

AN ABSTRACT OF THE THESIS OF

Leslie John Frederickson for the degree of Doctor of Philosophy

in Crop Science presented on November 10, 1982

Title: A Comparison of Two Methods of Divergent Mass Selection for
Heading Date in Two Winter Wheat (Triticum aestivum L. em Thell)

Crosses

Abstract approved:

Redacted for Privacy

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Responses to two cycles of mass selection for heading date, followed by selfing or intermating, were studied in two diverse winter wheat (Triticum aestivum L. em. Thell) crosses. Selection was bidirectional, resulting in early and late populations for each mating system, cycle, and cross. The influence of mass selection for heading date on the expressions of eight other agronomic traits was also studied.

Concurrent with selection for heading date, generation means and variances within crosses were used to obtain genetic information about each of the nine traits. Additive effects of genes were an important source of variation among Cross I generation means for most traits. Predicted response to selection for heading date was 7.1 and 9.1 days/cycle for 1981 and 1982, respectively. Most traits by which the parents differed in Cross II generations were primarily affected by non-additive genetic effects. Progress from selection for heading date was predicted to be 6.9 days/cycle in 1981, and 1.4 day/cycle in 1982.

Observed response to selection for heading date in Cross I showed gains of -4.8 and 5.5 days/cycle with selfing and -4.2 and 5.1 days/cycle with intermating. Further progress from selection for heading date could be achieved through additional cycles of selection and intermating in this cross. Response to selection for heading date with intermating in Cross II was superior to selfing in the early direction (6.0 vs. 5.0 days/cycle) and inferior to selfing in the late direction (0.9 vs. 1.9 days/cycle). These results were ascribed to an accumulation of minor genes via intermating and rapid fixation of recessive genes via selfing, for early and late selection, respectively.

Few large correlated responses in the eight unselected traits with selection for heading date were noted in either cross. In Cross I, intermating was more successful than selfing in retaining 'genetic variation' in most of the unselected traits. In Cross II, intermating showed a slight advantage in maintaining 'genetic variation' in unselected traits, probably due to the low levels of additive genetic variation present in this cross.

A COMPARISON OF TWO METHODS OF DIVERGENT MASS
SELECTION FOR HEADING DATE IN TWO WINTER WHEAT
(Triticum aestivum L. em Thell) CROSSES

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed November 10, 1982

Commencement June 1983

APPROVED:

Redacted for Privacy

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Date thesis is presented November 10, 1982

Typed by Kathleen Miller for Leslie John Frederickson

ACKNOWLEDGEMENTS

I would like to express my gratitude to Dr. W. E. Kronstad for his guidance and support throughout the pursuit of this study.

A sincere thanks is also extended to Drs. W. L. McCuistion, D. I. Mills, W. M. Proebsting, and K. E. Rowe for serving on my graduate committee and providing invaluable suggestions and guidance throughout the course of this investigation.

I would also like to acknowledge the assistance of Patrick Hayes, Mat Kolding, Dario Leal, Juan Salmeron and Jaime Tola for their help in taking field notes, and Kathie Miller for typing this thesis.

To all the staff, graduate students, and summer crew who helped plant, culture and harvest this thesis, thank you.

A special acknowledgement is given to my wife, Regina, and my daughters, Angela and Tamara, for their support and encouragement.

Appreciation to Oregon State University for providing the financial support and facilities which made this research possible is also extended.

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A COMPARISON OF TWO METHODS OF DIVERGENT MASS SELECTION
FOR HEADING DATE IN TWO WINTER WHEAT
(Triticum aestivum L. em Thell) CROSSES

INTRODUCTION

In conventional wheat breeding programs, cultivars and improved lines are carefully selected for two-way, three-way, or even four-way crosses. The genetic variability arising from these crosses is then exploited via selection for important agronomic traits. Natural self-pollination during ensuing generations of selection leads rapidly to homozygous lines. These lines are then tested for various agronomic and quality characteristics and released if found to be superior to existing cultivars. In addition, improved homozygous lines are re-cycled in the breeding program by using them as parents in two-way, three-way or four-way crosses.

This long-term mating and selection scheme has resulted in considerable crop improvement over the eighty-two years since the re-discovery of Mendel's Laws of Inheritance. However, using recurrent selection, a more rapid cycling between crossing and selection may be achieved, leading to even greater crop improvement. Recurrent selection has been used for many years in cross-pollinated crops. Advantages of this breeding method over the conventional longer-term crossing and selection method are: 1)

the frequent cycling of selection and intermating increases the probability of accumulating favorable alleles for selected traits into a 'breeding population'; 2) random fixation of genes affecting traits having low heritability is not as likely; and 3) linkage blocks may be broken and result in increased genetic variability.

Several problems associated with recurrent selection may restrict its adoption in the genetic improvement of self-pollinated crops. Some of these problems are: 1) recurrent selection requires a large number of crosses; 2) favorable gene combinations, which may be tightly linked, would be destroyed in the intermating phase of recurrent selection; 3) the literature on recurrent selection has been sparse and spread across many different self-pollinated crops, with little attempt to verify the theoretical basis of this breeding method; and 4) little or no research has been done on how breeding populations should be initiated and handled in self-pollinated crops.

This investigation was undertaken in an attempt to verify the theoretical advantages of recurrent selection, while keeping the number of crosses to a minimum. Specifically, the objectives of this study were: 1) determine the nature and amount of genetic variation for several important agronomic traits in two winter wheat populations; 2) predict and evaluate genetic progress from selection for heading date in breeding populations arising from recurrent, mass selection and mass selection with selfing; and 3) determine the correlative influence of selection for heading date on several other important agronomic traits in these populations.

LITERATURE REVIEW

Recurrent selection is a breeding system involving repeated cycles of selection and recombination with the objective of increasing the frequency of favorable genes for yield or other characteristics (Leonard et al., 1968). This breeding system is actually an array of breeding methods developed by corn breeders and geneticists in the early part of the present century. Corn breeders were experiencing problems associated with breeding self-pollinated crops in developing inbred lines for hybrid corn production. The historical development and acceptance of recurrent selection as a means of improving cross-pollinated crops should thus provide insight into its possible adoption by breeders of self-pollinated crops.

Early History of Recurrent Selection

In 1919, Hayes and Garber discussed the major problems confronting the corn breeder. Among these they included the importance of inbreeding and crossbreeding and their relationship to methods of corn improvement. Inbreeding was regarded as faster with respect to mass or ear-to-row selection in modifying the genotypical nature of a variety. The major criticism of self-fertilization in corn was the loss of vigor, which was found to be detrimental to hybrid corn seed production. Emerson and East (1913) had suggested that if a type of plant could not be found in a segregating population that might eventually yield a superior

strain, inter-crossing among a group of the more desirable individuals would "assuredly" result in obtaining a desired combination of genetic factors. This observation led Hayes and Garber (1919) to initiate a breeding program to produce a high-protein strain of corn (Minnesota No. 13) by a process of selfing, selection, and crossing among the selected individuals. While there is no indication in their paper that this process would be cyclic, other writers (Allard, 1960; Briggs and Knowles, 1967) have given credit to Hayes and Garber (1919) for originating the basic tenets of what would later (Hull, 1945) become known as recurrent selection.

East and Jones (1920) reported on several investigations on breeding for high-protein content of the corn kernel. They realized that selection for high-protein, combined with artificial self-pollination, would give high-protein strains in a shorter time than would any other breeding method. However, they noted that inbreeding reduced the yield, vigor, seed size, and seed number of the corn plant. To overcome this negative relationship between inbreeding and the expression of important agronomic traits, East and Jones (1920) suggested a cyclic breeding method wherein plants were to be selfed, selected and intercrossed generation after generation. Their plan was based "upon the plausible assumption that since the various inbred high-protein strains differ in their morphological features, similar protein percentages may be due to different genetic constitutions". After two cycles of selected matings between high-protein plants, these authors produced three

high-protein strains with greater vigor and better yield than inbred lines developed by self-pollination and selection. They also noted a reserve of genetic variability from which further improvement in protein content was expected.

Thirty years later, Sprague and Brimhall (1950) published the results from a recurrent selection scheme similar to that of East and Jones (1920). Their approach was "to evaluate a series of individual plants for a given character, truncate the frequency distribution at some desired level, and intercross the individuals comprising the truncated tail". That material would then be used to initiate the next cycle of selection. By following this procedure, Sprague and Brimhall (1950) hoped to establish a higher 'potential ceiling' in the expression of a trait than was possible using the then current system of inbreeding and selection. Because selections were based on individual phenotypes, the procedures developed by East and Jones (1920) and Sprague and Brimhall (1950) are known as simple or phenotypic recurrent selection (Allard, 1960) or mass selection (Sprague and Eberhart, 1977).

Jenkins (1940) suggested a breeding method, which later became known as recurrent selection for general combining ability (Penny et al., 1963), intended for the production of synthetic varieties of corn in areas not suited to growing hybrid corn. On the basis of earlier data (Jenkins, 1935), which showed that inbred lines became stable for yield prepotency early in the inbreeding process, Jenkins (1940) outlined the following breeding procedure: 1) isolate one-generation selfed lines; 2) test these lines in

topcrosses for yield and other characteristics to determine their relative endowments with respect to genes affecting these characters; 3) intercross the better-endowed selfed lines to produce a synthetic variety; 4) repeat the above process at intervals after each synthetic variety has had a generation or two of mixing, possibly with the inclusion of lines from unrelated sources. Jenkins (1940) recommended the use of the parental variety as the tester (which was heterogeneous), and in effect was testing the general combining abilities of individuals in his recurrent population.

The development of hybrid corn in the first part of this century resulted in a lot of speculation concerning the nature of hybrid vigor (Allard, 1960). Proceeding on the assumption that heterosis was the result of overdominance, Hull (1945) outlined a recurrent selection method which utilized an inbred tester to identify superior specific combining abilities among individuals in a breeding population. If heterosis was due to overdominance, he reasoned, then the use of an inbred tester would assure that for every recessive allele in the tester, a dominant allele would be identified in the recurrent population and conversely, for every dominant allele in the tester, a recessive allele would be identified in the recurrent population. Hull (1945) also mentioned that the extra generations of intermating called for in Jenkins' (1940) procedure were probably unnecessary, since "sufficient mixing occurs in proceeding from cycle to cycle".

A further development in recurrent selection methods came when Comstock et al. (1949) proposed reciprocal recurrent selection. Their method required three years to complete one cycle. Using a one-locus model, Comstock et al. (1949) compared the theoretical improvement limits and rates of improvement between recurrent selection for general combining ability, recurrent selection for specific combining ability and reciprocal recurrent selection. Under the assumptions of no epistasis, no linkage, and two alleles per locus, they concluded that reciprocal recurrent selection would be superior to selection for general combining ability for loci at which there is overdominance, and superior to recurrent selection for specific combining ability for loci at which there is partial dominance. They noted that the only difference between reciprocal recurrent selection and recurrent selection for general combining ability is the tester. In reciprocal recurrent selection, each source population serves as the other's tester. In recurrent selection for general combining ability, all selection material is tested against the same tester. The implication of this difference is that reciprocal recurrent selection may be used to improve the population mean and the population cross, whereas recurrent selection for general combining ability is used only for improving the population mean.

From 1950 to the early 1960's, many breeders of cross-pollinated crops, especially corn, were involved in short- and long-term selection experiments designed to verify the theoretical advantages of recurrent selection, and to identify the best methods

to apply to the genetic improvement of their crops. Sprague and Eberhart (1977) and Hallauer and Miranda (1981) provide excellent summaries of these investigations and note that recurrent selection, in one form or another, has been widely adopted by breeders of cross-pollinated crops. Hallauer and Miranda (1981) point out that recurrent selection was accepted after breeders realized its efficiency in increasing the frequency of favorable genes in breeding populations. Penny et al. (1963) had earlier noted that advance from selection is much more likely when selection is practiced on a population in which a trait(s) is exhibited to a high degree.

Theory of Recurrent Selection in Relation to Self-Pollination

Breeders of self-pollinated crops have traditionally used the pedigree and bulk methods of selection (hereafter referred to as conventional methods) which take advantage of the rapid fixation of genes due to self-pollination (inbreeding) and the concurrent increase in prepotency (Allard, 1960). These methods, however, have several disadvantages with respect to genetic progress from selection. Some of the more important disadvantages include: 1) large populations are required to ensure obtaining a desired type when selecting for a quantitatively-inherited trait; 2) selection for such traits must be delayed until later generations, risking random fixation of both favorable and unfavorable gene combinations; 3) the nature of selfing, which is a requisite of all conventional breeding methods, is such that opportunities for new

recombination are drastically reduced with each generation; and 4) the two-parent cross common in conventional breeding schemes restricts the gene pool, thus increasing the incidence of genetic vulnerability, particularly to insects, pathogens, and sudden changes in the environment.

Recurrent selection has been suggested as a means of alleviating these deficiencies, by providing for frequent intercrossing among selected individuals and a concomitant increase in the frequency of favorable genes. The successful adoption of recurrent selection in self-pollinated crops depends on a critical evaluation of its advantages and disadvantages as well as an empirical validation of its theory.

Advantages of Adapting Recurrent Selection to Self-Pollinated Crops

The population sizes necessary in the F_2 or F_3 generations to find a segregate combining all the desirable attributes of two parents is almost impossible to attain in practice. For example, with 10 loci segregating in an F_2 , the smallest perfect population size required for at least one individual of each genotype to be represented is 1,048,576 (Allard, 1960). Of these, only 9.1×10^{-11} percent would be expected to be homozygous for favorable alleles at all 10 loci. Recurrent selection, however, is a means of accumulating favorable alleles through the process of intermating selected individuals, thereby reducing the size of the population required to obtain a desired segregate. Sprague and Brimhall (1950) obtained an extreme deviate of 13.5% oil after two

cycles of recurrent selection for oil content in corn. Projecting this value to an F_2 population derived from a single cross, an estimated 12,450,000 individuals would have been necessary to give this value as an average maximum deviate.

An additional problem with conventional breeding methods in self-pollinated crops is the reduction of opportunities for genetic recombination with each generation of selfing. On selfing, the percentage of heterozygosity at one locus decreases in the familiar series $1/2$, $1/4$, $1/8$, ... Allard (1960) noted that the theoretical improvement limits associated with conventional inbreeding methods will be determined by the genotype of a single foundation plant. Thus, genes affecting traits with low heritability, such as grain yield, will be fixed at random in the early generations of selection. The intermating phase of recurrent selection provides an added opportunity for recombination among a number of individuals, resulting in theoretical improvement limits determined by the most favorable combination of genes contained in a group of foundation plants. In addition, the probability of maintaining a higher frequency of genes affecting traits with low heritability should increase.

A third problem with conventional inbreeding methods is also related to the amount of genetic recombination occurring with each generation of selfing. Linkage blocks, enhanced and maintained by inbreeding, may serve both as a stabilizing force in breeding, as suggested by Jensen (1970), and as a impediment to recombination (Jensen, 1970; Meredith and Bridge, 1971; Doggett, 1972). The

latter effect may result in a significant suppression of usable genetic variation (Jensen, 1970) and in maintenance of negative correlations between economically-important traits (Meredith and Bridge, 1971).

Al-Jibouri et al. (1958) noted that non-parental (i.e., recombinant) types occurred infrequently in the F_3 generation of a cross between two divergent strains of cotton. They also reported a negative association between fiber strength and high yield in a replicated test of the F_3 progenies. These results may have been caused by initial linkage blocks present in the F_1 . Miller and Rawlings (1967a) tested this hypothesis after six successive generations of 'mixed' (i.e., 50% of self-pollination) intermating, beginning with the F_2 . They noted a shift of genotypic correlations between several traits toward values observed in populations assumed to be more nearly in linkage equilibrium. The intermating phase of recurrent selection would be expected to breakup linkage blocks, thus freeing genetic variation for selection.

The effects of linkage block breakup on genetic variances can be dependent on whether linkages are in coupling or repulsion phase. If one parent contributes more favorable alleles to a cross than another, coupling phase linkages may be important and result in decreased genetic variance after intermating. If both parents contribute equally to a cross, repulsion phase linkages may be important and result in increased genetic variance after intermating (Pederson, 1974). The importance of six generations of

mixed intermating in cotton on breakup of linkage blocks and changes in genetic variance were reported by Miller and Rawlings (1967a). Declines in genetic variance occurred for six traits and an increase in genetic variance occurred for one trait. These authors suspected that initial coupling and repulsion phase linkages, respectively, may have been the cause of these results.

Current breeding practices in self-pollinated crops have also severely limited the genetic diversity available for continued crop improvement (Hanson, et al., 1967; Jensen, 1970, Brim and Stuber, 1973; Eslick and Hockett, 1974; McProud, 1979). With each advance in crop improvement, the probability of successful exploitation of new germplasm decreases (Eslick and Hockett, 1974). This is because the new sources of germplasm would contain successively larger numbers of non-adapted genes and relatively fewer numbers of genes for desirable traits.

McProud (1979) evaluated three barley breeding programs in different parts of the world. He found that 13 to 16 separate genetic sources of germplasm, most of which were introduced 50 years ago, have essentially been recombined through a 'long-cycle' phenotypic recurrent selection process. The average time to complete one full cycle of recurrent selection in each breeding program ranged from 6.5 to 10.5 years. This process has resulted in a very narrow germplasm base from which to make genetic improvement. McProud (1979) recommended devoting more resources to expanding the germplasm base and reducing the time between cycles of selection.

Hanson et al. (1967) discussed a typical breeding program in soybeans in terms of Malecot's (1948) coefficient of parentage. Beginning with eight improved soybean lines, these investigators assumed that the breeding material passed through a bottleneck of four lines for each cycle of improvement. After only two cycles, the coefficient of parentage would be 0.51, assuming no selection was practiced. "In other words, the probability is 0.51 that a locus in two random parents in the next cycle carries genes which are identical by descent." This has obvious implications concerning the amount of genetic diversity available for continued improvement of the crop. Hanson et al. (1967) suggested that recurrent selection might be used for the step-wise improvement of a population while minimizing the coefficient of parentage among breeding lines.

Problems Associated with Adapting Recurrent Selection to Self-Pollinated Crops

Among the problems associated with adapting recurrent selection to improvement of self-pollinated crops, perhaps the most restrictive are a result of the intermating phase of this breeding system. Two major problems can be cited: 1) the extensive crossing necessary is inhibited by the difficulty and expense involved with hand-pollinations; 2) artificial crossing generally results in relatively few seeds per cross, especially in cereal crops and an additional generation of selfing to obtain enough seed for the testing phase of recurrent selection may become necessary.

The advent of male sterility in several autogamous crop species, including barley (Suneson, 1962), sorghum (Stephens and Holland, 1954), and soybeans (Brim and Young, 1971), has greatly enhanced the intercrossing phase of recurrent selection. Ramage (1977) provides the following method of using genetic recessive male-sterility in barley for recurrent selection : 1) select for a particular character or combination of characters in a large number of male-sterile and male-fertile plants from a population that is segregating for both the desired character(s) and male-sterility; 2) intercross the selected plants using male-sterile plants as females and bulk the crossed seed; 3) grow out the F_1 generation to provide enough seed for the next cycle; 4) the F_2 generation is grown and provides the population from which the next cycle of selection is made.

Male sterility in wheat has been reported (Briggle, 1970), although its success in promoting outcrossing has been limited by environmental conditions and the genotype carrying the male-sterile gene (Ramage, 1977).

Alternative mating systems have been suggested in which the number of crosses necessary to carry on a recurrent selection program do not necessarily exceed those required in a conventional breeding program. Compton (1968) proposed a method of recurrent selection in self-pollinated crops which requires a minimum of crossing. In his procedure, n homozygous lines are paired at random to give $n/2$ single crosses. The F_1 seed is advanced to a desired generation for testing by single seed descent. The top

group of lines are selected after yield tests and their progeny are intercrossed, providing material for the next cycle. Compton (1968) estimated that three years per cycle would be required. He points out that gain from selection should be twice as great by selecting among lines from different single crosses rather than selecting among lines from the same single cross.

Jensen (1970) proposed a rather complex breeding program, which he called the diallel selective mating system. This method employs recurrent selection with a 'minimum' of crossing. He states that the system "provides for broad use of germplasm, simultaneous input of parents, creation of persistent gene pools, breaking of linkage blocks, freeing of genetic variability, and general fostering of genetic recombination."

Results from Experiments in Self-Pollinated Crops

The theoretical advantages of recurrent selection, with respect to self-pollinated crops, appear to heavily outweigh its disadvantages. However, experimental verification of that theory seems a necessary prerequisite to its adoption. Verification can take a number of forms, such as comparisons between recurrent selection and conventional breeding methods or short and long-term results from crop improvement via recurrent selection. Before discussing results of recurrent selection in self-pollinated crops, a short discussion of modern concepts in recurrent selection methods and the criteria used to select among them will be given.

Intra- and Inter-Population Improvement

Current methods of recurrent selection are divided into two broad categories, depending on the goals of the breeder (Hallauer and Miranda, 1981). Intra-population recurrent selection methods are used when the goal of the plant breeder is to develop a superior cross-bred or pure-line cultivar (i.e., improve the population mean). Inter-population recurrent selection methods are used when the goal is to improve the population cross.

Sprague and Eberhart (1977) list six alternative procedures for improving the population mean. These include mass selection (with or without pollen control), modified ear-to-row selection, half-sib selection, full-sib selection, S_1 or S_2 selection, and testcross selection with a broad-base or inbred-line tester. With respect to earlier nomenclature for recurrent selection, mass selection is identical to phenotypic recurrent selection; testcross selection is identical to recurrent selection for general combining ability when the tester has a broad genetic base and identical to recurrent selection for specific combining ability when the tester is an inbred line.

Two methods of improving the population cross (Sprague and Eberhart, 1977) are reciprocal recurrent selection (and a modification using a common inbred tester) and full-sib reciprocal recurrent selection. Selection intensity using full-sib reciprocal recurrent selection is double that of reciprocal recurrent selection because only half as many families must be evaluated.

Relative gain per year, for a selected trait, is an important criterion for choosing among the many recurrent selection methods (Sprague and Eberhart, 1977). The magnitude of the response to selection is a function of the selection intensity, amount of additive genetic variance, and the precision with which the genetic worth of an individual or family is measured (Falconer, 1960). Based on these considerations, if heritability is high, mass selection with pollen control should be the most efficient method of increasing the population mean (Sprague and Eberhart, 1977). In mass selection, parents are selected based on their individual performance. Selections, or their progeny are intercrossed to provide source material for the next cycle. If the intercrossing phase can be completed the same year that selections are made, one complete cycle per year is possible.

When heritabilities are relative low, recurrent selection methods involving some sort of family structure (i.e., half-sibs, full-sibs, S_1 -families) are recommended. Intra-population improvement procedures involving family performance testing suffer from a reduction in effective population size which may lead to increased inbreeding and less intense selection pressure than is possible with mass selection (Sprague and Eberhart, 1977).

Recurrent Selection vs. Selection with Selfing

Selection followed by selfing is an important step in the development of inbred lines for hybrid corn seed production. The first investigation providing evidence of the superiority of

recurrent selection over selection with selfing in improving the mean of a breeding population was reported by Sprague and Brimhall (1950). Beginning with a source population derived from reciprocal backcrosses involving the single cross Illinois High Oil x wx0s420, these investigators selfed each backcross population, analyzed the progeny for oil content, planted five ears from each population ear-to-row, and made all possible intercrosses among these ten progenies. This cycle was repeated by bulking equal quantities of seed from each cross to use as source material. In addition, seed from the original 10 selfed ears were planted ear-to-row and selections were made on a visual basis for plant type. These progeny were then selfed and analyzed for oil content after harvest. The two progeny from each family which expressed oil content to the highest degree were selected and their seed planted ear-to-row the following year. This procedure was followed for five generations of selfing. The results of these experiments showed that recurrent selection was 2.6 times as effective as selection during inbreeding in improving the oil content of the corn kernel.

