma and Knott (39) show that kernel weight is controlled by relatively few genes, possibly as few as four. If this is the case, then the small difference between the parents of population 2 could result in significant differences among lines in the F_4 generation. The genetic component of variance for kernel weight in population 3 was non-significant (P. = .05) and much smaller in magnitude than the components for populations 1 and 2. Parental means for kernel weight show a five gram difference between parents, very similar to the difference between the parents of population 1.

Heritability Estimates

Broad sense heritability estimates for population 1 were possible for only two of the four characters, heading date and kernel weight (Table IX). In population 2, heritability estimates were possible for four characters and in population 3, for only mature plant height and heading date. Johnson *et al*. (27) reported broad sense heritability estimates of .608 for plant height. His estimate, even though calculated by the same method used herein, was based on the F_1 generation which

TABLE IX

BROAD SENSE HERITABILITY ESTIMATES FOR ALL CHARACTERS IN ALL POPULATIONS

Character	Population 1	Population 2	Population 3
Mature Plant Height	0.0[a]	0.329	0.227
Heading Date	0.358	0.301	0.593
Yield	0.0[a]	0.409	0.0[a]
Kernel Weight	0.699	0.706	0.0[a]

[a] The estimate was considered 0.0 since σ_c^2 was not significantly (P. = .05) greater than zero for these characters.

undoubtedly contained some non-additive effects. For the estimates presented here, consideration must be given to the fact that one row plots were used. The heritability estimate for yield in population 2 is much larger than expected for this character and as usual when dealing with heritability the estimate may be influenced by a number of factors which cannot be controlled.

The heritability estimate for kernel weight for population 1 and 2 are of similar magnitude, being .699 and .706, respectively. Johnson *et al*. (27) reported a broad sense heritability estimate for kernel weight of .612 and Sharma and Knott (39) one of .693 which are similar to the results obtained here. Heritability estimates are usually used or applied to the population from which they were derived. The use of the broad sense estimates in this experiment rather than narrow sense heritability can be justified since most of the non-additive genetic effects are lost by the F_4 generation.

Since this experiment was grown only for one year the individual components and the heritability estimates are probably inflated due to the years and year interaction components not being available.

Expected Advance from Selection

The expected phenotypic advance that can be achieved by selection is given in Tables X, XI, and XII for populations 1, 2, and 3, respectively. Selection for mature plant height and heading date would be made in a negative direction. The expected advance in all cases is given in the same units used in the original measurement of the character. Any success in selection for any one character will depend on the effect

TABLE X

EXPECTED GENETIC GAIN IN FOUR CHARACTERS IN THE F_5 GENERATION FROM SELECTION IN THE F_4 GENERATION USING DIFFERENT SELECTION INTENSITIES--POPULATION 1

Character and Units	Percent Selected			
	20	15	10	5
Mature Plant Height (cm.)	—[a]	—[a]	—[a]	—[a]
Heading Date (days past March 31)	.93	1.03	1.16	1.36
Yield (g./plot)	—[a]	—[a]	—[a]	—[a]
Kernel Weight (g./1000 K)	1.76	1.95	2.21	2.59

[a] No estimate of genetic advance was possible since the heritability for these characters was estimated to be 0.0.

TABLE XI

EXPECTED GENETIC GAIN IN FOUR CHARACTERS IN THE F_5 GENERATION FROM SELECTION IN THE F_4 GENERATION USING DIFFERENT SELECTION INTENSITIES--POPULATION 2

Character and Units	Percent Selected			
	20	15	10	5
Mature Plant Height (cm.)	1.45	1.61	1.83	2.14
Heading Date (days past March 31)	0.70	0.77	0.88	1.03
Yield (G./plot)	16.42	18.18	20.64	24.16
Kernel Weight (g./1000 K)	1.89	2.09	2.37	2.78

TABLE XII

EXPECTED GENETIC GAIN IN FOUR CHARACTERS IN THE F_5 GENERATION FROM SELECTION IN THE F_4 GENERATION USING DIFFERENT SELECTION INTENSITIES--POPULATION 3

Character and Units	Percent Selected			
	20	15	10	5
Mature Plant Height (cm.)	1.25	1.39	1.58	1.84
Heading Date (days past March 31)	1.65	1.83	2.07	2.43
Yield (g./plot)	—[a]	—[a]	—[a]	—[a]
Kernel Weight (g./1000 K)	—[a]	—[a]	—[a]	—[a]

[a] No estimate of genetic advance was possible since the heritability for these characters was estimated to be 0.0.

it will have on the most important character yield. Considering mature plant height for population 1 it is noted that the simple correlation coefficient (Table XIII) is positive indicating that as plant height increased, so would yield. This would be an undesirable situation when selecting for shorter plants. This same situation exists for populations 2 and 3. An estimate of the genotypic correlation coefficient for mature plant height and yield, which was calculated only for population 2, was negative which indicates that selection for shorter plants might not adversely affect yield.

