

AN ABSTRACT OF THE THESIS OF

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Title: Methods of Evaluation, Effects of Intermating and Results
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The focus of this study was to determine if S_1 family recurrent selection might be successfully used for barley improvement. Objectives were: 1) to identify suitable methods of evaluating grain yield in small plots, 2) to study the effects of intermating on mean values and variances of selected agronomic characters, and 3) to evaluate the response to one cycle of S_1 family selection for grain yield. Genetic materials included parents, random F_3 lines from four single cross populations, and random S_1 lines from the Cycle 0 (C-0) population which was developed by intermating the four single crosses for two generations. Heading date, plant height, and grain yield were measured on F_3 and S_1 lines grown in unreplicated small (0.7 m^2) two row plots in two locations in 1979. The same traits were measured on bulk progenies of F_3 and S_1 lines grown in unreplicated large (6.0 m^2) plots in three locations in 1980.

Moving mean technique, which uses the mean grain yield of a number of adjacent plots as a covariable in an analysis of covariance,

improved the precision of yield trials. Error mean square of replicated parents was reduced between 0 and 80 percent at different experimental sites, depending on the magnitude of field variation. Comparison of grain yield of parents grown in both large and small plots in the same year-location indicated that grain yield in small plots was affected by competition effects associated with plant height. Additional evidence for the inaccuracy of small plot yield data was supplied by the higher positive correlation between grain yield and plant height in small plots as compared to large plots.

Breakup of favorably interacting associations of alleles by intermating was studied by comparing the mean of the four single crosses with the mean of the C-0 population. Two generations of intermating did not affect the mean values for plant height or grain yield, however the C-0 population headed significantly earlier due to the effect of rapid generation advancement in the intermating process. Two generations of intermating increased genetic variance for heading date and plant height, but no effect could be detected for grain yield. While some of the estimates of genetic variance for grain yield were negative, most were small and non-significant. Lack of genetic variation for grain yield is believed to be due to common parentage of the genetic materials in this study.

Response to selection for grain yield was evaluated with Cycle 1 (C-1) S_7 lines developed by intermating the highest yielding 10% of C-0 S_7 lines. The C-1 population was significantly higher yielding than parents and significantly taller than parents and the C-0

population. Since little genetic variation for grain yield was found in this study, the response to selection for grain yield shown in small plot tests is believed to be a manifestation of competition effects associated with the increased plant height of the C-1 population. Successful S_1 family recurrent selection in barley may require the development of populations with greater genetic variation for grain yield. If populations with more diverse parentage and greater genetic variability are developed, then S_1 family selection in concert with improved field plot techniques may result in continued grain yield improvement in barley.

Methods of Evaluation, Effects of
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Recurrent Selection in Barley

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TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
LITERATURE REVIEW	3
History of Recurrent Selection	4
Genetic Studies in Self-Pollinated Crops	9
Methods of Evaluation	22
MATERIALS AND METHODS	28
1979 Small Plot Experiment	29
Generation of Experimental Populations	29
Methods	30
Moving Mean Technique	33
Analysis	34
Estimates of Grain Yield Potential	35
1980 Large Plot Experiment	38
1980 Small Plot Experiment	40
Data Management	47
RESULTS	49
Methods of Evaluation	49
Effects of Intermating	63
Results of Selection	70
DISCUSSION	75
Methods of Evaluation	76
Effects of Intermating	81
Results of Selection	85
SUMMARY AND CONCLUSIONS	87
LITERATURE CITED	93
APPENDIX	99

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1.	Plot layout with numbered plots for 1979 and 1980 Small Plot Experiments.	31
2.	Relationship between the main grain yield of parental lines and Steptoe grown in large plots with their mean grain yield in small plots. Means represent an average across two locations, Holmes Farm and Moro, in 1980 Experiments.	62

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Effect of five configurations of moving mean covariables on error mean square for grain yield of parental lines, Steptoe, and bulk populations grown in two locations, 1979 Small Plot Experiment.	51
2. Effect of adjusting grain yield by moving means on genotype x location mean squares for grain yield of five populations grown in two locations, 1979 Small Plot Experiment.	52
3. Effect of five configurations of moving mean covariables on error mean square for grain yield of parental lines, Steptoe, and bulk populations grown in three locations, 1980 Large Plot Experiment.	53
4. Effect of adjusting grain yield by moving means on genotype x location mean squares for grain yield of five populations grown in three locations, 1980 Large Plot Experiment.	54
5. Effect of five configurations of moving mean covariables on error mean square for grain yield of parental lines and Steptoe grown in two locations, 1980 Small Plot Experiment.	55
6. Effect of adjusting grain yield by moving means on genotype x location mean squares for grain yield of three populations grown in two locations, 1980 Small Plot Experiment.	56
7. Correlation of five measures of grain yield potential estimated on F_3 or S_1 lines of four populations grown in two locations in 1979 with moving mean adjusted grain yield of the related F_4 or S_2 bulks grown in three locations in 1980.	60
8. Phenotypic correlations between mean values of heading date, plant height, visual evaluation, and grain yield of five populations grown in the 1980 Experiments.	61

	<u>Page</u>
9. Population means for heading date, plant height, grain yield, and 1000 kernel weight of five populations grown in two locations in the 1979 Small Plot Experiment.	64
10. Population means and tests of significance for heading date, plant height, and grain yield of five populations grown in three locations in the 1980 Large Plot Experiment.	65
11. Estimates of genetic variance, its standard error, and heritability on a single plot basis for heading date of five populations grown in the 1979 Small Plot Experiment and the 1980 Large Plot Experiment.	67
12. Estimates of genetic variance, its standard error, and heritability on a progeny mean basis for plant height of five populations grown in the 1979 Small Plot Experiment and the 1980 Large Plot Experiment.	68
13. Estimates of genetic variance, its standard error, and heritability on a progeny mean basis for moving mean adjusted grain yield of five populations grown in the 1979 Small Plot Experiment and the 1980 Large Plot Experiment.	69
14. Analysis of variance for heading date, plant height, and grain yield of parental lines and Steptoe planted with both field and greenhouse grown seed and grown in two locations in the 1980 Small Plot Experiment.	71
15. Tests of significance and means for heading date, plant height, and grain yield according to seed source for two populations, selected F ₄ lines, parental lines, and Steptoe grown in two locations in the 1980 Small Plot Experiment.	72
16. Estimates of genetic variance and its standard error for heading date, plant height, and grain yield for two populations and selected F ₄ lines grown in two locations in the 1980 Small Plot Experiment.	74

LIST OF APPENDIX FIGURES

<u>Figure</u>		<u>Page</u>
1	Diagram of the parental relationships of several spring barley lines.	114

LIST OF APPENDIX TABLES

<u>Table</u>		<u>Page</u>
1	Pedigrees and descriptions of parental lines.	99
2	Logistics of germplasm development and testing for three field experiments.	101
3	Summary of climatological data on a per month basis for the 1979 growing season at East Farm and Redmond.	103
4	Summary of climatological data on a per month basis for the 1980 growing season at Holmes Farm, Moro, and Klamath Falls.	104
5	Means for heading date, plant height, and moving mean adjusted grain yield of populations, bulk populations, parents and Steptoe grown at two locations in the 1979 Small Plot Experiment.	105
6	Means for heading date, plant height, and moving mean adjusted grain yield of populations, bulk populations, parents and Steptoe grown at three locations in the 1980 Large Plot Experiment.	106
7	Means for heading date, plant height, and moving mean adjusted grain yield of four populations, parents, and Steptoe according to seed source. Grown in two locations in the 1980 Small Plot Experiment.	107
8	Analysis of variance for heading date, plant height, actual grain yield and moving mean adjusted grain yield of five populations grown in two locations in the 1979 Small Plot Experiment.	108
9	Analysis of variance for heading date, plant height, actual grain yield and moving mean adjusted grain yield of five populations grown in three locations in the 1980 Large Plot Experiment.	109
10	Analysis of variance for heading date, plant height, actual grain yield, and moving mean adjusted grain yield for two populations and selected F ₄ lines grown at two locations in the 1980 Small Plot Experiment.	110

		<u>Page</u>
11	Estimates of parameters used to estimate the statistical index for populations grown in the 1979 Small Plot Experiment.	111
12	Estimates of gain from selection for S_1 family and conventional recurrent selection techniques at different levels of additive genetic variation.	112

METHODS OF EVALUATION, EFFECTS OF
INTERMATING AND RESULTS OF ONE CYCLE OF S_1 FAMILY
RECURRENT SELECTION IN BARLEY

INTRODUCTION

Progress from selection for grain yield per se in barley has been disappointing in recent years, and concern is being expressed regarding the possibility of a yield plateau. Short cycle recurrent selection techniques, which have been used extensively to improve grain yield and other traits in cross-pollinated crops, may be useful in a self-pollinated crop such as barley. Through more frequent intermating and selection, recurrent selection may result in more rapid increases in the frequency of favorable alleles and thus more rapid germplasm improvement. Perhaps recurrent selection is the breeding tool which can break the apparent yield plateau in barley.

The overall focus of this study was to determine if short cycle recurrent selection techniques such as S_1 family have a place in barley breeding (an S_1 family is the selfed progeny of a single, non-inbred plant). Specific objectives of this recurrent selection study were 1) to identify suitable methods of grain yield evaluation in small plots, 2) to study the effects of intermating on mean values and variances of selected agronomic characters, and 3) to evaluate the results of one cycle of S_1 family recurrent selection for grain yield.

The first objective is important because short cycle recurrent selection techniques like S_1 family require testing the progeny of a

single plant. Both accuracy and precision of yield trials will be adversely affected by the small quantity of seed produced by a single plant. Grain yield measurements may not be accurate because it is difficult to simulate the competitive conditions which exist in larger, solid stands of barley. There will be a loss of precision in yield trials because of insufficient seed for replicated tests. More advanced experimental procedures, such as the moving mean technique, may alleviate some of these difficulties. Any improvement in yield testing procedures will be beneficial for all barley breeding methods.

The second objective relates to the possible deleterious effects of intermating a normally self-pollinated crop. Favorably interacting associations of genes may be disrupted by the frequent intermating associated with recurrent selection. The second objective also relates to the potential for increased genetic variability due to the formation of new combinations of genes. The final objective, which deals with the response to selection, will help determine whether recurrent selection has a place in barley breeding.

LITERATURE REVIEW

Recurrent selection techniques have efficiently and effectively increased the rate of genetic improvement of cross-pollinated crops. These techniques are just beginning to have an impact on the breeding of self-pollinated crops. The meager research that is available is spread thinly across a wide array of crops, and it is not yet known whether recurrent selection will be as successful in self-pollinating crops as it has been in cross-pollinating crops. The self-pollinated crops - wheat, rice, barley, peas, and beans - are man's most important food sources. Increasing the rate of genetic improvement in these crops has obvious implications in the fight against world hunger.

The jumble of breeding techniques that are collectively known as recurrent selection have been developed by breeders of cross-pollinated crops and some techniques are not applicable to self-pollinated crops. Most of the techniques have been proposed and discussed based solely on theoretical considerations. Therefore, before addressing the literature on recurrent selection in self-pollinated crops, it will be useful to review the historical development and classification of recurrent selection techniques as well as some of the theoretical concepts which affect their application. The success of recurrent selection, or any method of plant improvement, depends upon adequate genotype evaluation techniques. The literature concerning this aspect of selection will also be reviewed.

History of Recurrent Selection

The history of recurrent selection is largely the history of corn breeding. The term 'recurrent selection' was introduced into plant breeding literature by Hull in 1945, and later defined by Hull (1952) to mean "reselection generation after generation, with interbreeding of selects to provide for genetic recombination. Thus selection among isolates, inbred lines, or clones is not recurrent until selects are interbred and a new cycle of selection is initiated."

While the term 'recurrent selection' is quite recent, the concept of cyclic systems of selection is much older. For instance, corn has probably been mass selected since its domestication. Mass selection in corn was widely practiced in the United States by farmers and breeders alike up until the 1920's. Selection had been shown to be quite effective in altering highly heritable traits such as grain color, plant height, ear height, date of maturity, and prolificacy. However, mass selection had not been shown to be effective for grain yield improvement (Allard, 1960; Sprague and Eberhart, 1977).

In 1896, Hopkins (1899) began a selection experiment using a more sophisticated form of recurrent selection called ear-to-row selection. Ear-to-row selection involves growing the progeny of an open-pollinated plant in rows and selecting both between and within the rows. The Burr White variety of corn was selected for both high and low levels of protein and oil. The success of this method in altering the chemical composition of the corn kernel (Dudley, Lambert, and Alexander, 1974) led many breeders to apply the ear-to-row technique to grain yield.

Richey (1922) summarizes the results: "In view of the expense, the uncertainty with which larger yields have been obtained, and the small increases secured during a series of years in the most favorable cases, so far there appears to be little to recommend ear-to-row breeding as a practical method of corn improvement."

Several authors felt that other methods of selection might more effectively modify kernel composition than ear-to-row methods. Hayes and Garber (1919) discussed a method to improve percent protein in Minnesota 13 corn synthetic. Plants were self-pollinated and the selfed seed was tested for percent protein. The best S_1 lines were selected and test crossed. The test crosses were evaluated for grain yield and the F_2 of the best yielding cross was reselected for vigor. This paper is often referred to as a first paper on recurrent selection. In fact, the only reselection after intermating of selects was the reselection for vigor. Throughout the paper, there is no evidence the authors looked upon their method as a cyclic breeding system.

On the other hand, East and Jones (1920) definitely employed the recurrent concept in their paper on selection for protein content in maize. The concept of testing large numbers of individuals to exhaust genetic possibilities was discussed and discarded as impractical. The procedure was "simply to cross different selected high protein lines, to self-pollinate the first-generation plants, and to select again from the progenies which represent segregating generations." In the strains selected by this procedure there remained a "reserve of genetic variability out of which it is possible, theoretically, to carry the percent of protein to a still higher level." Both Hayes and Garber

(1919) and East and Jones (1920) were interested in improving the value of an open-pollinated variety of corn.

The improvement of open-pollinated varieties was also the objective of the recurrent selection procedure proposed by Jenkins (1940). The procedure involved the following steps: (1) the isolation of one-generation selfed lines, (2) testing the lines in top crosses for yield and other characters, (3) intercrossing the best selfed lines to produce a synthetic variety, and (4) repetition of the above process at intervals after each synthetic variety has had a generation or two of intermating, possibly with the inclusion of lines from unrelated sources. Jenkins envisioned a continuous selection process, with newly developed synthetics being released to farmers as they became available. He went on to mention several ways in which the basic procedure might be altered.

The first recurrent selection system directed towards the improvement of a population so that improved inbred lines for F_1 hybrids might be selected from it was proposed by Hull (1945). The selection procedure involved: (1) self-pollinating plants in the corn population and using pollen of each plant separately on silks of a tester line, (2) recording yield performance of test hybrids, (3) growing ear-rows from selfed seed of the plant which had the higher yielding test hybrids and intercrossing. One cycle would require three years. This selection system would be superior to conventional selection systems for inbreds because, according to Hull, it would select for overdominance and hybrid vigor, because recurrent mild selection would soon build up a selection intensity far in excess of any feasible attainment by a single selection

without recombination, because the decline in genetic variation would be slow, and because it would break up linkages.

Hull (1945) clarified his concept of recurrent selection with the following statement: "Current corn breeding practice presumably includes successive cycles of breeding, although cycles occur irregularly and overlap a great deal. Better lines of one cycle are interbred to provide foundation stock for a succeeding cycle. The present plan is a variation of current practice in which the inbreeding interphase is eliminated and frequency of recurring cycles raised to a maximum."

Since Hull developed the term recurrent selection in 1945, many cyclic breeding systems have been proposed and evaluated. They require the selection of superior phenotypes in a breeding population and the intermating of the selects to form a new population. If the phenotypes are superior because they contain more of the favorable alleles, then these recurrent selection procedures will increase the frequency of favorable alleles. Selection can be based on the phenotype of an individual (mass selection) or on the mean phenotype of families. When families are used, three phases are involved: (1) forming families, (2) evaluating these families and selecting those that are superior, and (3) intercrossing the selected families to form the breeding population for the next cycle of improvement (Sprague and Eberhart, 1977).

Recurrent selection procedures have also been classified according to the objectives of the improvement program. The two categories are intrapopulation improvement and interpopulation improvement. Empig et al. (1972), Sprague and Eberhart (1977), and Gardner (1978) have

developed formulas and discussed the common intra- and interpopulation improvement techniques. Commonly used intrapopulation improvement techniques include:

1. Mass selection
 - a. with pollen control
 - b. without pollen control
2. Full-sib family
3. Half-sib family
 - a. ear-to-row (no replication)
 - b. replicated test
 - c. modified ear-to-row
4. S_1 family
5. S_2 family
6. Testcross (population as tester)

While these intrapopulation techniques are used to improve the population itself and the inbred lines derived from it, they also can result in improved hybrid performance (Moll and Stuber, 1974). The common interpopulation improvement techniques are:

1. Test cross
 - a. broad base tester
 - b. inbred tester
2. Reciprocal recurrent selection
3. Full-sib reciprocal recurrent selection

The interpopulation improvement techniques are used to improve the population cross and the F_1 hybrid from inbreds derived from each population. They also can result in improvement of the population itself (Moll and Stuber, 1974).

Summaries of the results of recurrent selection programs in corn have been provided by Sprague and Eberhart (1977) and Gardner (1978). The application of these techniques has lagged far behind in self-pollinated crops. To fully understand contemporary research on recurrent selection in self-pollinated and cross-pollinated crops, one needs a background of quantitative genetic theory. Only then will the concepts of genetic variability and heritability assume their proper role in making practical breeding decisions.