A similar investigation was reported by Sprague et al. (1952). Two cycles of phenotypic recurrent selection for oil content in the corn kernel were compared with five generations of selection followed by selfing. The source material came from a synthetic variety called 'Stiff Stalk'. Depending on the contrast used (i.e., gain per year or a contrast of extreme deviates), recurrent

selection was 1.3 to 3.0 times more effective in improving the population than selection followed by selfing.

Redden and Jensen (1974) compared the effectiveness of two cycles of mass selection with phenotypic assortative mating vs. mass selection with selfing to the F_4 for "green tiller" number in wheat and barley. In the barley investigation, mass selection with intermating of selects increased tiller number 13.9% at site 1 and 17.1% at site 2 over the base (F_2) population. Selection with selfing resulted in an 8.5% increase at site 1 and 10.3% at site 2. In the wheat investigation, at one site only, mass selection with intermating resulted in a 22.6% increase while selfing with selection gave a 18.5% increase in tiller number over the base population.

Short Term Results from Crop Improvement via Recurrent Selection

Results from experiments in self-pollinated crops reported to date have focused on intra-population improvement. Matzinger and Wernsman (1968) evaluated four cycles of mass selection with pollen control in tobacco. They obtained an 18% increase in green weight of leaves over the mean of the unselected base population. Gupton (1981) used phenotypic recurrent selection for increased leaf weight and decreased alkaloid content of Burley tobacco. Twenty-eight single crosses were used to generate the base population. Gupton (1981) reported a three-location average of 21.2% increase in leaf weight after three cycles of selection.

Percent total alkaloids were reduced an average 29.1% after five cycles of selection when tested at two locations.

In self-pollinated crops, S_1 -testing is the most commonly reported type of family performance testing (Brim and Burton, 1979; Byrne and Rasmusson, 1974; Kenworthy and Brim, 1979; McNeal et al., 1978; Miller and Fehr, 1979; Miller and Rawlings, 1967b; Prohaska and Fehr, 1981). In a typical S_1 selection cycle (Burton et al., 1971), individual plants from the source population (S_0) are selfed to produce the S_1 ; S_1 lines are yield-tested the second year; the top-yielding lines are intermated to produce material for the next cycle of selection.

Miller and Rawlings (1967b) reported on three cycles of S_1 testing in Upland cotton. Yield of third cycle selections exceeded that of the base population by 29.7%.

Byrne and Rasmusson (1974) evaluated progress from three cycles of combined mass selection and S_1 testing in wheat and barley. They selected the extreme 15 high and 15 low F_2 plants for strontium content of grain in both species. The subsequent F_3 families were also tested for strontium content and intercrosses were made among F_4 plants derived from the two highest or two lowest strontium-containing F_3 families. Response to selection was measured as a percent of the mean of the original parental cultivars. In the wheat investigation, they obtained an average response per cycle of selection of 7.4% in the high population and -12.4% in the low population. In the barley investigation, they obtained an average response per cycle of

selection of 12.2% in the high population and -11.2% in the low population.

A modified S_1 -testing procedure was employed by McNeal et al. (1978) for improving protein content of spring wheat. In their procedure, F_3 progeny rows, derived from nine crosses made among 12 homozygous lines previously selected for high protein, were evaluated for protein content. Those F_3 lines having high protein content were yield-tested and two high protein, high yielding lines from each cross were intercrossed in all possible combinations. In the next cycle, F_2 plants derived from the diallel were evaluated for vigor and agronomic appearance and selected F_3 seed was planted in progeny rows. These were then tested for protein content. The 10 highest and 10 lowest protein lines were selected from cycle one crosses and re-tested in the next year, due to unusually high protein contents obtained in the F_3 . A comparison of parents with 27 high-protein lines from the second cycle of selection showed an average increase of 2.5% in protein content.

S_1 testing was also used by Brim and Burton (1979) to increase protein in soybean seeds. They evaluated six cycles of recurrent selection in a base population derived from a cross of two highlyadapted experimental lines and five cycles of recurrent selection in a base population derived from a backcross of a highly-adapted experimental line to nine unadapted plant introductions. In addition, recurrent selection using smaller effective population sizes was practiced on material derived from

the previous two base populations. In the adapted population, six cycles of recurrent selection resulted in an increase of 2.1% protein over the original population. Recurrent selection using smaller effective population size gave a 1.2% increase in protein over the base population after four cycles. Five cycles of recurrent selection in the unadapted population yielded a 3.3% protein increase over the base population. Four cycles of recurrent selection in the same population using smaller effective population size increased protein by 2.7%. Brim and Burton (1977) noted a greater rate of progress from selection in the unadapted population and this was reflected by a higher realized heritability than that obtained in the adapted population. They believed the use of smaller effective population sizes would be more efficient in breeding programs, especially for short-term selection goals.

Kenworthy and Brim (1979) selected for increased yield in soybeans using S_1 testing. They obtained an average increase in yield of 134 kg/ha/cycle of selection over the unimproved population. A composite of lines derived from the third selection cycle yielded 16% more than the original population. They also reported on the effect of using two other selection criteria for increasing yield. Average yield increased when selection was based on efficiency, expressed as the ratio of seed weight to straw weight, and an index generated by summing the ranks of each test progeny for efficiency and yield were not significant.

Progress from one cycle of direct, and one cycle of indirect selection for protein content in soybeans was reported by Miller

and Fehr (1979). Indirect selection was based on a negative genetic correlation between protein and oil content of the soybean. The advantage of indirect selection of protein by direct selection for low oil content arises from the less expensive and more rapid method for measuring oil content. A separate population was generated for both selection criteria. Miller and Fehr (1979) obtained a 1.5% increase in protein by direct selection and a 0.8% increase by indirect selection, over their respective base populations.

Using a combination of full-sib and S_1 testing for increased percent total alkaloids of the cured tobacco leaf, Matzinger et al. (1972) reported an increase of 0.445% alkaloid content after two cycles of selection. In their original selection cycle, only full-sib families were evaluated. In cycles one and two, both full-sib and selfed families were evaluated. Selection was based on an index derived from weighted values of full-sib and selfed (S_1) families. The use of full-sib families provided two opportunities for recombination per cycle, although the extra generation required for family formation may have lowered the efficiency of this procedure.

Prohaska and Fehr (1981) followed three generations of intermating in the AP9 soybean population with two cycles of S_1 selection for resistance to iron deficiency chlorosis. They obtained a 9% reduction in chlorosis over the base population.

Mass selection followed by half-sib family selection for increased percent oil in soybeans was reported by Burton and Brim

(1981). Intermating was facilitated using the ms_1 male-sterile gene. After three cycles of selection, they obtained a 1.1% increase in oil content over the unselected base population. Both mass selection and within half-sib family selection were thought to have contributed to progress in improving oil content.

Additional Need for Experimentation

The success of intra-population improvement of several self-pollinated crops via recurrent selection has been reviewed. However, only three citations were found which demonstrated the superiority of recurrent selection over conventional inbreeding methods (Sprague and Brimhall, 1950; Sprague et al., 1952; Redden and Jensen, 1974). Of these, two (Sprague and Brimhall, 1950; Sprague et al., 1952) may have unfairly biased gain from selection in favor of recurrent selection, by practicing selection only within the inbred lines used for the selfing series. Individual, or mass selection was practiced on corn plants in the recurrent series. Falconer (1960) points out that within-family selection is rarely superior to individual selection.

Redden and Jensen (1974) also showed superior performance of recurrent selection over selection with selfing. Although there were differences in sample size between the recurrent and the selfing series, the only other difference in their comparison was due to mating system (i.e., phenotypic assortative mating vs. selfing). In fact, they state that "... this is the first

demonstration of the effect of mating system upon response to directed mass selection in a crop species under field conditions."

If recurrent selection is to replace or otherwise become a major part of current breeding methods in self-pollinated crops, much more attention must be focused on obtaining the following kinds of information via experimentation: 1) evaluation of the relative efficiencies of recurrent selection vs. conventional inbreeding methods; 2) comparisons of different family performance testing procedures (e.g., S_1 , half-sib, full-sib, etc.) for recurrent selection of traits having low heritability; and 3) long-term results of recurrent selection in self-pollinated crops.

MATERIALS AND METHODS

The primary objective of this investigation was to evaluate the relative effectiveness of recurrent selection and selection followed by selfing in the improvement of two winter wheat populations for heading date. Mating system (i.e., intermating or selfing) was the single criterion used to differentiate these two breeding methods. To meet this objective, the study was divided into two phases: the first phase involved two cycles of divergent mass selection for heading (i.e., selection for early and late heading date) and the second phase was concerned with an evaluation of the two breeding methods.

Heading date was chosen as the criterion of selection because: 1) it is an agronomically-important trait in winter wheat, 2) it has a high heritability, indicating mass selection should be effective; and 3) selections and crosses among selections can be made the same season. In addition, eight other agronomic traits were measured to evaluate the effects of mating system on correlated response to divergent mass selection for heading date.

Description of Plots

Three experimental sites were utilized over the course of this investigation. The first cycle of selection (1979-80) was carried out in plots located at the Botany and Plant Pathology Farm (a.k.a. East Farm), 1.6 km east of Corvallis. The second

selection cycle (1980-81) was carried out in plots grown at the Hyslop Agronomy Farm (a.k.a. Hyslop), 11 km northeast of Corvallis. The soil type at both locations is a Woodburn silt loam. The evaluation phase (1981-82) was conducted on plots grown at two locations: the Hyslop site and at a site in eastern Oregon, near Pendleton. The latter site has a Walla Walla silt loam soil.

Planting methods were identical in both the selection and the evaluation phases. Entries were hand-planted 15.3 cm apart within a row and 30.5 cm apart between rows. Rows were 3 m long. To provide for uniform competition, the winter barley cultivar 'Scio' was used as border at the ends of rows and on the edges of the replications. Scio was also used as filler within rows where wheat plants were missing (due to no emergence, winter injury, bird or rodent damage).

Weeds were controlled with fall applications of Karmex (1.68 kg A.I./ha) and Buctril (.14 kg A.I./ha) at locations in the Corvallis area. A spring application of Bronate (.86 L A.I./ha) plus Malonen (.28 kg A.I./ha) was used at the site near Pendleton. For the 1981-82 growing season only, the site at Hyslop was fumigated with a 63/33 mixture of methyl bromide and chloropicrin (420 kg/ha) prior to planting. No other herbicides were applied throughout the growing season.

In anticipation of possible infections by Septoria tritici and stripe rust (Puccinia striiformis), two applications of Tilt (.14 kg A.I./ha) were applied in the spring of 1982.

At the Corvallis sites, a total of 168 kg/ha/growing season of nitrogen was applied in three split applications using either 46-0-0 urea or 21-0-0 ammonium sulfate. Two applications of 32-0-0 anhydrous ammonia for a total of 5 kg/ha, were applied at the site near Pendleton. Climatological records for these sites are given in Appendix Table 1.

The Selection Phase

Two single crosses were made to generate the experimental populations used in this study. The three winter wheat cultivars, 'Kavkaz', 'Roussalka', and 'Hyslop' were selected to make the single crosses. Each of these cultivars is well-adapted to growing conditions observed in the Pacific Northwest. A general description and the pedigree of each cultivar is given in Appendix Table 2.

Kavkaz has shown excellent general combining ability when used in the Spring x Winter Wheat Breeding Program at Oregon State University. It was, therefore, used as a common parent in both crosses. The two other parents were selected in an attempt to generate two kinds of base populations from which to initiate selection: 1) Roussalka was chosen as a contrasting parent to Kavkaz. It has a much earlier heading date, and the resulting F_2 was expected to show a large amount of genetic variation for this trait. 2) Hyslop and Kavkaz have nearly identical heading dates, and since these cultivars are not related (Appendix Table

2), the F_2 derived from their hybridization was expected to show transgressive segregation for heading date.

Development of Experimental Populations

Before describing how populations were developed, a digression into the nomenclature used to identify crosses and populations will be given. Two crosses were used in this study: Roussalka/Kavkaz and Hyslop/Kavkaz. These will hereafter be referred to as Cross I and Cross II, respectively. The parental cultivars are abbreviated as follows: Kavkaz (KVZ); Roussalka (RSK); and Hyslop (HYS). Selfed generations are identified with the usual F (filial generation), with subscripts i, j , where i = the generation and j = the cross. Backcross generations are symbolized by $BC_{i,j}$, where i refers to the parent to which an $F_{1,j}$ was crossed. In both single crosses, KVZ is parent 2; RSK and HYS are thus parent 1 in their respective crosses. The j has the same meaning as in the F generations. The selected populations are identified by $C_i F_{i,j}$ or $I_i F_1$, preceded by an E for early or an L for late selection. C_i refers to the i th cycle of selection within single crosses and I_i refers to the i th cycle of selection in the populations derived from intercrossing selections from Cross I and Cross II. The $F_{i,j}$ have the same meaning as for the filial generations obtained by selfing. Thus, $EC_1 F_{4,1}$ refers to the first cycle population selected for early heading date from Cross I (RSK/KVZ); it has been advanced to the F_4 generation by selfing.

The parents, $F_{1,j}$'s and $F_{2,j}$'s of both single crosses (Table 1) were hand-planted at East Farm on November 3, 1979. Twenty seeds of the parents and $F_{1,j}$'s and 100 seeds of the $F_{2,j}$'s were sown in each of the three replications. The $F_{2,j}$'s constituted the base populations for the first cycle of selection for heading date.

Individual plants within each $F_{2,j}$ population were selected for heading date (measured as the number of days from January 1, until 50% of the heads on a plant were fully emerged from the boot). Selections were made within replications according to the method described by Gardner (1961). An entire replication of Cross I was destroyed by rodents. Therefore, selections were restricted to 200 individuals in each cross.

Four heading date populations within the F_2 of each cross were formed in the spring of 1980, in the manner described below. Individual plants from a given cross within a replication were visually scored for heading date. The first 10 individuals reaching the 50% heading stage were intercrossed, non-reciprocally, with each individual being used once as a female. Two spikes per plant were used per cross to ensure enough seed for the next cycle of selection. In addition, one unemasculated spike from each selection was covered with a glassine bag to assure self-pollination. Similarly, the last 10 plants within each replication to reach the 50% heading stage were selfed and intercrossed to generate the late-heading populations. Finally, an early- and a late-heading population were formed by intercrossing

selected individuals across single-cross populations. Only 40 seeds were obtained from each of these latter crosses due to the extreme difference in the head dates of the two single cross populations.

The populations required for a genetic analysis of the $F_{2,j}$'s were made in the greenhouse in the fall of 1979, and the spring of 1981. Parents and $F_{1,j}$'s were vernalized in a growth chamber for six weeks at 8°C and 8 hours illumination. Vernalization was 'fixed' by growing the material for one week at 15°C and 8 hours illumination. Plants were then transplanted into 15 cm plastic pots and placed in the greenhouse. Temperature was increased to 20°C and daylength was increased to 18 hours. Parents were hybridized to form F_1 's and $F_{1,j}$'s were backcrossed to each parent.

Materials for the second selection cycle were hand-planted at the Hyslop site on October 17, 1980. Twenty seeds of parents and $F_{1,j}$'s and 30 seeds of $BC_{i,j}$'s, $F_{2,j}$'s, $F_{3,j}$'s and selected populations were sown per replication (Table 1). Selections, crosses among selections, and selfing were handled in the manner described for the first selection cycle. The selection differential was also identical (i.e., 10 percent).

Three other traits were measured in addition to heading date in 1981, for the purpose of evaluating the effect of one cycle of selection for heading date on correlated response in these traits. Plant height was recorded as the height in cm from the soil surface to the tip of the main spike, excluding awns. Plant

maturity was measured as the number of days from January 1, until 50% of the spikes in a population lost their green color. Grain yield was taken on individual plants and recorded in grams per plant. Grain yield was not taken on individuals selected to form the cycle two populations in both the selfing and the intermated populations. This was necessary to remove bias from emasculations done in the intermated populations.

The Evaluation Phase

Parents, $F_{1,j}$'s, $F_{2,j}$'s, $F_{4,j}$'s, $BC_{i,j}$'s and both the first and second cycle populations were hand-planted at the Hyslop site on October 23, 1981 (Table 1). Twenty seeds of parents and $F_{1,j}$'s and 30 seeds of $BC_{i,j}$'s, $F_{2,j}$'s, $F_{4,j}$'s and the selected populations were sown per replication. A set of parents, $F_{2,j}$'s, and the second cycle populations were also planted at the site near Pendleton, on October 16, 1981 (Table 1). Seeding rates were identical to those used at the Hyslop site for the appropriate populations.

Traits measured in 1982, included heading date, plant height, and grain yield as described previously. In addition, population maturity, spikes/plant, 100-kernel weight, kernels/spike, harvest index, and biological yield were recorded.

Population maturity was measured as the number of days from January 1, until 50% of the spikes in a population were fully senesced. Spikes/plant were recorded as the number of seed-producing tillers per plant. One hundred-kernel weight was

Table 1. List of nomenclature and populations planted in each of three crop years.

1979-80	1980-81	1981-82	
East Farm	Hyslop	Hyslop	Pendleton
RSK	RSK	RSK	RSK
HYS	HYS	HYS	HYS
KVZ	KVZ	KVZ	KVZ
$F_{1,j}$	$F_{1,j}$	$F_{1,j}$	-
$F_{2,j}$	$F_{2,j}$	$F_{2,j}$	$F_{2,j}$
-	$F_{3,j}$	$F_{4,j}$	-
-	$BC_{i,j}$	$BC_{i,j}$	-
-	$EC_1 F_{1,j}$	$EC_1 F_{1,j}$	-
-	-	$EC_2 F_{1,j}$	$EC_2 F_{1,j}$
-	$EC_1 F_{3,j}$	$EC_1 F_{4,j}$	-
-	-	$EC_2 F_{4,j}$	$EC_2 F_{4,j}$
-	$LC_1 F_{1,j}$	$LC_1 F_{1,j}$	-
-	-	$LC_2 F_{1,j}$	$LC_2 F_{1,j}$
-	$LC_1 F_{3,j}$	$LC_1 F_{4,j}$	-
-	-	$LC_2 F_{4,j}$	$LC_2 F_{4,j}$
-	$EI_1 F_1$	$EI_1 F_1$	-
-	-	$EI_2 F_1$	-
-	$LI_1 F_1$	$LI_1 F_1$	-
-	-	$LI_2 F_1$	-

RSK = 'Roussalka'; HYS = 'Hyslop'; KVZ = 'Kavkaz';

$F_{i,j}$ = the i th generation of the j th cross;

$BC_{i,j}$ = backcross to the i th parent in the j th cross;

'Kavkaz' is always parent 2;

E = early selection;

L = late selection;

C_i = i th cycle of selection;

I_i = i th cycle of selection in cross between the two populations.

determined by counting 100 seeds from a plant and obtaining their weight in grams. The number of kernels/spike was derived by dividing plant grain yield by the product of the number of spikes/plant and 100-kernel weight. Harvest index was calculated as the ratio of grain yield to the weight of the total above-ground dry matter (i.e., biological yield), and expressed as a factor less than unity.

Genetic Evaluation

One of the objectives of this investigation was to determine the nature and amount of genetic variation for the traits measured in Crosses I and II. This objective is a necessary prerequisite to any evaluation of selection methods for the following reasons: 1) to make a decision on the proper unit of selection; 2) to obtain a reasonable expectation of the possible genetic advance from selection; and 3) to assess the probable effects of selection for one trait on the expression of other traits. For this purpose, a generation mean analysis, narrow-sense heritability, and various correlation estimates for the nine agronomic traits were computed. In addition, heritabilities and genetic correlations were used to estimate response to selection for heading date and correlated responses in the eight unselected traits.

Generation means for each cross were obtained from the parents, $F_{1,j}$'s, $F_{2,j}$'s, $F_{3,j}$'s, and $BC_{i,j}$'s grown in 1980-81. In 1981-82, $F_{4,j}$'s were substituted for the $F_{3,j}$'s. Entry means were used in these analyses.

Both three-parameter and six-parameter models were fit to the generation means using a weighted least squares procedure (Rowe and Alexander, 1980). Appropriate weights were computed as the reciprocals of the pooled standard errors of each generation mean. The adequacy of each model was tested by χ^2 with $n-p$ degrees of freedom, where n = the number of generation means and p = the number of parameters in the model. The expectations of the generation means are given in Table 2 (Mather and Jinks, 1970). Assumptions of both models are: 1) multiple alleles absent; 2) no linkage; 3) equal survival of all genotypes; 4) gene frequencies for all segregating loci equal to 0.5 and 5) environmental effects are additive with the genotypic value (Gamble, 1962; Mather and Jinks, 1971). Significance of gene effects were determined by computing standard errors from the variances of the appropriate generation means.

Narrow-sense heritability estimates for each trait were computed using 25 plants/plot variances pooled across replications for the appropriate $F_{2,j}$'s and $BC_{i,j}$'s as described by Warner (1952). Assumptions were: 1) no linkage; 2) gene frequencies at each locus by which the original parents differed equals 0.5; 3) regular diploid behavior at meiosis; 4) no epistasis; and 5) the non-heritable components of variance of the F_2 and of the back-crosses are of comparable magnitude. The following formula was used:

$$h_{n.s.}^2 = [(1/2)D]/V_{F_2}$$

Table 2. Expectations of generation means for three- and six-parameter models.

Generation	Parameters					
	m	(a)	(d)	(aa)	(ad)	(dd)
\bar{P}_1	1	1	0	1	0	0
\bar{P}_2	1	-1	0	1	0	0
\bar{F}_1	1	0	1	0	0	1
\bar{F}_2	1	0	1/2	0	0	1/4
\bar{F}_3	1	0	1/4	0	0	1/16
\bar{F}_4	1	0	1/8	0	0	1/64
\overline{BC}_1	1	1/2	1/2	1/4	1/4	1/4
\overline{BC}_2	1	-1/2	1/2	1/4	-1/4	1/4

m = the mean of the inbred population derived from a cross between two true-breeding lines.

(a) = pooled additive effects of genes.

(d) = pooled dominance effects of genes.

(aa) = pooled additive x additive effects of genes.

(dd) = pooled dominance x dominance effects of genes.

(ad) = pooled additive x dominance effects of genes.

With standard error equal to the square root of the following
(Ketata et al., 1976):

$$V(h_{n.s.}^2) = 2 \left\{ \frac{(V_{BC1} + V_{BC2})^2}{d.f.(F_2)} + \frac{V_{BC1}^2}{d.f.(BC_1)} + \frac{V_{BC2}^2}{d.f.(BC_2)} \right\} / V_{F2}$$

Where: $h_{n.s.}^2$ = narrow sense heritability estimate

$1/2D$ = additive genetic variance in the F_2

$$= 2(V_{F2}) - (V_{BC1} + V_{BC2})$$

V_{F2} = the total variance, pooled across replications,
in F_2

BC_i = the total variance, pooled across replications, in
the i th backcross

d.f. = degrees of freedom for the appropriate generation.

Phenotypic correlations were computed between heading date and each of the unselected traits within each $F_{2,j}$ population. Estimates were based on 100 randomly-selected plants per cross. Environmental correlations were estimated between heading date and each of the unselected traits within each $F_{1,j}$, based on 60 plants per cross. Genetic correlations were then derived in the following manner (Falconer, 1960):

$$r_g = (r_p - e_x e_y r_E) / h_x h_y$$

$$S.E.(r_g) = (1 - r_g^2/\sqrt{2})\sqrt{[(S.E.(h_y^2)(S.E.(h_x^2)))/h_y^2 h_x^2]}$$

Where r_g = the genetic correlation between traits X and Y

r_p = the phenotypic correlation between traits X and Y

r_E = the environmental correlation between traits X and Y

$e_i^2 = 1 - h_i^2$ for the i th trait

h_i^2 = the narrow-sense heritability for the i th trait.