The phenotypic correlation coefficients for heading date and yield (Tables XIII, XIV, and XV) are negative in all cases but significant only for population 2. In this case then selection for earlier heading would have no adverse effect on yield. The genotypic correlation coefficients for these two characters are of similar magnitude for populations 2 and 3, but is very small for population 1.

Kernel weight is considered one of the components of yield and as would be expected, the phenotypic correlation coefficient for kernel weight and yield in this study was positive and highly significant (P. = .01) for each population. The genotypic correlation coefficients for kernel weight and yield were rather low but consistent for populations 2 and 3. In some cases the component of variance estimate was negative and calculation of the genotypic correlation coefficient was not possible.

From the analysis of the F_4 generation, the expected advance at a given selection intensity was calculated. Table XVI gives the parent mean and the excepted F_5 generation mean for a particular character.

TABLE XIII

PHENOTYPIC CORRELATION COEFFICIENTS (TOP RIGHT) AND GENOTYPIC CORRELATION COEFFICIENTS (BOTTOM LEFT) FOR ALL CHARACTERS FOR POPULATION 1, LOCATION 1

Characters	Mature Plant Height	Heading Date	Yield	Kernel Weight
Mature Plant Height		.07 N.S.	.43**	.29**
Heading Date	.61		-.12 N.S.	-.10 N.S.
Yield	—[a]	—[a]		.34**
Kernel Weight	.05	-.01	—[a]	

[a] Negative mean square estimates did not allow calculation of these values.

NOTE: ** = Significantly greater than zero at the .01 level of probability.
N.S. = Not significantly greater than zero at the .05 level of probability.

TABLE XIV

PHENOTYPIC CORRELATION COEFFICIENTS (TOP RIGHT) AND GENOTYPIC CORRELATION COEFFICIENTS (BOTTOM LEFT) FOR ALL CHARACTERS FOR POPULATION 2, LOCATION 1

Characters	Mature Plant Height	Heading Date	Yield	Kernel Weight
Mature Plant Height		.12 N.S.	.16*	.12 N.S.
Heading Date	.30		-.37**	-.10 N.S.
Yield	-.36	-.88		.46**
Kernel Weight	.14	-.23	.18	

NOTE: * = Significantly greater than zero at the .05 level of probability.
** = Significantly greater than zero at the .01 level of probability.
N.S. = Not significantly greater than zero at the .05 level of probability.

TABLE XV

PHENOTYPIC CORRELATION COEFFICIENTS (TOP RIGHT) AND GENOTYPIC CORRELATION COEFFICIENTS (BOTTOM LEFT) FOR ALL CHARACTERS FOR POPULATION 3, LOCATION 1

Characters	Mature Plant Height	Heading Date	Yield	Kernel Weight
Mature Plant Height		.19**	.47**	.26**
Heading Date	—[a]		.10 N.S.	.08 N.S.
Yield	—[a]	-.41		.44**
Kernel Weight	—[a]	.29	.21	

[a] Negative mean square estimates did not allow calculation of these values.

NOTE: ** = Significantly greater than zero at the .01 level of probability.
N.S. = Not significantly greater than zero at the .05 level of probability.

TABLE XVI

EXPECTED F_5 POPULATION MEANS FOR ALL CHARACTERS AND ALL POPULATIONS USING A 5 PERCENT SELECTION INTENSITY AND PARENTAL MEANS FOR EACH POPULATION

		Characters			
Population	Parents	Mature Plant Height (cm.)	Heading Date (days)	Yield (g./plot)	Kernel Weight (g./1000 kernels)
	Seneca	120.3	38.8	176.9	35.7
1	Expected F_5 Means	-- [a]	29.2	-- [a]	36.1
	Knox 62	115.8	28.6	110.9	30.4
	Monon	110.1	28.3	244.4	31.1
2	Expected F_5 Means	109.0	28.5	218.4	33.4
	Triumph	109.7	28.8	162.8	29.6
	Knox 62	109.5	29.0	188.7	30.0
3	Expected F_5 Means	113.8	28.1	-- [a]	-- [a]
	Tenn. 9	119.1	38.3	173.3	35.0

[a] Expected advance not calculated since heritability was estimated to be 0.0.