Genetic Studies in Self-Pollinated Crops

There are two schools of thought in quantitative genetics of crops. The first school studies genetic and environmental variances using the generation means method. The genetic material studied often includes two inbred parents, backcrosses to each parent, the F_1 , and F_2 individual plants. Some of the important developmental and summary papers of this school include Fisher, Immer, and Tedin (1932), Mather (1949), Warner (1952), and Powers (1963).

The second school of quantitative genetic variation in plants studies components of variance. The main proponents of this school are Comstock, Robinson, and colleagues. Estimates of genetic and environmental parameters are usually obtained using half-sib and full-

sib families (Comstock and Robinson, 1948, 1952) or by appropriately arranged progenies from the cross of two inbred lines (Cockerham, 1954; Horner and Weber, 1956). A diallel cross also uses variance components to estimate genetic variances, but this method has been very heavily criticized (Gilbert, 1958; Baker, 1978).

The advantages and disadvantages of generation means and variance components were discussed by Gates (1963). The components of variance approach allows one to study almost any breeding population and allows study of genotype x environment interaction. Only the components of variance approach will be reviewed here because it is more relevant to the study of recurrent selection in plants.

Accurate estimates of genetic and environmental components of variance can provide a basis for critical evaluation of breeding and testing procedures. Unfortunately, estimates of genetic components of variance are often biased because they are estimated from inadequate data. One must also recognize that components of variance are subject to large sampling errors (Dudley and Moll, 1969).

Johnson et al. (1955) estimated genetic components of variance in two soybean crosses. The progenies studied were F_4 and F_5 bulks, each derived from random F_2 plants. Estimates of genetic variance for grain yield (bushels/acre) determined in a single environment were 5.99 and 2.94 for populations 1 and 2, respectively. Estimates of genetic variance for grain yield when studied in two locations for two years were 1.72 and 2.33 for populations 1 and 2, respectively. The estimate from a single environment was larger, the authors explained, because genotype x year,

genotype x location, and genotype x year x location interaction components were confounded within the genetic component.

Johnson et al. (1955) also estimated genetic components of variance for plant height (inches). Estimates of genetic variance obtained by testing in one environment were 9.86 and 9.98 for populations 1 and 2, respectively. Estimates of genetic variance obtained by testing in two locations for two years were 7.19 and 9.34 for populations 1 and 2, respectively. Genotype x environment interaction variances for plant height were quite small relative to the genetic variance.

An estimate of the genetic component of variance is an estimate of the variance of genotypic values. Genotypic values are estimated by testing individuals or lines in a sample of environments from a population of environments. The population of environments should be the set of years and locations for which the breeder is interested in developing new varieties. An appropriate and unbiased estimate of genetic variance can be obtained only when genotypes are evaluated in at least two years and at least two locations (Johnson et al., 1955; Gardner, 1963; Dudley and Moll, 1969). The importance of an unbiased estimate of genetic variance arises from the fact that, in practical breeding programs, the breeder is specifically concerned with the average genotypic value of lines over the range of environments encountered in a region. The unbiased genetic variation estimate will indicate whether progress is possible, and the unbiased heritability estimate derived from it will indicate the ease with which progress might be made.

Heritability is a useful descriptive statistic. It represents the proportion of the observed phenotypic variance for which heredity is responsible. It is used to make choices between different breeding schemes and to predict breeding progress. Unfortunately, the heritability statistic is not exactly clear or straightforward in plants (Hanson, 1963; Robinson, 1963). Narrow and broad-sense heritabilities are readily adaptable to the description of genetic variability in animals, where the reference unit is the individual animal. In plants, the reference unit is not so easily defined. It might be a plant, a field plot, replicated field plots in one environment, or replicated field plots in two or more environments. The different reference units affect the heritability estimate by changing the denominator from the phenotypic variance of individuals to the variance of phenotypic means of families of individuals. In addition, when progress from selection is estimated, the types of individuals or families evaluated will change the numerator of a heritability estimate. These problems were discussed by Hanson at the Statistical Genetics and Plant Breeding Symposium in 1963 (Hanson, 1963), and he concluded that the definition of heritability should be "the fraction of the selection differential expected to be gained when selection is practiced on a defined reference unit."

Dudley and Moll (1969) stress two basic points when progress from selection is being predicted: (1) the estimate of genetic variance used should, as far as possible, be free of genotype x environment interaction, and (2) the heritability value should be computed on the basis of the type of selection unit, which includes the type of progeny,

the type of plot, and the number of replications, location, and years the progenies will be evaluated.

The quantitative genetics of annual lespedeza, a self-pollinated forage crop, was studied by Hanson, Robinson, and Comstock in 1956 (Hanson et al., 1956). Three single cross populations were studied by growing F_2 families in the F_3 and F_4 generations in two locations over a two-year period. The progeny or family components of variance for the traits total yield and seed yield were generally much larger than the progeny x year and progeny x location components, approximately equivalent to the progeny x year x location component, and much smaller than the plot error variance. Heritability estimates were computed on both a single plot basis and a progeny mean basis, where the progeny mean is based on tests with two replications in two locations for two years. The heritability of total yield on a single plot vs. progeny mean basis was 10.2 vs. 39.0, 14.1 vs. 52.8, and 9.4 vs. 34.2 for populations 1, 2, and 3, respectively. The authors note that the heritability of a progeny mean is used to predict gain from selection. However, when heritability is used to characterize a particular trait, estimates on a single plot basis are more readily and conveniently used.

Tobacco is a largely self-pollinated crop. Estimates of additive, dominance, and additive x additive epistatic variances for several agronomic and chemical characters in a tobacco single cross were obtained by Matzinger et al. (1960). Estimates were derived from a North Carolina Design II experiment that included an analysis of F_3 lines. Families were grown in a two replication experiment in a single

environment. Estimates of components of variance that were larger than their standard errors were obtained for additive genetic variance for yield, value per cwt., plant height, number of leaves, leaf width, percent nicotine, and percent total alkaloids; dominance variance for value per cwt., number of leaves, and number of suckers; and additive x additive epistatic variance for plant height and leaf length. The assumption of no epistasis would have changed the estimates of additive and dominance variance for most characters, but only for leaf length would one have concluded that additive genetic variance was important when by more complete analysis it appeared to be primarily additive x additive epistasis.

Estimates of genetic variances for a second single cross in tobacco were presented in 1966 (Matzinger et al., 1966). The parents were Dixie Bright 244 and Coker 139. This single cross between two high-yielding, low-alkaloid varieties formed the base population for an alkaloid selection experiment. The traits studied included total alkaloids, yield, value per cwt., days to flower, plant height, number of leaves per plant, and number of suckers per plant. Estimates of additive genetic variance were significant for all traits except value per cwt. There was significant non-additivity for value per cwt. and plant height. Estimates were based on a North Carolina Design II experiment where families were grown with two replications in a single environment. The authors recognized the possible bias in the estimates of genetic variance due to genotype x environment interaction. They stated that other experiments had shown little evidence for genotype x environment interactions and felt that greater information could be

obtained from a given number of plots by maximizing the number of full-sib families at the expense of additional replications and environments.

The progress from two cycles of recurrent selection for increased alkaloids in the tobacco cross Dixie Bright 244 x Coker 139 were presented by Matzinger *et al.* (1972). The method of family selection was outlined by Cockerham and Matzinger (1966). Selection was based on both full-sib and selfed progenies. One cycle of selection raised mean alkaloid level from the average of the two parents in the unselected population to the higher parent. After two cycles of selection most families were above the high parent. The predominant genetic variance was additive, with little evidence of dominance or epistatic effects. The genetic variance following selection did not decrease, and continued progress from selection was expected.

A third population of tobacco, formed by the cross of SC 58 x Dixie Bright 244, was studied by Matzinger (1968). Full-sib and selfed progenies obtained from parent plants in the F_2 generation were evaluated with two replications in one environment. Genotype x environment interactions had been shown to be unimportant in tobacco. Significant estimates of additive genetic variance were obtained for yield, alkaloids, plant height, number of leaves, leaf length, leaf width, and number of suckers. None of the estimates of dominance variance was significant. A significant estimate of additive x additive epistatic variance was obtained for plant height.

The effect of five generations of random intercrossing in tobacco was studied to determine if internally balanced chromosome effects were

important (Humphrey et al., 1969). The base population, called the black shank synthetic, was formed by intermating eight tobacco varieties. Comparisons of generation means indicated small but significant epistatic effects for six out of eight characters. The decrease in yield and narrower leaves with increased generations of intermating suggested that internally balanced chromosomal effects were being disrupted. However, the magnitude was low and the effect would be more than offset by one generation of selection.

The results of four cycles of mass selection for green weight of leaves in the black shank synthetic was reported by Matzinger and Wernsman (1968). Plants could be evaluated prior to crossing; thus selection was practiced on both male and female parents. A linear increase of 44 grams of green leaves per plant per cycle was obtained. The realized heritability, computed as the linear regression of cycle means on the cumulated selection differential, was $.18 \pm .01$.

Cotton is not a strongly self-pollinated crop since it can have up to 50 percent outcrossing. Miller and Rawlings (1967a) studied the effect of six generations of intermating on genetic variances and covariances in a cross between an unadapted cotton strain of inter-specific origin with an adapted variety. The cross was made to combine the fiber strength of the first parent with the yield of the second parent. An analysis of the original single cross population showed a genetic correlation of $-.69$ between lint yield and fiber strength. This character association may have been due to linkage, pleiotropy, or a combination of both. Six generations of intermating reduced the genetic correlation between lint yield and fiber strength from $-.69$ to $-.35$.

Other genetic correlations also tended to shift toward values observed in populations assumed to be more nearly at linkage equilibrium.

Intermating decreased the genetic variances of six traits where coupling phase linkages might be expected to predominate and increased the genetic variation for one trait where repulsion linkages might have been important. Coupling might be expected to predominate if parents are quite different for a trait and repulsion if parents are similar for a trait.

Miller and Rawlings (1967b) conducted three cycles of S_1 family recurrent selection for lint yield in a single cross population of upland cotton. Between 81 and 90 S_1 progenies were evaluated each cycle in two or three replicates in two or three environments. The best six progenies were selected each cycle. Response to selection was evaluated by growing the six selected progenies of each cycle as well as both parents in a four-replicate, five-environment yield trial. Selected progenies had all reached the F_6 generation of inbreeding. Significant yield increases were recorded for each cycle of selection. Yield of third-cycle selections exceeded the mid-parent by 29.7 percent and high parent by 13.0 percent. Predicted increases in yield computed from original experiments agreed very closely with observed response. Response to selection was linear and was expected to continue.

The Deltapine 523 cotton variety served as the base population for three cycles of recurrent selection based both on individual and progeny row bases (Meredith and Bridge, 1973). Selection was for increased lint percentage, which is strongly correlated with lint yield. The base population and three cycles of selection were evaluated in replicated

experiments in four locations. Mean lint percent was 33.8, 35.4, 36.6, and 38.0 for cycles 0, 1, 2, and 3, respectively. Lint yield also increased significantly.

Soybeans are strongly self-pollinated. Brim and Cockerham (1961) estimated genetic variances in two single cross soybean populations. F_3 , F_4 , and F_5 progenies and full-sib families were evaluated with two replications in two locations over a two-year period. Eight traits were studied in each population. Additive genetic variance was the principle genetic component of variance for all characters in both populations. Significant dominance effects were present only for fruiting period and unthreshed weight in population II. Of the six estimates of additive x additive epistasis that were different from zero, two were negative. The authors estimated progress from selecting progenies derived by selfing F_2 , F_3 , F_4 , F_5 , and F_∞ parent plants. Expected progress increased with inbreeding but at a decreasing rate. The additional gain from continued inbreeding must be weighted against the time and effort involved in inbreeding. The authors stated that, in the populations studied, it would almost always be advantageous to inbreed the parents to the F_3 and often to the F_4 , before evaluating the progenies.

A base population for recurrent selection experiments was developed at North Carolina by backcrossing 9 exotic soybean lines to an adapted high-yielding line. Kenworthy and Brim (1979) compared three selection criteria for their ability to increase grain yield in this population. Three cycles of S_1 family selection were completed using the following selection criteria: seed yield, efficiency-expressed as the ratio seed weight/straw weight, and an index where seed yield and efficiency were

weighted equally. Selection was based on S_1 progeny performance in replicated hill plots at a single location. Average yield increases were 134, -2, and 38 kilograms per hectare per cycle for selection based on grain yield, efficiency, and index, respectively.

S_1 family recurrent selection was used to increase percent protein in two soybean populations by Brim and Burton (1979). Population I was a cross between two adapted lines and population II was generated by backcrossing 9 exotic introductions with high protein content to an adapted experimental line. The populations were divided into two groups, A and B, with the effective population size of IA and IIA about three times larger than that of IB and IIB. The populations were selected for four to six cycles. Percent protein increased significantly and linearly in all populations. Responses in percent protein were .33, .29, .67, and .59 percent protein per cycle of selection in populations IA, IB, IIA, and IIB, respectively. Differences in response due to effective population size were not significant.

The NP3R random mating grain sorghum population, which uses a genetic male-sterile to facilitate intermating, was studied by Jan-orn et al. (1976). Half-sib, full-sib, and S_1 randomly developed families were evaluated in two locations. Dominance variance exceeded additive genetic variance for grain yield per plant, grain yield per unit area, and kernels per plant, but the reverse was true for days to flower, height, 1000 kernel weight, yield per head, heads per plant, and kernels per head. Heritability on an individual plant basis was .88 for days to flower, and on a family basis was .89, .92, and .95 for half-sibs, full-

sibs, and S_1 families, respectively. Heritability on an individual plant basis was .09 for yield per hectare, and on a family basis was .55, .76, and .71 for half-sib, full-sib, and S_1 families, respectively. Heritability on a family basis involves testing the family with two replications in two locations. The authors stated that additive genetic variation appeared to be sufficient to permit substantial progress by any of the three family selection systems, but S_1 family was the most promising for increasing grain yield and yield components. For the highly heritable traits, such as plant height and days to flower, individual plant selection (mass selection) was expected to be most effective.

Estimates of genetic variation and heritability in three grain sorghum random mating populations were obtained by Ekebil et al. (1977). Estimates were based on 200 random S_1 lines from each population grown with two replications in one location over a two-year period. The NP3R population, composed of adapted lines, was higher yielding than NP5R, which contained exotic germplasm. However, the NP5R had twice as much genetic variability for yield and most other characters. NP7BR, a narrow-based population, yielded the same as NP5R but had less genetic variability. Genotype x year interaction variances were low relative to genetic variances, therefore heritabilities were generally high. Heritabilities for grain yield on a two-replicate, two-year basis were .74, .87, and .75 for populations NP3R, NP5R, and NP7BR, respectively. Predicted gains in yield from selecting the highest 20 percent of the families in each population were 10.2, 16.3, and 8.7 quintals (100 kilograms) per hectare for NP3R, NP5R, and NP7BR,

respectively. The authors felt that NP3R and NP5R were suitable for recurrent selection programs.

Three cycles of bi-directional recurrent selection for strontium (Sr) content were conducted in single cross populations of wheat and barley by Byrne and Rasmusson (1974). Selection for Sr content in grain was based on both individual and family performance. The average response per cycle in wheat was 7.4 percent for high and 12.4 percent for low levels of Sr. The average response per cycle in barley was 12.2 percent for high and 11.2 percent for low levels of Sr. In barley, high and low selection resulted in populations in cycle 3 that surpassed the high and low parental varieties. In wheat, neither the high nor the low population surpassed the high and low parental varieties.

Redden and Jensen (1974) selected for tillering in single cross populations of wheat and barley. Individual plants were selected for two cycles in both a selfing and an intermating series. Total response to selection in wheat was 22.6 percent when plants were intermated to produce populations for subsequent selection and 18.5 percent when plants were selfed to produce populations for subsequent selection. Total response to selection in barley was 17.1 percent in the intermating series and 8.7 in the selfing series at site 1, and 13.9 percent with intermating and 10.3 percent with selfing at site 2.

Two cycles of selection for grain protein content in spring wheat were conducted by McNeal et al. (1978). Second cycle progeny had higher grain protein percentages than first cycle progeny; however grain yield had decreased. A comparison of parents with 27 high protein lines from

the second cycle showed an average increase of 2.5 percent protein and an increase in protein yield of 12.0 grams per 2.4 meters of row.

Methods of Evaluation

Selection, no matter how intense, cannot produce gains in performance if the observed phenotype does not reflect the genotype of the plant. Today, it is widely believed that the early failures of mass and ear-to-row selection to improve grain yield in maize were due to ineffective identification of genetically superior individuals and families (Sprague and Eberhart, 1977; Gardner, 1978). The first, and often cited, effective intrapopulation grain yield improvement experiment was Lonquist's (1949) development of Syn-2 and Syn-3 populations from Krug open-pollinated maize. A likely reason for the success can be read in his materials and methods: "The 36 top-crosses were compared in 1944, using a triple lattice design with six replications. Plot size was 2 x 10 hills. Planting was done at an increased rate and later thinned to a uniform stand." Today breeders achieve more effective identification of genetically superior individuals and families by using improved field plot techniques, improved field designs, and replication both within and across environments (Gardner, 1978).

The history of the improvement of individual plant evaluation techniques is quite short. Gardner (1961) improved plant evaluation by overplanting and then thinning to obtain uniform stands, by using irrigation to reduce genotype x year interactions, and by selecting

superior plants from small grids to reduce micro-environmental variation. As a result, mass selection for grain yield within the Hays Golden open-pollinated corn variety achieved a gain of 3.08 percent per cycle of selection over 15 cycles of selection (Gardner, 1977).