Estimates of expected response to mass selection for heading date were computed using (Falconer, 1960):

$$R = ih\sigma_A.$$

Estimates of expected correlated response in trait Y when selection was for heading date were computed using (Falconer, 1960):

$$CR_y = ih_x r_g \sigma_{Ay}.$$

Where R = response to mass selection per cycle per year.

i = the standardized selection differential (i.e., selection intensity); at a selection differential of 10%, $i = 1.755$.

h_x = the square root of the heritability estimate for heading date

σ_{Ay} = the square root of the additive variance for trait y.

Response to Selection

The first selection cycle populations (1980-81) were planted in a split plot design with four replications. Single crosses

were treated as main plots and the populations derived from each single cross were treated as subplots. Heading date, plant height and grain yield were measured on 15 to 25 plants/plot in all four replications, depending on the entry. Lodging later in the summer prevented full assessment of plant maturity. Only 10 plants per entry per replication, for three replications were measured for plant maturity. An analysis of variance, based on 15 plants/plot means, was calculated for each trait using all entries. An additional analysis, based on plot means calculated from 25 plants/plot, was computed for each trait using only the $F_{2,j}$ and selected populations. Sums of squares for populations and cross x population interaction were partitioned into single degree of freedom comparisons. These comparisons formed the basis for determining response to the first cycle of selection for heading date over the four methods used (i.e., early-selfed, early intermated, late-selfed and late-intermated).

First and second-cycle populations were arranged in a randomized complete block design with four replications in 1981-82. This design was substituted for the split plot design used in 1980-81, to obtain more precision in estimating cross means. Heading date, spikes/plant, 100-kernel weight, kernels/spike, grain yield, harvest index, and biological yield were measured on 15 to 25 plants/plot, depending on the population, at the Hyslop site. Population maturity was also recorded. The material grown

at the site near Pendleton was evaluated for plant height, spikes/plant, 100-kernel weight, kernels/spike, grain yield, harvest index, and biological yield. These traits were measured on 15 to 25 plants per plot per replication, depending on the population.

A separate analysis of variance was calculated on a plot mean basis for both locations and using all entries at 15 plants/plot/replication. For evaluation of selection response for the two directions of selection for heading date under two systems of mating, an additional analysis of variance using only $F_{2,j}$'s and the first (Hyslop site only) and second cycle populations was computed for each location. Analyses for each trait were based on population means derived from 25 plants per plot.

Sums of squares for crosses, methods of selection, and the cross x methods of selection interaction were partitioned into single degree of freedom contrasts to assess response to selection. In a combined analysis for both locations, error terms were either heterogeneous between locations (Appendix Table 9) or the location x treatment interaction was significant. Heterogeneity of location error mean squares was tested using an F-test of the ratio of the larger error mean square to the smaller error mean square (Snedecor and Cochran, 1967). Heterogeneity among the treatment x location interaction sums of squares was determined using Bartlett's chi-square test (LeClerc et al., 1962). To ensure that tests of significance did not cause too many Type I

errors, treatment mean squares were tested against the interaction term. If the interaction term was heterogeneous, individual treatment effects were tested against their own interaction with locations (Cochran and Cox, 1957).

A least squares procedure for comparing progress from different selection methods was used at the Hyslop site only (Eberhart, 1964). Since only two cycles of selection were completed, the following linear model was employed:

$$Y_{ij} = \mu_0 + \beta_{1j}x_{ij} + \delta_{ij}$$

Where: Y_{ij} = the mean of the ij th entry.

i = the cycle of selection for the j th method

μ_0 = the mean of the base population (F_2)

β_{1j} = the linear coefficients for the j th method

$x_{j'ij} = 0$ for $j' \neq j$
 $= i$ for $j' = j$

δ_{ij} = deviations not explained by the regression of response to selection on methods of selection.

RESULTS

Results of this investigation will be presented in three sections. In the first section, the genetic evaluation of heading date and eight other traits in Crosses I and II will be described. Next, the effect of two systems of mating on response to divergent mass selection for heading date will be evaluated. Finally, the correlative influence of selection for heading date under both mating systems on eight unselected traits will be characterized.

Appendix Table 1 contains summary data on temperature and precipitation for the three crop years. The initial selection cycle for heading date occurred in the 1979-80 crop year. Therefore, the effects of climatological conditions in the succeeding two crop years will be compared with 1979-80 data at the Hyslop site, with respect to the selection experiments.

The total amount of precipitation in 1980-81, at the Hyslop site, was only eight percent less than in the previous crop year (Appendix Table 1). There was a 31% increase in precipitation in 1981-82 compared to 1979-80 at Hyslop; however, most of that increase occurred during the winter months. The plots at the Hyslop site suffered from waterlogging in isolated areas during 1981-82, resulting in an estimated 10% reduction in stand. The site at Pendleton received 57% more precipitation in 1981-82 than the long term average for that location. Plant development at the Pendleton site was excellent; however, heavy rainfall prior to

harvest (Appendix Table 1) resulted in considerable lodging and delayed plant development.

Temperatures over all three crop years at East Farm and/or Hyslop were similar (Appendix Table 1). Minimum temperatures for the first half of 1982, were one to two degrees centigrade lower than the previous two crop years, and this may have had an effect on the onset of spring plant growth in 1982. Maximum temperatures at the Pendleton site were similar to those at Hyslop in 1981-82. Minimum temperatures were uniformly cooler over the growing season at Pendleton when compared to the Hyslop site.

No significant disease occurred at either the Hyslop or Pendleton sites in 1981-82. However, a severe infection of Septoria tritici occurred the previous year at Hyslop.

Genetic Evaluation

Analyses of variance indicated that significant differences existed among the entries used in this investigation for each of the traits measured in 1981 and 1982. A combined analysis of variance for the two crop years was not generated because of the different field plot designs employed in the two years and since entries in both years were not identical (i.e., F_3 's were grown in 1980-81 and F_4 's were grown in 1981-82).

Generation means and their within-plot variances for the seven generations derived from Crosses I and II are given in Tables 3 and 4, respectively. An examination of both tables reveals later plant development in the 1981-82 crop year, compared to 1980-81. This

Table 3. Observed generation means, within-plot variances, and midparent values (MP) for nine agronomic traits measured in Cross I (1981-1982).

Trait	Generation/Year §																	
	Roussalka		Kavkaz		MP		F _{1,1}		F _{2,1}		F _{3,1}		F _{4,1}		BC _{1,1}		BC _{2,1}	
	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982
Heading Date (days)	\bar{x}^\dagger 121.6	131.7	147.1	147.3	134.4	139.5	130.4	139.3	139.2	140.6	137.2	-	-	142.6	132.2	136.6	137.6	145.1
	v 4.1	4.0	24.1	1.0	-	-	4.1	2.7	29.5	23.1	69.9	-	-	22.6	22.8	10.3	14.4	9.3
Plant Height (cm)	\bar{x} 92.0	85.5	130.4	120.3	111.2	102.9	117.6	114.3	119.4	103.8	105.0	-	-	99.9	105.4	97.5	127.2	114.1
	v 31.0	31.6	122.2	56.9	-	-	53.1	31.4	242.1	121.7	127.3	-	-	106.8	122.6	102.8	191.6	113.7
PM† (days)	\bar{x} 176.3	184.5	192.8	191.8	184.6	188.1	187.6	187.0	187.9	189.8	188.5	-	-	193.5	188.6	188.9	189.0	191.5
	v 1.9	-	22.1	-	-	-	17.3	-	14.9	-	28.0	-	-	-	7.4	-	15.3	-
Grain Yield (g)	\bar{x} 10.2	37.6	26.0	55.1	18.1	46.4	23.4	49.9	23.7	48.2	20.5	-	-	40.3	18.9	41.3	24.7	43.7
	v 16.4	161.7	220.9	303.4	-	-	84.8	381.6	159.2	473.1	132.9	-	-	323.7	96.6	260.1	155.7	460.4
Spikes/plant (no.)	\bar{x} -	16.2	-	18.8	-	17.5	-	16.8	-	17.9	-	-	-	16.1	-	16.2	-	15.0
	v -	22.8	-	27.4	-	-	-	30.2	-	59.3	-	-	-	33.3	-	25.5	-	58.7
100-Kernel Weight (g)	\bar{x} -	5.00	-	5.54	-	5.27	-	5.51	-	5.34	-	-	-	5.24	-	5.21	-	5.41
	v -	0.09	-	0.06	-	-	-	0.09	-	0.20	-	-	-	0.24	-	0.28	-	0.18
Kernels/spike (no.)	\bar{x} -	45.9	-	52.3	-	49.1	-	53.0	-	51.0	-	-	-	46.2	-	47.8	-	56.5
	v -	42.0	-	97.6	-	-	-	62.0	-	84.2	-	-	-	95.2	-	76.3	-	160.0
Harvest Index	\bar{x} -	0.43	-	0.35	-	0.39	-	0.39	-	0.39	-	-	-	0.40	-	0.40	-	0.36
	v -	0.001	-	0.001	-	-	-	0.005	-	0.002	-	-	-	0.004	-	0.005	-	0.002
Biological Yield (g)	\bar{x} -	86.5	-	155.4	-	121.0	-	127.6	-	121.9	-	-	-	100.4	-	103.2	-	119.1
	v -	855.3	-	2094.3	-	-	-	2230.7	-	2527.9	-	-	-	1893.9	-	1254.4	-	2958.5

† PM = Plant Maturity (1981), Population Maturity (1982). ‡ \bar{x} = generation mean; v = within-plot variance.

§ Traits measured in 1981 were Heading Date, Plant Height, Plant Maturity and Grain Yield only; in 1982, Heading Date, Plant Height, Population Maturity, Grain Yield, Spikes/plant, Kernel Weight, Kernels/spike, Harvest Index and Biological Yield were measured. The F₄ generation was substituted for the F₃ generation in 1982.

Table 4. Observed generation means, within-plot variances, and midparent values (MP) for nine agronomic traits measured in Cross II (1981-1982)

Trait	Generation/Year ⁵																	
	Hyslop		Kavkaz		MP		F _{1,2}		F _{2,2}		F _{3,2}		F _{4,2}		BC _{1,2}		BC _{2,2}	
	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982	1982	1982	1981	1982	1981	1982	1981	1982
Heading Date (days)	\bar{x}^{\dagger} 147.6 v 1.6	150.0 1.0	147.1 24.1	147.3 1.0	147.7 -	148.6 -	141.6 7.4	145.3 1.5	143.1 25.0	151.9 8.7	144.9 19.3	- -	- -	150.6 18.6	145.8 18.1	147.0 8.6	140.3 12.4	146.5 6.5
Plant Height (cm)	\bar{x} 99.2 v 64.3	96.8 35.9	130.4 122.2	120.3 56.9	116.2 -	108.6 -	122.3 53.0	119.4 52.2	120.4 223.5	128.2 162.7	117.1 341.7	- -	- -	111.9 346.0	107.8 194.7	107.6 177.3	128.4 162.2	120.9 90.7
PM [†] (days)	\bar{x} 191.5 v 7.5	194.5 -	192.8 22.1	191.8 -	191.4 -	193.1 -	189.3 2.1	191.3 -	191.1 12.0	194.5 -	191.5 23.5	- -	- -	197.3 -	191.4 9.2	194.0 -	191.2 9.7	191.1 -
Grain Yield (g)	\bar{x} 12.1 v 35.6	55.2 552.6	26.0 220.9	55.1 303.4	17.9 -	55.1 -	21.9 116.3	59.3 593.9	19.0 132.1	45.5 702.4	17.9 165.6	- -	- -	46.9 703.1	17.3 120.7	52.4 549.0	21.0 100.9	49.7 399.8
Spikes/plant (no.)	\bar{x} - v -	21.6 75.2	- -	18.8 27.4	- -	20.2 -	- -	18.7 60.2	- -	22.8 143.1	- -	- -	- -	17.0 69.9	- -	17.7 57.4	- -	17.1 36.5
100-Kernel Weight (g)	\bar{x} - v -	4.72 0.07	- -	5.54 0.06	- -	5.13 -	- -	5.57 0.15	- -	4.85 0.23	- -	- -	- -	5.02 0.22	- -	5.23 0.20	- -	5.57 0.11
Kernels/spike (no.)	\bar{x} - v -	53.6 52.9	- -	52.3 97.6	- -	52.9 -	- -	59.2 107.5	- -	42.1 164.0	- -	- -	- -	54.9 149.0	- -	56.8 97.9	- -	57.3 98.6
Harvest Index	\bar{x} - v -	0.40 0.001	- -	0.35 0.001	- -	0.38 -	- -	0.40 0.004	- -	0.34 0.011	- -	- -	- -	0.37 0.006	- -	0.39 0.003	- -	0.35 0.003
Biological Yield (g)	\bar{x} - v -	135.0 2970.9	- -	155.4 2094.3	- -	145.2 -	- -	146.8 2872.9	- -	144.6 5150.4	- -	- -	- -	125.5 4037.5	- -	132.6 3033.2	- -	140.4 2523.1

[†]PM = Plant Maturity (1981), Population Maturity (1982). \bar{x} = generation mean; v = within-plot variance.

⁵ Traits measured in 1981 were Heading Date, Plant Height, Plant Maturity and Grain Yield only; in 1982, Heading Date, Plant Height, Population Maturity, Grain Yield, Spikes/plant, Kernel Weight, Kernels/spike, Harvest Index and Biological Yield were measured. The F₄ generation was substituted for the F₃ generation in 1982.

phenomenon can be seen by the delay in heading dates and plant or population maturities of most of the generations grown in those years. Another difference noted is a general reduction in plant height from 1981 to 1982, due to cooler winter and spring temperatures in 1982, which delayed the onset of plant growth (Appendix Table 1). Grain yields in 1982 were at least double those in the previous crop year, among comparable generations. This result may be explained by possible beneficial effects of soil fumigation in the fall of 1981, and the lack of leaf diseases in the spring of 1982.

Gene Effects

Joint scaling tests were used on generation means in both crosses to determine the kinds of gene effects controlling the expression of nine agronomic traits. The kinds and relative magnitudes of genetic effects varied both among crosses and between years, for those traits common to the two years (Tables 5 and 6).

Estimates of gene effects for two years are available for heading date, plant height, and grain yield, only. Maturity was also measured in both years but was recorded on a per plant basis in 1981 and on a population basis in 1982. Due to the many differences between the two single crosses studied, results of this investigation will be presented for each cross individually.

Cross I

Lack of fit to both three- and six-parameter models for heading date in 1981, indicated that linkage and/or trigenic epistatic effects of genes affected variation among Cross I

Table 5. Estimates of gene effects on nine agronomic traits using three- and six- parameter models for seven generations in Cross I.

Model and Effect ⁺	Trait and Year												
	Heading Date		Plant Height		Plant or Population Maturity		Grain Yield		Spikes/Plant	100-Kernel Weight	Kernels/Spike	Harvest Index	Biological Yield
	1981	1982	1981	1982	1981	1982	1981	1982	1982	1982	1982	1982	1982
	1981	1982	1981	1982	1981	1982	1981	1982	1982	1982	1982	1982	1982
3-parameter													
m	135.01**	139.99**	110.14**	100.66**	184.18**	190.19**	18.44**	42.66**	16.75**	5.24**	48.23**	0.39**	108.88**
(a)	-12.26**	- 7.64**	-18.85**	-16.36**	- 7.30**	- 3.42*	- 7.96**	- 6.22*	-0.69	-0.26**	-3.74*	0.04**	-25.47**
(d)	- 3.48	- 0.14	8.25	12.29**	7.57	- 1.70	6.49**	4.78	-0.28	0.23**	4.96	-0.01	14.26
χ^2	73.61	17.33	15.16	6.27	35.82	25.20	1.59	3.43	2.85	1.29	4.89	1.61	4.33
P	<.005	<.001	<.005	.25-.10	<.005	<.005	.90-.75	.75-.50	.75-.50	.95-.90	.50-.25	>.90	.75-.50
6-parameter													
m	141.05**	142.54**	95.38**	98.70**	185.66**	193.62**	18.89**	41.37**	16.74**	5.24**	44.04**	0.41**	101.22**
(a)	-12.65**	- 7.76**	-19.04**	-17.40**	- 8.28**	- 3.63**	- 7.76**	- 8.41	-1.25	-0.27**	-3.16**	0.04**	-33.37**
(d)	- 5.20	- 0.98	50.90	7.46	10.77	- 3.83	9.44	- 1.76	-2.74	0.03	18.72**	-0.07*	11.32
(aa)	- 6.84	- 3.04*	15.56	4.27*	- 1.02	- 5.36**	- 0.94	4.34	0.56	0.03	5.05**	-0.02*	17.96
(ad)	14.95*	- 1.46	- 6.37	1.83	16.12**	2.01	3.62	9.53	3.80	0.15	-11.10**	0.00	27.02
(dd)	- 5.47	- 2.30	-28.55	8.15*	- 8.88	- 2.33	- 4.89	10.55	2.86	0.24	- 9.80**	0.05*	15.56
χ^2	4.77	1.01	3.17	0.27	0.79	1.05	0.35	1.21	0.99	0.11	0.004	0.19	1.38
P	.05-.025	.5-.25	.10-.05	.75-.50	.50-.25	.50-.25	.75-.50	.50-.25	.50-.25	.75-.50	>.90	>.90	.25-.10

*,** significant at the 0.05 and 0.01 levels of probability, respectively.

⁺m = the mean of the inbred population derived from a cross between two true-breeding lines; (a) = pooled additive effects of genes; (d) = pooled dominance effects of genes; (aa) = pooled additive x additive effects of genes; (ad) = pooled additive x dominance effects of genes; (dd) = pooled dominance x dominance effects of genes.

Table 6. Estimates of gene effects on nine agronomic traits using three- and six-parameter models for seven generations in Cross II.

Model and Effect +	Heading Date		Plant Height		Plant or Population Maturity		Grain Yield		Spikes/Plant	Biological Yield	100-Kernel Weight	Kernels/Spike	Harvest Index
	1981	1982	1981	1982	1981	1982	1981	1982	1982	1982	1982	1982	1982
3-parameter													
m	145.76**	148.99**	115.13**	110.15**	192.38**	194.53**	17.70**	50.27**	18.69**	136.13**	5.08**	51.82**	0.37**
(a)	1.90	1.30*	-16.50**	-12.17**	-0.54	1.67	-5.56**	0.46	0.88	-9.64	-0.41**	1.87	0.03**
(d)	-4.71*	-3.24	7.29**	11.55	-2.98**	-2.78	3.32*	3.02	-.82	6.16	.42	3.75	.01
x ²	19.21	65.80	1.82	24.67	0.94	17.01	1.07	3.06	5.76	1.60	25.30	23.40	5.45
P	<.005	<.005	.90-.75	<.005	.95-.90	<.005	.90-.75	.75-.50	.25-.10	.90-.75	<.005	<.005	.25-.10
6-parameter													
m	147.45**	154.26**	117.22**	118.23**	191.38**	198.67**	17.63**	46.84**	18.15**	127.10**	4.78**	56.08**	0.37**
(a)	0.23**	1.38	-15.58**	-11.52	.65**	1.38**	-6.91**	.09	1.16	-10.34	-0.41	.32	0.02*
(d)	-11.67**	-11.65	2.41	4.39	1.04**	-10.77**	.59	-5.19	-2.54	9.71	0.94	-31.78	-0.04
(aa)	-0.13	-5.73	-2.54	-10.39	0.77**	-5.58**	1.37**	8.49**	1.52	16.67	0.38	-2.25	.007
(ad)	10.47**	-1.10	-10.01*	0.31	1.65**	2.99	6.32**	5.03	-0.41	6.05	0.02	26.99	.03
(dd)	5.84**	2.66	2.72	-3.03	-3.15**	3.37	3.72**	17.59**	3.19	10.24	-0.16	34.63	0.07
x ²	.002	22.93	0.22	13.60	.0003	0.21	.008	0.03	3.54	.50	17.38	12.23	1.67
P	>.90	<.005	.75-.50	<.005	>.90	.75-.50	>.90	.90-.75	.10-.05	.90-.75	<.005	<.005	.25-.10

*,** significant at the 0.05 and 0.01 levels of probability, respectively.

+ m = the mean of the inbred population derived from a cross between two true-breeding lines; (a) = pooled additive effects of genes; (d) = pooled dominance effects of genes; (aa) = pooled additive x additive effects of genes; (ad) = pooled additive x dominance effects of genes; (dd) = pooled dominance x dominance effects of genes.

generation means for this trait (Table 5). Both additive and the (ad) type of digenic epistasis affected the expression of this trait. However, the magnitudes and signs of these significant gene effects may have been influenced by unexplained variation among the generation means (Mather and Jinks, 1971).

Additive effects of genes were as important as dominance effects in determining variation among Cross I generation means for grain yield in 1981. Dominance effects were positive (Table 5). Additive effects were the only significant gene effects for plant height. However, additive effects were confounded with significant digenic interactions in the expression of plant maturity, making a unique interpretation of its relative importance impossible (Hayman, 1958). The following year, additive effects of genes explained most of the variation among Cross I generation means for grain yield, and biological yield. Additive effects for heading date and population maturity were confounded with significant digenic epistasis, but represented the only significant main effects for these traits.

Both additive and positive dominance effects of genes were important in the expressions of plant height, 100-kernel weight and kernels/spike in 1982. However, significant digenic epistasis for plant height and kernels/spike made interpretation of the relative importance of the two main effects for these traits difficult. Hayman (1958) suggested that an approximation to epistasis-free estimates of m , (a) and (d) could be obtained from the three-parameter model. In Cross I generation means, plant height

appeared to be equally affected by both additive and dominance effects in the direction of taller plant stature. Dominance effects of genes were six times the magnitude of additive effects for kernels/spike. Variation among 1982 Cross I generation means for spikes/plant was explained by the midparent value.

Plant maturity was affected by the (ad) type of epistasis in the direction of later maturity in 1981. The following year, digenic epistatic effects of the (aa) type were important in the expressions of heading date, plant height, population maturity, kernels/spike, and harvest index; the (ad) type of epistasis affected the expression of kernels/spike; and the (dd) type of epistasis affected variation among generation means for plant height, kernels/spike, and harvest index. The signs of the three interaction terms depended on the trait; signs were negative for population maturity and positive for plant height. Kernels/spike was affected by positive additive epistasis and negative non-additive epistasis, with the latter effects about twice the magnitude of the former. Variation among Cross I generation means for harvest index was affected by negative additive epistasis and positive non-additive epistasis; again, non-additive epistasis was twice as large as additive epistasis.

Cross II

In 1981, the six parameter model was sufficient to explain variation among generation means for every trait measured (Table 6). In 1982, however, heading date, plant height, 100-kernel weight, and kernels/spike were affected by more complex inheritance

than could be explained by either model. Nevertheless, significant additive effects were noted for heading date, plant height and 100-kernel weight; dominance and digenic epistatic effects were not detected.

Additive effects of genes did not account for the major portion of variation among Cross II generation means for any trait measured in 1981. Furthermore, main effects were confounded with digenic interactions for each trait. Based on the three-parameter model (Table 6), however, additive effects of genes were more important than dominance effects in the expressions of plant height and grain yield in 1981, and dominance effects explained all the variability due to main effects among generation means for heading date and plant maturity. The following year, additive effects were important for harvest index, dominance effects affected population maturity, and variation among Cross II generation means for spikes/plant and biological yield was explained by the mid-parent value. Dominance was in the direction of the earlier maturing parent, in terms of plant or population maturity and heading date and in the direction of the taller and higher-yielding parent in both years.

Digenic interactions were more important in 1981 than in 1982. The (aa) type of interaction affected the expressions plant maturity and grain yield in both years and of population maturity in 1982; (ad) effects were important for heading date, plant height, plant maturity, and grain yield in 1981, only; and the (dd) type of epistasis affected heading date and plant maturity in 1981,

and grain yield in both years. Significant epistatic effects were positive for heading date and negative for plant height. The signs of the epistatic terms for each of the other traits differed depending on the type of epistasis. Except for population maturity, non-additive epistatic parameters were larger than the additive type.

