Selection for yield in F3S and F4S of two winter wheat crosses employing hill plots
by G Hollis Spitler

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Crop and Soil Science
Montana State University

Abstract:
Wheat (Triticum aestivum L.) breeding programs evaluate large numbers of experimental lines to distinguish the best yielding cultivars. Current procedures use row plots, which are costly, and require relatively large amounts of land and seed. Efforts to identify superior genotypes in segregating (early) generations have been hampered by these restrictions.

Progeny of two winter wheat crosses (VT159/'Froid' and 'Roughrider'/'Centurk') were used to investigate early generation direct and indirect selection for grain yield employing a replicated single hill plot technique. Indirect selection criteria for grain yield were biological yield and harvest index. Eight F3 families per cross were selected based on F3 and F4 performance in experiments grown in 1980 and 1981, respectively.

Selection response was evaluated by comparing the performance of the selected F3-derived F5 lines, or bulked lines, to random F3-derived F5 lines and to the mid-parent value of each cross. The F5 row plots experiments were grown in three different environments.

Early generation direct and indirect selection for yield employing hill plots was successful in both crosses. The degree of success for direct or indirect yield selection varied depending on the cross. Yield of the direct and indirect yield selected F5s suggested hill plot Selection for yield, biological yield or harvest index in winter wheat F3s and F4s would be successful. Genetic variability of each population was maintained via the single seed descent method of producing random F5s. Although both early generation selection and single seed descent were successful in determining high yielding F5 lines, the single seed descent method would increase economy in time and labor.

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APPROVAL

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G. Hollis Spitler

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Wheat (*Triticum aestivum* L.) breeding programs evaluate large numbers of experimental lines to distinguish the best yielding cultivars. Current procedures use row plots, which are costly, and require relatively large amounts of land and seed. Efforts to identify superior genotypes in segregating (early) generations have been hampered by these restrictions.

Progeny of two winter wheat crosses (VT159/'Froid' and 'Roughrider'/'Centurk') were used to investigate early generation direct and indirect selection for grain yield employing a replicated single hill plot technique. Indirect selection criteria for grain yield were biological yield and harvest index. Eight F3 families per cross were selected based on F3 and F4 performance in experiments grown in 1980 and 1981, respectively.

Selection response was evaluated by comparing the performance of the selected F3-derived F5 lines, or bulked lines, to random F3-derived F5 lines and to the mid-parent value of each cross. The F5 row plots experiments were grown in three different environments.

Early generation direct and indirect selection for yield employing hill plots was successful in both crosses. The degree of success for direct or indirect yield selection varied depending on the cross. Yield of the direct and indirect yield selected F5s suggested hill plot selection for yield, biological yield or harvest index in winter wheat F3s and F4s would be successful. Genetic variability of each population was maintained via the single seed descent method of producing random F5s. Although both early generation selection and single seed descent were successful in determining high yielding F5 lines, the single seed descent method would increase economy in time and labor.

INTRODUCTION

Wheat (*Triticum aestivum* L.) breeding programs evaluate large numbers of experimental lines to distinguish the best yielding cultivars. Current procedures use row plots, which are costly, and require relatively large amounts of land and seed. Efforts to identify superior progeny in segregating (early) generations of wheat have been hampered by these restrictions.

Hill plots reduce cost, land area and seed requirements. Hill plot evaluations compare favorably with row plots for heading data, plant height, protein percentage, harvest index and yield components. Hill plots have been useful for certain qualitative genetic studies and in certain disease investigations. The use of hill plots as an indicator of comparative yield in wheats needs clarification. Successful early generation selection for yield requires that the identification of early generation yield selections relate to later generation high yielding progeny.

The objectives of this investigation were to evaluate for direct and indirect selection for grain yield employing hill plots. Biological yield and harvest index were the indirect selection criteria employed.