The history of family, line, or variety evaluation techniques can be divided into pre-Fisher and post-Fisher periods. Early in the twentieth century, crop experiments were conducted using single row plots, without randomization or replication. Control of errors due to soil variation was often achieved through the use of systematically arranged controls or checks. Variety yield was then expressed either as the difference from the mean of the nearest checks, or as a percent of the nearest checks (LeClerg, 1966).

R. A. Fisher is responsible for developing, in the 1920's, most of the experimental methods used today. The analysis of variance procedure for a randomized complete block design was first given in correspondence by Fisher to "Student" (Student, 1923). The principles of experimental design and statistical analysis were established in Fisher's first book, Statistical Methods for Research Workers (Fisher, 1926). His second book, The Design of Experiments (Fisher, 1935), discussed the basic principles of field experimentation in detail. The principles of experimental design advocated by Fisher showed the importance of replication, randomization, and properly designed blocks. Replication is used to provide an estimate of experimental error and to increase the precision of variety mean yield estimates. Randomization is used to make the estimates of experimental error and mean value unbiased.

Blocking, or 'local control' increases experimental precision because variation between blocks does not affect experimental error.

Yates (1936) pointed out serious statistical objections to the use of percent of checks and difference from checks methods to adjust plot yields for soil variation. Such procedures were shown to almost certainly over-adjust plot yields. Yates suggested, if controls are used, that yield adjustment should be accomplished through analysis of covariance procedures developed by Fisher (1932). The adjustment factor, estimated by an analysis of covariance, is determined so errors are minimized. The overadjustment of plot yield which occurs when the difference between check plots and variety plots is used was demonstrated in wheat by Townley-Smith and Hurd (1973) and in oats by Baker and McKenzie (1967). The use of percent of control plots was shown to overadjust barley yields by Mak et al. (1978).

The 1936 paper by Yates not only pointed out common problems when checks are used for error control but also observed that checks require extra time and labor. To reduce time and labor costs, and at the same time avoid the use of excessively large blocks when many varieties are tested, Yates proposed the incomplete block design (Yates, 1936). Current literature on the most extensively used incomplete block designs was surveyed by LeClerg (1966). The designs included lattices (simple and triple), balanced lattices, lattice squares, rectangular lattices, and cubic lattices. Of the 676 experiments surveyed, only 17, or 2 percent, were less efficient (less precise) than the randomized complete block design.

A 'moving average' was used by Richey (1924) to reduce error in a corn experiment with checks planted in alternate rows. Richey found that the moving average reduced probable errors by about one-half. The moving average was used as an index of productivity and was actually a ratio of sums. The moving average for each plot was the sum of the actual yield of a given plot and its two neighbors divided by the sum of the overall mean yield of the varieties grown on the three plots. The yield of each plot was then regressed on the moving average to obtain the adjustment factor. Variety yields were adjusted and then analyzed. Richey recognized that the extensive use of checks in this test limited the number of strains that could be tested and stated that the use of checks was in no way fundamental to the proposed method of yield adjustment.

Richey (1926) reanalyzed the barley data presented by Student (1923). This experiment had no checks. Analysis using a moving average gave an average probable error of a difference that was 12.5 percent less than the error reported by Student. Student had analyzed the data as a randomized block design. Richey further pointed out that the randomized block method would become less and less satisfactory as the number of strains in the experiment increased. Also, the moving average was much more flexible than replication blocking, because the number of plots used to compute the average can be changed to meet the needs of the experiment. There appears to be no further reference to the work of Richey except by LeClerc (1966) who misinterpreted it.

Grain yield of wheat lines was expressed as a percentage of a moving average by Knott (1972). The moving average was the mean of the nearest

seven hybrid plots ignoring the checks but including the plot in question. The experiment had check plots every five plots and grain yield was also expressed as a percent of the average of the nearest two checks. An analysis of variance of the actual data gave an Error Mean Square (MSE) of 423 and a Coefficient of Variation (CV) of 20.6 percent. Yield expressed as a percentage of adjacent checks gave an MSE of 277 and a CV of 17.5 percent. Yield expressed as a percent of a moving average gave an MSE of 231 and a CV of 15.1 percent. Knott concluded that since the use of checks increased the size of the test, a moving average would be most efficient.

A covariance technique using a moving average to reduce errors was proposed by Buker et al. (1972). This technique uses a productivity map. The productivity map is a second field map where the actual yield of a plot is replaced by the actual yield minus the average yield of the variety grown on the plot. A covariable for each plot is then obtained by averaging two or more adjacent productivity values. An analysis of covariance using this covariable frequently resulted in improved efficiencies of 50 to 75 percent over randomized block designs and slight improvement over lattice designs. The technique did not add any plots, restrict plot layout, treatment number, nor require equal observations per treatment, and the additional computer time was said to be insignificant. This method of analysis was later called Productivity Covariance Analysis (PCA) by Buker and Alvey (1979), and was significantly superior to a randomized block design in 61 percent of 655 corn trials. The average error reduction was 36 percent. PCA was at least as efficient as a lattice design.

Townley-Smith and Hurd (1973) applied a 'moving mean' technique to reduce experimental error in wheat yield trials. The moving mean for each plot was the mean of a number of adjacent hybrid plots. Actual plot yield was adjusted by subtracting its moving mean. The moving mean technique was superior to randomized complete block designs in all 13 experiments. The optimum number of plots to include in the moving mean varied from 4 to 18. Moving mean technique was compared to the use of checks and was superior. The disadvantages of moving means, the authors said, are the need for complete randomization and the need to harvest all plots.

The moving mean technique was applied to several forage grasses by Lawrence and Townley-Smith (1975). The moving mean was subtracted from the actual yield to obtain an adjusted yield. The moving mean gave a lower MSE than the randomized block design in 55 of 59 trials and was equal in the remaining four. Lattice designs were equivalent to moving means for reduction of MSE.

Control plots, moving means, and lattice designs were compared for error control in barley nurseries by Mak et al. (1978). Control or check plots were grown every third plot. Errors in the traits grain yield and percent protein were studied. The use of percent of the moving mean or percent of checks was inferior to the use of covariance, and occasionally inferior to a randomized block design. The use of covariance of check plots or moving means was equal to the lattice design for error control.

MATERIALS AND METHODS

Objectives of this recurrent selection study are: 1) to identify suitable methods of grain yield evaluation in small plots, 2) to determine the effects of intermating on the mean value and variance of heading date, plant height, and grain yield, and 3) to evaluate the response to one cycle of selection for grain yield. The barley germplasm used in this study consisted of the following single cross populations:

Single cross 1 (SC-1): Woodvale/CI1237//PI372083

Single cross 2 (SC-2): Steptoe/M21//Kar1

Single cross 3 (SC-3): Short Wocus//Robur

Single cross 4 (SC-4): Blazer/M22//M22/Zephyr

Pedigrees and descriptions of the parents are given in Appendix Table 1. Single cross populations were chosen based on an expectation of high grain yield and genetic diversity. A fifth population was developed by intermating the four single cross populations for two generations.

Objectives of this study were carried out by growing the five breeding populations or their progeny in a series of three field experiments. These experiments are labeled the 1979 Small Plot Experiment, the 1980 Large Plot Experiment, and the 1980 Small Plot Experiment. Logistics of the development and testing of breeding populations is outlined in Appendix Table 2.

1979 Small Plot Experiment

Generation of Experimental Populations

F_2 populations of each of the four single crosses were grown in the summer of 1978 at the Klamath Experiment Station. Fifty random F_3 lines of each population were formed by harvesting seed of fifty random F_2 plants in each population. The F_3 seed was counted, weighed on a Sybron Digimetric scale to determine seed weight, and prepared for planting in the Spring of 1979.

An intermated population, the Cycle 0 (C-0) base population for a recurrent selection program was developed by intermating the four single cross populations for two generations. The first intermating generation was accomplished in summer 1978 by mating random F_2 plants from the four single cross populations in all possible inter- and intra-population combinations. Twenty crosses were obtained for each of the 10 possible combinations. Plants were grown from first generation intercrosses in the greenhouse during fall of 1978. The second intermating generation was accomplished by intermating these plants at random. One-fourth of the attempted crosses set seed, and 179 crosses were obtained. These 179 crosses represent the C-0 population. A single plant was grown from each cross in the greenhouse during winter of 1979. S_1 lines were formed by allowing the plants to self-pollinate. The S_1 seed was harvested, counted, weighed on a Sybron Digimetric scale to determine seed weight, and prepared for field planting in Spring of 1979. Plants in the greenhouse were grown rapidly so that S_1 lines would be ready for spring planting. As a result, late

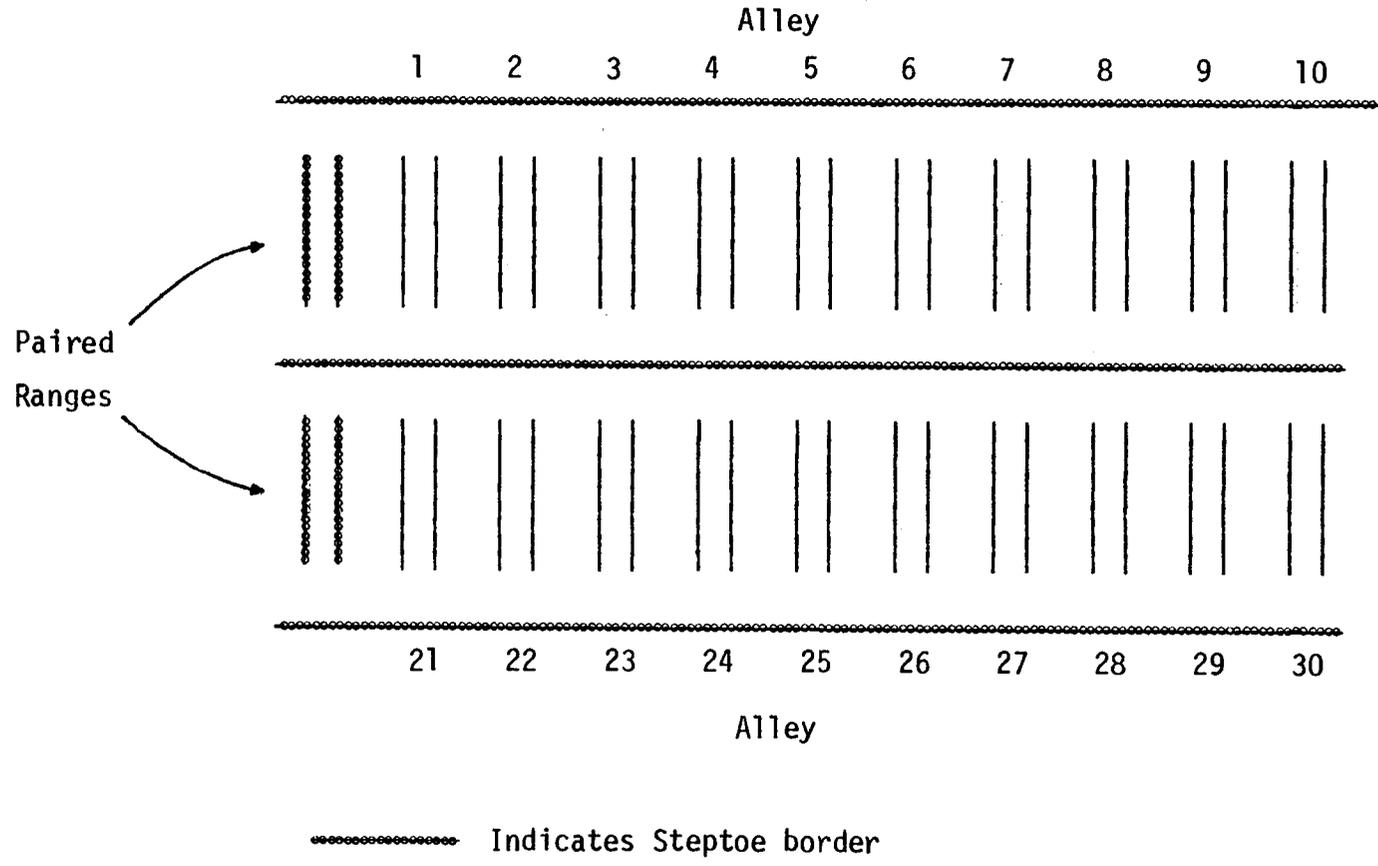
flowering plants were not intercrossed in the fall greenhouse period, and 19 late maturing plants were not harvested in the winter greenhouse period. Thus, only 160 S_1 lines from the C-0 population were prepared for spring planting.

Bulks of each of the single cross populations were prepared by compositing an equal quantity of seed from each of the fifty F_3 lines in the population. A bulk of the C-0 population was not created because of insufficient seed.

Methods

The parental lines (excluding Robur), 'Steptoe' (as a check), bulk populations, 50 F_3 lines from each single cross population, and 160 S_1 lines from the C-0 population were planted at East Farm near Corvallis on March 22, 1979. A second planting was made near Redmond at the Central Oregon Experiment Station on March 24, 1979. The F_3 and S_1 lines were not replicated within the locations. The parental lines, Steptoe, and the bulk populations were replicated at each location. Plots were two rows, 91 centimeters long, with 30 centimeters between rows. Entries were completely randomized and hand seeded with 160 seeds per plot. Plots were grown in paired ranges (Figure 1) and a single, solid seeded row of Steptoe barley was grown 30 centimeters from the edge of each range to serve as a border. Both locations have a sandy loam soil and received 90 kg of nitrogen per hectare prior to planting. Irrigation water was applied as needed from sprinklers mounted on movable pipe. Weed control was accomplished by applying .42 kg/ha A.I. Bromoxnil at the three to five leaf stage.

Figure 1. Plot layout with numbered plots for 1979 and 1980 Small Plot Experiments.



Plant height, visual evaluation, and grain yield data were taken on each plot in both locations. Heading date data were taken only at East Farm and was measured as the number of days from planting until 50% of the heads emerged from the boot. Plant height was the average distance in centimeters from the soil surface to the middle of the head. Visual evaluation is a visual rating from 1 (poor) to 9 (excellent), which characterized the agronomic value of an entry. Visual evaluation was based on expected grain yield, plant height, straw strength, and disease resistance. Grain yield was measured by harvesting the entire plot with a sickle, threshing it in a stationary Vogel grain harvester, and weighing the grain on a Mettler PS15 electronic scale. Grain yield per plot was then transformed to quintals (100 kg) per hectare.

During the two-week period following planting at East Farm, pheasants dug up and ate seeds from approximately 40% of the plots. Ten percent of the plots were severely damaged and were discarded. Grain weight of the partially damaged plots was corrected by the following formula:

$$\text{corrected grain weight} = \text{harvested grain weight} + \left(\frac{\text{harvested grain weight}}{6-X} \right) \left(\frac{X}{2} \right)$$

where X is the length, in feet (30 cm), of the portion of the plot that was damaged. One month after planting there were patches of yellow and stunted plants at East Farm. Plant samples were taken to Paul A. Koepsell, Extension Plant Pathologist, who identified the pathogen as Helminthosporium sativum, a foot rot fungus. Leaf rust Puccinia hordei Oth., was present late in the growing season at East Farm but was not serious. There were no serious disturbances at Redmond except for

gopher damage on 12 plots. Grain yield on these plots was corrected in the aforementioned manner.

Moving Mean Technique

Five configurations of moving mean covariables were computed for each plot in each location. The moving mean covariable for a given plot is the mean grain yield of a number of nearby plots. Using the plot numbers in Figure 1, the five configurations used to compute the moving means for plot number 6 include the following plot numbers:

Nearest 3 plots: numbers 5, 7, and 26

Nearest 5 plots: numbers 5, 7, 25, 26, and 27

Nearest 9 plots: numbers 4, 5, 7, 8, 24, 25, 26, 27, and 28

Nearest 13 plots: numbers 3, 4, 5, 7, 8, 9, 23, 24, 25, 26, 27, 28, and 29

Nearest 6 plots: numbers 3, 4, 5, 7, 8 and 9.

When moving means needed to be computed for plots at the end of a range the nearby plots were all on one side of the plot of interest. For instance, the moving mean which includes the nearest 5 plots for plot number 1 consists of plots number 2, 3, 21, 22, and 23.

Grain yield of the replicated parental lines, Steptoe, and bulk populations were analyzed as a completely randomized design to estimate experimental error at each location. Five configurations of moving means were used as covariables in an analysis of covariance in an attempt to reduce experimental error (Steel and Torrie, 1980; Snedecor and Cochran, 1973). The best moving mean covariable was chosen at each location based on the lowest error mean square for grain yield of the

replicated entries at that location. A regression coefficient (b) was estimated for the best moving mean at each location. The regression coefficient was then used to adjust the grain yield of each entry at each location with the following formula:

$$Y_A = Y - b(MM - \overline{MM})$$

where; Y_A = the adjusted grain yield,
 Y = the actual grain yield of a given plot,
 MM = the moving mean covariable for a given plot, and
 \overline{MM} = the average moving mean covariable.

Analysis

Plant height, visual evaluation, actual grain yield, and moving mean adjusted grain yield were analyzed in each population using the following form of the analysis of variance:

<u>Source of Variation</u>	<u>Degrees of freedom</u>	<u>Mean Square</u>	<u>Expected Mean Squares</u>
Environment	$e-1$		
Genotype	$g-1$	MS_g	$\sigma^2 + \sigma_{ge}^2 + e\sigma_g^2$
Genotype x Environment	$(e-1)(g-1)$	MS_{ge}	$\sigma^2 + \sigma_{ge}^2$

where: e = the number of environments,
 g = the number of genotypes,
 σ^2 = the variance of plots treated alike,
 σ_{ge}^2 = the variance due to interactions of genotypes and environments, and
 σ_g^2 = the variance due to genotypes.