Only in the case of kernel weight in population 1 was the expected advance expected to have an advantage over the best parent and the advantage was only slight, 36.1 grams to 35.7 grams for 'Seneca.' In population 2 the expected F_5 generation means for mature plant height would be only slightly better than the best parent 'Triumph' and in the case of kernel weight in population 2 the expected F_5 generation mean would be 2.3 grams better than the best parent 'Monon.' In population 3, only in the case of heading date would the expected F_5 generation mean be better than the best parent and again the advantage is very small, about 0.9 day.

CHAPTER V

DISCUSSION

It was mentioned earlier in Chapter II that Gyawali found that the F_1 of the crosses of the parents of population 1 and population 3 exhibited heterosis for yield over the best parent while the F_1 of the cross 'Monon' x 'Triumph' (population 2) did not exhibit heterosis. A direct comparison of these random F_4 lines to the F_1 would be interesting but such a comparison was not available in this study. An alternate then would be to compare these random F_4 lines to the parents of the lines as was done when the F_1's were compared with the parents to determine if and how much heterosis was exhibited. The question raised in the introduction was "Could lines of a particular hybrid be isolated in later generations that would be equal to or better than the F_1 of that hybrid?" Considering yield as the most important criteria, the results of this study indicate that only in population 2 was there sufficient genetic variation in yield that would allow selection for superior lines in the following generations and Table XVI, page 43, shows that the expected advance for yield in population 2 does not approach the best parent.

Considering characters other than yield, it is possible, if the predictions hold true, to isolate lines in the F_5 generation that would be superior to the best parent of that population for a particular character. In all cases, however, the advantage over the best parent is very small and there is some doubt that the advantage is real. Only for heading date in population 3 could one expect any real gain where the expected F_5 population mean is about one day earlier than the best parent 'Knox 62.'

On the basis of Gyawali's results, it should be possible to find lines in later generations that would equal or better the best parent of that particular population. General combining ability is considered a reflection of additive gene action and the effect of such action would not be lost as segregation occurred and homozygosity within lines was approached.

Gyawali (20) found, however, both general and specific combining ability to be statistically significant (P. = .05). If specific combining ability accounted for most of the heterotic response in the F_1 then one would expect that the effect of particular gene combinations in the F_1 would be lost in subsequent generations as segregation occurred and lines approached homozygosity. This is based on the theory that the gene frequency of the F_1 and F_4 random lines is the same but the genotypic frequencies of the F_1 and F_4 random lines differ.

It is observed in Table III, page 23, that the mean yield for population 1 is 11 grams over the best parent 'Seneca.' This discrepancy is probably due to random variation of testing. It is doubtful that the 11 gram advantage shown is real since similar results were not obtained in the other cross which exhibited heterosis in the F_1 ('Knox 62' x 'Tenn. 9'). It is also noted from Table III that there is about a 70 gram difference in yield between 'Knox 62' in population 1 and 'Knox 62' in population 3. Again, this difference is probably due to random variation. The population 3 mean yield is actually below the lowest yielding parent 'Tenn. 9.'

The population means for all other characters in all populations usually fall midway between the parent means for a particular character except in the case of heading date for population 3 where the population mean is very near the best parent 'Knox 62.'

Populations 1 and 3 will now be termed heterotic populations since the F_1's of each of these populations exhibited heterosis and population 2 will be termed the non-heterotic population since the F_1 of this population did not exhibit heterosis. Gyawali (20) found that general combining ability contributed more to the heterotic response of the F_1 than did specific combining ability although specific combining ability was also significant (P. = .05). Since general combining ability is considered a reflection of additive gene action its effect would not be lost in subsequent generations and as segregation occurred and homozygosity of loci was approached, differentiation among lines would occur. In this study, however, the heterotic populations showed no diversity among lines for yield while the non-heterotic population did. This suggests that, although Gyawali (20) found general combining ability to be more important than specific combining ability, the heterotic response of the F_1 may depend more on specific rather than general combining ability.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Three populations of common bread wheat were studied to gain an estimate of the genetic variability associated with four agronomic characters in each population. Two of the populations (population 1 and 3) exhibited heterosis for yield in the F_1 generation while population 2 did not. The main purpose of the study was to determine if homozygous lines, derived from a particular hybrid, could be isolated in later generations that would be as good or better than the F_1 of that particular cross.