LITERATURE REVIEW

Early Generation Direct Selection for Yield

In breeding programs of self-pollinated species the sequence of trait selection is determined by the priority of the breeding objectives and heritability of the trait. The primary objective of most wheat breeding programs is yield. Yield is generally treated as a quantitative trait with selection in later generations when high homozygosity is expected. Highly heritable traits such as disease resistance and plant height are routinely selected for in early generations (Allard, 1960; Shebeski, 1967; Briggs and Knowles, 1967).

Harrington (1932) may have first expressed the usefulness of early generation analysis as a predictive tool by showing F2 analysis could accurately predict the value of crosses. In their classic barley (*Hordeum vulgare* L.) study Harlan et al. (1940) concluded the yield of F2 and subsequent bulked generations could predict which crosses would produce the best selections. Harrington (1940) demonstrated that replicated F2 bulk test could estimate the yielding potentiality of wheat crosses. He also showed unselected F3 bulk tests may have supplementary value in this regard. Immer (1941) substantiated these findings in his work with F2, F3, and F4 barley bulks.

Boyce et al. (1947) reported early generation selection in wheat using F2 bulks could separate different crosses for high yield potential and the mean of the population was increased when selected F2-derived F3s were compared to rejected F2-derived F3s.

Lupton and Whitehouse (1951) examined the F2 progeny and pedigree methods of breeding self-pollinating cereals. They concluded the effectiveness of the F2 progeny method, which involves early generation F4 line testing, was equal to the pedigree method which generally yield tested lines at the F6 generation. Grafius et al. (1952) placed little value on early generation testing for yield in barley bulks and emphasized mid-parent values in selecting best parents. Their results indicated the best yielding parents produced best yielding progeny. Frey (1954) concluded the performance of F2 derived oat (*Avena sativa* L.) lines indicated the best F3 derived lines. Thus, the final selections among crosses could be made at the F3 generation. Further selections within the best F3 derived lines of chosen crosses could be made in the F6 to the F10 generations. Fowler and Heyne (1955) concluded that if early generation testing was to be effective environmental factors would have to be controlled, similar to Grafius et al. (1952). They also suggested parental performance might predict the potentials of hard red winter wheat crosses better than early generation testing. Shebeski (1967) showed F3 wheat yield tests could identify which F2-derived F3 lines would be best for further selection. Wheat and barley investigators found similar results when testing F2 and F3 bulks (Smith and Lambert, 1968; Jordaan and Laubscher, 1968; McGinnis and Shebeski, 1968). Although early generation bulk tests of both F3s and F4s predicted which crosses would produce the best F5 lines, F3 bulk tests were more efficient predictors.

Hurd (1969) presented a wheat breeding method for semi-arid climates incorporating early generation testing which consisted of: (1) growing large F2 populations from crosses of well adapted parents having diverse origins; (2) selecting a thousand plus F2 plants from these populations when grown under simulated moisture stress; (3) yield testing F3 lines, reselecting F4 lines through F7 and testing under several location environments; and (4) testing the potential new cultivars as F8-F10, under a maximum number of location-year trials. He successfully used early generation testing to develop new lines.

Early generation bulk testing had become an acceptable procedure by many researchers by the 1970s. Acknowledging its usefulness, some studies began examining procedures for detecting differences within early generation populations. Knott (1972) concluded even though selected F2-derived F3 lines yielded significantly more than unselected F2-derived F3 lines, this effect was not large enough to be of value in wheat breeding.

F3 yields from replicated designed experiments supported F2 single plant analysis as a predictive procedure for determining the origin of the best yielding F3 lines (DePauw and Shebeski, 1973; Skorda, 1973; Shebeski and Evans, 1973).

Knott and Kumar (1975) introduced single seed descent procedures to wheat breeding and compared it to early generation testing for determining high yielding lines. Both procedures were equal for line determination, but single seed descent increased economy in labor and time.

In spring wheat, early generation bulk tests more accurately predicted high yielding F5 sources than mid-parent analysis if the selection intensity is at 25 percent (Cregan and Busch, 1977). Comparing the pedigree method to early generation testing Salmon et al. (1978) concluded the predicability of high yielding lines was equal.