The hypothesis that there is no genetic variation among the genotypes for the trait studied, $H_0: \sigma_g^2 = 0$, was tested by $F = MS_g/MS_{ge}$ with $g-1$ and $(g-1)(e-1)$ degrees of freedom. Genetic variation was estimated by setting the observed mean squares equal to the expected mean squares and solving for the components. Standard errors of variance components were obtained according to the methods given by Kempthorne (1975). Heritability of F_3 or S_1 lines was estimated by dividing genetic variance by the variance of phenotype means. The variance of phenotype means is MS_g/e .

Heading date data were taken in a single location. Error variance ($\hat{\sigma}^2$) for heading date was estimated from an analysis of the parental lines, Steptoe, and the bulk populations. Phenotypic variance ($\hat{\sigma}_p^2$) for heading date was estimated directly by the variance of the observed heading date of the entries in each population. Genetic variance for heading date was estimated by $\hat{\sigma}_p^2 - \hat{\sigma}^2$. The hypothesis that there is no genetic variation for heading date, $H_0: \sigma_g^2 = 0$, was tested by $F = \hat{\sigma}_p^2 / \hat{\sigma}^2$ with the appropriate degrees of freedom. Heritability was estimated by the ratio $\hat{\sigma}_g^2 / \hat{\sigma}_p^2$. Standard errors of variance estimates were also obtained according to the methods outlined by Kempthorne (1975).

Estimates of Grain Yield Potential

The following methods were used to estimate grain yield potential of lines in all populations grown in the 1979 Small Plot Experiment: (1) visual evaluation, (2) actual grain yield, (3) moving mean adjusted grain yield, (4) a 'statistical' index and (5) a 'best guess' index.

Both indices have weights on both visual evaluation and moving mean adjusted grain yield.

The statistical index is computed using estimates of genetic and phenotypic variances and covariances. Estimates of the genetic and phenotypic covariances between two traits are obtained from an analysis of cross products. The analysis of cross products is completely analogous to the analysis of variance previously described. Thus, the mean cross product for genotypes (MCP_g) replaces the mean square for genotypes (MS_g), and the genetic component of covariance between traits 1 and 2 (σ_{g12}) replaces the genetic component of variance (σ_g^2). Estimates of components of covariance are obtained in the same manner as the components of variance, by setting the observed mean cross product equal to the expected mean product and solving for the components. Just as the phenotypic variance for a trait is obtained by MS_g/e , the phenotypic covariance between two traits is obtained by MCP_g/e . The following set of simultaneous equations (Robinson et al., 1951) was used to estimate the weights to apply to visual evaluation and grain yield when constructing the statistical selection index:

$$b_v P_{vv} + b_y P_{vy} = G_{vy}$$

$$b_v P_{vy} + b_y P_{yy} = G_{yy}$$

where; b_v = the relative weight applied to visual evaluation,
 b_y = the relative weight applied to grain yield,
 P_{vv} = the phenotypic variance of visual evaluation,

P_{vy} = the phenotypic covariance between visual evaluation and grain yield,

G_{vy} = the genetic covariance between visual evaluation and grain yield,

P_{yy} = the phenotypic variance of grain yield, and

G_{yy} = the genetic variance of grain yield.

The solution of the simultaneous equations will give the desired weights to use in the statistical selection index. The weights are then used in the following formula to estimate index values for selection:

$$I = b_v V + b_y Y$$

where; I = the index value for a given line
 V = the mean visual evaluation for a given line, and
 Y = the moving mean adjusted grain yield for a given line.

Statistical index values were computed for each line in each of the five populations.

The best guess index was also computed for each line in each of the five populations. In addition, best guess index was computed for all F_3 lines as though they were from a single population. Index values were computed by adding the product of .3 times the standardized visual evaluation to the product of .7 times the standardized grain yield. A standardized variable has a mean of zero and a variance of one. Weights

for grain yield and visual evaluation were judgementally chosen based on the importance and reliability of data on both traits.

1980 Large Plot Experiment

Parental lines (except Robur), Steptoe, bulk populations, 21 random S_2 bulks from the C-0 population, and 21 random F_4 bulks from each of the four single cross populations were planted on April 3, 1980 near Moro at Kaseberg's farm, on April 17, 1980 at Holmes Farm near Corvallis, and on May 1, 1980 near Klamath Falls at the Klamath Experiment Station. The 21 random S_2 and F_4 bulks were obtained by harvesting the seed produced by S_1 and F_3 lines grown the previous year in the 1979 Small Plot Experiment. Bulk populations for all five populations were obtained by compositing equal quantities of seed from all lines in the respective populations. Only the parental lines (excluding PI372083), Steptoe, and the bulk populations were replicated at each location and had three replications. Entries were completely randomized. Plots were 6 rows, 1.5 meters wide and 6.1 meters long. Planting was done with a seed drill at a rate of 100 kg per hectare which is the commercial seeding rate for this area. Soil type at all locations was a silt loam. Holmes Farm received 55 kg of nitrogen per hectare, Moro received 110 kg of nitrogen per hectare, and Klamath Falls received 135 kg of nitrogen per hectare prior to planting. Irrigation water was applied as needed from sprinklers mounted on movable pipe. Weed control was accomplished by applying .42 kg/ha A.I. Bromoxynil at the three to five leaf stage. Prior to harvest, plots were cut back

with hand-held sickle to 4.27 meters at Holmes Farm and to 3.81 meters at Klamath Falls. Plots were cut back to 4.27 meters at Moro by a Hege plot combine.

Plant height, visual evaluation, and grain yield data were taken on each plot at each location. Heading date data were taken at Holmes Farm only. Heading date, plant height, and visual evaluation were measured as previously described. Grain yield was measured by harvesting the plots with a Hege plot combine and weighing the grain on a Mettler PS15 electronic scale. Grain yield was transformed into quintals per hectare.

Moving means were computed for each plot and used as previously described to reduce experimental error for grain yield. Five configurations of moving means were used and they consisted of the mean grain yield of the nearest 4, 6, 8, 10, and 12 plots in the same range as the plot of interest. The moving mean plots were generally placed with equal numbers of plots on either side of the plot of interest. However, when the plot of interest was near the end of the range then the majority of the plots included in the moving mean were on one side of the plot of interest. Moving mean plots were always in the same range as the plot of interest. The grain yield of the replicated parental lines, Steptoe, and the bulk populations were analyzed at each location to estimate experimental error. Analyses included an analysis of variance with no moving mean and five analyses of covariance, one for each configuration of moving mean. The analysis with the lowest error mean square was chosen and grain yields were adjusted as previously mentioned.

Estimates of genetic variances for heading date, plant height, and grain yield were obtained, tested for significance, standard errors computed, and heritabilities estimated as previously indicated. The covariance between trait means of F_3 and S_1 lines grown in the 1979 Small Plot Experiment and trait means of the corresponding F_4 and S_2 bulks grown in the 1980 Large Plot Experiment were estimated using standard statistical methods. Five methods used to estimate grain yield potential of F_3 and S_1 lines in the 1979 Small Plot Experiment were correlated with moving mean adjusted grain yield in the 1980 Large Plot Experiment using standard statistical procedures. Comparisons of the means of the different populations were tested for significance using Cochran's approximate t-test (Snedecor and Cochran, 1973), which allows unequal variances and numbers of observations. All possible correlations between the entry means for heading date, plant height, visual evaluation, and grain yield were computed for each population in the 1980 Large Plot Experiment.

1980 Small Plot Experiment

The best 10 percent of the F_3 lines grown in the 1979 Small Plot Experiment were selected based on the 'best guess' index of the single cross populations as a whole. Of the 18 lines selected, nine came from SC-1 and nine came from SC-2. Five individual F_3 plants were harvested from each selected F_3 line from a space planted nursery grown in the summer of 1979 at the Klamath Experiment Station. The F_4 seed was

counted, weighed on a Sybron Digimetric scale to determine seed weight, and prepared for planting.

The best 10 percent of the S_1 lines grown in the 1979 Small Plot Experiment were selected based on the best guess index. S_2 seed of the 16 selected lines was planted on two dates in the greenhouse in the fall of 1979. The plants were intercrossed at random and 210 crosses set seed. These crosses constitute the Cycle 1 (C-1) population of the recurrent selection program. A single plant was grown from each cross during the winter of 1980 and allowed to self-pollinate. Plant growth in the greenhouse was far superior to the previous year due to improved lighting and better plant care. The seed of 208 S_1 lines was harvested, counted, weighed on a Sybron Digimetric scale to determine seed weight, and prepared for planting.

In addition, during the 1980 winter greenhouse period, 14 random plants from the C-0 population, four plants of each parental line (excluding Robur), and four plants of Steptoe were grown and allowed to self-pollinate. The 14 S_1 lines from the C-0 population were used to compute progress from selection. The parental lines and Steptoe were used to study the effect of seed source on plant growth. The seeds were harvested, counted, weighed on a Sybron Digimetric scale to determine seed weight, and prepared for planting.

Field and greenhouse grown seed of parental lines and Steptoe, 208 C-1 S_1 lines, 14 C-0 S_1 lines, and 90 F_4 lines were planted near Moro at Kaseberg's farm on April 3, 1980 and at Holmes Farm near Corvallis on April 17, 1980. Both field and greenhouse grown seed of each parental line and Steptoe was grown with four replications in both locations. No

other entries were replicated. Plots were similar to the 1979 Small Plot Experiment except that the distance between rows within the plot was reduced from 30 to 22 centimeters and the distance between rows between plots was increased from 30 to 38 centimeters. Border was 'Anza', a semi-dwarf spring wheat cultivar, and seeding rate was increased from 160 to 200 kernels per plot. Soil type at both locations was a silt loam. Holmes Farm received 55 kg of nitrogen per hectare and Moro received 110 kg of nitrogen per hectare prior to planting. Irrigation water was applied as needed from sprinklers mounted on movable pipe. Weed control was accomplished by applying .42 kg/ha A.I. Bromoxynil at the three to five leaf stage.

Plant height, visual evaluation, and grain yield data were taken on each plot as previously reported. Heading date was also measured as previously reported but only at Holmes Farm. There were no serious problems with plant growth except at Moro where a combination of shallow planting and rodent attack caused thin stands. The length in feet (30 cm) of damaged plot was estimated and grain yield was corrected as in the 1979 Small Plot Experiment. Moving means were computed and used as in the 1979 Small Plot Experiment. All possible correlations between entry means for heading date, plant height, visual evaluation, and grain yield were computed for the C-1 population.

Since the groups of genotypes grown in the 1980 Small Plot Experiment differed in seed source, it became necessary to evaluate the effect of seed produced in the greenhouse on subsequent plant growth. Greenhouse and field-grown seed effects were analyzed on the parental

lines and Steptoe for heading date, plant height, and grain yield using the following analysis of variance:

<u>Source of Variation</u>	<u>Degrees of freedom</u>	<u>Mean Squares</u>
Entries	$gs-1$	
Genotypes	$g-1$	
Seed source	$s-1$	MS_S
Genotype x Seed source	$(g-1)(s-1)$	MS_{gs}
Entries x Environments	$(gs-1)(e-1)$	MS_{ge}
Pooled Error	$(r-1)gse$	MS

where; g = the number of genotypes (8),
 s = the number of seed sources (2),
 e = the number of environments, and
 r = the number of replications per environment (4).

The hypothesis that there is no genotype x seed source interaction for the trait studied, Test A, is tested by $F = MS_{gs}/MS_{ge}$ with $(g-1)(s-1)$ and $(gs-1)(e-1)$ degrees of freedom. Since MS_{ge} is not estimable for heading date, Test A is obtained by $F = MS_{gs}/MS$ with $(g-1)(s-1)$ and $(r-1)gse$ degrees of freedom. The hypothesis that there are no seed source effects for the traits studied, Test B, is tested by $F = MS_S/MS_{gs}$ with $s-1$ and $(g-1)(s-1)$ degrees of freedom.

There are several mean comparisons that could be tested in the 1980 Small Plot Experiment. Mean comparison 1 is greenhouse grown parental lines vs. C-1 S_1 lines. Mean comparison 2 is C-0 S_1 lines vs. C-1 S_1 lines. Mean comparison 3 is C-1 S_1 lines vs. selected F_4 lines. Mean

comparison 4 is selected F_4 lines vs. field grown parental lines. Unfortunately, many of these comparisons are confounded by seed source effects. If neither Test A nor Test B of the parental lines is significant, then all four mean comparisons could be made. If Test A is significant, then only mean comparison 4 would be appropriate. If just Test B is significant, then only mean comparison 3 would be improper. Thus the mean comparisons that can be tested depend upon tests of significance of seed source effects and seed source x genotype interactions for that trait in the parental lines. Mean comparisons were tested using Cochran's approximate t-test (Snedecor and Cochran, 1973), which allows unequal numbers of observations and unequal variances. The mean of parental lines is 1/7 times the sum of the values for all parents except Robur, which is a winter type. The value of Blazer/M22 is included a second time in place of M22/Zephyr because SC-4 is a self-pollination.

Genetic effects for heading date, plant height, and grain yield for the selected F_4 lines within each single cross population were analyzed using the following form of the analysis of variance:

<u>Source of Variation</u>	<u>Degrees of freedom</u>	<u>Mean Squares</u>	<u>Expected Mean Squares</u>
F_4 lines	$ab-1$		
F_3 groups	$a-1$	MS_a	$\sigma^2 + \sigma_{ge}^2 + e\sigma_{F_4/F_3}^2 + eb\theta^2$
F_4 lines/ F_3	$a(b-1)$	MS_b	$\sigma^2 + \sigma_{ge}^2 + e\sigma_{F_4/F_3}^2$
F_4 lines x Env.	$(ab-1)(e-1)$	MS	$\sigma^2 + \sigma_{ge}^2$

where;

- a = the number of F_3 groups
- b = the number of F_4 lines within each F_3 group (5),
- e = the number of environments,
- σ^2 = the variance of plots treated alike,
- σ_{ge}^2 = the variance due to interaction of F_4 lines and environments
- σ_{F_4/F_3}^2 = the pooled variance of genetic effects of F_4 lines from the same F_3 lines, and
- θ^2 = the variation due to genetic effects of selected F_3 lines.

The hypothesis that no genetic differences exist between the F_4 lines within the F_3 groups of each single cross for the trait studied, $H_0: \sigma_{F_4/F_3}^2 = 0$, is tested by $F = MS_b/MS$ with $a(b-1)$ and $(ab-1)(e-1)$ degrees of freedom. For heading date, MS is not estimable, thus the test is $F = MS_b/MS_e$ with the appropriate degrees of freedom and MS_e equal to the error variance for heading date of parental lines. The hypothesis that no genetic differences exist between F_3 groups of each single cross for the trait studied, $H_0: \theta^2 = 0$, is tested by $F = MS_a/MS_b$ with $a-1$ and $a(b-1)$ degrees of freedom. Since the F_3 groups are selected, it is clear that they are a fixed effect. Nevertheless, in many cases they will be dealt with as though they are a random effect because this will often be more informative. Estimates of variance components were obtained by setting expected mean squares equal to observed mean squares and solving for the components. Estimates of the

standard errors of variance components were obtained according to the methods of Kempthorne (1975).

Estimates of genetic variances for heading date, plant height, and grain yield of the C-0 and C-1 populations were obtained, tested for significance, and standard errors and heritability estimated as previously mentioned. Realized heritability of grain yield was estimated using the following formula:

$$\frac{(C_{180} - C_{080})/C_{080}}{(C_{079S} - C_{079})/C_{079}}$$

where; C_{180} = the mean grain yield of the C-1 population in 1980,
 C_{080} = the mean grain yield of the C-0 population in 1980,
 C_{079S} = the mean grain yield of selected lines in the C-0 population in 1979, and
 C_{079} = the mean grain yield of the C-0 population in 1979.

This is a selection response divided by selection differential (gain over reach) type of heritability estimate that is adjusted for differences in yield performance due to different testing environments.

The number of additional cycles of recurrent selection required to increase the mean grain yield of the C-1 population to the mean grain yield of Steptoe was estimated in two ways. The first estimate was obtained by dividing the grain yield difference between Steptoe and the C-1 population by the grain yield difference between the C-1 and C-0 populations. The second estimate was obtained by dividing the

difference between Steptoe and the C-1 population by the expected gain from selection in the C-1 population. Expected gain from selection was obtained by multiplying the C-1 heritability estimate times the selection differential. The selection differential is the difference between the mean grain yield of the best 10 percent of the C-1 S_1 lines identified with the best guess index, and the mean grain yield of the C-1 population.

The small plot experiments at Holmes Farm and Moro in 1980 were planted in the vicinity of the 1980 Large Plot Experiments grown in the same two locations. Parental lines and Steptoe were grown in both experiments. Their mean grain yield across locations was computed for both plot types and plotted on a graph. Standard error of mean grain yield was computed for both plot types using experimental error.

Data Management

All field data were punched onto computer cards and analyzed by a Cyber model, Control Data Computer. Data analysis was handled by programs written in the Fortran language. Data were first entered into the Moving Mean program which computed the five moving mean covariables for each plot and stored the results on a permanent computer file. These results were then entered in the Ancova program which computed an analysis of variance and five analyses of covariance for the replicated lines at each location. The Combine program took the results of both the Moving Mean and Ancova programs and adjusted the grain yield by the

moving mean covariable, computed analyses of variance for all traits, and provided the necessary information for selection. Simpler analyses were done with a Hewlett-Packard model 33E programmable calculator.

RESULTS

Results of the field experiments will be presented in three sections. Each section relates to one of the objectives of this recurrent selection study. The first section deals with methods used to evaluate germplasm. The second section reports the effect of intermating on means and variances of several agronomic characters. The final section evaluates the response to one cycle of selection for grain yield.