Heritabilities and Correlations

Estimates of narrow-sense heritabilities for the nine agronomic traits measured on populations derived from Crosses I and II are given in Table 7. This table also provides estimates of phenotypic, genetic, and environmental correlations between heading date and each of the other traits under investigation. These estimates were then used to predict the correlated response in each of the eight agronomic traits when selection was for heading date.

Cross I

Populations of this cross showed high estimates of heritability for heading date and plant height in 1981, and for heading date only in the following year. Moderate estimates of heritability for Cross I were obtained for spikes/plant in 1982 and low estimates of heritability were obtained for plant maturity and grain yield in 1981, and for plant height, grain yield, biological yield, 100-kernel weight, kernels/spike and harvest index in 1982.

Estimates of genetic and environmental correlations between heading date and each of the other traits measured in 1981 were not significant. However, in 1982, these estimates indicated that significant negative genetic relationships existed between heading

Table 7. Estimates of narrow-sense heritabilities (h^2) and phenotypic (r_p), genetic (r_g) and environmental correlations (r_e)[†] of heading date with eight other traits.

Trait	Cross	h^2		r_p		r_g		r_e	
		1981	1982	1981	1982	1981	1982	1981	1982
Heading Date	I	.74**	1.00**						
	II	.78**	.27						
Plant Height	I	.70**	.23	-.09	-.03	-.07	-.06	-.13	-.03
	II	.40	.35	.06	-.44**	-.33	-.45	-.34*	-.44**
Maturity [‡]	I	.46		-.11	--	-.02	--	-.27	--
	II	.42		.29	--	.26	--	.41*	--
Grain Yield	I	.42	.48	-.27**	-.41**	-.40	-.59**	-.12	-.52**
	II	.32	.65*	-.06	-.52**	.31	-1.00**	-.59**	-.16
Spikes/Plant	I		.58*		-.31**		-.41*		-.43**
	II		1.00**		-.47**		-.91**		-.14
Biological Yield	I		.33		-.32**		-.56*		-.49**
	II		.92**		-.50**		-.92**		-.17
100-Kernel Weight	I		.00		-.29**		.00		-.35**
	II		.67*		-.26*		-.80**		.16
Kernels/Spike	I		.00		-.10		.00		-.31
	II		.80**		-.39**		-.79**		-.06
Harvest Index	I		.00		-.51**		.00		-.20
	II		1.00**		.20		.39*		-.05

*,** significant at the 0.05 and 0.01 levels of probability, respectively.

[‡]Plant maturity was measured in 1981 and population maturity was measured in 1982.

[†] r_p was calculated using 100 $F_{2,j}$ plants; r_e was calculated using 60 $F_{1,j}$ plants; r_g was derived from r_p and r_e .

date and grain yield, spikes/plant and biological yield (Table 7). Also, in 1982, significant negative environmental associations of grain yield, spikes/plant, biological yield, and 100-kernel weight with heading date were detected. Based on a non-significant estimate of genetic correlation between heading date and harvest index in 1982, the significant phenotypic correlation coefficient suggests an environmental relationship between these two traits.

Cross II

In this cross, estimates of heritability for heading date in 1981, and for spikes/plant, biological yield, harvest index and kernels/spike in 1982, were high. Moderate estimates of heritability were obtained for grain yield and 100-kernel weight in 1982. Heritability estimates were low for plant height, plant maturity, and grain yield in 1981, and for heading date and plant height in the following year.

None of the estimates of genetic correlation with heading date were significant in 1981; however, the following year significant, negative genetic correlations were obtained with heading date for all traits except plant height and harvest index (Table 7). The latter trait showed a significant, positive genetic association with heading date. Negative environmental correlations existed between heading date and plant height in both years, and between heading date and grain yield in 1981.

Response to Selection for Heading Date

Response at Hyslop - 1981

An analysis of variance for first cycle populations grown at

the Hyslop site in 1981, showed differences in response to selection for heading date between crosses and methods of selection to be highly significant (Appendix Table 3). Block effects were also significant and the coefficient of variation was low.

A partition of selection methods and the cross x selection method sums of squares showed that selection for heading date was effective in both directions and under both mating systems, but the magnitudes of these responses were dependent on the cross. Significant differences between mating systems were not detected in either cross.

Cross I

Significant changes in mean heading date in the selfed cycle one populations were obtained in both directions (Table 8). Predicted changes in heading date for the first cycle of selection did not correspond very closely with observed changes (Table 9). The early-selected population was 7.6 days earlier and the late-selected population was 2.3 days earlier than predicted. Selected populations were neither as early as 'Roussalka' nor as late as 'Kavkaz' (Appendix Table 4). One cycle of selection in either direction did not result in a detectable change in within-plot variance when compared to the base ($F_{2,1}$) population (Table 8). The $F_{2,j}$ variances were used as an indication of the amount of genetic and environmental variation for heading date and discrepancies from this variance in the selected populations were interpreted as a change in the 'genetic variation' for that trait.

Table 8. Population means and within-plot variances for heading date in Crosses I and II measured on 25 plants/population/block at Hyslop (1981).

Population		Cross	
		I	II
$F_{2,j}$	\bar{x}	139.0	143.2
	v	29.5	25.0
$EC_1F_{3,j}$	\bar{x}	124.4	139.1
	v	28.3	25.2
$EC_1F_{1,j}$	\bar{x}	125.0	138.0
	v	19.5	29.7
$LC_1F_{3,j}$	\bar{x}	143.8	150.1
	v	28.2	5.8**
$LC_1F_{1,j}$	\bar{x}	144.1	148.9
	v	20.3	5.2**
LSD (.05)		0.9	0.9

**within-plot variance of selected population significantly smaller than within-plot variance of $F_{2,j}$ at $P = 0.01$.

\bar{x} = populations means v = within-plot variances

Table 9. Predicted⁺ and observed[†] responses to divergent mass selection for heading date in Crosses I and II.

Population	Cross I		Cross II	
	1981	1982	1981	1982
EC ₁ F _{3(4),j} [§]	-14.7*	-7.0*	-4.1*	-6.4*
EC ₂ F _{4,j}	-	-2.7*	-	-3.5*
EC ₁ F _{1,j}	-14.1*	-5.3*	-5.2*	-6.5*
EC ₂ F _{1,j}	-	-3.2*	-	-5.4*
LC ₁ F _{3(4),j}	4.8*	7.2*	7.0*	2.2*
LC ₂ F _{4,j}	-	3.8*	-	1.6*
LC ₁ F _{1,j}	5.1*	5.7*	5.8*	0.4
LC ₂ F _{1,j}	-	4.4*	-	1.5*
Predicted	7.1	9.1	6.9	1.4

*Observed responses significantly different ($P=0.05$) from mean performance of the selections from one cycle to the next.

⁺Predicted responses are expressed as a deviation from the mean of the appropriate F_{2,j} population.

[†]Observed responses are expressed as a deviation from the mean performance of the selections from one cycle to the next.

[§]Number in parentheses refers to the F₄ generation grown in 1982.

Intermating following divergent mass selection for heading date was also successful in changing selected population means in the direction of selection (Table 8). Observed response to selection in either direction did not agree with prediction (Table 9). However, the same relationship of predicted response to each direction of selection as occurred in the selfed populations was observed. Means of first cycle populations did not attain the values of either parent for heading date (Appendix Table 4). No significant changes in within-plot variance in selected populations occurred.

Cross II

Gain from selection for heading date in both directions under selfing were significant (Table 8). With respect to the original parents, the $EC_1F_{3,2}$ and $LC_1F_{3,2}$ population means were earlier and later, respectively, than 'Hyslop' and 'Kavkaz' (Appendix Table 4). Predicted response to selection for heading date in Cross II more closely resembled observed responses than in Cross I (Table 9). A highly significant reduction in within-plot variance in the $LC_1F_{3,2}$ population was detected (Table 8).

Significant gains from selection followed by intermating were also obtained (Table 8). These changes in mean heading date were not as large as those predicted (Table 9), nor were these gains of the same absolute magnitude as those obtained under selfing (Table 8). Mean heading date in $EC_1F_{1,2}$ was significantly earlier than both original parents; but the mean heading date of $LC_1F_{1,2}$ was not significantly later than either parent

(Appendix Table 4). A highly significant reduction in within-plot variance of the late-selected population was observed (Table 8).

Contrasts of Selection Methods

In Cross I, response to selection for early heading date was approximately three times as great as response to selection for late heading date when expressed as a deviation from the $F_{2,1}$ population mean (Table 9). No differences were detected between mating systems in response to selection for heading date (Table 9).

Response to divergent mass selection for heading date in Cross II populations was similar in both directions for both systems of mating. However, with selection for early heading date, the intermated population was slightly earlier than the selfed population, and with selection for late heading date, the selfed population was later than the intermated population ($P = 0.05$).

Intercrosses

The intercross populations exhibited both the earliness of Cross I populations and the lateness of Cross II populations (Appendix Table 4). EI_1F_1 was significantly earlier than the $EC_1F_{1,2}$ and significantly later than any of the $EC_1F_{i,1}$ populations. Similarly, LI_1F_1 was later than the late-selected Cross I populations and earlier than the late-selected Cross II populations ($P = 0.05$). Means of both EI_1F_1 and LI_1F_1 were significantly different from the $F_{2,j}$ populations for heading date.

Response at Hyslop - 1982

Means squares for heading date of selected and unselected control populations for 1982, are given in Appendix Table 5. Highly significant differences among crosses and methods of selection were detected. Block effects were also highly significant and the coefficient of variation was quite low.

A partition of selection methods and the cross x selection methods sums of squares revealed highly significant effects for response to selection, direction of selection, mating system under late selection, cycle x direction, cross x response, cross x cycle, cross x direction, and cross x mating system under early selection interactions (Appendix Table 5).

Cross I

Significant, but non-linear, changes in heading date with cycles of selection were observed in both directions of selection under selfing (Table 10 and Figure 1). With respect to the original parental cultivars, the early-selected cycle two population was as early as 'Roussalka' and the late-selected cycle two population was significantly later than 'Kavkaz' (Appendix Table 6).

Predicted changes in heading date in 1982, agreed closely with observed responses in the selfed cycle one populations, but observed responses in cycle two populations were approximately half of that predicted (Table 9), for both directions of selection. Concurrent with the preceeding observation was a decrease in "genetic variance" for heading date, as determined by a contrast of the $F_{2,1}$ within-plot variance with those of both cycle two selfed populations (Table 10).

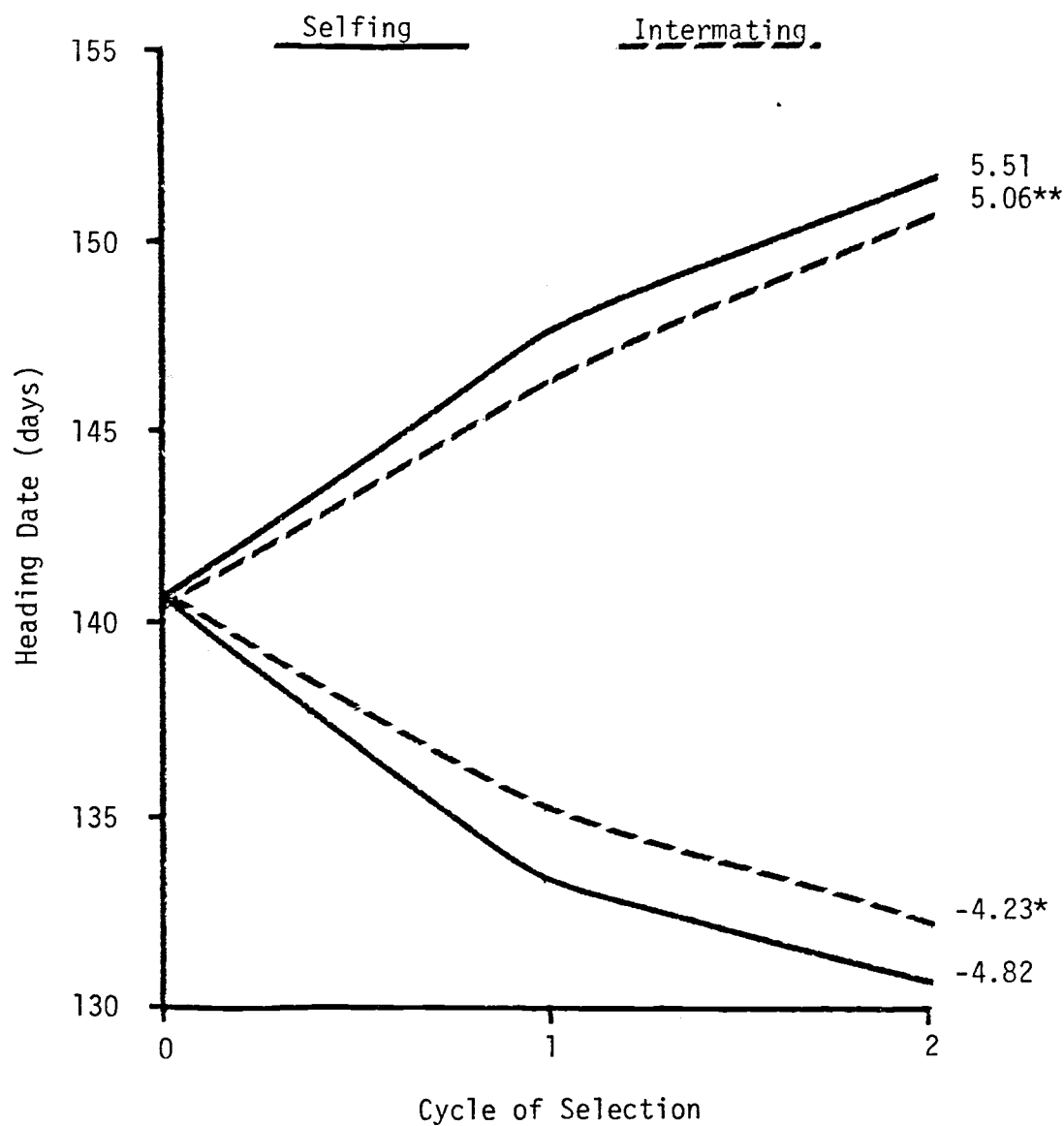


Fig. 1. Response to two cycles of divergent mass selection for heading date under two systems of mating in Cross I.

*,** Linear regression coefficients of population means on cycles of selection for heading date significant at 0.05 and 0.01 levels of probability, respectively.

Table 10. Population means and within-plot variances for heading date in Crosses I and II measured on 25 plants/population/block at Hyslop (1982).

Population		Cross I	Cross II
$F_{2,j}$	$\bar{x}^{\#}$	140.6	151.9
	v	23.1	8.7
$EC_1F_{4,j}$	\bar{x}	133.6	145.5 ⁺
	v	15.3	20.7 ⁺
$EC_2F_{4,j}$	\bar{x}	130.9	142.0
	v	11.2*	7.4
$EC_1F_{1,j}$	\bar{x}	135.3	145.4
	v	23.4	10.2
$EC_2F_{1,j}$	\bar{x}	132.1	140.0
	v	11.4*	13.7
$LC_1F_{4,j}$	\bar{x}	147.7	154.1
	v	12.3	11.4
$LC_2F_{4,j}$	\bar{x}	151.6	155.7
	v	6.6**	7.0
$LC_1F_{1,j}$	\bar{x}	146.3	152.2
	v	7.3**	8.4
$LC_2F_{1,j}$	\bar{x}	150.7	153.7
	v	5.1**	6.1
LSD (.05)		1.4	1.4

*,** within-plot variance of selected population significantly smaller than within-plot variance of $F_{2,j}$ at $P = 0.05$ and 0.01 , respectively.

⁺ within-plot variance of selected population significantly greater than within-plot variance of $F_{2,j}$ at $P = 0.05$.

[#] \bar{x} = population mean; v = within-plot variance.

Response to selection for heading date in the intermated populations over two cycles was significantly linear, with an average -4.23 days/cycle in $EC_iF_{1,1}$ and 5.06 days/cycle in $LC_iF_{1,1}$ gain from selection (Figure 1). As in the selfing series, cycle two populations exceeded the heading date of the later parent and equalled the heading date of the early parent used to generate Cross I (Appendix Table 5).

Predicted response to selection for heading date was approximately three days greater than occurred in both intermated cycle one populations (Table 9). However, reductions in observed response from selection between cycles one and two were not as large as occurred in the selfed populations. Despite the linearity of response to selection the intermated populations, both cycle two populations showed a reduction in within-plot variance (Table 10).

Cross II

Significant linear response to selection for heading date over cycles of selection was observed in the $LC_iF_{4,2}$ populations (Figure 2). Response to selection for early heading date was significant in each cycle but non-linear (Figure 2). Both cycle two populations exceeded the respective extremes in heading date when compared to 'Hyslop' and 'Kavkaz' (Appendix Table 6).

Observed responses with early selection under selfing and over both cycles were 2.5 to 4.6 times greater than predicted (Table 9), primarily because the estimate of heritability was low and non-significant in 1982 (Table 7). Observed response in both late-selected populations closely resembled predicted response (Table

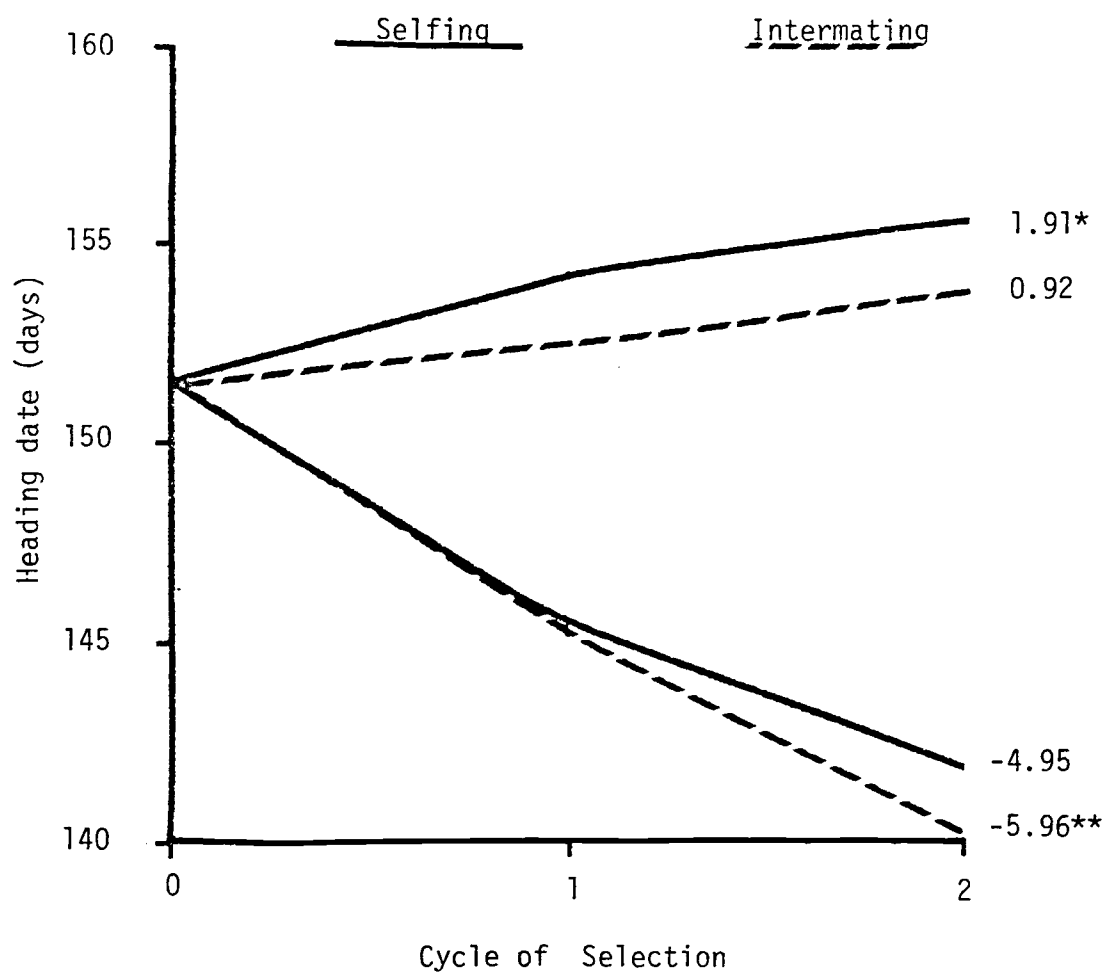


Fig. 2. Response to two cycles of divergent mass selection for heading date under two systems of mating in Cross II.

*,** Linear regression coefficients of population means on cycles of selection for heading date significant at 0.05 and 0.01 levels of probability, respectively.

9). Expected loss of 'genetic variation' for heading date in either selfed cycle two population did not occur (Table 10); in fact, the within-plot variance of $EC_1F_{4,2}$ was significantly greater than the $F_{2,2}$ within-plot variance.

Heading dates of early-selected intermated populations showed a linear response of -5.96 days/cycle to selection for heading date (Figure 2); the $LC_1F_{1,2}$ population mean was not significantly different than the mean of the base population (i.e., $F_{2,2}$) and the $LC_2F_{1,2}$ population mean was only 1.8 days later than the base population (Table 10). Nevertheless, both late- and early-selected cycle two population means exceeded the corresponding later and earlier parents used to generate Cross II (Appendix Table 6).

Observed response to selection for early heading date was up to five times greater than predicted, while response to selection for late heading date closely resembled the predicted gain in cycle two and was half the predicted gain in cycle one (Table 9). No loss of 'genetic variation' for heading date was detected in either cycle two population (Table 10).

Contrasts of Selection Methods

Table 11 shows the standard partial regression coefficients of observed population means on methods of selection. The relative magnitudes of the standard partial regression coefficients for mating systems and directions of selection gives an indication of the importance of each method in response to selection (Snedecor and Cochran, 1967). These comparisons, combined with statistics

Table 11. Coefficients of determination and standard partial regression coefficients for the multiple regression of response to selection for heading date on four "methods" of selection in Crosses I and II.

Method	Cross I	Cross II
$EC_{iF_{4,j}}$	-.44**	-.60**
$EC_{iF_{1,j}}$	-.37**	-.70**
$LC_{iF_{4,j}}$.50**	.28**
$LC_{iF_{1,j}}$.45**	.14*
R^2	.99	.99

*,** corresponding partial regression coefficient significant at 0.05 and 0.01 levels of probability, respectively.

⁺methods of selection were early-selfing, early-intermating, late-selfing, and later-intermating.

taken from Tables 9 and 10, indicate that, in Cross I, selection followed by selfing was slightly more effective in changing heading date in either direction than selection followed by intermating. The only significant difference detected between these mating systems occurred between $EC_1F_{4,1}$ and $EC_1F_{1,1}$, where the former population was 1.7 days earlier than the latter (Table 10). Selection for late heading date in Cross I was more effective under both systems of mating than selection for early heading date (Table 11), although this difference was not large.

In Cross II, early selection followed by intermating was more important than early selection followed by selfing in increasing earliness (Table 11). The standard partial regression coefficient of $LC_iF_{1,2}$ was half the magnitude of the coefficient for $LC_iF_{4,2}$; this result agrees with the difference in heading date means between the two populations (Table 10). Gain from selection for early heading date was more effective than gain from selection for late heading date (Table 11); as in Cross I, this result is opposite of what occurred in 1981.

Intercrosses

Significant gain from selection for heading date in both directions was detected between cycles one and two of the intercross populations (Appendix Table 6). The early-selected intercross populations were earlier than the $EC_iF_{1,2}$ and later than the $EC_iF_{1,1}$, for comparable cycles of selection. The $LC_2F_{i,2}$ populations were later than LI_2F_1 and no significant differences between $LC_2F_{4,1}$ and LI_2F_1 were

found. The LI_2F_1 population mean was significantly later than that of the $LC_2F_{1,1}$ (Appendix Table 6).