O'Brien et al. (1978 I & II) examined four spring wheat crosses in early generation tests, and concluded: (1) selection was effective when the environmental and genotype by environment variances were small relative to the total genotypic variance of a cross; (2) final yield of selected lines was dependent on both the original mean performance of the cross and the effectiveness of the selection within the cross; (3) replicated F3 yield test provided estimates for the population mean of a cross and the genetic variation within a cross indicated which cross or crosses should receive subsequent evaluation; (4) optimum allocation of a plant breeder's resources to early generations and subsequent selection within identified populations requires consideration of the goal to maximize selection response while maintaining acceptable levels of sample variation; and (5) the F5 replicated yield test demonstrated significant selection response for yield in the two crosses having the greatest genetic variation.

Indirect Yield Selection

The preceding methods of yield selection in early generations involved the direct approach, either restrictive or less likely unrestrictive (Allard, 1960; Rosielle and Frey, 1975). Yield was evaluated directly for the amount of grain produced by the selections. Restriction was based on simple inheritance or highly heritable traits (i.e., disease resistance, plant height, or maturity).

Indirect yield selection requires procedure criteria that: (1) measure a large number of plants with greater speed; (2) have higher heritability than yield; (3) are highly correlated with yield; and (4) are repetitious in these requirements (Searle, 1965; Fischer and Kertesz, 1976). Indirect yield selection has proceeded in two directions: (1) yield components (i.e., plants per acre, seeds per plant and weight per seed) and (2) yield efficiency which uses biological yield (total above ground dry weight) and harvest index (ratio of grain yield over biological yield) (Woodworth, 1931; Donald, 1962).

In bread wheat, Sprague (1926) found high correlations between grain yield, and the average number of spikes per area. Larger correlation coefficients were obtained for spaced plants than plants in rows for this relationship. Quisenberry (1928) related spring wheat yield with spikes per unit area and seeds per spike. In common and durum wheat, Waldron (1929) indicated seeds per spike was the most important yield component. High positive correlations of yield with grain size and weight were noted in hard red spring wheat by Bridgeford and Hayes (1931).

Early generation yield component selection did not increase wheat yield according to Boyce et al. (1947). Seeds per spike was the most reliable estimate of yield in barley and oat cultivars although these differences were influenced by environmental factors (Stoskopf and Reinbergs, 1966). Early generation (F1 and F2) heritabilities for yield components in winter wheat were similar between generations and high for spikes per area, seed per spike, and seed weight (Fonseca and Patterson, 1968). The components were highly correlated to grain yield but grain yield heritability varied between generations. A high negative correlation between spikes per area and seeds per spike placed limitations on selection for either to increase grain yield. This negative relationship between yield components explains the "component compensation" relationship found in small grain research (Donald and Hamblin, 1976). Oat isoline evaluation demonstrated yield component compensation in conventional stand conditions (Brinkman and Frey, 1977). Environmental factors prevented yield components from functioning independently although their inheritance may be independent.

The term "migration coefficient," coined by E. S. Beaven (1914), refers to the partitioning of vegetative plant products into final cereal grain yield (Donald and Hamblin, 1976). In bread wheat, Sprague (1926) reported a positive correlation between grain yield and straw weight per area. Niciporovic (Black and Watson, 1960) suggested that yield advances would be made by close examination of biological yield and economic yield to find a "coefficient of effectiveness," now termed "harvest index."

A close association was found for high yield with high harvest index. This resulted from the production of more grain relative to straw and chaff production (weight) in high yielding semidwarf spring wheats (Syme, 1970). Increased grain producing efficiency was accomplished without increased total biological yield (Syme, 1970; Donald and Hamblin, 1976).

A three year study of cereals indicated a high degree of variability in harvest index, especially in winter wheat (Singh and Stoskopf, 1971). Reduction in plant height reduced stem weight and increased harvest index in winter wheat. Harvest index was positively correlated to grain yield but negatively correlated to total vegetative dry weight (Singh and Stoskopf, 1971; Chaudhary et al., 1977). These interactions were noted (Singh and

Stoskopf, 1971) and considered a drawback to successful use of harvest index in early generation testing (Whan et al., 1981).