A summary of climatological data for the 1979 growing season is presented in Appendix Table 3. Higher than normal temperatures and lower than normal precipitation contributed to reduced plant height and grain yield at Redmond. Helminthosporium sativum, a foot rot of barley, caused patches of stunted plant growth at East Farm in 1979.

Crop growth was excellent at all locations in 1980. Temperatures were often below normal and rainfall above normal during the critical months of April, May and June. A summary of 1980 climatological data is given in Appendix Table 4.

Methods of Evaluation

Moving means were used in all three field experiments in an attempt to reduce experimental error for grain yield. The appropriate moving mean was chosen at each location based on an analysis of parents and checks (Tables 1, 3 and 5) and was used to adjust the grain yield of all lines of all populations grown at that location. This, in turn,

affected the genotype x location mean squares for grain yield in each population (Tables 2, 4 and 6).

The effect of moving mean covariables on error mean square (MSE) for grain yield of lines replicated at each location in the 1979 Small Plot Experiment is given in Table 1. At East Farm, a standard analysis of variance of parental lines, Steptoe, and bulk populations gave a MSE of 96.6 and a coefficient of variation (CV) of 27 percent. The analysis of covariance, using the mean grain yield of the nearest 3 plots as a covariable, resulted in the lowest MSE (61.7) and the lowest CV (21%). Thus the use of a moving mean resulted in a 36 percent reduction in experimental error. The analysis of covariance, again using the mean grain yield of the nearest 3 plots as a covariable, was used to estimate the regression coefficient. The regression coefficient, $b = .746$, was used to adjust grain yield of all lines grown at East Farm in the 1979 Small Plot Experiment.

At Redmond (Table 1), the greatest reduction in EMS occurred with a moving mean consisting of the nearest 6 plots. Analysis of covariance, using the mean grain yield of the nearest 6 plots as a covariable, reduced MSE from 81.3 to 16.3, an 80 percent reduction. The CV was reduced from 23 to 10 percent. The regression coefficient, $b = 1.00$, was used to adjust grain yield of all lines grown at Redmond in the 1979 Small Plot Experiment.

Genotype x location mean squares for grain yield of five populations were considerably reduced by adjusting grain yield with moving means (Table 2). The genotype x location mean square represents the failure of the difference between genotypes to remain constant from location to

Table 1. Effect of five configurations of moving mean covariables on error mean square for grain yield of parental lines, Steptoe, and bulk populations grown in two locations, 1979 Small Plot Experiment.

Moving Mean Covariable	Error Mean Square for Grain Yield (q/ha)	
	East Farm	Redmond
No Covariable	96.6 (.27)†	81.3 (.23)
Nearest 3 plots	61.7 (.21)	28.1
Nearest 5 plots	79.2	34.9
Nearest 9 plots	88.3	28.4
Nearest 13 plots	79.0	29.4
Nearest 6 plots	90.9	16.3 (.10)
Mean Grain Yield (q/ha)	36.9	39.8

† Coefficients of variation are presented in parenthesis for the standard analysis of variance (no covariable) and for the moving mean covariable with greatest reduction in error mean square.

Table 2. Effect of adjusting grain yield by moving means of genotype x location mean squares for grain yield of five populations grown in two locations, 1979 Small Plot Experiment.

Population	d.f.	Genotype x Location Mean Square for Grain Yield (q/ha)	
		Actual	Adjusted by Moving Mean
SC-1	41	92.4	70.1
SC-2	46	132.5	75.8
SC-3	43	95.2	62.7
SC-4	42	150.5	90.5
C-0	140	111.2	64.6

Table 3. Effect of five configurations of moving mean covariables on error mean square for grain yield of parental lines, Steptoe, and bulk populations grown in three locations, 1980 Large Plot Experiment.

Moving Mean Covariable	Error Mean Square for Grain Yield (q/ha)		
	Holmes Farm	Moro	Klamath Falls
No Covariable	12.3 (.075)†	34.4 (.104)	28.1 (.097)
Nearest 4 plots	12.8	23.4 (.085)	28.3
Nearest 6 plots	12.8	29.7	29.0
Nearest 8 plots	12.5	31.1	27.4
Nearest 10 plots	12.5	33.5	26.5
Nearest 12 plots	12.3 (.075)	33.0	26.2 (.094)
Mean Grain Yield (q/ha)	46.8	56.7	54.4

† Coefficients of variation are presented in parenthesis for the standard analysis of variance (no covariable) and for the moving mean covariable with greatest reduction in error mean square.

Table 4. Effect of adjusting grain yield by moving means on genotype x location mean squares for grain yield of five populations grown in three locations, 1980 Large Plot Experiment.

Population	d.f.	Genotype x Location Mean Square for Grain Yield (q/ha)	
		Actual	Adjusted by Moving Mean
SC-1	40	66.3	58.4
SC-2	38	60.5	60.3
SC-3	38	28.0	23.7
SC-4	38	15.8	17.7
C-0	40	42.3	40.2

Table 5. Effect of five configurations of moving mean covariables on error mean square for grain yield of parental lines and Steptoe grown in two locations, 1980 Small Plot Experiment.

Moving Mean Covariable	Error Mean Square for Grain Yield (q/ha)	
	Holmes Farm	Moro
No Covariable	28.2 (.112)†	49.5 (.123)
Nearest 3 plots	26.4	49.3
Nearest 5 plots	25.8	49.2
Nearest 9 plots	25.9	49.6
Nearest 13 plots	24.6	47.5
Nearest 6 plots	21.7 (.099)	41.3 (.112)
Mean Grain Yield (q/ha)	47.2	57.2

† Coefficients of variation are presented in parenthesis for the standard analysis of variance (no covariable) and for the moving mean covariable with greatest reduction in error mean square.

Table 6. Effect of adjusting grain yield by moving means on genotype x location mean squares for grain yield of three populations grown in two locations, 1980 Small Plot Experiment.

Population	d.f.	Genotype x Location Mean Squares for Grain Yield (q/ha)	
		Actual	Adjusted by Moving Mean
C-0	13	41.2	28.6
C-1	207	65.7	60.1
F ₄ lines	89	81.7	74.6

location. It has two causal components; experimental error within each location and the differential effect of the locations on genotype performance. The reduction of genotype x location mean squares due to adjustment of grain yield by moving means represents a reduction in the experimental error component.

The effect of five arrangements of moving means on the MSE for grain yield is given in Table 3 for each of three locations used in the 1980 Large Plot Experiment. At Holmes Farm, moving means were unable to reduce MSE. Plot yields at Holmes Farm were not adjusted by a moving mean covariable. At Moro, the best configuration for the moving mean was the nearest four plots. An analysis of covariance, using the mean grain yield of the nearest four plots as a covariable, reduced the MSE from 34.4 to 23.4, a 32 percent reduction. The CV was reduced from 10.4 to 8.5 percent. The regression coefficient, $b = .841$, was used to adjust grain yield of all lines grown at Moro in the 1980 Large Plot Experiment.

At Klamath Falls, an analysis of variance of replicated lines without a moving mean covariable gave an MSE of 28.1, which corresponds to a CV of 9.7 percent. The greatest reduction in MSE occurred with a moving mean covariable consisting of the nearest 12 plots, which gave a MSE of 26.2 and a CV of 9.4 percent. This is a seven percent reduction in MSE. The analysis of covariance, using the mean grain yield of the nearest 12 plots as a covariable, was used to estimate the regression coefficient. The regression coefficient, $b = .539$, was used to adjust the grain yield of all lines grown at Klamath Falls in the 1980 Large Plot Experiment.

Genotype x location mean squares for grain yield of five populations grown in three locations in the 1980 Large Plot Experiment (Table 4) are only moderately reduced by moving mean adjustments. The genotype x location mean square for SC-4 was slightly increased by adjusting grain yield with a moving mean.

The effect of moving means on MSE for grain yield of lines replicated at each of two locations is given in Table 5 for the 1980 Small Plot Experiment. At Holmes Farm, an analysis of variance using no moving mean gave a MSE of 28.2 and a CV of 11.2 percent. The greatest reduction in MSE occurred with a moving mean consisting of the nearest 6 plots, which gave a MSE of 21.7 and a CV of 9.9 percent. This is a 23 percent reduction in MSE. The analysis of covariance, using the mean grain yield of the nearest 6 plots as a covariable, was used to estimate the regression coefficient. The regression coefficient, $b = .649$, was used to adjust the grain yield of all lines grown at Holmes Farm in the 1980 Small Plot Experiment.

At Moro, the best configuration of moving mean was also the nearest 6 plots. Analysis of covariance, using the mean grain yield of the nearest 6 plots as a covariable, reduced the MSE from 49.5 to 41.3, a 17 percent reduction. This reduced the CV from 12.3 to 11.2 percent. The regression coefficient, $b = .529$, was used to adjust grain yield of all lines grown at Moro in the 1980 Small Plot Experiment.

Adjustment of grain yield in both locations of the 1980 Small Plot Experiment by moving means (Table 6) reduced genotype x location mean squares.

Five measures of grain yield potential were taken on each F_3 or S_1 line grown in the 1979 Small Plot Experiment. The correlations of these measures with moving mean adjusted grain yield of their F_4 or S_2 bulk progenies grown in the 1980 Large Plot Experiment are shown in Table 7 (single cross 4 is not included because it is a self-pollination). Best guess index and grain yield adjusted by a moving mean had consistently higher correlations with grain yield in 1980 than raw grain yield data. No other measurement of grain yield potential showed a consistent effect across all populations. Statistical index was generally inferior to the best guess index. On the average, visual evaluation was superior to raw yield data and inferior to moving mean adjusted grain yield. Single cross 3, the only winter x spring cross, had consistently negative correlations for these comparisons.

Phenotypic correlations between several traits are shown in Table 8. These correlations were estimated primarily to indicate which traits were being identified when plots were visually evaluated. Correlations between characters were relatively consistent across populations except for SC-3 which is a winter x spring cross. Visual evaluation was not related to grain yield except in SC-3. Progenies with high visual evaluation were much shorter and later heading. The correlation between grain yield and plant height tended to be negative for the populations grown in the 1980 Large Plot Experiment, but was positive, moderately large, and significant in the C-1 population grown in the 1980 Small Plot Experiment.

The relationship between grain yield in large plots vs. small plots is shown in Figure 2. The plotted means are from parental lines and

Table 7. Correlation of five measures of grain yield potential estimated on F₃ or S₁ lines of four populations grown in two locations in 1979 with moving mean adjusted grain yield of the related F₄ or S₂ bulks grown in three locations in 1980.

Population	Visual Evaluation	Grain Yield (raw data)	Grain Yield (Adjusted by moving mean)	Index (statistical)	Index (best guess)
SC-1	.26	-.08	.12	.14	.18
SC-2	.19	.41	.51*	.15	.48*
SC-3	-.28	-.42	-.27	-.24	-.30
C-0	.15	.11	.23	.13	.24

* Significant at the .05 level of probability.

Table 8. Phenotypic correlations between mean values of heading date, plant height, visual evaluation, and grain yield of five populations grown in the 1980 experiments.†

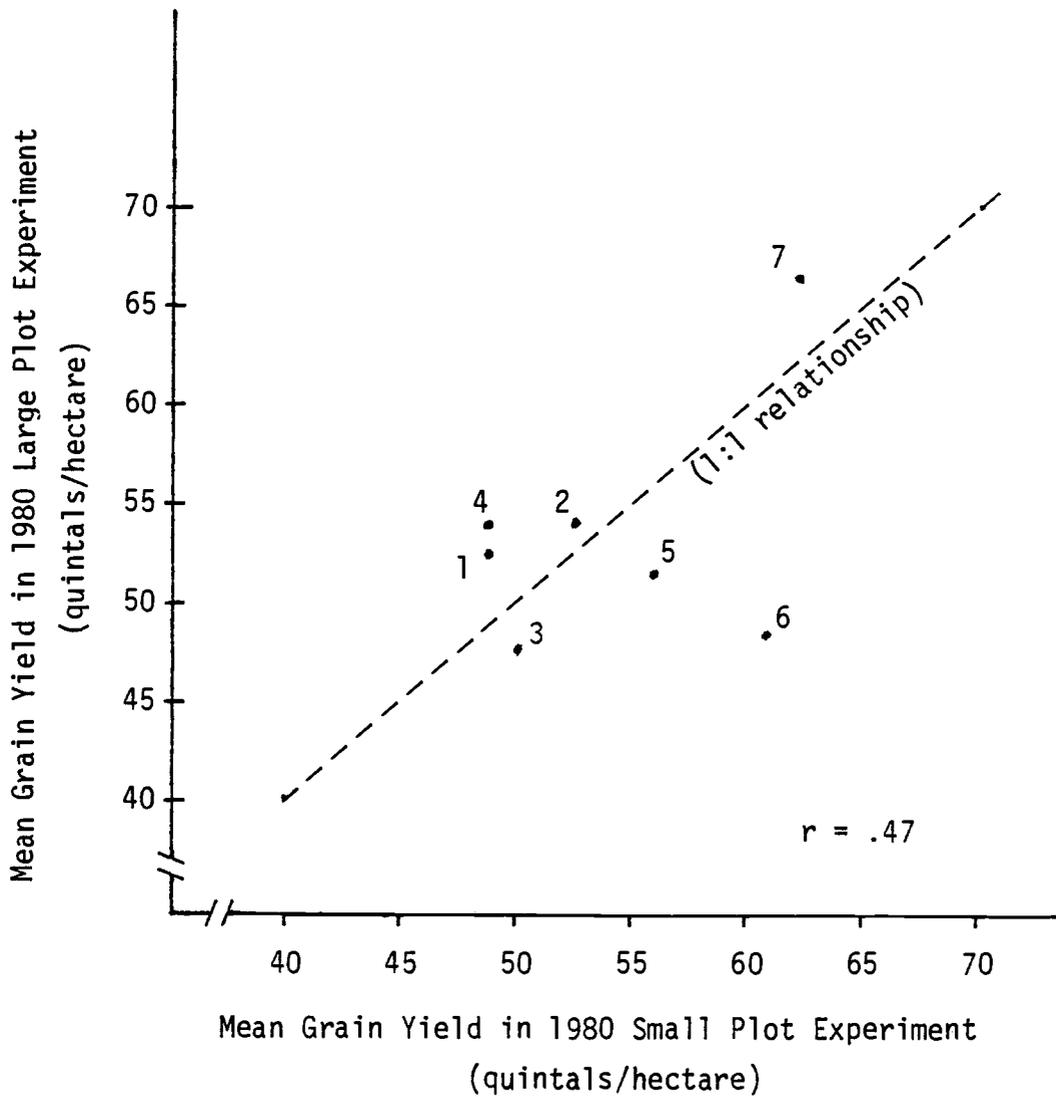
	<u>Visual Evaluation</u>	<u>Plant Height</u>	<u>Heading Date</u>
<u>Plant Height</u>			
SC-1	-.79**		
SC-2	-.78**		
SC-3	-.05		
C-0	-.81**		
C-1	-.65**		
<u>Heading Date</u>			
SC-1	.41	-.29	
SC-2	.57**	-.28	
SC-3	.16	.12	
C-0	.22	-.26	
C-1	.26**	-.17*	
<u>Grain Yield</u>			
SC-1	.16	-.11	-.12
SC-2	.10	-.41	-.55*
SC-3	.65**	-.31	-.08
C-0	.06	-.01	.10
C-1	-.13	.42**	-.28**

† Populations SC-1, SC-2, SC-3, and C-0 grown in large plots.
Population C-1 grown in small plots.

* Significant at the 5% level of probability

** Significant at the 1% level of probability.

Figure 2. Relationship between mean grain yield of parental lines and Steptoe grown in large plots with their mean grain yield in small plots. Means represent an average across two locations, Holmes Farm and Moro, in 1980 experiments.



1. M22/Zephyr
2. Blazer/M22
3. Karl
4. Steptoe/M21

5. Woodvale/CI1237
6. Short Wocus
7. Steptoe

Steptoe which were grown in both large and small plots at both Holmes Farm and Moro in 1980. Grain yields do not appear to fit the expected 1:1 relationship. Standard errors of mean grain yield, calculated from experimental error, are 1.7 and 2.0 quintals/hectare for large and small plots, respectively. This may be an underestimate of the appropriate error term needed to evaluate deviations from the expected 1:1 relationship. Parents 2 and 4 have short height, parent 1 is intermediate, and parents 3, 5, and 6 are all tall (Appendix Tables 6 and 7). Steptoe, the check, is also tall.

Effects of Intermating

Measurements of heading date, plant height, and grain yield were taken on F_3 or S_1 lines of five populations grown in the 1979 Small Plot Experiment. The means of these traits for five populations are shown but not compared in Table 9. They are not compared because of the vastly different 1,000 kernel weight of the seed planted. The C-0 population was grown from seed that was produced in the greenhouse, while the single cross populations were grown from seed that was produced in the field.

The mean of the C-0 population can be compared to the average of the single cross populations in the 1980 Large Plot Experiment (Table 10), because all plots were grown from field produced seed. The mean of the S_2 bulks of the C-0 population was significantly different from the mean of F_4 bulks of the single cross populations for heading date but not for plant height or grain yield.

Table 9. Population means for heading date, plant height, grain yield, and 1,000 kernel weight of five populations grown in two locations in the 1979 Small Plot Experiment.

Population	Population Means			
	Heading Date (days)	Plant Height (cm)	Grain Yield (q/ha)	1,000 kernel† Weight (grams)
SC-1	71	65	42.5	40.6
SC-2	71	72	45.0	37.8
SC-3	68	69	38.8	53.1
SC-4	71	60	33.6	38.8
C-0	69	65	33.3	26.8

† Weight of seed planted in the 1979 Small Plot Experiment.