Response at Pendleton - 1982

Individual plant data for heading date were not taken at the Pendleton site in 1982. Instead, the range of heading dates within populations were used to approximate the effects of selection for heading date by comparing ranges between selected populations, parents, and unselected controls (Appendix Table 8). In general, early-selected populations were earlier than the appropriate base population and late-selected populations were later than the appropriate base population. In addition, cycle two populations of both crosses were as early or as late as the corresponding early or late parent used to derive the crosses.

Correlated Response to Selection for Heading Date

As previously mentioned, selection in populations of Crosses I and II was restricted to divergent mass selection for heading date, under two systems of mating. Correlated responses in other traits to selection for heading date were also investigated.

Correlated Response at Hyslop - 1981

Mean squares from an analysis of variance of selected populations and their unselected controls for correlated response in each of three traits is given in Appendix Table 3. Significant changes in plant height and plant maturity occurred after one cycle of selection for heading date. Changes in grain yield of selected populations were not detected. Block effects were not detected and

coefficients of variation ranged from a low of 1.4% for plant maturity, to a high of 18.0% for grain yield (Appendix Table 3). The coefficient of variation for plant height was low at 4.0%.

A partition of the sums of squares for methods of selection and the cross x methods of selection interaction showed that significant effects of divergent mass selection for heading date on plant height and plant maturity were largely dependent on the cross in which they were measured and the direction of selection (Appendix Table 3).

Cross I

Selection for early heading date was accompanied by significant decreases in both plant height and plant maturity in the selfed populations (Table 12). The late-selected population was also shorter than the average of the base population, but was significantly later-maturing. In contrast to the original parental cultivars, neither selected population was as short as 'Roussalka' nor as late as 'Kavkaz' (Appendix Table 4). Observed correlated responses in both unselected traits did not agree closely with predictions (Table 13) for either direction of selection for heading date. Further, correlated response in plant height resulted in a significant loss of 'genetic' variance for this trait in both selected populations (Table 12).

Divergent mass selection for heading date followed by inter-mating resulted in significant reductions in plant height and plant maturity in the $EC_1F_{1,1}$, a significant reduction in plant height and a significant increase in plant maturity in the

Table 12. Population means and within-plot variances for three agronomic traits measured in Cross I on 25 plants/population/block at Hyslop (1981).

Population		TRAIT		
		Plant Height (cm)	Plant Maturity (days)	Grain Yield (g)
F _{2,1}	\bar{x}^+	119.4	188.0	23.4
	v	242.1	14.9	159.2
EC ₁ F _{3,1}	\bar{x}	104.6	182.7	20.0
	v	61.3**	28.9	81.5
EC ₁ F _{1,1}	\bar{x}	102.5	182.6	20.2
	v	91.3*	14.9	110.0
LC ₁ F _{3,1}	\bar{x}	110.2	193.1	18.2
	v	99.4*	23.2	118.5
LC ₁ F _{1,1}	\bar{x}	106.1	192.4	17.5
	v	153.2	17.3	113.6
LSD (.05)		4.7	3.3	3.6

*,** within plot variances of selected populations significantly smaller than within-plot variance of F_{2,1} at P = 0.05 and 0.01, respectively.

⁺ \bar{x} = population mean; v = within-plot variance.

Table 13. Predicted⁺ and observed[‡] correlated responses in three agronomic traits to divergent mass selection for heading date in Crosses I and II (1981).

Population	Plant Height (cm)		Plant Maturity (days)		Grain Yield (g)	
	I [‡]	II [‡]	I	II	I	II
EC ₁ F _{3,j}	-14.8*	-4.3	-5.3*	0.8	-3.4	1.2
EC ₁ F _{1,j}	-16.8*	-4.7	-5.4*	-2.4	-3.1	0.6
LC ₁ F _{3,j}	- 9.2*	-4.9*	5.1*	3.9*	-5.2	-0.4
LC ₁ F _{1,j}	-13.3*	0.5	4.5*	0.4	-5.9	-0.1
Predicted	- 1.4	-4.9	-0.1	0.9	-4.9	3.1

*Observed response significantly different from F_{2,j} population mean at P = 0.05.

⁺Predicted & observed responses are expressed as a deviation from the mean of the appropriate F_{2,j} population.

[‡] I = Cross I; II = Cross II.

$LC_1F_{1,1}$ population (Table 12). Both intermated populations exhibited the same plant height and plant maturity relationships with the parental cultivars as occurred in the selfed populations (Appendix Table 4). Predicted correlated responses in the unselected traits were of a smaller magnitude than observed correlated response, and only the $EC_1F_{1,1}$ population suffered a loss of 'genetic variation' in plant height with selection for heading date (Tables 12 and 13).

Cross II

In this cross, plants selected for late heading date, followed by selfing, were on average, shorter than the mean of the base population and later in plant maturity (Table 14). No correlated responses in plant height or plant maturity were detected for selection of early heading date. Selected populations were intermediate in plant height when compared to 'Hyslop' and 'Kavkaz' and did not differ in plant maturity (Appendix Table 4). Selection for heading date in either direction had no effect on the within-plot variances for the two unselected traits (Table 14).

Intermating following divergent mass selection for heading date had no effect on any of the unselected traits (Table 14). The difference in mean plant height of the $F_{2,2}$ and $EC_1F_{1,2}$ populations did approach significance, however ($P = 0.10$).

Contrasts of Selection Methods

Correlated response in plant height with selection for early heading date was greater than occurred with selection for late heading date in Cross I selfed populations (Table 12). No other

Table 14. Population means and within-plot variances for three agronomic traits measured in Cross II on 25 plants/population/block at Hyslop (1981).

Population ⁺		TRAIT		
		Plant Height (cm)	Plant Maturity (days)	Grain Yield (g)
F _{2,2}	\bar{x}	120.4	191.1	19.0
	v	223.5	12.0	132.1
EC ₁ F _{3,2}	\bar{x}	116.1	191.9	20.2
	v	362.6	13.9	144.4
EC ₁ F _{1,2}	\bar{x}	115.7	188.7	19.6
	v	276.0	9.3	100.0
LC ₁ F _{3,2}	\bar{x}	115.6	195.0	18.6
	v	348.0	12.4	117.9
LC ₁ F _{1,2}	\bar{x}	120.9	191.5	18.9
	v	315.2	10.3	129.2
LSD (.05)		4.7	3.3	3.6

⁺ \bar{x} = population mean; v = within plot variance.

differences in correlated response, in the three unselected traits, between mating systems or directions of selection were detected.

In Cross II, selection for late heading date, under inter-mating, was ineffective in changing plant height and plant maturity, although significant correlated responses in these traits occurred in the $LC_1F_{3,2}$ population (Table 14). No other differences between mating systems were detected. Selection for late heading date under selfing was superior to selection for early heading date under the same mating system for correlated response in plant maturity.

Intercrosses

The effects of selection for heading date on plant height and plant maturity in the first cycle intercross populations were not directly measureable because no control population was available (i.e., no F_2). Nevertheless, examination of Appendix Table 4 shows that early selected population more closely resembled Cross II populations in plant height and early-selected Cross I populations in plant maturity. The LI_1F_1 population was similar to Cross I populations in plant height and Cross II populations in plant maturity. The means of the EI_1F_1 population for plant height and plant maturity were significantly taller and earlier, respectively, than the means of the LI_1F_1 population.

Correlated Response at Hyslop - 1982

Analyses of variance showed highly significant differences occurred among both crosses and methods of selection for correlated

response in plant height, population maturity, spikes/plant, biological yield, 100-kernel weight, and harvest index (Appendix Table 5). Highly significant differences among crosses were also obtained for grain yield, and among methods of selection for kernels/spike. Block effects were significant for four of the eight unselected traits and coefficients of variation ranged from a low of 1.0% for population maturity to a high of 15.5% for grain yield.

Partitioning the sums of squares for methods of selection and the cross x methods of selection interaction into single degree of freedom comparisons revealed few consistent trends (Appendix Table 5). Effects of mating system on correlated response in the eight unselected traits were dependent on both the direction of selection and the cross in which they were observed.

Cross I

Concurrent with selection for early heading date, followed by selfing, significant reductions in plant height, population maturity, spikes/plant, and biological yield were observed (Table 15). In addition, significant increases in 100-kernel weight and harvest index with selection for early heading date occurred. Of these traits, only correlated response in population maturity was significantly linear over cycles of selection (Table 16). Selection for late heading date resulted in a significant increase in population maturity for the first cycle of selection. Except for correlated response in population maturity and spikes/plant for $EC_iF_{4,1}$, no further changes in any of the other traits, following a second

Table 15. Population means and within-plot variances for eight traits measured in Cross I on 25 plants/
population/block at Hyslop (1982).

Population		Plant Height (cm)	Population Maturity (days)	Grain Yield (g)	Spikes/ Plant (no.)	Biological Yield (g)	100-Kernel Weight (g)	Kernels/ Spike (no.)	Harvest Index
F _{2,1} [§]	\bar{x}	103.8	189.8	48.2	17.9	121.9	5.34	51.0	0.39
	v	121.67		473.14	59.31	2527.94	0.20	84.23	.0017
EC ₁ F _{4,1}	\bar{x}	94.1	186.6	40.2	14.7	89.6	5.57	49.1	0.45
	v	60.45*		332.89	41.24	1483.77	0.26	60.70	.0038 ⁺
EC ₂ F _{4,1}	\bar{x}	92.2	183.4	46.6	17.1	103.6	5.68	49.8	0.45
	v	45.09*		265.45	28.82*	1124.61*	0.16	230.50 ⁺⁺	.0023
EC ₁ F _{1,1}	\bar{x}	98.5	189.5	47.6	16.8	107.8	5.68	55.5	0.44
	v	81.21		463.56	51.97	2121.34	0.26	547.44 ⁺⁺	.0031
EC ₂ F _{1,1}	\bar{x}	97.3	186.1	44.3	15.6	99.1	5.68	50.8	0.44
	v	72.98		423.43	38.06	1783.11	0.20	163.93	.0030
LC ₁ F _{4,1}	\bar{x}	103.2	197.8	44.8	16.0	111.5	5.36	52.4	0.40
	v	84.5		405.23	35.96	2275.08	0.15	340.28 ⁺⁺	.0025
LC ₂ F _{4,1}	\bar{x}	107.3	197.8	51.0	17.6	128.6	5.48	55.6	0.39
	v	51.4*		581.19	51.38	3473.8	0.18	801.50 ⁺⁺	.0014
LC ₁ F _{1,1}	\bar{x}	103.0	197.5	48.1	16.3	117.0	5.60	52.0	0.41
	v	106.31		417.63	33.63*	2239.87	0.16	68.35	.0013
LC ₂ F _{1,1}	\bar{x}	101.1	198.3	45.5	16.0	114.3	5.60	54.1	0.39
	v	121.39		565.39	57.44	3264.33	0.20	651.42 ⁺⁺	.0018
LSD (.05)		4.2	2.4	8.2	2.9	19.4	0.16	6.8	.02

*within plot variance of selected population significantly smaller than within-plot variance of F_{2,j} at P=0.05.

⁺, ⁺⁺ within-plot variance of selected population significantly greater than within-plot variance of F_{2,j} at P=0.05 and 0.01, respectively.

[§] \bar{x} = population mean; v = within plot variance.

Table 16. Linear regression coefficients of observed population means for eight agronomic traits on cycles of selection for heading date in Cross I (Hyslop Farm, 1982)

Trait	Population			
	$EC_{iF_{4,1}}$	$EC_{iF_{1,1}}$	$LC_{iF_{4,1}}$	$LC_{iF_{1,1}}$
Plant height (cm)	-5.79	-3.24	1.73	-1.34
Population Maturity (days)	-3.18**	-1.81	4.03	4.28
Grain Yield (g)	-0.76	-1.96	1.41	-1.34
Spikes/Plant (no.)	-0.40	-1.15**	-0.15	-0.95
100-Kernel Weight (g)	0.17	0.17	0.07	0.13
Kernels/Spike (no.)	-0.60	-0.10	2.30	1.55
Harvest Index	0.03	0.03	0.00	0.00
Biological Yield (g)	-9.13	-11.41	3.36	-3.81

**significant at the 0.01 level of probability.

cycle of selection for heading date, were observed (Table 17). The number of spikes/plant significantly increased from cycle one to cycle two in $EC_iF_{4,1}$ to the level of the base population.

Predicted changes in unselected traits measured on the selfed populations were in good agreement with observed correlated response in spikes/plant (first cycle only) and biological yield, and one-tenth of that observed in plant height (Table 17), with selection for early heading date. The significant increase in harvest index was not expected. With respect to parental cultivars used to generate Cross I, the $LC_2F_{4,1}$ population exceeded the higher parent in mean expression of population maturity (Appendix Table 6). Correlated responses in plant height, spikes/plant, and biological yield were also accompanied by a significant loss of 'genetic variation' for these traits in the $EC_2F_{4,1}$ population. The $LC_2F_{4,1}$ population showed a significant loss of 'genetic variation' for kernels/spike.

In the early-selected intermated populations, selection for heading date resulted in reduced plant height and population maturity, and increased 100-kernel weight and harvest index (Table 15). Regression of $EC_iF_{1,1}$ population means for spikes/plant on cycles of selection for heading date showed a significant loss of 1.2 spikes/cycle of selection (Table 16), although the selected population means for spikes/plant did not differ from that of the base population (Table 15). Positive correlated responses in population maturity and 100-kernel weight to selection for late heading date were also observed. For each of these traits, except

Table 17. Predicted⁺ and observed⁺ correlated responses (CR) in eight agronomic traits to divergent mass selection for heading date in Crosses I and II (1982).

Trait	Cross	Predicted CR								
			EC ₁ F _{4,j}	EC ₂ F _{4,j}	EC ₁ F _{1,j}	EC ₂ F _{1,j}	LC ₁ F _{4,j}	LC ₂ F _{4,j}	LC ₁ F _{1,j}	LC ₂ F _{1,j}
Plant Height (cm)	I	-0.5	-9.8*	-1.8	-5.3*	-1.2	-0.6	4.0	-0.8	-1.9
	II	-3.1	-23.5*	8.5*	-18.2*	-0.3	-16.1*	-1.8	-9.6*	-4.0
Population Maturity (days)	I	--	-3.1*	-3.3*	-0.3	-3.4*	8.0*	0.1	7.8*	0.8
	II	--	-2.5*	1.1	-1.9	-2.6*	3.9*	0.1	3.1*	0.6
Grain Yield (g)	I	-15.6	-8.0	6.4	-0.6	-3.3	-3.4	6.2	-0.1	-2.6
	II	-19.5	-3.7	3.8	-0.2	1.7	4.4	-6.6	10.1*	-4.4
Spikes/Plant (no.)	I	-4.2	-3.2*	2.4	-1.1	-1.2	-1.9	1.6	-1.6	0.3
	II	-11.5	-6.6*	0.4	-6.3*	-0.3	-1.7	-1.2	-1.8	0.4
100 Kernel Weight (g)	I	0.0	0.23*	0.11	0.34*	0.00	0.02	0.12	0.26*	0.00
	II	-0.3	0.08	0.16	0.14	0.05	0.04	-0.09	0.18*	-0.29
Kernels/Spike (no.)	I	0.0	1.9	0.7	4.5	-4.7	1.4	3.2	1.0	2.1
	II	-8.3	14.1*	1.2	16.0*	3.0	10.4*	-1.8	14.1*	-2.3
Harvest Index	I	0.00	0.06*	0.00	0.05*	0.00	0.01	-0.01	0.02	-0.02
	II	0.04	0.05*	0.00	0.06*	0.01	0.03*	-0.02	0.01	0.02
Biological Yield (g)	I	-28.4	-32.3*	14.0	-14.1	-8.7	-10.4	17.1	-4.9	-2.7*
	II	-57.8	-32.7*	11.1	-27.2*	2.4	-1.7	-13.6	18.4	-20.0

*Observed response significantly different from mean performance of the selections from one cycle to the next.

⁺Predicted responses are expressed as a deviation from the mean of the appropriate F_{2,j} population; observed responses are expressed as a deviation from the mean performance of the selections F_{2,j} from one cycle to the next.

population maturity, all changes occurred in the first cycle of selection. The $EC_1F_{1,1}$ population did not show significant correlated response in population maturity, but the $EC_2F_{1,1}$ did.

Observed changes in each of the unselected traits measured on intermated populations did not agree with predictions (Table 17). Although predicted, changes in spikes/plant and biological yield were not observed. Correlated responses in 100-kernel weight and population maturity matched the mean of 'Kavkaz' for the former trait in both selected populations and exceeded the mean of 'Kavkaz' for the latter trait in the $LC_2F_{1,1}$ population (Appendix Table 6). Of the correlated responses that did occur, none resulted in a significant reduction in 'genetic variation' in both cycle two populations (Table 15).

Cross II

Plant height, population maturity, spikes/plant, and biological yield were all reduced by selection for early heading date under selfing (Table 18). In addition, the $EC_iF_{4,2}$ populations showed significant increases in kernels/spike and harvest index over the base population. Selection for late heading date resulted in a reduction in plant height and increases in population maturity, kernels/spike and harvest index. Of these correlated responses, only changes in the $LC_iF_{4,2}$ populations for spikes/plant was significantly linear over cycles of selection (Table 19). In addition, a significant increase in plant height between cycles one and two was observed for the $EC_iF_{4,2}$

Table 18. Population means and within-plot variances for eight traits measured in Cross II on 25 plants/ population/block at Hyslop (1982).

Population		Plant Height (cm)	Population Maturity (days)	Grain Yield (g)	Spikes/ Plant (no.)	Biological Yield (g)	100-Kernel Weight (g)	Kernels/ Spike (no.)	Harvest Index
F _{2,2} §	\bar{x}	128.2	194.5	47.5	22.8	144.6	4.85	42.1	0.34
	v	162.69		702.41	143.07	5150.13	0.23	164.03	.0105
EC ₁ F _{4,2}	\bar{x}	104.8	192.0	43.9	16.2	112.0	4.93	56.2	0.39
	v	227.48		513.05	62.77	3152.60	0.34	200.52	.0033**
EC ₂ F _{4,2}	\bar{x}	113.2	193.1	47.7	16.6	123.1	5.09	57.4	0.39
	v	272.60		478.83	45.58**	2798.05*	0.21	280.76	.0040*
EC ₁ F _{1,2}	\bar{x}	110.0	192.6	47.4	16.5	117.5	4.99	58.1	0.40
	v	242.90		445.44	52.20**	2432.75*	0.17	148.59	.0028**
EC ₂ F _{1,2}	\bar{x}	109.7	190.1	49.1	16.2	119.6	5.04	61.1	0.41
	v	270.15		579.99	52.82*	3168.90	0.29	194.34	.0021**
LC ₁ F _{4,2}	\bar{x}	112.1	198.4	52.0	21.1	143.0	4.89	52.5	0.37
	v	301.06		563.43	84.95	3897.74	0.24	625.36 [‡]	.0059
LC ₂ F _{4,2}	\bar{x}	110.3	198.4	45.4	19.9	129.3	4.80	50.7	0.35
	v	482.98 [‡]		350.09*	63.00*	2447.28*	0.18	793.79 [‡]	.0032**
LC ₁ F _{1,2}	\bar{x}	118.6	197.6	57.7	21.0	163.0	5.03	56.2	0.35
	v	249.94		852.64	108.61	6696.46	0.37	472.44 [‡]	.0040
LC ₂ F _{1,2}	\bar{x}	114.6	198*2	53.3	21.4	143.0	4.74	53.9	0.37
	v	212.19		620.82	71.41*	4298.06	0.20	238.72	.0016**
LSD (.05)		4.2	2.4	8.2	2.9	19.4	0.16	6.8	0.02

*,** within plot variance of selected population significantly smaller than the within-plot variance of the F_{2,j} at P = 0.05 and 0.01, respectively.

[‡]within-plot variance of selected population significantly greater than the within-plot variance of the F_{2,j} at P = 0.01.

§ \bar{x} = population mean; v = within-plot variance.

populations (Table 17), although mean plant height of $EC_2F_{4,2}$ was still less than the mean of the base population (Table 18).

Observed correlated responses for both directions of selection for heading date under selfing did not agree very closely with predicted correlated response in plant height, spikes/plant, biological yield, and 100-kernel weight (Table 17). There was close agreement between observed and predicted correlated response in harvest index for both directions of selection, disregarding the sign of these changes. Except for population maturity, both cycle two populations were well within the limits of expression of each of the other unselected traits when compared to the original parents (Appendix Table 6). Depending on the direction of selection, correlated responses in spikes/plant, biological yield, grain yield and harvest index also resulted in a loss of 'genetic variation' for these traits in cycle two populations (Table 18).

In conjunction with divergent mass selection for heading date, followed by intermating, negative correlated responses were observed in plant height and biological yield for both directions of selection (Table 17). The $EC_iF_{1,2}$ populations also showed a significant, but non-linear reduction in spikes/plant and a significant, linear decline in population maturity with cycles of selection for heading date (Tables 18 and 19). The $LC_iF_{1,2}$ populations showed a non-linear, but significant, decrease in the mean expression of 100-kernel weight (in cycle two), significant, non-linear increases in population maturity, grain yield, 100-kernel weight (in cycle one), and kernels/spike; and a significant

Table 19. Linear regression coefficients of observed population means for eight agronomic traits on cycles of selection for heading date in Cross II (Hyslop Farm, 1982)

Trait	Population			
	$EC_{iF_{4,2}}$	$EC_{iF_{1,2}}$	$LC_{iF_{4,2}}$	$LC_{iF_{1,2}}$
Plant Height (cm)	-7.50	-9.27	-8.95	-6.81
Population Maturity (days)	-0.72	-2.22*	1.97	1.85
Grain Yield (g)	0.07	0.79	-1.08	2.88
Spikes/Plant (no.)	-3.10	-3.30	-1.45*	-0.70
100-Kernel Weight (g)	0.12	0.10	-0.03	-0.05
Kernels/Spike (no.)	7.65	9.50	4.30	5.90
Harvest Index	0.03	0.04	0.01	0.02*
Biological Yield (g)	-10.78	-12.52	-7.65	-0.82

*significant at 0.05 level of probability.

linear increase in the mean expression of harvest index with cycles of selection for late heading date.

Predicted correlated response in Cross II intermated populations in plant height and 100-kernel weight were of a lower magnitude than observed (Table 17). The $EC_iF_{1,2}$ did not show a significant correlated response in 100-kernel weight, and the $LC_iF_{1,2}$ did not show a significant change in spikes/plant, although significant responses were predicted (Table 17). As in the selfed cycles two populations, the mean population maturity of the $LC_2F_{1,2}$ population was significantly later than either of the original parental cultivars (Appendix Table 6). In addition, mean kernels/spike of the $EC_2F_{1,2}$ population exceeded both 'Hyslop' and 'Kavkaz' in the expression of this trait. Selection for heading date in either direction also resulted in a significant loss of 'genetic variation' for spikes/plant and harvest index (Table 18).

Contrasts of Selection Methods

The relative importance of different mating systems and directions of selection on correlated response to selection for heading date in Crosses I and II is given in Table 20. Early selection with selfing in Cross I was superior to intermating for correlated response in plant height and population maturity. Intermating after selection for early heading date was more important than selfing for correlated response in 100-kernel weight. With selection for late heading date, intermating was superior to selfing for determining correlated response in both population

Table 20. Coefficients of determination and standard partial regression coefficients for the multiple regression of correlated response in eight agronomic traits to selection for heading date on four 'methods' of selection in Crosses I and II (1982).