Under restrictive versus unrestrictive selection in oats increases in harvest index increased grain yields (Rosielle and Frey, 1975). Restrictions (no late or tall selections) allowed biological yield to remain equal as harvest index and grain yield increased. Unrestricted selection increased all three traits.

Gene action of harvest index in wheat is reported largely additive, with a moderate to high heritability, encouraging the use of harvest index selection in early segregating generations to improve yield (Bhatt, 1976 and 1977). In an extensive review on biological yield and harvest index Donald and Hamblin (1976) concluded: (1) choose parental material with high harvest index and biological yield; (2) assess lines for high harvest index and biological yield under high population density and high fertility; (3) use these criteria in early generation testing under densities beyond commercial ones; and (4) adjust biological yield for tallness.

Bhatt and Derera (1978) used harvest index to select for yield in near isogenic lines of wheat. They found a high positive correlation between high harvest index in F5 lines and high yielding F7 lines. Nass (1980), using harvest index in F2 selections, found F4 lines from high harvest index F2s yielded 9 percent more than F2 derived low harvest index F4 lines. Space planted F2 spring wheat could be used to predict high yield in F4 bulks by using high biological yield criteria for tall F2 selections and high harvest index criteria for semidwarf F2 selections (McVetty and Evans, 1980, II). Grain yield variation in several winter wheat cultivars was accounted for by harvest index (95%) and biological yield (99%) under various plot conditions (Frederickson, 1979).

Field Plot Technique

The need for smaller plots in evaluating early generation selection was recognized by Harrington (1940) when he used 2.4 m rows to examine F2 bulks. Bonnett and Bever (1947) implemented the hill plot technique by planting one head per hill to remove off-types in small grain pure seed production. A comparison study in oats and spring barley indicated hill plots had higher variability for yield than conventional row plots and were only valuable when screening large numbers of lines or when seed and land resources were limited (Ross and Miller, 1955).

Working in oats, Frey (1959) suggested replicated hill plots at several fertility levels could be implemented in early generation testing. Higher coefficients of variation for hill plots (13.1% to 21.8%) compared to row plots (8.0% to 12.8%) in oats were noted by Jellum et al. (1963), although they reported hill plots out-performed row plots for predicting high yielding of lines in early generation testing. Genetic correlations for grain yield in oats between row and hill plots was 0.98 percent and variability was similar for plant height, weight per volume, spike per panicle, panicle per plant, and 100 seed weight (Frey, 1965). Grain yield coefficients of variability were calculated at two to five times larger for hill plots than 4.9 m row plots.

Genetic correlations for measuring attributes in hill and row plots were nearly perfect for grain yield, plant height, and heading date (Frey, 1965), suggesting hill plots would be useful for early generation yield selection. Winter wheat F2 selections in hill and row plots provided similar results for all characteristics including yield and yield components (Fonseca and Patterson, 1968). LeClerg (1966) emphasized the economic advantages of hill plots over row plots in early generation testing involving many individual plants and limitations on labor, land and time. Economic value of hills in early generation or hybrid testing was emphasized by Jensen and Robson (1969). They found more than twice as many replications were needed for hills to equal the precision of one replication in row yield experiments.

A comparison of hill and row plots in common and durum wheats reported hill plots very useful for genetic studies and early generation selection (Baker and Leisle, 1970). As with oat hill plots the genotypic correlations were higher than phenotypic correlations.

Conventional single hill plot design was found to enhance or suppress yield more than row plots or multi-hill designs in an examination of competition among oats cultivars (Smith et al., 1970). Spring wheat hill plots spaced at 61 cms demonstrated harvest index on a plant or single shoot basis had a significantly positive correlation to plot yield. Yield per plant was correlated to plot yield (Fischer and Kertesz, 1976). Harvest index in wheat hill plots was correlated with yield in row plots and high harvest index in hill plots indicated high yielding lines in rows (Bhatt and Derera, 1978). A positive phenotypic correlation between harvest index in row and hill plots was found in winter wheat (Frederickson, 1979). Furthermore, row plot grain yield had a positive phenotypic correlation with harvest index in hill plots. Harvest index and biological yield accounted for 95 to 99 percent, respectively, of the yield variation within hill and row plots.