Table 10. Population means and tests of significance for heading date, plant height, and grain yield of five populations grown in three locations in the 1980 Large Plot Experiment.

Populations	Population Means		
	Heading Date (days)	Plant Height (cm)	Grain Yield (q/ha)
SC-1	60.8	85	51.4
SC-2	60.2	95	51.4
SC-3	57.8	89	46.1
SC-4	60.3	75	54.7
SC-average	59.8	86	50.9
C-0	57.4	91	52.6
<u>Tests of Significance</u>			
C-0 vs. SC-average	**	ns	ns

** Significant at the 1% level of probability.

ns Not significant.

Estimates of genetic variance for heading date (Table 11) in the C-0 population were consistently larger than the estimates in the single cross populations. Single cross 4 had exceptionally low estimates of genetic variation for heading date. Single crosses 1, 2, and 3 were intermediate. The magnitude of the heritability estimates follow the same pattern as the estimates of genetic variance. Heritability was much larger in 1980 than in 1979. Heritability estimated by regressing 1980 data on 1979 data produced one value larger than one.

Estimates of genetic variance for plant height (Table 12) in the C-0 population were consistently larger than the estimates in the single cross populations. Single crosses 3 and 4 had low estimates of genetic variance and in two cases are not significant. Single crosses 1 and 2 had intermediate estimates of genetic variance for plant height. Heritabilities generally followed the magnitude of the genetic variance estimates. Heritabilities in the 1980 Large Plot Experiment were larger than in the 1979 Small Plot Experiment. Regression of plant height in 1980 on plant height in 1979 gave heritability estimates greater than one for two populations.

Few of the estimates of genetic variance for grain yield (Table 13) were significant and one-third are negative. Two-thirds of the estimates had standard errors greater than the estimates themselves. Heritabilities were variable, but generally quite low. Analyses of variance of all traits measured in the 1979 Small Plot and 1980 Large Plot Experiments are given in Appendix Tables 8 and 9.

Table 11. Estimates of genetic variance, its standard error, and heritability on a single plot basis for heading date of five populations grown in the 1979 Small Plot Experiment and the 1980 Large Plot Experiment.

Population	Genetic Variance for Heading Date (days)			Heritability on a Single Plot Basis		
	1979 Small Plot Experiment	1980 Large Plot Experiment	Covariance between 1979 and 1980 data	1979 Small Plot Experiment	1980 Large Plot Experiment	Regression of 1980 data on 1979 data †
SC-1	2.3** (.9) ††	4.9** (1.6)	3.0** (1.1)	.58	.95	.90
SC-2	3.8** (1.2)	5.5** (1.7)	3.8** (1.3)	.70	.96	1.13
SC-3	3.2** (1.1)	6.4** (2.0)	5.0** (1.7)	.66	.96	.87
SC-4	.5 (.6)	.1 (.1)	.5* (.3)	.22	.23	.24
C-0	6.0** (1.0)	8.4** (2.6)	7.8** (2.6)	.78	.97	.83

† Regression of F_4 or S_2 progeny on F_3 or S_1 parents.

†† Estimates of standard errors in parenthesis.

* Significant at the 5% level of probability.

** Significant at the 1% level of probability.

Table 12. Estimates of genetic variance, its standard error, and heritability on a progeny mean basis for plant height of five populations grown in the 1979 Small Plot Experiment and the 1980 Large Plot Experiment.

Population	Genetic Variance for Plant Height (cm)			Heritability on a Progeny Mean Basis [†]		
	1979 Small Plot Experiment	1980 Large Plot Experiment	Covariance between 1979 and 1980 data	1979 Small Plot Experiment	1980 Large Plot Experiment	Regression ^{††} of 1980 data on 1979 data
SC-1	38** (14)§	101** (35)	76** (26)	.59	.87	1.00
SC-2	16 (16)	124** (41)	70** (26)	.24	.93	1.31
SC-3	27** (11)	27** (11)	9 (7)	.53	.75	.37
SC-4	15 (10)	19** (8)	15** (6)	.36	.74	.70
C-0	59** (10)	153** (49)	91** (33)	.70	.94	1.06

[†] One plot in each of two locations for 1979 Small Plot Experiment and for regression of 1980 data on 1979 data. One plot in each of three locations for 1980 Large Plot Experiment.

^{††} Regression of F_4 or S_2 progeny on F_3 or S_1 parents.

§ Estimates of standard errors in parenthesis.

** Significant at the 1% level of probability.

Table 13. Estimates of genetic variance, its standard error, and heritability on a progeny mean basis for moving mean adjusted grain yield of five populations grown in the 1979 Small Plot Experiment and in the 1980 Large Plot Experiment.

Population	Genetic Variance for Grain Yield (q/ha)			Heritability on a Progeny Mean Basis [†]		
	1979 Small Plot Experiment	1980 Large Plot Experiment	Covariance between 1979 and 1980 data	1979 Small Plot Experiment	1980 Large Plot Experiment	Regression ^{††} of 1980 data on 1979 data
SC-1	16.6 (13.5) _§	-4.5 (6.2)	3.3 (6.8)	.32	-.30	.06
SC-2	3.4 (11.4)	5.7 (9.1)	15.2* (7.4)	.08	.22	.37
SC-3	8.8 (10.7)	34.4** (13.2)	-10.1 (8.5)	.22	.81	-.25
SC-4	-15.1 (11.6)	1.3 (2.6)	-.3 (4.8)	-.50	.18	-.01
C-0	16.7** (7.0)	-2.7 (4.4)	4.0 (4.3)	.34	-.25	.08

[†] One plot in each of two locations for 1979 Small Plot Experiment and for regression of 1980 data on 1979 data. One plot in each of three locations for 1980 Large Plot Experiment.

^{††} Regression of F_4 or S_2 progeny on F_3 or S_1 parents.

_§ Estimates of standard errors in parenthesis.

* Significant at the 5% level of probability.

** Significant at the 1% level of probability.

Results of Selection

The C-0 and C-1 populations, selected F_4 lines, parental lines, and Steptoe were grown in the 1980 Small Plot Experiment. Unfortunately, many of the comparisons between these populations were confounded by seed source effects. Some of the lines were planted with seed grown in the greenhouse and some with seed grown in the field. In order to determine which comparisons could be made, the effect of different seed sources on performance of parental lines and Steptoe was analyzed.

The analyses of variance of seed source effects on heading date, plant height, and grain yield of the parental lines and Steptoe are given in Table 14. Test A, the test for presence of genotype x seed source interaction, was significant for heading date but not for plant height or grain yield. Test B, the test of seed source effects, was significant for both heading date and grain yield.

Since Test A was significant for heading date, the only appropriate comparison for heading date (Table 15) was F_4 lines vs. parents and the difference was significant. Neither Test A or B was significant for plant height, thus all height comparisons were proper. C-1 population was taller than both population C-0 and parental lines. Selected F_4 lines did not significantly differ in height from either the C-1 population or the parental lines. Comparison of mean grain yield of selected F_4 lines vs. C-1 population was not proper because seed source effects were significant. Population C-1 was not significantly higher yielding than population C-0 but was significantly higher than the parental lines. Selected F_4 lines were also higher yielding than the

Table 14. Analysis of variance for heading date, plant height, and grain yield of parental lines and Steptoe planted with both field and greenhouse grown seed and grown in two locations in the 1980 Small Plot Experiment.

Source of Variation	d.f.	Mean Square Heading Date (days)	d.f.	Mean Squares	
				Plant Height (cm)	Grain Yield (q/ha)
Genotypes (G)	7	131.7**	7	666.8**	334.5**
Seed Source	1	30.3*	1	7.0	296.6*
G x Seed Source	7	2.7**	7	103.5	38.0
Entry x Location			15	56.9	25.2
Pooled Error	48	.7	96	26.4	38.9

* Significant at the 5% level of probability.

** Significant at the 1% level of probability.

Table 15. Tests of significance and means for heading date, plant height, and grain yield according to seed source for two populations, selected F₄ lines, parental lines, and Steptoe grown in two locations in the 1980 Small Plot Experiment.

Genotypes	Seed Source†	Means		
		Heading Date (days)	Plant Height (cm)	Grain Yield (q/ha)
C-0 S ₁ Lines	G	60.6	76.3	50.0
C-1 S ₁ Lines	G	59.8	83.1	53.6
Parental Lines	G	61.9	76.8	49.9
Steptoe	G	57.3	90.0	56.9
Selected F ₄ Lines	F	62.4	79.7	53.7
Parental Lines	F	60.3	78.8	51.3
Steptoe	F	55.8	85.0	60.2
<u>Tests of Significance</u>				
C-1 vs. parents	G+G	no test	**	**
C-1 vs. C-0	G+G	no test	*	ns
F ₄ lines vs. C-1	F+G	no test	ns	no test
F ₄ lines vs. parents	F+F	*	ns	*

† G indicates greenhouse grown seed, F indicates field grown seed.

* Significant at the 5% level of probability.

** Significant at the 1% level of probability.

ns Not significant.

parental lines. When interpreting these mean comparisons, one must recognize that different means are estimated with different precision.

A realized heritability for grain yield of .21 was estimated using the difference between the C-0 and C-1 populations (Table 15) divided by the selection differential from the 1979 Small Plot Experiment. The number of additional cycles of recurrent selection required to raise mean grain yield up to the level of Steptoe was estimated in two ways. An estimate of .9 additional cycles of selection was obtained by dividing the difference between Steptoe and the C-1 population by the difference between the C-1 and C-0 populations. An estimate of .7 additional cycles of selection was obtained by dividing the difference between Steptoe and the C-1 population by the product of grain yield heritability (.41) times the selection differential (11.1) of the C-1 population.

Estimates of genetic variation for heading date, plant height, and grain yield for germplasm tested in the 1980 Small Plot Experiment (Table 16) were all significant except for grain yield of F_4 lines within F_3 groups in both single cross populations. Estimates of genetic variance for heading date and grain yield in the C-0 population appeared to be larger than the estimates in the C-1 population. Variation of all three characters tended to be about the same for the C-1 population and F_3 groups of both single crosses. Genetic variation of F_4 lines within F_3 groups was always considerably less than genetic variation between F_3 groups, as would be expected. Analyses of variance of all traits measured in the 1980 Small Plot Experiment are given in Appendix Table 10.

Table 16. Estimates of genetic variation and its standard error for heading date, plant height, and grain yield for two populations and selected F₄ lines grown in two locations, 1980 Small Plot Experiment.

Genotypes	Estimates of Genetic Variation		
	Heading Date (days)	Plant Height (cm)	Grain Yield (q/ha)
C-0 S ₁ Lines	25.1** (9.4) [†]	74.** (37.)	47.8** (23.3)
C-1 S ₁ Lines	5.4** (.6)	88.** (11.)	20.6** (5.8)
<u>Selected F₄ Lines</u> ^{††}			
SC-1 F ₃ groups	7.8** (3.9)	53.** (27.)	22.3** (12.9)
SC-1 F ₄ Lines/F ₃	3.4** (.9)	26.** (9.)	-5.7 (9.1)
SC-2 F ₃ groups	8.7** (4.2)	89.** (44.)	24.0** (14.1)
SC-2 F ₄ lines/F ₃	2.6** (.8)	28.** (10.)	-.5 (10.1)

† Standard errors in parenthesis.

†† Variation estimates for F₃ groups are functions of fixed effects.

** Significant at the 1% level of probability.

DISCUSSION

Short cycle recurrent selection techniques have been used successfully to improve grain yield and other traits in cross-pollinated crops. The same techniques may be just as useful in self-pollinated crops such as barley. Most recurrent selection methods have been developed and discussed based on quantitative genetic theory. Quantitative genetic theory deals with the nature of genetic and environmental variation. This relates to recurrent selection since an appropriate form of recurrent selection is chosen based, in part, on the magnitude and nature of the genetic and environmental variation of the trait selected (Empig et al., 1972; Sprague and Eberhart, 1977; Gardner, 1978).

Short cycle recurrent selection techniques are seldom used by breeders of self-pollinated crops because it is difficult to intermate self-pollinated crops. This obstacle has been overcome in barley by the discovery and use of genetic male sterility (Suneson, 1945). There are two additional problems which should be investigated before recurrent selection is applied to the improvement of self-pollinated crops. The first problem is the possibility that frequent intermating might breakup favorably interacting associations of alleles which have evolved over centuries of self-pollination (Pederson, 1974). The second problem deals with evaluation trials. Due to the rapid cycling of many recurrent selection techniques, there often is little seed available for testing. Procedures for identifying superior segregates, particularly for grain yield, may need to be improved.

The results of this investigation of recurrent selection will be discussed as they apply to the following subjects: 1) methods of evaluation, 2) effects of intermating, and 3) results of selection.

Methods of Evaluation

The following procedures were utilized in the 1979 and 1980 Small Plot Experiments to more effectively identify superior yielding segregates in the populations studied: 1) family selection, 2) testing in multiple locations, 3) solid seeding, 4) border-harvest entire plot, 5) two row plots, 6) altered row spacing, 7) moving mean technique, and 8) index selection.

Progenies were evaluated as families instead of individuals because plant to plant environmental variation can largely be eliminated when families are evaluated. In addition, families can be replicated and this will reduce the effects of plot to plot environmental variation. If plots are replicated over several locations, then even greater reductions in environmental variation are possible (Hanson, 1963).

Barley is normally grown in a solid stand and more accurate yield testing would best be accomplished with solid seeded plots. A row of border was grown along the edge of the plots to reduce border effects. This allowed the entire plot to be harvested; thus the small quantity of seed available for testing was used efficiently.

Plots consisted of two short rows instead of a single long row. This reduces competition effects from adjacent rows (Hanson et al., 1961). In addition, plots (1980 Small Plot Experiment only) were grown

with reduced space between rows within the plot and increased space between rows between plots to reduce competition effects (Compton, 1977).

The results of this experiment indicated that competition effects from adjacent plots still exert a strong effect on grain yield in small plots. The grain yield of parents in the 1980 Small Plot Experiment did not appear to fit the expected 1:1 relationship with their grain yield in large plots. Deviations from the expected 1:1 relationship appear to be due to differences in plant height. Grain yield of taller parents was higher than expected in small plots. Grain yield of shorter parents was lower than expected in small plots. Phenotypic correlations between grain yield and plant height in both large and small plots offer further evidence that competition effects due to plant height existed in the small plot experiments. Correlations between grain yield and plant height were generally low and negative when measured on different populations in large plots. The correlation between grain yield and plant height in the C-1 population, which was grown in small plots, was positive, moderately large, and significant. Thus, grain yield of lines tested in small plots was influenced by competition effects associated with plant height. Perhaps some form of index or adjustment for plant height differences can alleviate this problem. More study is needed before small plots can be used effectively to evaluate genotypes.

The performance of a genotype will vary depending upon its location in a field. While the variation in performance may have many different causes, in the following discussion its cause will be referred to as variation in 'soil fertility'. Variation in 'soil fertility' can

increase the plot to plot experimental error. Moving means were very effective in reducing the portion of experimental error for grain yield due to variation in 'soil fertility'. The smallest moving mean, consisting of the mean grain yield of the nearest 3 plots, gave superior error reduction at East Farm in 1979. This was expected since very rapid changes in 'soil fertility' were caused by a patchy attack of Helminthosporium sativum. A moving mean consisting of the nearest 6 plots gave the greatest reduction in error for grain yield at Redmond in 1979. This moving mean configuration was developed after observing the nature of soil variation at Redmond.

There was little variation in soil fertility at the locations used in the 1980 Large Plot Experiment. Moving means were not capable of substantial error reduction at any location except Moro. While the soil did appear to be more variable at Moro, there may be another cause for the 32 percent error reduction. Plots at Moro were cut back to a "uniform" length by a Hege combine, while plots at the other two locations were cut back by hand-held sickles. It is difficult to drive a Hege combine straight along the edge of the plots, and the irregular path of the combine may have created the variation in grain yield which the moving mean removed.

The small plot experiment of 1980 was grown on fairly uniform soils. While experimental error was reduced by about 20 percent in both locations, the CV was not reduced substantially. A 20 percent reduction in error is a small actual reduction when error is already low.

Reduction of experimental error results in more precise estimates of grain yield potential. Adjustment of grain yield of F_3 and S_1 lines in

the 1979 Small Plot Experiment by a moving mean brought about a consistently higher correlation with grain yield of related F_4 and S_2 bulks grown in the 1980 Large Plot Experiment.

The moving mean technique will be useful when a substantial portion of the experimental error is due to variation in soil fertility. Other situations in which a moving mean can be useful can be deduced from the formula for the standard error of the mean (Steel and Torrie, 1980):

$$s_{\bar{x}} = \sqrt{\frac{\text{MSE}}{n}}$$

When the number of plots of each genotype (n) is small, then a moderate reduction in error mean square (MSE) may result in a meaningful reduction of the standard error of the mean ($s_{\bar{x}}$). The number of plots of each genotype (n) will be small in most recurrent selection programs since there is little seed available for testing. When n is large, such as in advanced yield trials with multiple replications and locations, a moderate error reduction will not bring about a substantial reduction in the standard error of the mean. In an advanced yield trial, one might consider the change in $s_{\bar{x}}$ achieved by dropping a replication and using the moving mean technique. One must also consider the cost of an extra replication and compare it to the cost involved in computing and using a moving mean.

Some of the experiments reported in the literature show large reductions in error when a moving mean is used (Knott, 1972; Buker and Alvey, 1979; Townley-Smith and Hurd, 1973). These experiments appear to be similar to the 1979 Small Plot Experiment, which was grown on extremely variable soil. The 1980 experiments were grown on much more uniform soils. Moving means will not produce such substantial

reductions in error when greater care is used to select an experimental site.