Trait	Cross	R^2	Standard Partial Regression Coefficients			
			$EC_{iF4,j}$	$EC_{iF1,j}$	$LC_{iF4,j}$	$LC_{iF1,j}$
Plant Height	I	0.92	-0.90**	-0.38	0.33	-0.03
	II	0.42	-0.64	-0.68	-0.60	-0.29
Population Maturity	I	0.94	-0.52*	-0.32	0.43*	0.45*
	II	0.92	-0.29	-0.52	0.46	0.41
Grain Yield	I	0.27	-0.22	-0.10	0.39	0.04
	II	0.51	-0.29	-0.08	-0.17	0.54
Spikes/Plant	I	0.18	-0.19	-0.32	0.13	-0.27
	II	0.78	-0.73	-0.75	-0.12	0.03
100-Kernel Weight	I	0.77	0.75	0.85**	0.11	0.59
	II	0.62	0.42	0.36	-0.30	-0.30
Kernels/Spike	I	0.58	-0.33	0.17	0.56	0.36
	II	0.65	0.68	0.92	0.24	0.50
Harvest Index	I	0.83	0.53	0.53	-0.24	-0.19
	II	0.78	0.58	0.87**	0.02	0.14
Biological Yield	I	0.61	-0.49	-0.39	0.36	0.08
	II	0.61	-0.58	-0.59	-0.21	0.19

*,**corresponding partial regression coefficient significant at 0.05 and 0.01 levels of probability, respectively

maturity and 100-kernel weight, although the partial regression coefficients for 100-kernel weight were not significant. Selection for early heading date, under both systems of mating, was more important than selection for late heading date in determining the magnitude of correlated response in plant height and 100-kernel weight. For correlated response in population maturity, superiority of direction of selection depended on the mating system.

In Cross II, intermating with early selection for heading date was more important than selfing in determining correlated response in population maturity and harvest index (Table 20). Early selection in either mating system was superior to late selection for heading date in affecting change in harvest index. As in Cross I, the relative importance of direction of selection for heading date on changes in population maturity was dependent on the mating system in effect.

Intercrosses

The effects of divergent mass selection for heading date on eight other traits in the intercross populations is given in Appendix Table 6. Significant correlated response in these traits between cycles of selection for heading date was detected in the LI_1F_1 populations for 100-kernel weight and population maturity.

The EI_2F_1 population was most similar to Cross I populations in the expressions of population maturity, spikes/plant, biological yield, 100-kernel weight, kernels/spike,

and harvest index. Mean expressions of spikes/plant, biological yield, 100-kernel weight, and kernels/spike in the LI_2F_1 population were comparable to Cross II populations. Grain yields in both cycle two intercross populations were intermediate in expression between populations of Crosses I and II. None of the intercross populations expressed any of the eight unselected traits to a greater or lesser extent than the populations derived from the two single crosses.

Correlated Response at Pendleton - 1982

Analyses of variance for the seven traits measured on populations grown at the Pendleton site showed significant differences between crosses for all but three of these traits (Appendix Table 7). All but two of these unselected traits exhibited a significant effect for correlated response, and all but one trait were affected by direction of selection for heading date over both crosses. However, a partition of the sums of squares for crosses and the cross x methods interaction revealed significant interactions between crosses, mating systems and directions of selection for most of the unselected traits.

Block effects were significant for all but two of the traits measured at Pendleton (Appendix Table 7). Coefficients of variation ranged from a low of 2.9% for 100 kernel weight to a high of 14.3% for biological yield, and were, on the whole, smaller than occurred at Hyslop (Appendix Table 5).

Cross I

Significant correlated response in several traits to divergent mass selection for heading date followed by selfing, were observed (Table 21). Selection for early heading date resulted in decreased mean expressions for plant height, grain yield, spikes/plant, and biological yield. Selection for late heading date was followed by positive correlated responses in grain yield and kernels/spike. Neither selected population exceeded the limits of expression for any trait set by 'Roussalka' and 'Kavkaz' (Appendix Table 8). However, selection in either direction for heading date resulted in a loss of 'genetic variability' for harvest index as noted by a reduction in within-plot variance (Table 21).

Response to selection for early heading date in the intermated population also effected decreases in plant height and biological yield, and increases in 100-kernel weight and harvest index (Table 21). The only correlated response observed in the $LC_2F_{1,1}$ population was an increase in kernels/spike. With respect to the parental cultivars used to generate Cross I, means of both cycle two populations exceeded both parents for grain yield (Appendix Table 7). In addition, means for harvest index in $EC_2F_{1,1}$ and spike/plant and biological yield in $LC_2F_{1,1}$ exceeded the mean values for these traits in 'Roussalka' and 'Kavkaz'. Significant losses in 'genetic variation' for 100-kernel weight in $EC_2F_{1,1}$ and for harvest index in $LC_2F_{1,1}$, with selection for heading date were also detected (Table 21).

Table 21. Population means and within-plot variances for seven traits measured in Cross I on 25 plants/population/block at Pendleton (1982).

Population		Plant Height (cm)	Grain Yield (g)	Spikes/Plant (no.)	Biological Yield (g)	100-Kernel Weight (g)	Kernels/Spike (no.)	Harvest Index
F _{2,1}	\bar{x}^+	82.7	30.5	13.4	71.2	4.71	48.0	0.43
	v	74.45	180.81	23.74	778.38	0.20	96.70	.0044
EC ₂ F _{4,1}	\bar{x}	70.5	27.1	11.7	57.9	4.75	48.3	0.47
	v	40.51	156.61	22.68	724.74	0.19	74.55	.0014**
EC ₂ F _{1,1}	\bar{x}	76.2	28.9	11.9	60.8	4.92	48.3	0.48
	v	50.90	172.35	19.65	755.45	0.10*	107.12	.0035
LC ₂ F _{4,1}	\bar{x}	85.8	33.9	13.3	77.9	4.74	52.8	0.43
	v	49.47	298.02	32.90	1496.41	0.18	81.58	.0013**
LC ₂ F _{1,1}	\bar{x}	84.0	32.8	12.8	76.9	4.83	52.8	0.43
	v	100.16	191.64	23.61	1058.98	0.14	71.42	.0012**
LSD (.05)		4.9	3.1	1.6	9.0	0.14	3.7	.04

*,** within-plot variance of selected population significantly smaller than within-plot variance of F_{2,1} at P = 0.05 and 0.01, respectively.

⁺ \bar{x} = population mean; v = within-plot variance.

Cross II

The selfed population selected for early heading date was, on the average, shorter, had lower grain yield, fewer spikes/plant, and lower biological yield than the mean of the base population (Table 22). In addition, positive correlated responses in 100-kernel weight and kernels/spike were observed in this population. The $LC_2F_{4,2}$ population exhibited a decrease in plant height and 100-kernel weight and an increase in kernels/spike. Mean expression for kernels/spike of the $EC_2F_{4,2}$ population was significantly greater than its expression in both 'Hyslop' and 'Kavkaz' (Appendix Table 7). No significant loss of 'genetic variation' for any of the unselected traits were observed in either selected population (Table 22).

Significant changes in all but mean expression for 100-kernel weight were recorded in the $EC_2F_{1,2}$ population (Table 22). Correlated response in kernels/spike and harvest index was positive, while changes in the other unselected traits were negative. Correlated response in the $LC_2F_{1,2}$ population was identical for each trait measured as occurred in the $LC_2F_{4,2}$ population. With respect to the parental cultivars, the $EC_2F_{1,2}$ exhibited significantly greater kernels/spike than either parent (Appendix Table 7). Within-plot variance for each of the unselected traits in both intermated populations did not change as a result of selection for heading date (Table 22).

Contrasts of Selections Methods

In Cross I, selection for early heading date under intermating resulted in a greater correlated response in 100-kernel weight than

Table 22. Population means and within-plot variances for seven agronomic traits measured in Cross II on 25 plants/population/block at Pendleton (1982).

Population		Plant Height (cm)	Grain Yield (g)	Spikes/Plant (no.)	100-Kernel Weight (g)	Kernels/Spike (no.)	Harvest Index	Biological Yield (g)
F _{2,1}	\bar{x}^+	98.4	29.3	15.7	4.30	42.7	0.37	77.8
	v	70.0	188.6	32.5	0.23	85.3	0.0033	1116.1
EC ₂ F _{4,2}	\bar{x}	90.9	25.3	10.3	4.45	54.3	0.41	59.9
	v	211.3**	173.9	21.6	0.17	236.5**	0.0033	892.7
EC ₂ F _{1,2}	\bar{x}	90.9	26.1	10.9	4.37	54.0	0.42	61.1
	v	117.7	164.0	22.8	0.20	142.9	0.0024	795.5
LC ₂ F _{4,2}	\bar{x}	84.8	27.9	14.1	4.14	46.7	0.37	75.3
	v	260.2**	172.8	28.3	0.26	76.9	0.0021	1076.0
LC ₂ F _{1,2}	\bar{x}	89.2	31.7	14.7	4.07	51.5	0.40	79.7
	v	92.5	237.3	38.3	0.18	82.2	0.0032	1530.4
LSD (.05)		4.9	3.1	1.6	0.14	3.7	0.04	9.0

**within-plot variance of selected population significantly greater than within-plot variance of F_{2,2} at P = 0.01.

⁺ \bar{x} = population mean; v = within-plot variance.

selfing; however, early selection with selfing resulted in shorter plant stature than with intermating (Table 21). No significant differences between mating systems for correlated response in any of the seven unselected traits when selection was for late heading date were observed. Selection for late heading date under both systems of mating resulted in significantly greater mean expressions for plant height, grain yield, biological yield and kernels/spike than selection for early heading date. In addition, selection for early heading date with intermating effected a higher mean expression for harvest index than selection for late heading date under the same mating system.

The $LC_2F_{1,2}$ population had a greater mean yield and a higher number of kernels/spike than the $LC_2F_{4,2}$ population (Table 22). Differences in other traits for the two mating systems were not significant. Differences between directions of selection and mating systems, in terms of correlated response, were more variable than what was observed in Cross I. Under selfing, selection for late heading date resulted in higher mean values for spikes/plant and biological yield; early selection for heading date under the same mating system resulted in greater population expression of plant height, 100-kernel weight and kernels/spike. With intermating, selection for late heading date effected a smaller change in grain yield, spikes/plant, and biological yield when compared to selection for early heading date. However, selection for early heading date also increased values for 100-kernel weight and harvest index; these correlated responses

were not noted with selection for late heading date followed by intermating.

Combined Correlated Response at Hyslop and Pendleton - 1982

Combined analyses of variance of selected and unselected populations grown at Hyslop and Pendleton in 1982, for seven traits, is given in Appendix Table 9. Significant population x location interactions were detected for plant height, biological yield and 100-kernel weight. Significant cross x location interactions were observed for plant height, spikes/plant, biological yield, and 100-kernel weight. Individual effects of selection methods showed significant interactions with locations for plant height and 100-kernel weight, with the interaction involving plant height dependent on the cross. Mating systems behaved identically across locations and, except for plant height, locations had no effect on direction of selection.

The significant cross x location effect in the combined analysis for plant height (Appendix Table 9) was a result of a change in relationship between early- and late-selected populations between the two locations. At Hyslop, population means for plant height were approximately of the same magnitude (Table 18); at Pendleton, however, late-selected populations, especially the $LC_2F_{4,2}$, were shorter than early-selected populations (Table 22).

DISCUSSION

Recurrent selection has proven to be a very effective method for the genetic improvement of cross-pollinated crops, especially corn. However, there are several problems associated with recurrent selection which have apparently restricted its adoption by breeders of self-pollinated crops. Chief among these problems is the time and expense involved in making large numbers of crosses with each cycle of selection. Another major constraint is a lack of empirical evidence that recurrent selection is superior to conventional inbreeding methods, in terms of both short- and long-term crop improvement.

The major advantage of recurrent selection over conventional inbreeding methods is a step-wise accumulation of favorable alleles while maintaining genetic variation for unselected traits (Allard, 1960). This is accomplished by frequent intermating of selected families or individuals. Therefore, differences in the relative effectiveness of the two breeding methods should manifest themselves in the mating system employed. This investigation was designed to differentiate recurrent selection from conventional inbreeding and to determine if two cycles of selection for heading date would show any consistent superiority of either mating system in response to selection or in correlated response in several other traits.

Results of this investigation will be discussed in terms of:

- 1) the kinds and amount of genetic variability in heading date and eight other agronomic traits available for crop improvement; 2) the evaluation of response to selection for heading date under two

systems of mating; and 3) the effect of selection for heading date on other important agronomic traits under the same two systems of mating.

Genetic Evaluation

Selection in variable plant populations cannot be effective unless that variation has a genetic component. Since the criterion of selection in this study was heading date on an individual plant basis, response to selection was dependent on a moderate to high narrow-sense heritability. The magnitude of heritability of a trait is dependent on the number of genes involved, the type of gene action, and the size of the genotype-environment interaction (Falconer, 1960). An analysis of types of gene effects affecting the expression of heading date, and eight other traits, was therefore undertaken in two winter wheat crosses.

To determine the types of gene effects influencing nine agronomic traits, seven generations of both Cross I and Cross II were grown at Hyslop in each of two years (1981 and 1982). Estimates of narrow-sense heritability were also obtained for each trait from the pooled variances of $F_{2,j}$ and $BC_{i,j}$ populations. Finally, estimates of heritability, genetic correlations, and correlations between heading date and eight unselected traits in the $F_{1,j}$ and $F_{2,j}$ populations were used to predict response and correlated response to selection for heading date.

Cross I

Cross I was derived from the homozygous parents 'Roussalka' and 'Kavkaz'. These parents expressed contrasting heading dates, plant

height, plant and population maturity, grain yield, biological yield, harvest index, and 100 kernel weight. 'Roussalka' had the lower mean expression for each of these traits, except harvest index. The two parents had identical spikes/plant and joint scaling tests suggested that they shared the same genes for this trait.

The results of joint scaling tests on Cross I generations for heading date indicated that generation means were skewed toward the earlier 'Roussalka' by the action of linked or epistatic genes in 1981 and by (aa) effects in 1982. In addition to the information on the nature of gene action for heading date, high estimates of narrow-sense heritability for this trait were obtained in both years, indicating selection should be effective. However, the 1981 joint scaling tests indicated a larger epistatic effect, in the direction of earliness in both heading date and plant maturity, than occurred in 1982. If the non-additive epistasis observed in 1981, were to remain constant over cycles of selection, then selection for late heading date might eventually become more effective than selection for early heading date as gene frequencies in populations selected in either direction became differentiated. This result would also depend on the amount of inbreeding that occurred, since inbreeding would be expected to 'fix' only additive types of gene action.

Much of the literature on the inheritance of heading date in wheat suggests that epistasis is not a common type of gene action for this trait (Amaya et al., 1972; Bhatt, 1972; Edwards et al., 1976). However, Ketata et al. (1976) found significant additive x additive epistasis for heading date in a 'Centurk' x 'Bezostaia 1'

cross grown in 1973. Edwards et al. (1976) reported no epistasis in this cross when it was grown in 1974 at the same location. Results of these studies suggest an environmental influence on the expression of epistasis in winter wheat. The nature of this environmental influence was not discussed in either of the preceeding papers.

The inheritance of the unselected traits was also studied. The pattern of inheritance of plant height in 1981 showed only additive effects of genes. This result agrees with the high estimate obtained for narrow-sense heritability of plant height in 1981. The following year, significant additive x additive interaction favoring taller plant height, as well as positive non-additive effects were detected. However, the estimate of heritability in 1982, was low and non-significant. These results, combined with no observed correlations of heading date with plant height, indicated that selection for heading date would not affect the expression of plant height.

Joint scaling tests on Cross I generation means for maturity, as measured by plant maturity in 1981 and population maturity in 1982, indicated that these traits were under somewhat different genetic control. In 1981, non-additive epistatic effects skewed generation means towards the later maturing 'Kavkaz'. In 1982, means were earlier than predicted on a three-parameter model due to significant (aa) epistasis. The estimate of narrow-sense heritability for plant maturity and the three correlation coefficients estimated between heading date and plant maturity in 1981 were not significant and

indicated that correlated response in plant maturity with selection for heading date would not occur.

Variation in grain yield among Cross I generation means was equally determined by additive and dominance effects in 1981. Dominance alleles were contributed by the higher-yielding parent - 'Kavkaz'. In 1982, however, differences between generation means in the expression of grain yield were fully accounted for by additive effects of genes.

The relationship between the classic components of yield to the inheritance of yield per se in Cross I can be characterized as follows: 'Kavkaz' contributed dominance factors for greater 100-kernel weight and additive x additive epistatic effects for greater kernels/spike, and neither parent donated contrasting alleles for spikes/plant. Grain yield and most of the components of grain yield had low, non-significant estimates of narrow-sense heritability in both years and for the appropriate traits (i.e., components of yield were not measured in 1981). Despite the apparent lack of genetic variability for spikes/plant, a moderate, but significant, estimate of heritability was obtained for this trait. In addition, the estimate of genetic correlation between heading date and spikes/plant was significant and suggested a negative correlated response in spikes/plant would occur with selection for heading date.

The inheritance of harvest index, as determined by joint scaling tests, indicated that variation among Cross I generation means could be explained by additive, dominance and epistatic effects of genes. However, variation among generation means for the

components of harvest index, namely grain yield and biological yield, was completely explained by additive gene effects in 1982. Negative dominance and the (aa) interaction parameter apparently cancelled out the effect of the positive (dd) epistatic term, making Cross I generation means for harvest index behave as if influenced by additive effects only. This conclusion is supported by the results of the three-parameter model, which showed only additive effects of genes controlling variation among Cross I generation means for this trait.

The narrow-sense heritability estimate for harvest index was zero, presumably because of the large effects of non-additive gene action detected by the six-parameter joint scaling test. No correlated response to selection for heading date was expected. A significant negative phenotypic correlation between heading date and harvest index, accompanied by non-significant genetic and environmental correlations, leads to the conclusion that any change in harvest index would be more a function of environmental influences than genetic. However, since harvest index is the ratio of grain yield to biological yield, changes in harvest index with selection for heading date may occur as a result of changes in either of its components, both of which exhibited significant, negative associations with heading date in 1982.

Cross II

'Hyslop' and 'Kavkaz' were hybridized to derive the seven generations used to evaluate the inheritance of the nine agronomic traits. The two parents had contrasting expressions of plant height, 100-kernel weight, and harvest index. It is interesting to

note that means for heading date, plant maturity, and grain yield differed between years to the extent that, in 1981, 'Hyslop' was lower-yielding than 'Kavkaz' and had identical heading date and plant maturity but in 1982 'Hyslop' had identical grain yield and was later in both heading date and population maturity than 'Kavkaz'. These results imply a genotype x environmental interaction for these traits. In addition, no significant differences between the two parents were obtained for spikes/plant, biological yield or kernels/spike in 1982.

Gene action for heading date was completely different in the two years, as shown by the results of joint scaling tests and estimates of narrow-sense heritability for this trait. In 1981, the mean value for heading date of the $F_{1,2}$ showed significant heterobeltiosis in the direction of earliness. Both dominance and non-additive types of epistasis contributed to the heterobeltiosis, with additive effects showing minimal contribution to variation among generations. The estimate of narrow-sense heritability for heading date was significant and high and was apparently biased upwards by epistasis. Since the signs of the interaction parameters influence the magnitude of the F_2 variance (Mather and Jinks, 1971), the observed positive effects of the (ad) type of epistasis were expected to increase variance in the $F_{2,2}$ and subsequent selfed generations. When the signs of (d) and (dd) are opposite, as in this cross, F_2 variance is expected to decrease. Therefore, it seems that the relatively higher (ad) effect had a greater effect on increasing $F_{2,2}$ variation for heading date than the negative (dd)

effect had in decreasing variation, resulting in an overestimate of narrow-sense heritability.

In 1982, the inheritance of heading date in Cross II was too complex to be explained by the three- or six-parameter models. Also, a low, non-significant estimate of narrow-sense heritability was obtained, indicating selection for heading date would be ineffective. Apparently, environmental factors (i.e., temperature) between the two crop years were such that genes that did not express themselves for heading date in 1981, did so in 1982, or vice versa. This conclusion is also supported by the significant difference in heading dates between 'Hyslop' and 'Kavkaz' in 1982.

Joint scaling tests on Cross II generations for maturity, as measured by plant maturity in 1981, and population maturity in 1982, revealed large effects of dominance and epistasis in both years. In 1981, 'Kavkaz' contributed dominance and epistatic effects towards earlier plant maturity, and in the following year, towards earlier population maturity.

The heritability estimate of plant maturity in 1981, was moderate but non-significant. In addition, a non-significant genetic correlation between heading date and plant maturity indicated that selection for heading date would have no pleiotropic effects on plant maturity. However, as suggested by a significant and positive environmental association with heading date, selection for heading date was expected to result in a change in plant maturity due to environmental influences. In other words, populations selected for early heading date would be exposed to

temperatures and photoperiod effects also favorable to early plant maturity.

Environmental factors between the two crop years apparently had a major influence on the inheritance of plant height in Cross II. In 1981, primarily non-additive epistatic effects were contributed by 'Hyslop' in the direction of shorter plant height, while positive dominance effects were contributed by 'Kavkaz'. The following year, although the three-parameter model indicated significant additive effects, neither genetic model was sufficient to explain the nature of gene action. Heritability estimates for both years were low and non-significant. Further, the association of heading date with plant height over years suggested that any changes in this trait with selection for heading date would be a result of environmental factors, such as a shortened period of vegetative growth.

Variation among generations in Cross II for grain yield was largely the result of positive effects of epistasis from 'Kavkaz' and negative effects of epistasis from 'Hyslop' in 1981. The three-parameter model indicated that additive effects were more important than dominance effects in determining grain yield. Even so, a moderate, but non-significant estimate of heritability was obtained in 1981. In 1982, however, variation among generation means for grain yield was fully explained by positive genic interactions, with no additive effects apparent. The moderate, but significant heritability estimate in 1982, was probably biased upward by additive x additive epistatic effects. Estimates of genetic correlation between heading date and grain yield were non-significant in 1981, and significant in 1982. If correlated

response in grain yield to selection for heading date were to occur, the above results indicate that the change would be small, due to the magnitude of non-additive epistatic effects in both years.

As already mentioned, differences between 'Hyslop' and 'Kavkaz' for grain yield, spikes/plant, and kernels/spike were not detected in 1982. In spite of these results, 'Kavkaz' exhibited significantly greater mean 100-kernel weight, suggesting that some unmeasured yield component enabled 'Hyslop' to attain the same grain yield as 'Kavkaz'. Joint scaling tests indicated that both parents had identical genes for spikes/plant; however, these tests were unsuccessful in determining the effects of genes on variation among generation means for 100 kernel weight and kernels/spike.

Moderate to high estimates of heritability were obtained for spikes/plant, 100 kernel weight, and kernels/spike in 1982. Since variation among generation means for spikes/plant and kernels/spike can be explained by the midparent values, estimates of heritability for these traits were probably biased by sampling errors and/or differential responses of the $F_{2,2}$ vs. the backcrosses to the environment (Warner, 1952). Although both three- and six-parameter models did not fit generation means for 100-kernel weight, the three-parameter model indicated that additive effects may be important in the expression of this trait. In addition, trigenic or higher order interactions may have contributed to the size of the heritability estimates.

Large negative estimates of genetic correlation between heading date and the two yield components, spikes/plant and 100-kernel weight, suggested correlated response in these traits with selection

for heading date could be expected. How much the genetic correlations were influenced by the biased estimates of heritability, can only be determined by selection experiments.

Joint scaling tests on harvest index were effective in showing that variation among generations of Cross II was due to additive effects of genes. Since biological yield was explained by the value of the midparent, the significant difference between 'Hyslop' and 'Kavkaz' in harvest index is difficult to assess. It seems probable that, due to the shorter stature of 'Hyslop' and the approximately 20 g difference in biological yield between 'Hyslop' and 'Kavkaz', experimental error was too large to detect a true difference between parents for biological yield.

The greater "efficiency" expressed by 'Hyslop' in producing grain yield, as determined by harvest index, may explain its ability to yield as well as 'Kavkaz' despite its lower 100-kernel weight. A significant, positive genetic correlation between heading date and harvest index suggested that selection for heading date in Cross II populations would result in a correlated response in harvest index.