The analysis of variance for population 1 revealed that only heading date and kernel weight had significant (P. = .05) genetic components of variance. The analysis of variance for population 2 revealed that all four characters had significant (P. = .05) genetic components of variance and in population 3, only mature plant height and heading date had significant (P. = .05) genetic components of variance. Heritability estimates were calculated and are all in the range expected for these characters except for the estimate for yield in population 2. All estimates are considered biased to some extent by the year and year interaction components for which no estimate was obtained. Calculation of the expected advance from selection revealed that only in the case of heading date in population 3 and kernel weight and mature plant height in population 2 could you expect a genetic advance that would better the best parent of the respective population. Coefficients of variation for each character in each population were within acceptable range except for yield which was about three times as great in all three populations. The severe lodging and disease at all locations probably caused considerable unaccountable variation in yield and thus the high coefficients of variation for this character.

A biomodal distribution for heading date in population 2 suggests that two major genes control this character with an underdetermined number of minor genes having some effect.

Evidence presented here shows that the non-heterotic population (population 2) offered more variation in the F_4 generation than did the heterotic populations and only in population 2 could one expect any advance for yield. The data also show that it would not be possible to "fix" the heterosis of the F_1 in homozygous lines of later generations. The high coefficients of variation for yield may be some indication that the precision was not such that small differences could be measured.

Gyawali (20) found that the greatest heterotic response in the F_1 was due to general combining ability although specific combining ability was also significant (P. = .05). In this study no direct comparison of the F_4's and F_1's was possible and the experiment was not designed to distinguish types of gene action; however, evidence presented tends to indicate that specific combining ability may be more important in explaining the heterotic response of the F_1's than is general combining ability. The evidence is by no means conclusive but only accentuates the need for more investigations in this area before hybrid wheat becomes a reality.

LITERATURE CITED

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1. Allard, R. W., and J. Harding. 1963. Early generation analysis and prediction of gain under selection in derivatives of a wheat hybrid. Crop Sci. 3:454-456.

2. Ausemus, E. R., J. B. Harrington, L. P. Reitz, and W. W. Worzella. 1946. A summary of genetic studies in hexaploid and tetraploid wheats. Agron. J. 38:1082-1083.

3. Ayad, Mohamed A. G. 1952. Inheritance studies of some qualitative and quantitative characters in Egyptian varieties of wheat. Proc. Egyptian Academy of Science 8:26-38.

4. Baker, R. J., V. M. Bendelow, and M. L. Kaufmann. 1968. Inheritance of and interrelationships among yield and several quality traits in common wheat. Crop Sci. 8:726-729.

5. Boyce, S. W. 1948. A preliminary study of the inheritance of grain weight in wheat. New Zealand J. of Sci. and Tech. 30:13-22.

6. Briggle, L. W. 1963. Heterosis in wheat--a review. Crop Sci. 3:407-412.

7. _______, E. L. Cox, and R. M. Hayes. 1967. Performance of a spring wheat hybrid, F_2, F_3, and parent varieties at five population levels. Crop Sci. 5:465-470.

8. _______, H. D. Petersen, and R. M. Hayes. 1967. Performance of a winter wheat hybrid, F_2, F_3, and parent varieties at five population levels. Crop Sci. 5:485-490.

9. _______, and L. P. Reitz. 1963. Classification of Triticum species and of wheat varieties grown in the United States. U.S. Dept. Agric. Tech. Bul. 1278.

10. Brown, C. M., R. O. Weibel, and R. D. Seif. 1966. Heterosis and combining ability in common winter wheat. Crop Sci. 6:382-383.

11. Burton, G. W. 1952. Quantitative inheritance in grasses. Proc. 6th International Grassland Congress 1:277-283.

12. Comstock, R. E., H. F. Robinson. 1952. Genetic parameters, their estimation and significance. Proc. 6th International Grassland Congress 1:284-291.

13. Crumpacker, D. W., and R. W. Allard. 1962. A diallel cross analysis of heading date in wheat. Hilgardia 32:275-318.

14. Fonseca, S., and F. L. Patterson. 1968. Hybrid vigor in a seven-parent diallel cross in common winter wheat. Crop Sci. 8:85-88.

15. ______, and ______. 1968. Yield component heritabilities and interrelationships in winter wheat. Crop Sci. 8:614-617.