Several different types of index selection were studied. Visual evaluation is a kind of index selection. In this study, visual evaluation was based upon expected grain yield, plant height, straw strength, and disease resistance. Visual evaluation of F_3 and S_1 lines in the 1979 Small Plot Experiment appeared to estimate grain yield potential better than raw grain yield data but poorer than moving mean adjusted grain yield.

The relationship between visual evaluation and other important traits was studied in the 1980 Large Plot Experiment. Visual evaluation was strongly associated with plant height. Shorter plants were rated much higher than taller plants. Late heading plants also tended to have high visual evaluation. Early heading plants may have had low visual evaluation because the straw was bent and broken by standing fully mature in the field for longer periods of time.

Visual evaluation had a significant positive correlation with grain yield in the SC-3 population. The correlation in other populations was generally positive but low. Since only SC-3 had significant variation for grain yield in this experiment, visual evaluation by a "novice" was able to detect differences in grain yield in this as well as other studies (Salmon and Larter, 1978). Visual evaluation of grain yield potential is inexpensive and quick and allows the breeder to practice more intense selection, but this advantage must be weighed against the disadvantage of less effective identification of superior genotypes.

Two types of selection indices with weights on both moving mean adjusted grain yield and visual evaluation were studied. The weights of the "statistical" index (Appendix Table 11) were determined from estimates of genetic and phenotypic variances and covariances (Robinson et al., 1951). Weights of .7 for grain yield and .3 for visual evaluation were deemed appropriate for the "best guess" index. The best guess index, as a measure of grain yield potential of S_1 and F_3 lines in 1979, had as high a correlation with grain yield in 1980 as any other measure of grain yield potential. The poor performance of the statistical index is probably due to unreliable estimates of genetic and phenotypic variances and covariances. This is a common problem with "statistical" indices (Subandi et al., 1973; Eberhart, 1977).

Best guess index of grain yield and visual evaluation is recommended for selection in barley populations. The rationale for choosing an index over direct selection for grain yield comes from the selection experiences of corn programs. Recurrent selection for high corn yield has increased corn yield, but the resulting populations are agronomically unacceptable, primarily due to increased lodging and ear dropping (Gardner, 1976). Best guess index is recommended so that high yielding, agronomically acceptable varieties might some day be developed from the improved populations.

Effects of Intermating

An intermated population, the C-0 population, was developed by intermating four single cross populations for two generations. The mean

of the C-0 population was compared to the overall mean of the four single cross populations to determine if intermating had caused a breakup of favorable epistatic associations of alleles. The effect of intermating on genetic variability was studied by comparing the genetic variance of the C-0 population with the genetic variance within each of the single cross populations.

The mean heading date of the C-0 population was 2.4 days earlier than the mean of the four single cross populations. This significant change is not believed to be due to the breakup of epistatic gene combinations. A simpler explanation is that the earliness of the C-0 population was caused by selection. Plants grown in the greenhouse in the fall of 1978 and the winter of 1979 were grown rapidly so that C-0 S_1 lines would be ready to plant in the spring of 1979. Late flowering plants were not intercrossed and late maturing plants were not harvested to form the C-0 S_1 lines. This selection is the most likely explanation for the earliness of the C-0 population. Plant height and grain yield were not significantly altered by two generations of intermating. Humphrey et al. (1969) found small but significant changes occurred in six out of eight characters after intermating tobacco for five generations. The results of this study agree with the results of Humphrey since there were no substantial changes in mean performance after several generations of intermating, except for the changes due to selection.

The effect of intermating on genetic variation for heading date, plant height, and grain yield was also studied. The C-0 population had consistently larger estimates of genetic variation than any of the four

single cross populations for both heading date and plant height. The increases in genetic variation are believed to be due to an increased number of loci segregating for each trait. Miller and Rawlings (1967a) interpreted the change in genetic variation after six generations of intermating as a breakup of coupling or repulsion phase linkages. Such a basis for the observed increase in genetic variation in the C-0 population cannot be stated for this study since the C-0 population was not studied through several generations of intermating.

Effects of intermating on genetic variation for grain yield were not detected. Estimates of genetic variance for grain yield for each of the five populations were small and often negative. Only three of fifteen estimates were significant. The failure to detect significant genetic variation for grain yield could be ascribed to insufficient genotypes and replications, but that would not alter the fact that there was relatively little genetic variation for grain yield in these populations. This was surprising since the crosses were chosen based on an expectation of genetic diversity. A further, in-depth study of the pedigrees of most of the varieties included in this study (Appendix Figure 1) revealed extensive common parentage (Aberg and Wiebe, 1946; Malting Barley Improvement Association, 1977). The large proportion of genes that must be identical by descent probably caused the lack of genetic variability found in the five populations (Falconer, 1960). Much of the common parentage of barley varieties could be attributed to the strict quality requirements of the malting and brewing industry but that would not explain why soybeans have an equally narrow gene base (Luedders, 1977).

Contemporary breeding methods used in self-pollinated crops, whether they are pedigree, bulk, or single seed descent, can be considered as cyclic breeding methods since pure line parents are intercrossed and the pure line progeny that are eventually selected are again used as parents to begin another cycle of selection. Therefore, contemporary breeding methods can be characterized by recurrent selection and quantitative genetic terminology. The coefficient of inbreeding (F) measures the probability that the two alleles at any locus are identical by descent. Changes in the coefficient of inbreeding from cycle to cycle are a function of 'effective population size' (Falconer, 1960). Effective population size of the entire barley breeding population is reduced by three characteristics of contemporary breeding methods. The first characteristic is the use of homozygous pure lines as parents. The second characteristic is the unequal contribution of different parents to the selected progeny. The third characteristic is the small number of parents that contribute to progeny. Each of these characteristics contribute to a small effective population size in barley breeding populations. Small effective population sizes increase the probability that genes at a locus are identical by descent. A high coefficient of inbreeding is a reasonable explanation for the lack of genetic variability for grain yield that was found in this barley study.

Results of Selection

Response to one cycle of selection for grain yield was studied by growing C-1 S_1 lines, C-0 S_1 lines, selected F_4 lines and parents in the 1980 Small Plot Experiment. C-1 S_1 lines were developed by intermating the best 10% of the C-0 S_1 lines grown in the 1979 experiment. F_4 lines were selected from the best 10% of the F_3 lines grown in the 1979 experiment. There are five F_4 lines per selected F_3 line. Superior lines were identified using the best guess index.

One cycle of S_1 family selection for grain yield increased plant height. The C-1 population was significantly taller than both the C-0 population and the mean of the parents. Selection for grain yield also increased grain yield of both C-1 S_1 lines and F_4 lines as compared to the mean of the parents. Relatively large and significant estimates of genetic variability for grain yield were found for C-0 S_1 lines, C-1 S_1 lines, and between F_3 groups of F_4 lines. These results do not agree with the results of other experiments included in this study. Since previous estimates of genetic variability for grain yield were small and non-significant, small responses to selection and small estimates of genetic variability for grain yield were expected.

The unexpected results of the response to selection experiment can be explained by the fact that this experiment was grown in small plots. Competition effects associated with plant height have been shown to affect grain yield in small plots. Taller plants yield higher than expected and shorter plants yield less than expected in small plots. Significant genetic variation for plant height exists in the C-0

population, the C-1 population, and between F_3 groups of F_4 lines. Variation for plant height may have caused variation for grain yield. Since the selected C-1 population was taller, the increased plant height probably caused the observed increase in grain yield.

Short cycle recurrent selection techniques such as S_1 family are unlikely to be very successful in populations with as little genetic variability for grain yield as the populations included in this study. Contemporary breeding methods in self-pollinated crops may be more successful in populations with small amounts of genetic variability. The characteristics of contemporary breeding methods which allow them to be successful in populations with little genetic variability are 1) very intense selection, 2) adequate seed for precise testing, and 3) increased additive genetic variation between lines due to selfing (Cockerham, 1954; Horner and Weber, 1956). There is no need to maintain a large 'effective population size' when selecting for grain yield in the C-0 population since there is little genetic variation to conserve. Total response to selection is likely to be small.

Short cycle recurrent selection techniques such as S_1 family are more effective in populations with greater amounts of additive genetic variation. Such populations might include parents which have not been used to develop present day elite lines. Populations for recurrent selection with exotic germplasm have been developed and selected in soybeans (Hanson et al., 1967; Kenworthy and Brim, 1979), sorghum (Eckebil et al., 1977) and corn (Hallauer, 1978). Diverse populations such as these, if improved while maintaining large effective population sizes, hold promise for continued yield improvement.

SUMMARY AND CONCLUSIONS

The objectives of this investigation of recurrent selection for grain yield in barley were as follows: 1) to assess the ability of several methods of genotype evaluation to identify superior yielding lines when little seed is available for testing, 2) to study the effects of two generations of intermating on means and variances of selected agronomic characters, and 3) to observe the results of one cycle of S_1 family recurrent selection for grain yield.

The base genetic materials for this study were four single cross populations and an intermated (C-0) population which was developed by intermating the four single crosses for two generations. These genetic materials or lines derived from them were grown in three field experiments - the 1979 Small Plot Experiment, the 1980 Large Plot Experiment, and the 1980 Small Plot Experiment.

Fifty random F_3 lines from each single cross and 160 random S_1 lines from the C-0 population were grown with parental lines and 'Steptoe' check in small (0.7 m^2) two-row plots at two locations in 1979. In the 1980 Large Plot Experiment, 21 random F_4 bulks from each single cross, 21 random S_2 bulks from the C-0 population, parents, and Steptoe were grown in large (6.0 m^2) plots at three locations. The seed harvested from F_3 and S_1 line in 1979 constitute the F_4 and S_2 bulks grown in 1980. In both experiments the only material replicated within locations was the parents and Steptoe. Data were collected on a plot basis for heading date, plant height, visual evaluation, and grain yield. Visual

evaluation is a rating from 1 (poor) to 9 (excellent) which characterizes the agronomic value of a line.

Moving mean covariables consisting of the mean grain yield of the nearest 3, 5, 9, 13, and 6 plots were computed for the 1979 Small Plot Experiment and used in analyses of covariance of parents and Steptoe at each location in an attempt to reduce experimental error for grain yield. Moving mean covariables were also computed for the 1980 Large Plot Experiment. The covariables consisted of the mean grain yield of the nearest 4, 6, 8, 10, and 12 plots. Analyses of covariance using each moving mean covariable were computed for the grain yield of parents and Steptoe at each location. A regression coefficient was estimated from the analysis of covariance which gave the greatest reduction in error mean square at each location. The regression coefficient was then used to adjust the grain yield of all lines grown at that location.

The following five measures of grain yield potential were estimated for F_3 and S_1 lines grown in 1979: 1) visual evaluation, 2) actual grain yield, 3) moving mean adjusted grain yield, 4) 'statistical' index, with weights on visual evaluation and moving mean adjusted grain yield determined from genetic and phenotypic variances and covariances, and 5) 'best guess' index, with weights of .3 on visual evaluation and .7 on moving mean adjusted grain yield. Weights for the 'best guess' index were chosen based on what seemed appropriate. These five measures of grain yield potential of F_3 and S_1 lines were evaluated by their correlation with grain yield of related F_4 and S_2 bulks. Phenotypic correlations between heading date, plant height, visual evaluation, and grain yield were also computed using the 1980 large plot data.

Analyses of variance were computed for heading date, plant height, actual grain yield, and moving mean adjusted grain yield for each population in each experiment. The effect of intermating on means was studied by comparing the mean of the C-0 population with the mean of the four single cross populations. Genetic variance for each character and its standard error were estimated from the analyses of variance as well as the covariance between 1979 and 1980 data. The effect of intermating on genetic variation was studied by comparing the genetic variance of the C-0 population with the genetic variance within each single cross population. Complete pedigrees of the parents were determined and studied in order to answer questions regarding the magnitude of genetic variation found for grain yield.

Results of one cycle of selection for grain yield were studied in the 1980 Small Plot Experiment by growing 14 random C-0, S_1 lines, 208 random Cycle-1 (C-1) S_1 lines, 90 selected F_4 lines from the single crosses, parents, and Steptoe in two locations. C-1 S_1 lines were developed by intermating the best 10% of C-0 S_1 lines. Five F_4 lines represented each of the best 10% of the F_3 lines. Superior lines were identified using the 'best guess' index.

Heading date, plant height, visual evaluation, and grain yield were measured on a plot basis. Moving means were used to reduce experimental error for grain yield as in the 1979 Small Plot Experiment. Analyses of variance were computed for each character.

Response to selection was studied by comparing the mean of the C-1 population with the mean of the C-0 population or the mean of the parents. Response to selection was also studied by comparing the mean

of F_4 lines with the mean of the parents. Genetic variances and their standard errors were also estimated and compared.

Phenotypic correlations between heading date, plant height, visual evaluation, and grain yield were determined for the C-1 population. The accuracy of yield information from small plots was studied by comparing the grain yield of parents and Steptoe in the 1980 small plots with their grain yield in the 1980 large plots.

Based on the results of this investigation, the following conclusions were drawn:

1. Grain yield of lines tested in small plots was influenced by competition effects associated with plant height.
2. Moving mean technique was very effective in reducing experimental error for grain yield which was due to variation in soil fertility.
3. Moving mean techniques are likely to be most useful in yield trial situations where the number of replications is small. Such situations are common in recurrent selection studies since limited seed is available for testing.
4. Moving mean techniques can also be useful when adequate seed is available for testing by allowing a reduction in the number of replications without increasing the standard error of genotype means.
5. A 'statistical' selection index may not be very useful in plants due to the difficulty of obtaining reliable estimates of genetic and phenotypic variances and covariances.

6. A 'best guess' index of grain yield and visual evaluation is recommended for plant selection in barley because it should result in improved grain yield yet maintain the agronomic acceptability of the population.
7. Intermating four single cross populations for two generations did not alter mean values for plant height or grain yield.
8. Intermating four single cross populations for two generations brought about earlier heading dates in the intermated population. Changes in heading date are believed to be due to inadvertent selection.
9. Intermating four single cross populations for two generations increased genetic variability for heading date and plant height. The increases could be explained by increases in the number of segregating loci.
10. Very small estimates of genetic variability for grain yield were found in all five populations. Lack of genetic variability is believed to be due to the large proportion of genes likely to be 'identical by descent', which may be caused by the small effective population sizes of contemporary breeding methods in self-pollinated crops.
11. One cycle of S_1 family selection increased both plant height and grain yield, but increased grain yield may be a function of increased plant height since yield testing was done in small plots.

12. Significant estimates of genetic variation for grain yield in the C-0 and C-1 populations as well as between F_3 groups in the 1980 Small Plot Experiment are believed to be a function of the significant genetic variation for plant height found in the populations.
13. Successful implementation of short cycle recurrent techniques in barley appears to be dependent upon the development of diverse populations with adequate genetic variability for grain yield.
14. Continued grain yield improvement in barley may be dependent upon the development of populations with diverse parents not heretofore used in breeding improved barley lines. These populations should be improved with strict attention to maintaining adequate 'effective population sizes'.

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Appendix Table 1. Pedigrees and descriptions of parental lines.

Single cross 1 (SC-1): Woodvale/CI1237//PI372083

Woodvale/CI1237 is an advanced experimental line developed in Oregon. Woodvale is a tall, six-row, spring feed barley and is a reselection of 27 shorter, earlier maturing, glossy headed types from Vale. CI1237 is a barley yellow dwarf tolerant line.

PI372083 is a short statured, spring, six-row, feed barley introduced from Omsk, U.S.S.R. Its Russian name is Omskij 13709.

Single cross 2 (SC-2): Steptoe/M21//Karl

Steptoe/M21 is a short statured, spring, six-row, feed barley advanced line developed in Oregon. Steptoe is a very high yielding six-row feed barley developed from the cross: Washington 3564/Unitan. M21 is a short statured advanced line from the cross: Jotun/Kindred//Vantage/3/Trophy/4/Dickson/5/M60-105.

Karl is a tall, six-row, spring malting barley developed from the cross: Traill//Good Delta/Everest/3/Traill.

Single cross 3 (SC-3): Short Wocus/Robur

Short Wocus is a tall, stiff strawed, six-row feed barley reselected from Wocus in Oregon. Wocus is a selection from the cross: Coast/Lion//Winter Club.

Robur is a short statured, six-row, winter feed barley developed in France and is resistant to leaf rust.

Single cross 4 (SC-4): Blazer/M22//M22/Zephyr

Blazer/M22 is a short statured, six-row, spring barley advanced line developed in Oregon. It was bulked in the F_4 generation. Blazer is a tall, six-row malting barley developed from

Appendix Table 1. (continued)

Trail, Orange lemma, and Gem. M22 is a short statured advanced line from the cross: Jotun/Kindred//Vantage/3/Trophy/4/Dickson/5/M59-38/6/Beacon.

M22/Zephyr is an intermediate height, advanced six-row barley developed in Oregon. Zephyr is a two-row malting barley selected in the Netherlands from the cross: Heine 2149/Carlsberg II. M22 is mentioned above.