The combination of estimates of gene effects, narrow-sense heritability estimates, and various correlation coefficients appear to be effective tools for plant breeders in understanding and predicting the consequences of selection. In this investigation, two single crosses were studied: Cross I showed a greater magnitude of additive genetic variability for most of the traits than Cross II. This was expected from the contrasting expressions for most of the traits in 'Roussalka' and 'Kavkaz'. In Cross II, parental cultivars were quite similar in expression of most of the traits

studied and genetic variability within generations derived from this cross was largely non-additive and epistatic in nature.

Selection for heading date was expected to be more effective in Cross I than in Cross II. In the latter cross, gain from selection for heading date was predicted to be a result of unique combinations of primarily interacting genes or, alternatively as a result of a breakup of linkages between heading date genes.

Correlated responses to selection for heading date were largely predicted to be small and mainly due to environmental effects. In Cross I, 100-kernel weight and harvest index showed moderate, negative environmental associations with heading date. Plant height, kernels/spike, and population maturity were not expected to change as a result of selection for heading date. However, significant pleiotropic effects of heading date genes on the expressions of grain yield, spikes/plant, and biological yield were detected.

Correlated responses in Cross II populations, with selection for heading date, were expected to occur in harvest index as a result of pleiotropy and in grain yield, spikes/plant, kernels/spike, and biological yield as a result of environmental influences (e.g., photoperiod, temperature, moisture stress).

Response to Selection for Heading Date

Results from two cycles of divergent mass selection for heading date, obtained for two years on populations from cycle one and for two locations on populations from cycle two, indicated that selection in either direction was highly effective under both systems of mating. In Cross I, the early-selected cycle two

populations were as early as 'Roussalka' at Hyslop, and indications at Pendleton suggested that at least some of the individuals in these populations were earlier than 'Roussalka', especially in the intermated population. Both late-selected cycle two populations in Cross I were later-heading than 'Kavkaz'. In Cross II, cycle two populations exceeded their respective earlier and later parents for the appropriate directions of selection.

Since the effects of mating system on response to selection for heading date were not consistent between crosses, cycles of selection, or directions of selection, results of this study will be discussed separately for each of these variables.

In Cross I, selfed populations showed a slight, but non-significant, superiority over intermated populations in response to selection for both years. Since the only difference between the populations selected in each direction was the mating system in effect, two conclusions seem justified. First, sampling variation probably accounted for the small discrepancies between mating systems for response to selection; second, selection followed by intermating did not result in an obvious "accumulation" of heading date alleles in selected populations.

The foregoing results were not entirely unexpected. In Cross I, the major portion of genetic variation for heading date appeared to be additive, even though joint scaling tests of both genetic models failed to explain all the variation among generation means in 1981. Further, the estimates of narrow-sense heritability for heading date for both years were high, and observed response to selection was as great as or greater than predicted. Each of these

results suggests that heading date in Cross I was controlled by a few major genes. Therefore, two cycles of selection for this trait were expected to be equally effective under both systems of mating.

Two results indicated that additional cycles of selection for heading date in Cross I would show an advantage for intermating. First, although heading date appeared to be controlled by a few major genes, the environmentally-influenced epistatic effect on heading date suggested that minor genes may be accumulated by intermating. These minor genes would only be expressed under favorable photoperiod or temperature conditions. This conclusion is indirectly supported by the range of heading dates taken on cycle two populations at Pendleton. The $EC_2F_{1,1}$ population appeared to be more highly skewed toward earlier heading date than both 'Roussalka' and the $EC_2F_{4,1}$ population. The second result which suggests that minor genes control heading date in Cross I is that both late-selected cycle two populations were significantly later than 'Kavkaz'. Intermating after selection would be expected to 'accumulate' these genes, whereas selfed cycle two populations are essentially composed of homozygous plants with no further improvement expected.

Most of the variation among Cross II generation means for heading date, as detected by joint scaling tests in 1981, was due to dominance and non-additive epistasis. Therefore, the significant response to divergent mass selection for heading date suggests that the first cycle of selection probably acted on a few major genes. Also, gain from selection in the second cycle was due to either a breakup of linked genes or an accumulation of genes with smaller

effects. Some indication of these conclusions was shown by the greater response to selection for early heading date under inter-mating, vs. selfing, in both years and the increase in response to late-selection in the cycle two intermated population noted in 1982. Except for $EC_1F_{4,2}$ vs. $EC_1F_{1,2}$ in 1982, all differences were significant.

Effects of mating system on response to selection for heading date were also inconsistent between cycles of selection in both crosses. Response to selection was non-linear in both selfed Cross I populations and in each of the Cross II populations, except the $EC_1F_{4,2}$. Possible causes of the non-linear response observed in these populations include environmental change between observations on each cycle of selection; sampling variation; and a reduction in additive genetic variation with selection (Falconer, 1960).

The influence of environment on differences between population means for each selection cycle is expected to be small, since all populations were grown in the same year for each determination of response to selection. However, since effects of genes for heading date were different in the two years studied, it seems reasonable to assume that selection for heading date in each cycle acted on different gene combinations.

Sampling variation may have had a significant influence on measures of response to selection in each cycle. No records were kept on the pedigrees of individual plants, making it impossible to determine the number of progeny representing each selected individual in cycle one or cycle two populations. The most probable effect of differential viability on progeny of selected individuals

would be a bias in selection intensity in favor of those individuals leaving the most surviving offspring (Falconer, 1960).

The influence of a reduction in additive genetic variance with selection for heading date over two cycles was not directly measured. However, a comparison of within-plot variances between selected populations and their appropriate $F_{2,j}$ showed significant losses occurred only in the late-selected cycle two populations in Cross I. Although significant changes in within-plot variances of Cross II populations were not observed, the $F_{2,2}$ did exhibit a reduction in this variance ($P = 0.05$) between 1981 and 1982 possibly due to the expression of linked or epistatic genes in 1982. It seems unlikely that selection, which was effective in these populations, would have left the same array of linked and/or interacting genes as occurred in the $F_{2,2}$. Therefore, it must be assumed that in 1982 the within-plot variances of Cross II selected populations were reduced by selection, albeit to the level of the $F_{2,2}$.

The direction of selection for heading date also had an influence on response to selection in both Crosses and under both systems of mating. In 1981, selection for early heading date in Cross I was more effective than selection for late heading date. In the following year, response to selection in either direction was close to symmetrical. Mating system did not appear to have an influence on the asymmetry in response observed in either year.

Falconer (1960) lists the following causes of asymmetry in response to selection: 1) differences in selection differential; 2) genetic asymmetry; 3) selection for heterozygotes; 4) inbreeding

depression and 5) maternal effects. The bias in favor of selection for early heading date in 1981, probably cannot be ascribed to any of the preceding causes, as these usually require several cycles of selection to identify. With a single cycle of selection, it seems improbable that changes in gene frequency for heading date would have been large. The non-additive epistasis observed in Cross I generations may have affected the expression of heading date in early-selected cycle one populations by skewing the population mean toward earliness. In 1982, a smaller magnitude of epistasis was detected, with most 'explained' variation among generation means determined by additive effects of genes. This result agrees with the small asymmetry in selection response noted in 1982. The switch from positive (ad) epistasis in 1981 to negative (aa) epistasis in 1982, may have been due to somewhat cooler spring temperatures than occurred the previous year (Appendix Table 1). The possibility exists that temperatures favorable for the expression of interacting earliness genes in 1982 were not high enough to activate these genes. Pirasteh and Welsh (1980) observed a significant increase in earliness among both spring and winter wheat cultivars with an increase in temperature.

Selection for late heading date in Cross II was more effective than selection for early heading date in 1981; however, differences in response in each direction were not of the magnitude of Cross I populations. Unlike Cross I, the asymmetry observed in 1981 may have been a manifestation of Falconer's "genetic asymmetry" (1960). Since no significant additive effects were detected for heading date in 1981, it seems reasonable to assume that selection acted on one

or two major genes in the first cycle. Due to the presence of dominance gene effects in the direction of earliness, distinguishing homozygotes and heterozygotes for early heading date would have been difficult. However, the ability to select homozygous recessive late heading plants would have been easier. Cycle one populations selected for early heading date would be expected to segregate for both early and late-heading date alleles, resulting in a later population mean than predicted and more genetic variability than in populations selected for late heading date. These expectations were observed, with both late-selected populations showing a significant loss of 'genetic variability' and a greater mean response to selection.

In 1982, the greater response noted for selection for early heading date in Cross II seems to have been a result of gene effects skewing the mean of the base population toward late heading date as compared to the midparent. Since a joint scaling test of the six-parameter model did not explain variation among generation means in 1982, it was not possible to reach any conclusions regarding this observation.

Results from recurrent selection within intercross populations showed significant gains from selection in both directions between cycles one and two. When both years are considered, neither intercross population exceeded the earliest selected populations in Cross I, or the latest selected populations in Cross II. Two conclusions are possible: 1) Cross I contained all possible alleles for early heading date when compared to Cross II while Cross II contained all possible alleles for late heading date when compared

to Cross I; or 2) sample sizes used to initiate recurrent selection in the intercross populations were too small to adequately sample the heading date genes available in both crosses. The latter explanation appears to be the more likely, since cycle one intercross populations were initiated from intercrosses between a single plant in Cross I and a single plant in Cross II for each direction of selection.

The theoretical advantage of recurrent selection (i.e. higher ceiling of performance via step-wise changes in gene frequency) was not observed in this investigation in a dramatic way. Heading date in both crosses appeared to be controlled by a few major genes which were efficiently identified in selection under both systems of mating. However, some of the results did indicate an eventual advantage for intermating. First, when compared to the base populations ($F_{2,j}$), individuals within the selected-selfed populations have an inbreeding coefficient of 0.75, discounting the effects of selection. Although the coefficient of inbreeding in intermated cycle two populations cannot be calculated because individual pedigrees are not known, it seems reasonable to assume that it is lower than in the selfed population.

Another result which indicates an eventual advantage for intermating was the presence of linked and/or minor genes detected in both single crosses for heading date. Additional cycles of selection followed by intermating would be expected to breakup the linkage blocks, if present, or accumulate favorable minor genes affecting heading date.

Finally, in Cross II only, selection for early heading date followed by intermating showed an advantage for this mating system over selfing. This result was ascribed to an accumulation of heading date genes with small effects over cycles of selection. Since the frequency of heterozygotes in cycle one populations was relatively high, a second cycle of selection followed by selfing may have resulted in random fixation of both early and late-heading alleles. However, intermating was apparently successful in accumulating favorable alleles for early heading date. Since 'genetic variability' for heading date as determined by a comparison of within-plot variances of selected populations with the $F_{2,2}$, still exists in cycle two populations, intermating should continue to show an advantage over selfing with selection for early heading date.

Correlated Response to Selection for Heading Date

Indirect effects of selection for heading date on several other important agronomic traits were studied on cycle one populations in each of two years and on cycle two populations at two locations. Correlated response to selection for heading date was expected to arise due to one or more of the following relationships: 1) chance fixation of unselected traits with selection for heading date, 2) a significant genetic and/or environmental correlation between heading date and the unselected trait; and 3) linkage between heading date genes and genes affecting the unselected trait (Falconer, 1960).

Although significant estimates of genetic and/or environmental correlations of heading date with each of the unselected traits were not obtained, correlated responses to selection for heading date

were observed in each of the unselected traits. As with response to selection for heading date, however, the effects of mating system on correlated responses were not consistent between crosses, cycles of selection or directions of selection.

Cross I

Of the unselected traits measured in Cross I, correlated responses in plant height, plant maturity, 100-kernel weight, kernels/spike and harvest index were not expected, due to non-significant estimates of genetic correlation with heading date. However indirect effects of selection for heading date on 100-kernel weight and harvest index were expected to occur due to environmental associations with heading date.

Observed changes in plant height, which were all in the direction of shorter plant stature for both directions of selection, may have been the result of chance selection of plants with shorter stature than the base population during selection for heading date. Indirect evidence for this hypothesis comes from the comparison of the effect of mating system on each of the observed correlated responses in plant height. The selfed populations showed a significantly greater correlated response in plant height with early selection than did the intermated populations at Hyslop in 1982. These results were not detected in 1981, but the $EC_2F_{4,1}$ population at Pendleton, was significantly shorter than the $EC_2F_{1,1}$ population. Intermating, following selection for heading date in either direction was apparently successful, however, in retaining genetic variability for plant height; not only did the mean plant heights of both cycle two intermated populations more

closely resemble the $F_{2,1}$, but the intermated populations did not lose 'genetic variability' for plant height, as did the selfed populations.

The case for indirect effects of selection for heading date on plant and population maturity is less clear. Of all the traits measured, plant or population maturity was the only trait which consistently showed a response in each cycle of selection and in the same direction as selection for heading date. However, none of the various correlation coefficients between heading date and plant maturity in 1981, were significant, suggesting correlated response in this trait would result from random fixation of maturity genes with selection for heading date, if it occurred at all. One possible explanation for the failure to detect an environmental correlation between these two traits is that the environmental differences affecting the $F_{1,1}$ generation, which was used to obtain estimates of environmental correlation, did not influence either plant maturity or heading date. The two most important environmental factors affecting the expression of either trait are temperature and photoperiod (Pirasteh and Welsh, 1980), and these two factors were not variable within the $F_{1,1}$ generation.

Correlated response in kernels/spike was not observed in selected populations at the Hyslop site. Most of the variation among generation means for kernels/spike was due to non-additive effects of genes, including epistasis, with the estimate of heritability being low. However, at Pendleton, late selected cycle two populations under both systems of mating showed a significant increase in kernels/spike over the base population. These results

suggest that kernels/spike was under somewhat different genetic control at the two sites.

Grain yield, spikes/plant and biological yield all showed significant genetic associations with heading date in 1982, at Hyslop. Further, each of these associations were inversely related to heading date. At Hyslop, only the selfed populations selected for early heading date showed correlated responses in spikes/plant and biological yield. At Pendleton, the $EC_2F_{4,1}$ population showed a reduction in grain yield, spikes/plant, and biological yield and the $EC_2F_{1,1}$ population exhibited a loss in mean expression for biological yield, only. In addition, selection for late heading date followed by selfing resulted in an increase in grain yield at Pendleton. Differences between mating systems for each of these unselected traits were non-significant, even through the selfed populations effected correlated response in a greater number of traits. Combined with the observed loss of 'genetic variation' for spikes/plant and biological yield in the selfed populations, these results indicate that selection for heading date followed by intermating was more effective at maintaining genetic variability for these traits than selfing.

Cycles of selection for heading date had no major impact on correlated responses in the eight unselected traits. Population maturity was the only trait which showed a significant change between cycles of selection, and this change occurred only in the early-selected populations under both systems of mating. Since heritabilities of both heading date and the unselected traits and the genetic and environmental correlations between them are expected

to decline with selection, correlated responses in the second cycle may not have been large enough to detect. Miller and Rawlings (1976b) noted a tendency for genetic correlations between lint yield in Upland cotton and various other traits to decrease rapidly with selection for lint yield.

Differences in correlated response were also noted between directions of selection for heading date. Except for population maturity, the greatest magnitudes of correlated response to selection were observed with selection for early heading date. In addition, individual unselected traits expressed themselves to a greater or lesser degree in early- and late-selected populations, respectively. At the Hyslop site, for example, plant height, spikes/plant, harvest index, and biological yield all underwent change with selection for early heading date but were unaffected by selection for late heading date. Since none of the foregoing traits showed a significant genetic association with heading date, it seems likely that environmental factors may have been the cause of the discrepancies between directions of selection and correlated response.

Cross II

Plant height and plant maturity did not show significant genetic associations with heading date in either year these estimates were obtained. Indirect effects of selection for heading date on these traits were expected to arise from environmental and/or non-additive genetic variation only. None of the selected populations suffered a reduction in within-plot variance for these traits in either year or location; in fact, several of the

populations exhibited increases in within-plot variance over the base population. These results suggest that pleiotropy between heading date and these traits did not exist, and that selection for heading date under either system of mating did not have a detrimental or beneficial effect on their expression.

Selection for early heading date in Cross II was expected to have a positive, pleiotropic effect on grain yield, spikes/plant, biological yield, 100-kernel weight and kernels/spike and a negative effect on harvest index. Conversely, selection for late heading date was expected to have the opposite effects on these traits. Results at both locations in 1982, showed little similarity with these predictions possibly due to stress late in the growing season. Populations selected for early heading date under both systems of mating generally expressed higher values for 100-kernel weight and harvest index and lower values for grain yield, spikes/plant, and biological yield at both locations than populations selected for late heading date. Accompanying these correlated responses were significant reductions in within-plot variance for harvest index and spikes/plant for both mating systems and directions of selection, and of biological yield and grain yield for early-selected and late-selected selfed populations, respectively. Apparently, the failure of observed indirect effects of selection for heading date to agree with predictions for grain yield and 100-kernel weight were the result of the presence of non-additive genetic variation for these traits. Non-additive effects of genes would be expected to bias estimates of heritability and genetic correlations which were used to predict correlated responses (Falconer, 1960).

Joint scaling tests on Cross II generation means for spikes/plant and biological yield indicated that parents shared identical alleles for these traits. The significant reduction in biological yield noted at both locations, with selection for heading date may have been a result of the shorter plant stature which accompanied selection for heading date. However, the decrease in spikes/plant, which was observed at both locations with selection for early heading date under both systems of mating, was probably a function of the amount of time to form tillers before plants changed from vegetative to reproductive growth. This conclusion is not supported by a significant estimate of environmental correlation between heading date and spikes/plant, however.

As in Cross I, cycles of selection for heading date had no major impact on correlated responses in the eight unselected traits. Most of the correlated responses that did occur did so in the first cycle of selection. Further, not even population maturity showed correlated response in both cycles of selection for heading date. Due to the lack of genetic variability or the large amount of non-additive gene action affecting most of the unselected traits in Cross II, predicted correlated responses were probably too high, and correlated responses with a second cycle of selection for heading date were either too small to detect or non-existent.

The effect of direction of selection on correlated responses in Cross II was dependent on the particular unselected trait under consideration. Plant height, plant or population maturity, kernels/spike, harvest index, and biological yield generally responded the same in both directions of selection for heading date.

Correlated responses in grain yield and 100-kernel weight were greater with selection for late heading date and correlated response in spikes/plant was greater with selection for early heading date. The only advantage of mating system detected was in correlated response in grain yield and 100 kernel weight in the $LC_1F_{1,2}$ population, although a second cycle of selection for late heading date reduced the mean expressions of these traits to the level of the selfed populations. No single interpretation of these results is possible. When the major association between heading date and any of the unselected traits was due to environmental causes, as with plant maturity and plant height, correlated response to selection for heading date was on the same order of magnitude in both directions. Grain yield, spikes/plant, kernels/spike, 100-kernel weight, harvest index, and biological yield all showed significant genetic associations with heading date. However, differences in environment (e.g., photoperiod, temperature, moisture stress) appeared to account for the greater correlated responses observed in either direction of selection for heading date. Spikes/plant and harvest index were affected more by selection for early heading date. The decrease in spikes/plant may have been the result of a shorter interval between vegetative and reproductive growth in the early selected populations. However, the increase in harvest index may have occurred because of a combination of no change in grain yield and a significant reduction in biological yield with selection for early heading date.

Intercrosses

Results of selection for heading date in the intercross

populations showed a tendency for early-selected populations to resemble Cross I populations in plant or population maturity, spikes/plant, biological yield, 100-kernel weight, and kernels/spike. The LI_1F_1 populations were more similar to Cross II populations in the expressions of these same traits. The only correlated response to selection for heading date between cycles of selection was a reduction in 100-kernel weight in the LI_2F_1 to the level of the $F_{2,2}$ population. These results suggest that direction of selection, as it affected duration of growth, had a marked influence on the phenotypes of individuals in the intercross populations. Further, even though a direct estimate of pleiotropic effects of heading date genes on these traits was not available, the tendency for the EI_1F_1 to resemble Cross I and the LI_1F_1 to resemble Cross II suggests that pleiotropy or linkage is involved.

Both conventional inbreeding and recurrent selection for an agronomically-important trait, such as heading date, would be expected to affect the expression of correlated traits. The advantages of recurrent selection over conventional breeding methods in this respect are twofold: first, if a true genetic correlation exists between two traits, recurrent selection for one of them should result in a step-wise improvement in both traits (assuming, of course that heritabilities and the genetic correlation are of sufficient magnitude). The second advantage of recurrent selection over conventional inbreeding would occur in a situation where the genetic correlation between two traits was either very low or non-existent. In this case, selfing would result in random fixation

of the unselected trait with the first selection, whereas recurrent selection would be expected to maintain genetic variation for the unselected trait assuming population sizes were large enough and the unselected trait did not reduce fitness in plants expressing it.

Neither of the advantages listed above were observed in a dramatic way in this investigation. However, two cycles of selection for heading date may have been insufficient to cause any major changes in the unselected traits. Few of the selected populations suffered a significant loss in 'genetic variation' for the unselected traits in Cross I and most of those that did were in the selfing series. This result suggested that intermating was more effective than selfing at maintaining genetic variation for these traits with selection for heading date. In Cross II, selected populations under both systems of mating exhibited roughly equivalent losses in 'genetic variation' in the unselected traits with selection for heading date. This result was probably due to lack of additive genetic variation for most of the unselected traits in Cross II.

SUMMARY AND CONCLUSIONS

The objectives of this investigation were: 1) to determine the kinds and relative magnitudes of genetic variation affecting several agronomic traits in two winter wheat populations; 2) to predict and evaluate genetic progress from selection for heading date in breeding populations arising from recurrent, mass selection and mass selection with selfing; and 3) determine the correlative influence of selection for heading date on several other important agronomic traits in these populations.

The two single crosses 'Roussalka'/'Kavkaz' and 'Hyslop'/'Kavkaz', were used to generate the populations for genetic analysis and selection. Generations required for a genetic analysis were derived by crossing and backcrossing in the greenhouse in the fall of 1979, and the spring of 1981. These materials were then hand-planted at the Hyslop Agronomy Farm in each of two years (1981 and 1982) and individual plant data were taken on heading date, plant height, plant maturity and grain yield in 1981; and for heading date, plant height, grain yield, spikes/plant, 100 kernel weight, kernels/spike, harvest index and biological yield in 1982. In addition, population maturity was measured on a population basis in 1982.

Generation means, weighted by the reciprocals of their standard errors, were fit to genetic expectations based on three- and six-parameter models by a least squares procedure. Goodness of fit was tested by chi-square and expectations provided estimates of additive and dominance main effects and of three kinds of digenic epistatic effects, for nine agronomic traits.

Pooled variances of $F_{2,j}$ and $BC_{i,j}$ generations were used to estimate narrow-sense heritabilities of all nine traits. The narrow-sense heritability estimate for heading date was then used to predict response to selection for heading date in each single cross.

Correlation coefficients between heading date and each of the eight unselected traits were obtained within each $F_{1,j}$ and $F_{2,j}$ population and provided estimates of environmental and phenotypic correlation, respectively. These parameters, combined with the estimates of narrow-sense heritability for all nine traits, were then used to derive genetic correlation with heading date and predicted correlated response in each of the unselected traits with selection for heading date.

Divergent mass selection for heading date under two systems of mating (selfing and intermating) was initiated within the $F_{2,j}$ population of each single cross in 1980. A selection differential of 10% was employed in each direction of selection. The unit of selection was an individual F_2 plant; when 50% of the spikes on an individual plant had fully emerged from the boot, a single head was covered with a glassine bag to generate the selfed populations. In addition, crosses between individual plants within single crosses were made non-reciprocally, within each of two replications. The intercross populations were initiated by intermating individual selected plants within the $F_{2,j}$ of both single crosses for each direction of selection. The 10 populations were then planted in the fall of 1980. In the spring of 1981, a second cycle of selection for heading date was carried out within each of these populations, maintaining the appropriate system of mating and 10% selection intensity.