16. Freeman, G. F. 1919. Heredity of quantitative characters in wheat. Genetics 4:1-93.

17. Frey, K. J. 1954. The use of F_2 lines in predicting the performance of F_3 selections in two barley crosses. Agron. J. 46:541-544.

18. _____, and T. Horner. 1955. Comparison of actual and predicted gains in barley selection experiments. Agron. J. 47:186-188.

19. Graybill, F. A., F. Martin, and G. Godfrey. 1956. Confidence intervals for variance ratios specifying genetic heritability. Biometrics 12:99-109.

20. Gyawali, K. K. 1966. Heterosis and combining ability in winter wheat. M. S. Thesis. The University of Tennessee.

21. ______, C. O. Qualset, and W. T. Yamazaki. 1968. Estimates of heterosis and combining ability in winter wheat. Crop Sci. 8:322-324.

22. Hanson, D. H., H. F. Robinson, and R. E. Comstock. 1956. Biometrical studies of yield in segregating populations of Korean lespedeaz. Agron. J. 48:268-272.

23. Heyne, E. G., and G. S. Smith. 1967. Wheat breeding. K. S. Quisenberry (ed.). Wheat and wheat improvement. Am. Soc. of Agron., Madison Wisconsin.

24. Hicks, C. R. 1966. Fundamental concepts in the design of experiments. Holt, Rinehart and Winston. New York, N. Y.

25. Jensen, N. E. 1966. Broadbase hybrid wheats. Crop Sci. 6:376-377.

26. Johnson, H. W., H. F. Robinson, and R. E. Comstock. 1955. Estimates of genetic and environmental variability in soybeans. Agron. J. 47:314-318.

27. Johnson, V. A., K. J. Biever, A. Haunold, and J. W. Schmidt. 1966. Inheritance of plant height, yield of grain and other plant and seed characteristics in a cross of hard red winter wheat. Crop Sci. 6:336-338.

28. Kaw, R. N. 1966. Genetic variability in quantitative characters of Indian barley. Ind. J. Agr. Sci. 36:301-310.

29. Kihara, H. 1951. Substitution of nucleus and its effects on genome manifestations. Cytologia 16:177-193.

30. Kronstad, W. E., and W. H. Foote. 1964. General and specific combining ability estimates in winter wheat (Triticum aestivum). Crop Sci. 4:616-619.

31. Lofgren, J. R., K. F. Finney, E. G. Heyne, L. C. Bolte, R. C. Hoseney, and M. D. Shogren. 1968. Heritability estimates of protein content and certain quality and agronomic properties in bread wheat (Triticum aestivum L.). Crop Sci. 8:563-567.

32. McNeal, F. H., M. A. Berg, and C. A. Watson. 1968. Reciprocal crosses and their influence on wheat quality. Crop Sci. 8:485-487.

33. Nettevich, E. D. 1968. The problem of utilizing heterosis of wheat. Euphytica 17:54-62.

34. Rasmusson, D. C., and R. L. Glass. 1965. Effectiveness of early generation selection for four quality characters in barley. Crop Sci. 5:389-391.

35. _______, and _______. 1967. Estimates of genetic and environmental variability in barley. Crop Sci. 7:185-188.

36. Sage, G. C. M. 1967. Male-sterility and the exploitation of hybrid vigor. Ann. Appl. Biol. 59:319-321.

37. Schlehuber, A. M., D. C. Abbott, B. R. Jackson, and B. C. Curtis. 1967. Correlated inheritance of maturity and quality factors in a hard red winter wheat cross. Crop Sci. 7:13-16.

38. Schmidt, J. W., and V. A. Johnson. 1966. Sterility - fertility interaction in wheat. Second Int. Wheat Gen. Sym., Sweden, 1963.

39. Sharma, D., and D. R. Knott. 1964. Inheritance of seed weight in a wheat cross. Can. J. Gen. and Cytol. 6:419-425.

40. Shebeski, L. H. 1966. Quality and yield studies in hybrid wheat (Triticum aestivum L.). Can. J. Genet. Cytol. 8:375-386.

41. Steel, R. G., and J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw Hill Book Company, Inc. New York, N. Y.

42. Wallace, A. T., G. K. Middleton, R. E. Comstock, and H. F. Robinson. 1954. Genotypic variances and covariances of six quantitative characters in oats. Agron. J. 46:484-488.

43. Watson, I. A., and K. S. McWhorter. 1968. Bulk method of producing hybrid wheat. Crop Sci. 8:124-125.

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