Appendix Table 2. Logistics of germplasm development and testing for three field experiments. †

<u>Time Period</u>	<u>Intermated Population</u>	<u>Single Cross Populations</u>
Summer 1978	Intermate random F_2 plants from four single cross populations in all possible combinations. (field)	Harvest 50 random F_2 plants from each of ² four single cross populations to form F_3 lines. (field)
Fall 1978	Intermate plants grown from cross-pollinated seed from Summer of 1978. (greenhouse)	
Winter 1979	Form 160 random Cycle 0 (C-0) S_1 lines by selfing the plant grown from a single seed from each cross made in Fall 1978. (greenhouse)	

<u>1979 Small Plot Experiment</u>		
Spring and Summer 1979	Test 160 C-0 S_1 lines in two locations. Select best 10% based on 'best guess' index. (field)	Test 50 F_3 lines per single cross ³ in two locations. Identify best 10% based on 'best guess' index. Harvest five F_3 plants per selected F_3 line from space planted F_3 rows. (field)

Fall 1979	Intermate best 10% of C-0 S_1 lines. (greenhouse)	
Winter 1980	Form 208 random Cycle 1 (C-1) S_1 lines by selfing the plant grown from a single seed of each cross made in Fall 1979.	

Appendix Table 2. (continued)

<u>Time Period</u>	<u>Intermated Population</u>	<u>Single Cross Populations</u>
<u>1980 Small Plot Experiment</u>		
Spring and Summer 1980	Test 208 C-1 S_1 lines in two locations. (field)	Test 90 selected F_4 lines (five from each selected F_3 line) in two locations. (field)
<u>1980 Large Plot Experiment</u>		
Spring and Summer 1980	Test 21 random S_2 bulks in three locations. S_2 bulks are formed by harv- esting seed produced by S_1 lines grown in Spring 1979. (field)	Test 21 random F_4 bulks of each single cross in three locations. F_4 bulks are formed by harvesting seed produced by F_3 lines grown in Spring 1979. (field)

[†]Field or greenhouse indicates the environment which the plants were grown for each population and time period.

Appendix Table 3. Summary of climatological data on a per month basis for the 1979 growing season at East Farm and Redmond.[†]

<u>Location</u>	<u>Month</u>	<u>Temperature °F</u>		<u>Precipitation (inches)</u>	
		<u>Average</u>	<u>Departure from normal</u>	<u>Average</u>	<u>Departure from normal</u>
East Farm	March	48.4	2.9	2.89	-1.31
	April	50.3	.2	2.93	.88
	May	55.6	-.1	2.11	.34
	June	61.1	.1	.38	-.77
	July	66.5	.6	.43	.10
	August	64.8	-1.0	2.67	2.12
Redmond	March	41.7	1.9	1.00	.51
	April	44.4	-1.0	.53	.20
	May	53.7	1.7	.17	-.73
	June	60.0	1.7	.24	-.80
	July	67.2	1.5	.07	-.25
	August	64.5	1.2	1.25	.89

[†]Source: Climatological Data Oregon. Environmental Data Service, Asheville, N.C. Vol. 85.

Appendix Table 4. Summary of climatological data on a per month basis for the 1980 growing season at Holmes Farm, Moro, and Klamath Falls.[†]

<u>Location</u>	<u>Month</u>	<u>Temperature °F</u>		<u>Precipitation (inches)</u>	
		<u>Average</u>	<u>Departure from normal</u>	<u>Average</u>	<u>Departure from normal</u>
Holmes Farm	March	45.7	.2	4.02	.18
	April	51.1	1.0	3.63	1.58
	May	54.0	-1.7	1.46	-.31
	June	58.1	-2.9	1.75	.60
	July	66.6	.7	.24	-.09
	August	63.4	-2.4	.01	-.54
Moro	March	40.0	-.7	.94	-.01
	April	49.4	2.3	.89	.17
	May	53.2	-1.3	1.27	.41
	June	56.6	-4.5	1.37	.58
	July	67.2	-1.2	.16	-.04
	August	63.2	-3.8	.11	-.16
Klamath Falls	March	36.7		.76	
	April	45.6		.65	
	May	50.3		.73	
	June	54.4		.84	
	July	66.7		.02	
	August	63.0		.00	

[†]Source: Climatological Data Oregon. Environmental Data Service, Asheville, N.C. Vol. 86.

Appendix Table 5. Means for heading date, plant height, and moving mean adjusted grain yield of populations, bulk populations, parents and Steptoe grown at two locations in the 1979 Small Plot Experiment.

Genotypes	Heading Date (days)	Plant Height (cm)	Grain Yield (q/ha)
Single Cross 1	71	65	42.5
Bulk Population	70	70	49.8
Woodvale/CI 1237	75	68	42.1
PI 372083	71	53	32.6
Single Cross 2	71	72	45.0
Bulk Population	68	75	43.9
Steptoe/M21	71	60	40.0
Karl	66	67	37.5
Single Cross 3	68	69	38.8
Bulk Population	68	71	38.7
Short Wocus	69	65	33.8
Single Cross 4	71	60	33.6
Bulk Population	70	60	37.5
Blazer/M22	71	63	41.3
M22/Zephyr	65	60	27.1
C-0 Population	69	65	33.3
Steptoe	66	68	34.3

Appendix Table 6. Means for heading date, plant height and moving mean adjusted grain yield of populations, bulk populations, parents and Steptoe grown at three locations in the 1980 Large Plot Experiment.

Genotype	Heading Date (days)	Plant Height (cm)	Grain Yield (q/ha)
Single Cross 1	60.8	85	51.4
Bulk population	60.0	91	50.0
Woodvale/CI 1237	65.0	92	52.6
PI 372083	60.0	75	47.6
Single Cross 2	60.2	95	51.4
Bulk Population	59.0	98	53.0
Steptoe/M21	61.6	76	53.7
Karl	57.0	99	50.1
Single Cross 3	57.8	89	46.1
Bulk Population	56.6	92	46.9
Short Wocus	57.0	96	50.5
Single Cross 4	60.3	75	54.7
Bulk Population	60.3	75	51.5
Blazer/M22	60.6	74	56.0
M22/Zephyr	53.0	87	52.3
C-0 Population	57.4	91	52.6
C-0 Bulk Population	56.6	96	51.5
Steptoe	56.3	92	63.9

Appendix Table 7. Means for heading date, plant height, and moving mean adjusted grain yield of four populations, parents, and Steptoe according to seed source. Grown in two locations in the 1980 Small Plot Experiment.

Genotype	Seed Source [†]	Heading Date (Days)	Plant Height (cm)	Grain Yield (q/ha)
C-0 S ₁ lines	G	60.6	76.3	50.0
C-1 S ₁ lines	G	59.8	83.1	53.6
SC-1 F ₄ lines	F	61.3	81.6	55.5
SC-2 F ₄ lines	F	63.4	77.8	51.9
Woodvale/CI 1237	G	68.3	81.3	49.2
Woodvale/CI 1237	F	66.0	85.0	54.2
PI 372083	G	61.3	72.5	47.3
PI 372083	F	59.5	74.4	48.7
Steptoe/M21	G	62.3	75.6	44.6
Steptoe/M21	F	60.5	73.8	48.1
Karl	G	58.0	86.3	52.2
Karl	F	57.8	88.8	49.2
Short Wocus	G	60.0	81.9	52.8
Short Wocus	F	57.0	85.6	56.9
Blazer/M22	G	61.8	70.0	51.4
Blazer/M22	F	60.5	71.9	51.0
M22/Zephyr	G	53.0	83.8	47.0
M22/Zephyr	F	53.8	73.1	48.6
Steptoe	G	57.3	90.1	56.9
Steptoe	F	55.8	85.0	60.2

[†]G indicates greenhouse grown seed, F indicates field grown seed.

Appendix Table 8. Analysis of variance for heading date, plant height, actual grain yield and moving mean adjusted grain yield of five populations grown in two locations in the 1979 Small Plot Experiment.

Population and Source of Variation	Mean Squares						
	Heading Date		Plant Height		Grain Yield		
	df	(days)	df	(cm)	df	Actual (q/ha)	
Single Cross 1							
Genotypes (G)	49	3.9**	49	128**	41	173*	103
G X Location			49	53	41	92	70
Single Cross 2							
Genotypes	49	5.4**	49	131	46	138	83
G X Location			49	100	46	133	76
Single Cross 3							
Genotypes	49	4.9**	49	101**	43	146	80
G X Location			49	47	43	95	63
Single Cross 4							
Genotypes	47	2.1	49	82	42	109	60
G X Location			49	53	42	151	91
C-0 Population							
Genotypes	140	7.6**	140	168**	140	116	98**
G X Location			140	50	140	111	65
Replicated Lines							
Exp. Error	28	1.7	70	53	67	89	39

*Significant at the 5% level of probability.

**Significant at the 1% level of probability.

Appendix Table 9. Analysis of variance for heading date, plant height, actual grain yield and moving mean adjusted grain yield of five populations grown in three locations in the 1980 Large Plot Experiment.

Population and Source of Variation	Mean Squares					
	Heading Date		Plant Height		Grain Yield	
	df	(days)	df	(cm)	Actual (q/ha)	Moving Mean Adjusted (q/ha)
Single Cross 1						
Genotypes (G)	20	5.2**	20	347**	62	45
G X Location			40	44	66	58
Single Cross 2						
Genotypes	20	5.8**	19	403**	87	77
G X Location			38	30	61	60
Single Cross 3						
Genotypes	20	6.6**	19	109**	112**	127**
G X Location			38	27	28	24
Single Cross 4						
Genotypes	19	.3	19	76**	25	22
G X Location			38	20	16	18
C-0 Population						
Genotypes	20	8.7**	20	489**	33	32
G X Location			40	30	42	40
Replicated Lines						
Exp. Error	24	.3	72	20	25	21

*Significant at the 5% level of probability.

**Significant at the 1% level of probability.

Appendix Table 10. Analysis of variance for heading date, plant height, actual grain yield, and moving mean adjusted grain yield for two populations and selected F₄ lines grown at two locations in the 1980 Small Plot Experiment.

Population and Source of Variation	Mean Squares					
	Heading Date		Plant Height		Grain Yield	
	df	(days)	df	(cm)	Actual (q/ha)	Moving Mean Adjusted (q/ha)
C-0 Population						
Genotypes (G)	13	25.8**	13	198**	126*	124**
G X Location			13	49	41	29
C-1 Population						
Genotypes	207	6.1**	207	212**	104**	101**
G X Location			207	36	66	60
Selected F ₄ Lines						
Single Cross 1						
F ₃ groups	8	43.1**	8	613**	239**	286**
F ₄ lines/ F ₃ groups	36	4.0**	36	80**	77	63
Single Cross 2						
F ₃ groups	8	46.5**	8	978**	300**	314**
F ₄ lines/ F ₃ groups	36	3.3**	36	84**	73	74
F ₄ lines x Loc.			89	29	82	75
Replicated Lines						
Exp. error	48	.7	96	26	39	32

*Significant at the 5% level of probability.

**Significant at the 1% level of probability.

Appendix Table 11. Estimates of parameters used to estimate the statistical index for populations grown in the 1979 Small Plot Experiment.

Population	Parameters [†]						
	P_{vv}	P_{vy}	P_{yy}	G_{vy}	G_{yy}	b_y	b_v
SC-1	1.9206	37.6737	2855.1	13.6905	918.4	.307098	1.104331
SC-2	2.3677	32.6621	2280.4	15.7997	187.7	-.016534	6.901131
SC-3	.5342	14.9484	2218.4	2.2785	487.0	.235121	-2.314073
C-0	1.0068	13.1799	2708.3	-4.6855	924.4	.388738	-9.742822

[†] P_{vv} = Phenotypic variance for visual evaluation.

P_{vy} = Phenotypic covariance between visual evaluation and grain yield.

P_{yy} = Phenotypic variance for grain yield.

G_{vy} = Genetic covariance between visual evaluation and grain yield.

G_{yy} = Genetic variance for grain yield.

b_y = relative weight applied to grain yield.

b_v = relative weight applied to visual evaluation.

Grain yield was adjusted by moving mean and expressed in grams per plot.

Appendix Table 12. Estimates of gain from selection for S_1 family and conventional recurrent selection techniques at different levels of additive genetic variation.[†]

Additive Genetic Variation (q/ha) ²	Gain from Selection (q/ha/year)	
	S_1 family	Conventional
0	0	0
5	.46	.60
10	.86	1.00
15	1.23	1.30
20	1.56	1.56
25	1.87	1.79
30	2.16	1.99

[†] Gain from conventional selection is based on the selection of the best 10 out of 400 random F_5 derived F_7 bulks tested with two replications in three locations over a two year period. Gain from S_1 family selection is based on the selection of the best 20 out of 200 random S_1 lines tested with one replication in two locations in a single year. Gains from selection, assuming no dominance or epistatic genetic variance, were crudely estimated using the following formulas:

$$\text{Gain from Conventional selection} = (2.32) \left(\frac{1}{8}\right) \frac{1.9\sigma_A^2}{\sqrt{1.9\sigma_A^2 + \frac{\sigma_{gy}^2}{2} + \frac{\sigma_{gl}^2}{3} + \frac{\sigma_{gyl}^2}{6} + \frac{\sigma_{ec}^2}{12}}}$$

$$\text{Gain from } S_1 \text{ family selection} = (1.74) \left(\frac{1}{3}\right) \frac{\sigma_A^2}{\sqrt{\sigma_A^2 + \frac{\sigma_{gy}^2}{1} + \frac{\sigma_{gl}^2}{2} + \frac{\sigma_{gyl}^2}{2} + \frac{\sigma_{es}^2}{2}}}$$

where; σ_A^2 = additive genetic variance,
 σ_{gy}^2 = 10, the variance due to interaction of genotypes and years,
 σ_{gl}^2 = 10, the variance due to interaction of genotypes and locations,

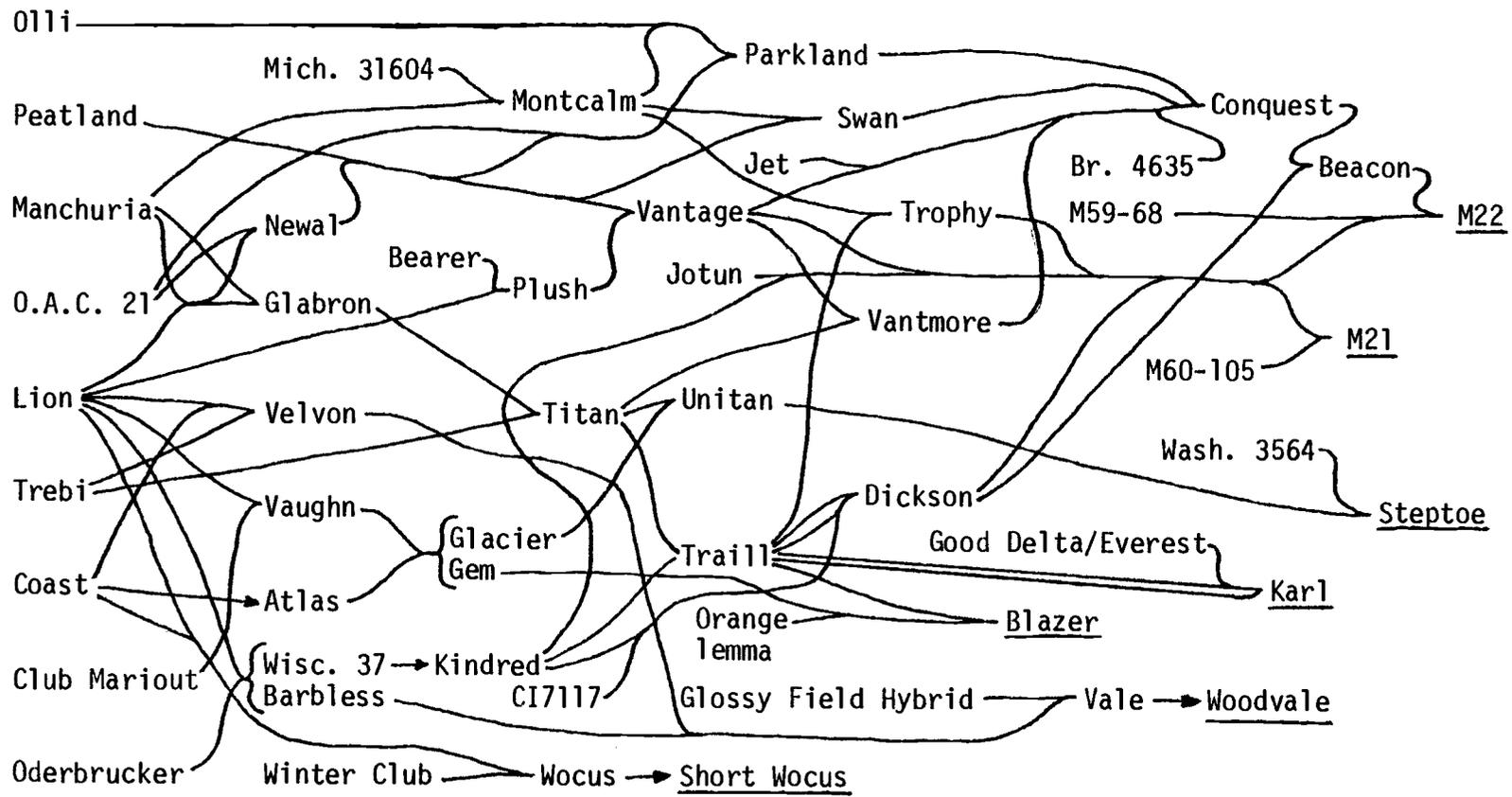
Appendix Table 12. (continued)

$\sigma_{gy1}^2 = 10$, the variance due to interaction of genotypes, years,
and locations,

$\sigma_{ec}^2 = 20$, the experimental error from testing F_6 and F_7 bulks,

$\sigma_{es}^2 = 30$, the experimental error from testing S_1 lines.

Appendix Figure 1. Diagram of the parental relationships of several spring barley lines.[†]



[†] Source: Aberg and Wiebe (1946) and Malting Barley Improvement Association (1977).