Response to divergent mass selection for heading date was evaluated on cycle one populations in both 1981 and 1982, at the Hyslop site, and on cycle two populations at both the Hyslop and Pendleton sites in 1982. Observed response was measured as a deviation of the mean performance of the selected populations from one cycle to the next, with the mean performance of the $F_{2,j}$ representing cycle zero. A direct measure of heading date, on an individual plant basis, was not obtained at the Pendleton site. Instead, the range of heading dates within each population vs. the unselected control, was used as an indication of response to selection for heading date.

Analyses of variance were computed on a plot mean basis for each year at the Hyslop site. Sums of squares for selection methods and the cross x selection methods interaction were partitioned into single degree of freedom contrasts. These effects were the basis for determining the influence of mating system and direction of selection on response to selection for heading date. Genetic parameters estimated from the generation means of each single cross were then used to interpret the effects of mating systems and directions of selection on observed response to selection for heading date.

Correlated response to divergent mass selection for heading date was also evaluated, using the same populations and statistical tools as were used to determine response to selection for heading date. In 1981, plant height, plant maturity, and grain yield were measured at the Hyslop site. The following year, plant height, grain yield, spikes/plant, 100-kernel weight, kernels/spike, harvest index and biological yield were measured at Hyslop. Each of the preceding traits were measured on an individual plant basis. In addition, population maturity

was recorded in 1982, on a population basis. Unselected traits measured at the Pendleton site were identical to those at Hyslop, except for population maturity in 1982.

The conclusions of this investigation are as follows:

1. Of the two single crosses studied, Cross I showed the greatest amount of additive genetic variation for the nine agronomic traits. This was expected due to the contrasting expressions for each trait in the parental cultivars, 'Roussalka' and 'Kavkaz'.
2. Genetic variation for most of the traits studied in Cross II was non-additive, with linkage and/or digenic or higher order epistasis important in most traits.
3. Selection for heading date was expected to be more effective in Cross I populations, but transgressive segregation was not expected.
4. Due to the nature of gene action in Cross II, response to selection for heading date was expected to result from either breakup of linkage blocks, or unique combinations of interacting genes.
5. Correlated responses to selection for heading date were predicted to be small and largely due to environmental effects or chance fixation of genes affecting unselected traits in both single crosses.
6. Response to selection for heading date was equally effective under both systems of mating in Cross I. Selection apparently acted on a few major genes showing large additive effects in both cycles of selection.

7. The presence of minor genes, governed by additive and/or additive x additive epistasis, for heading date were detected in Cross I via selection, indicating an eventual advantage for intermating with additional cycles of selection for heading date.
8. The asymmetry in response to direction of selection for heading date noted in 1981, was thought to be the result of non-additive epistatic effects in the direction of early heading date in Cross I. Only a small asymmetry for direction of selection was noted the following year, possibly due to environmental factors which did not 'turn on' epistatic genes.
9. Response to selection for heading date in Cross II showed an advantage for intermating with early selection and an advantage for selfing for late selection. These results were attributed to an accumulation of minor genes via intermating and rapid fixation of recessive genes via selfing.
10. The advantage for selection of early heading under both systems of mating over selection for late heading date in 1982, was interpreted as the result of linkage and/or trigenic epistasis skewing the $F_{2,2}$ population toward later heading date.
11. The failure to observe an advantage for intercrossing between single crosses was ascribed to small sample size in the initial cycle of selection for heading date.
12. Few large correlated responses in the eight unselected traits with selection for heading date were noted in either cross. In general, correlated responses measured at the two sites in 1982, were identical for mating systems, directions of selection, and

crosses.

13. Intermating in Cross I was more successful than selfing in retaining 'genetic variation' for unselected traits when no genetic or environmental association between heading date and the unselected traits existed.
14. Intermating in Cross I was also more successful than selfing in retaining 'genetic variation' in unselected traits which showed a significant genetic correlation with heading date.
15. In Cross II, neither system of mating showed an advantage with respect to correlated response to selection for heading date. This was interpreted as a result of the lack of additive genetic variability in most of the unselected traits.
16. Intermating between the two single cross populations skewed intercross population means toward Cross I with early selection and toward Cross II with late selection for heading date, with respect to the unselected traits. Environmental factors and possible pleiotropy or linkage were the most likely causes of these results.
17. The genetic parameters for heading date and the unselected traits estimated in 1981 and 1982, were seen as useful tools to a plant breeder for understanding and predicting the consequences of selection and correlated response to selection for important agronomic traits.

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APPENDICES

Appendix Table 1. Meteorological data for the 1979-80, 1980-81 and 1981-82 crop years for the experimental sites in the area of Corvallis, Oregon and the 1981-82 crop year for the experimental site near Pendleton, Oregon.

Month	1979-80 East Farm			1980-81 Hyslop Agronomy Farm			1981-82 Hyslop Agronomy Farm			1981-82 Pendleton		
	Max. (°C)	Min. (°C)	Precipitation (mm)	Max. (°C)	Min. (°C)	Precipitation (mm)	Max. (°C)	Min. (°C)	Precipitation (mm)	Max. (°C)	Min. (°C)	Precipitation (mm)
September	24.7	10.0	55	24.6	5.9	24	25.1	8.5	79	26.1	5.9	38
October	19.7	7.7	183	19.5	5.2	47	16.5	4.9	140	16.4	1.9	41
November	10.7	2.3	104	12.4	4.3	160	12.4	4.3	171	12.6	1.2	61
December	9.9	2.8	159	9.2	2.9	288	9.3	2.8	355	7.0	-1.3	83
January	7.1	-1.2	170	7.1	-1.2	58	6.1	0.4	183	7.0	-3.8	66
February	10.4	1.9	99	10.4	1.9	113	9.6	1.6	181	7.9	-1.6	47
March	12.1	3.1	102	12.1	3.1	76	12.4	2.0	90	11.4	0.4	51
April	16.7	4.5	92	16.7	4.5	60	14.3	2.4	116	15.2	0.5	39
May	18.3	6.2	37	18.3	6.2	76	20.0	5.9	12	20.4	4.8	12
June	12.9	9.0	44	19.9	9.0	66	23.5	10.6	38	26.9	10.8	28
July	27.0	11.3	6	27.0	11.3	3	25.4	10.8	11	30.2	11.6	26
August	26.3	8.5	0	26.3	8.5	0						
Total			1051			971			1376			492
Long Term Average			1008			1008			1008			314

Appendix Table 2. Pedigree and description of cultivars.

Kavkaz

Lutescens 314-h-147/Bezostaja 1. A hard red common winter wheat cultivar released by Russia in 1971. It has large, cylindrical, white-chaffed spikes without awns. It is a tall, mid-season cultivar with poor tillering, large seed, and high yield potential.

Roussalka

Was-Nibay/Steriling B x C54. A hard red common winter wheat cultivar from Bulgaria. It has a mid-dense, awned spike. It is a semi-dwarf, early cultivar with poor tillering, medium kernel weight, and high yield potential.

Hyslop

Nord Desprez/Pullman Selection 101*2. A soft white common winter wheat cultivar released by Oregon State University in 1970. It has a mid-dense, awned spike. It is a semi-dwarf, mid-season cultivar with good tillering capacity, large seed, and high yield potential.

Appendix Table 3. Analysis of variance and partition of sums of squares for four agronomic traits of selected populations grown at Hyslop (1982).

Source of Variation	df	Heading Date	Plant Height	Grain Yield	df	Plant Maturity
Blocks	3	8.11*	62.84	18.09	2	22.48
Crosses (C)	1	737.88**	807.93**	3.17	1	114.47
Error a	3	0.60	24.89	5.89	2	6.94
Selection Methods (M)	4	464.07**	125.27**	12.86	4	69.43**
Response to Selection (R)	1	23.74**	398.19**	27.18	1	0.21
Direction of Selection (D)	1	1831.49**	95.46*	24.04	1	255.98**
Mating system-early (MSE)	1	0.27	5.86	0.08	1	8.12
Mating system-late (MSL)	1	0.77	1.58	0.15	1	13.42
C X M	4	48.68**	76.24*	9.97	4	22.45*
C X R	1	50.23**	201.98**	35.58	1	1.06
C X D	1	139.24**	10.66	2.55	1	75.76**
C X MSE	1	2.87	2.79	0.74	1	7.07
C X MSL	1	2.38	89.54*	1.02	1	5.89
Error b	24	0.81	20.75	12.34	16	7.30
CV (%)		0.65	4.03	17.97		1.42

*,** Significant at the 0.05 and 0.01 levels of probability, respectively.

Appendix Table 4. Entry means for four agronomic traits measured on 15 plants/entry/block at Hyslop (1981).

Entry	Heading Date (days)	Plant Height (cm)	Plant Maturity (days)	Grain Yield (g)
RSK	121.6	92.00	176.34	10.21
HYS	147.55	99.16	191.50	12.10
KVZ	147.93	130.37	192.80	25.96
F _{1,1}	130.38	117.12	188.00	23.03
F _{1,2}	141.63	122.33	189.27	21.93
F _{2,1}	138.28	121.00	187.95	25.23
F _{2,2}	143.73	118.00	191.10	17.78
F _{3,1}	135.95	103.83	188.50	19.88
F _{3,2}	144.38	116.67	191.47	17.74
BC _{1,1}	132.13	107.67	188.77	20.04
BC _{2,1}	137.68	124.67	189.00	23.09
BC _{1,2}	145.73	106.92	191.60	15.90
BC _{2,2}	140.65	126.08	191.34	20.09
EC ₁ F _{3,1}	123.38	104.67	182.67	18.92
EC ₁ F _{1,1}	124.50	103.40	182.60	20.74
EC ₁ F _{3,2}	138.38	118.92	191.87	20.17
EC ₁ F _{1,2}	137.43	115.35	188.73	19.25
LC ₁ F _{3,1}	143.90	111.08	193.10	20.31
LC ₁ F _{1,1}	143.93	107.54	192.40	18.50
LC ₁ F _{3,2}	150.50	117.00	195.03	19.65
LC ₁ F _{1,2}	148.65	123.27	191.52	21.90
EI ₁ F ₁	128.83	115.76	180.87	20.80
LI ₁ F ₁	147.74	107.55	190.66	21.12
LSD (.05) ⁺	1.30	5.36	4.25	4.69

⁺LSD based on standard error for subplot treatments for the same mainplot.

Appendix Table 5. Analysis of variance and partition of sums of squares for nine agronomic traits of selected populations grown at Hyslop (1982)

Source of Variation	df	Mean Squares								
		Heading Date	Plant Height	Population Maturity	Grain Yield	Spikes/ Plant	100-Kernel Weight	Kernels/ Spike	Harvest Index	Biological Yield
Blocks	3	5.57**	106.97**	8.98*	5.04	2.75	0.14**	56.72	.0010**	110.16
Crosses (C)	1	1139.35**	3259.36**	175.78**	170.68*	124.96**	7.00**	71.80	.0339**	9032.46**
Methods (M)	8	1386.42**	195.46**	163.71**	63.67	20.68**	0.10**	66.56**	.0042**	1342.37**
Response (R)	1	14.50**	766.49**	15.18*	0.04	60.67**	0.20**	398.69**	.0083**	1228.96*
Cycle (Cy)	1	2.98	0.56	10.97	0.42	0.89	0.00	0.48	.0000	0.12
Direction (D)	1	2882.10**	637.55**	1246.97**	239.52**	94.83**	0.34**	27.90	.0247**	7872.77**
Mating System-Early (MSE)	1	0.28	63.39**	5.28	48.82	0.09	0.01	84.64	.0001	121.77
Mating System-Late (MSL)	1	19.26**	9.74	0.28	64.92	7.28	0.09*	13.02	.0001	310.15
Cy x D	1	169.13**	19.45	23.15**	64.47	0.10	0.09*	0.28	.0003	358.67
Cy x MSE	1	3.01	33.29	7.03	69.36	8.83	0.02	6.38	.0001	502.63
Cy x MSL	1	0.10	33.24	0.78	21.84	0.05	0.05*	1.10	.0004	343.90
Cross x Methods	8	21.52**	80.76**	20.87**	47.04	11.68*	0.03	76.43**	.0005	330.66
C x R	1	25.39**	270.64**	5.94	30.66	10.91	0.04	267.29**	.0002	0.27
C x Cy	1	16.76**	2.62	5.94	36.43	2.62	0.04	0.32	.0002	399.97
C x D	1	114.09**	53.03	108.94**	22.52	65.45**	0.00	203.48**	.0005	305.16
C x MSE	1	12.37	30.58	32.00**	3.67	0.19	0.01	1.61	.0013*	66.96
C x MSL	1	1.15	146.93**	0.78	124.48	3.53	0.04	38.16	.0000	905.76*
C x Cy x D	1	1.19	90.97**	7.22	71.55	0.32	0.09*	75.09	.0002	782.81*
C x Cy x MSE	1	0.99	44.55**	6.13	29.39	4.37	0.00	25.31	.0001	94.02
C x Cy x MSL	1	0.21	6.76	0.03	61.29	6.07	0.00	0.21	.0013*	90.29
Error	51	0.93	8.67	2.83	33.40	4.23	0.01	22.87	.0002	186.09
CV (%)		0.70	2.76	0.87	12.10	11.59	2.18	8.98	3.87	11.22

*,**significant at the 0.05 and 0.01 levels of probability, respectively.

Appendix Table 6. Entry means for nine agronomic traits measured on 15 plants/entry/block at Hyslop (1981).

Entry	Heading Date (days)	Plant Height (cm)	Population Maturity (days)	Grain Yield (g)	Spikes/Plant (no.)	100-Kernel Weight (g)	Kernels/Spike (no.)	Harvest Index	Biological Yield (g)
RSK	131.7	85.5	184.5	37.6	16.2	5.00	45.9	0.43	86.5
HYS	150.0	96.8	194.5	55.2	21.6	4.72	53.6	0.40	135.0
KVZ	147.3	120.3	191.8	55.1	18.8	5.54	52.3	0.35	155.4
F _{1,1}	139.3	114.3	187.0	49.9	16.8	5.51	53.0	0.39	127.6
F _{1,2}	145.3	119.4	191.3	59.3	18.7	5.56	59.2	0.40	146.8
F _{2,1}	141.1	103.6	189.8	46.7	17.2	5.31	51.5	0.39	117.6
F _{2,2}	152.0	127.1	194.5	48.2	22.7	4.91	43.6	0.34	145.0
F _{4,1}	142.8	99.3	193.5	37.8	15.5	5.19	44.8	0.39	94.6
F _{4,2}	150.9	111.6	197.3	45.9	16.5	5.00	55.2	0.36	123.5
BC _{1,1}	136.9	98.0	188.9	41.7	16.5	5.27	47.7	0.40	102.4
BC _{2,1}	145.3	113.5	191.5	43.0	14.2	5.45	58.0	0.37	115.7
BC _{1,2}	146.7	108.8	194.0	53.7	18.7	5.20	55.6	0.39	137.5
BC _{2,2}	146.5	119.8	191.1	49.6	17.1	5.58	58.4	0.35	139.4
EC _{1F_{4,1}}	133.6	94.1	186.6	40.2	14.7	5.57	49.1	0.45	89.6
EC _{2F_{4,1}}	130.3	91.7	183.4	47.8	17.1	5.66	52.1	0.45	106.4
EC _{1F_{4,2}}	144.8	107.0	192.0	47.7	17.4	4.96	56.8	0.39	121.0
EC _{2F_{4,2}}	141.8	115.5	193.1	50.6	17.6	5.07	56.7	0.38	132.2
EC _{1F_{1,1}}	135.4	98.0	189.5	45.9	16.8	5.65	51.8	0.43	105.3
EC _{2F_{1,1}}	132.1	97.2	186.1	45.7	15.7	5.67	51.5	0.43	101.8
EC _{1F_{1,2}}	145.3	110.6	192.6	49.5	17.5	4.98	58.0	0.40	121.7
EC _{2F_{1,2}}	139.8	107.9	190.1	48.2	16.2	5.06	60.6	0.41	117.2
LC _{1F_{4,1}}	147.7	102.4	197.8	42.7	15.5	5.26	52.8	0.40	105.7
LC _{2F_{4,1}}	151.7	107.1	197.8	51.8	18.0	5.49	54.6	0.40	130.4
LC _{1F_{4,2}}	154.1	112.1	198.4	52.0	21.1	4.89	52.5	0.37	143.0
LC _{2F_{4,2}}	156.0	110.5	198.4	43.5	19.6	4.80	51.6	0.35	124.8
LC _{1F_{1,1}}	146.2	102.9	197.5	47.3	16.1	5.57	52.0	0.41	115.3
LC _{2F_{1,1}}	150.9	100.4	198.3	46.3	16.0	5.62	55.4	0.39	116.2
LC _{1F_{1,2}}	152.0	118.8	197.6	58.0	21.2	5.04	53.6	0.35	164.1
LC _{2F_{1,2}}	154.1	115.3	198.2	53.5	22.0	4.76	53.9	0.37	144.2
EI _{1F₁}	138.0	117.0	190.8	50.7	17.9	5.50	50.2	0.39	125.7
EI _{2F₁}	136.9	114.5	188.9	45.5	16.5	5.36	51.5	0.40	111.7
LI _{1F₁}	150.6	110.8	196.0	56.1	17.4	5.27	60.4	0.38	148.0
LI _{2F₁}	153.0	109.6	199.0	50.9	18.9	4.98	54.4	0.39	128.3
LS0 (.05)	1.8	5.7	2.7	10.5	3.6	0.24	6.9	0.02	25.2

Appendix Table 7. Analysis of variance and partition of sums of squares for seven agronomic traits of selected populations grown at the Pendleton site (1982).

Source of Variation	df	Plant Height	Grain Yield	Spikes/ Plant	100-Kernel Weight	Kernels/ Spike	Harvest Index	Biological Yield
Blocks	3	1.07	23.45**	4.43*	.06**	61.79**	.0019*	59.88
Crosses (C)	1	1211.49**	66.16**	3.32	2.72**	.41	.0261**	32.19
Methods	4	106.73**	48.66**	19.68**	.07**	58.56**	.0046**	674.69**
Response (R)	1	268.89**	3.20	27.72**	.01	211.05**	.0055**	213.95*
Direction (D)	1	118.73**	177.17**	50.20**	.25**	.67	.0118**	2457.01**
Mating System-Early (MSE)	1	32.49	7.37	.77	.01	.14	.0003	15.84
Mating System-Late (MSL)	1	6.81	6.92	.00	.00	22.37	.0007	11.37
Cross x Methods	4	150.48**	8.25	5.79**	.06**	67.36**	.0005	22.77
C x R	1	53.29*	5.02	8.16*	.03	66.25**	.0000	57.05
C x D	1	478.95**	3.12	13.62*	.14**	180.50**	.0002	2.25
C x MSE	1	31.36	.91	.12	.06*	.12	.0001	2.82
C x MSL	1	38.32	23.93	1.25	.03	22.56	.0015	28.94
Error	27	11.33	4.68	1.20	.01	6.53	.0005	37.96
CV (%)		3.8	13.6	12.6	2.9	8.0	7.4	14.3

*,**significant at the 0.05 and 0.01 levels of probability, respectively.

Appendix Table 8. Entry means for seven agronomic traits measured on 15 plots/entry/replication at Pendleton and ranges for population heading date (1982).

Entry	Range of Heading Dates (days)	Plant Height (cm)	Grain Yield (g)	Spikes/ Plant (no.)	100-Kernel Weight (g)	Kernels/ Spike (no.)	Harvest Index	Biological Yield (g)
RSK	143-144	65.9	21.4	11.1	4.46	42.4	0.44	49.0
HYS	154-156	76.9	29.6	15.6	3.96	47.6	0.39	75.4
KVZ	154-156	91.2	22.6	9.1	5.04	47.7	0.36	61.8
F _{2,1}	144-153	82.5	30.3	13.0	4.67	49.1	0.43	69.9
F _{2,2}	144-161	100.0	28.5	15.6	4.28	42.2	0.37	75.2
EC ₂ F _{4,1}	143-144	70.2	26.4	11.2	4.75	48.4	0.47	56.5
EC ₂ F _{4,2}	146-156	93.2	25.9	10.4	4.48	55.1	0.41	62.1
EC ₂ F _{1,1}	123-148	76.6	30.0	12.6	4.88	47.7	0.49	62.6
EC ₂ F _{1,2}	146-150	92.6	25.9	10.7	4.39	54.6	0.43	60.2
LC ₂ F _{4,1}	151-159	86.5	33.8	13.1	4.76	53.3	0.43	77.6
LC ₂ F _{4,2}	155-164	82.5	28.1	14.5	4.10	46.8	0.37	74.7
LC ₂ F _{1,1}	152-162	84.8	34.3	13.5	4.83	52.7	0.43	81.4
LC ₂ F _{1,2}	156-164	89.6	31.7	14.6	4.08	51.6	0.40	80.5
LSD (.05)		4.6	5.5	2.3	0.18	5.6	0.04	14.0

Appendix Table 9. Combined analysis of variance with a partition of sums of squares for seven traits measured on selected populations grown at Hyslop and Pendleton (1982).

Source of Variation	df	Plant Height	Grain Yield	Spikes/ Plant	100-Kernel Weight	Kernels/ Spike	Harvest Index	Biological Yield
Locations (L)	1	10,064.47**	6,851.87**	546.42**	9.8465**	149.33**	.0178**	55,916.17**
Crosses(C)	1	3,349.79**	5.72	48.30**	6.8494**	1.75	.0431*	2,046.32
Methods (M)	4	313.77**	47.08	42.83**	0.1899**	151.76**	.0104**	1,514.07**
Response (R)	1	900.02**	1.58	76.34**	0.1285*	567.44**	.0129	1,151.78
Direction (D)	1	328.52**	172.54*	94.48**	0.6277**	8.73	.0271*	4,892.30**
Mating System-Early (MSE)	1	26.28	1.56	0.51	0.0011	9.46	.0005	8.28
Mating System-Late (MSL)	1	0.27	12.62	0.00	0.0023	21.39	.0011	3.92
Cross x Methods	4	265.08**	45.33	17.91*	0.0915*	190.55**	.0008	175.12
C x R	1	250.78*	0.61	21.13*	0.0909	275.42**	.0003	103.31*
C x D	1	570.49**	9.64	40.58**	0.1712*	439.53**	.0007	39.88
C x MSE	1	101.25	4.11	1.14	0.0470	2.67	.0002	0.19
C x MSL	1	137.78*	167.76*	8.78	0.0570	44.56*	.0021	557.11
Population x Location	9	26.79*	20.84	3.18	0.0219*	7.82	.0002†	213.19†
Location x C	1	74.91**	83.08	19.10**	0.0823**	4.98	.0002	1,384.75*
Location x M	4	18.10	10.18	1.41	0.0199	7.79	.0001	64.12
L x R	1	46.38*	1.63	1.67	0.0649*	10.73	.0001	175.62
L x D	1	7.37	32.36	0.09	0.0065	3.22	.0001	0.02
L x MSE	1	8.61	6.71	3.84	0.0078	12.95	.0000	72.36
L x MSL	1	10.04	0.03	0.04	0.0003	4.26	.0000	8.49
L x C x M	4	23.45	15.94	0.97	0.0088	8.56	.0003	69.37
L x C x R	1	30.38	15.59	0.31	0.0036	25.85	.0001	0.27
L x C x D	1	49.91*	0.37	1.32	0.0118	3.86	.0001	17.60
L x C x MSE	1	4.59	11.40	0.34	0.0195	4.53	.0009	3.78
L x C x MSL	1	8.90	36.41	1.90	0.0002	0.00	.0001	255.83
Pooled Error	54	10.19	16.57 ⁺	2.76 ⁺	0.0100	14.19 ⁺	.0004 ⁺	100.97 ⁺

*,**significant at the 0.05 and 0.01 levels of probability, respectively.

⁺ error mean squares for Hyslop and Pendleton heterogeneous. † interaction mean square heterogeneous.