O'Brien et al. (1979) studied early generation testing of F3 selections in spring wheat in hill and row plots and concluded: (1) hill selection efficiency was 50-75 percent that of single row plots; (2) hill plots must be replicated two to four times more than row plots for similar information; and (3) hill plots used less seed and land but hand labor was increased.

MATERIALS AND METHODS

Genetic Materials

Crosses, F1s, and F2s

Two winter wheat crosses involved parents differing in adaptation in the first cross but having similar adaptation in the second cross. In the first cross a soft red winter wheat from France designated 'VT159', from male sterile plants of the cultivar 'Heima', was the female parent and the winterhardy hard red winter wheat cultivar 'Froid', C.I. 13872 (MT1904-7, bulk winterhardiness selection) was the male parent. The second cross involved two hard red winter wheat cultivars, 'Roughrider', C.I. 17439 (NE63265/Hume/3/Yogo/Frontana/2* Minter) as the female parent and 'Centurk', CI 15075 (Kenya 58/Newthatch/3/Hope/2* Turkey/4/Cheyenne/5/Parker) as the male parent. The two crosses were designated cross V/F and R/C, respectively.

F1 plants originated from crossed seed of one spike of a female plant pollinated by one spike of a male plant. The crossed seeds planted in single head rows (3.0 m long and 0.3 m apart) generally resulted in 8 to 12 plants spaced at various distances within the row (Figure 1). Bulked F2 seed from the F1 plants was the basis for the F2 generation grown in the inoculated stem rust (*Puccinia graminis* Pers. f. sp. *tritic* Eriks & Henn.) nursery. Approximately 1800 to 2000 F2 plants of each cross were grown (6 rows 15.3 m long and 0.3 m apart with plants spaced approximately 0.03 m to 0.07 m apart within a row). Two hundred and fifty stem rust resistant plants with acceptable agronomic appearance (good tillering and good straw strength) were harvested. This selection provided 190 V/F cross and 192 R/C cross plants with a minimum of 300 seeds (approximately 10 gms) to become F2-derived F3 entries.

F2-Derived F3s and F4s

Based on the F3 hill experiment performances ten percent of the F2-derived F3s were selected for grain yield, biological yield and harvest index from each cross. This provided 18 yield selected, 19 biological yield selected and 17 harvest index selected F3s for the V/F cross. Twelve selections were in common for yield and harvest index. Nineteen yield and biological yield selected F3s (18 in common) and 18 harvest index selected F3s (one in common with a yield selection) were advanced for the R/C cross. One F3 experiment replication harvested for yield became the seed source of the selected F3-derived F4s. Two F3 experiment replications were used for head selection sources for the F3-derived F4 head rows and were not harvested for yield. Four heads per hill per replication were taken at random from each F3 selected for F4 testing. Four heads were kept as reserve and four were planted as the F3-derived F4 head rows from each F3 selected for F4 testing (Figure 1).

Ten percent selection for each selection criteria (yield, biological yield and harvest index) resulted in a total of 39 F2-derived F4s in the V/F cross, and a total of 37 F2-derived F4s in the R/C cross (Figure 1).

Reselected F2-derived F4 bulks identified the appropriate F3 family source of the four F3-derived F4 head rows that became the selected F3-derived F5 lines. The 4 head rows combined became the F5 selected family bulked line.

Unequal selection intensities resulted from treating each selection criteria as one yield selection group. The planned reselection intensity of 20 percent became 25 percent for yield and 10 percent for biological yield and harvest index in the F2-derived F4s (Figure 1).

F3-Derived F5s

Twenty-five percent selection intensity for yield resulted in 5 families, or a total of 20 F3-derived F5 lines and 5 bulked F3-derived F5 lines from each cross advanced to the F5 yield tests (Figure 1). Ten percent selection intensity for biological yield and harvest

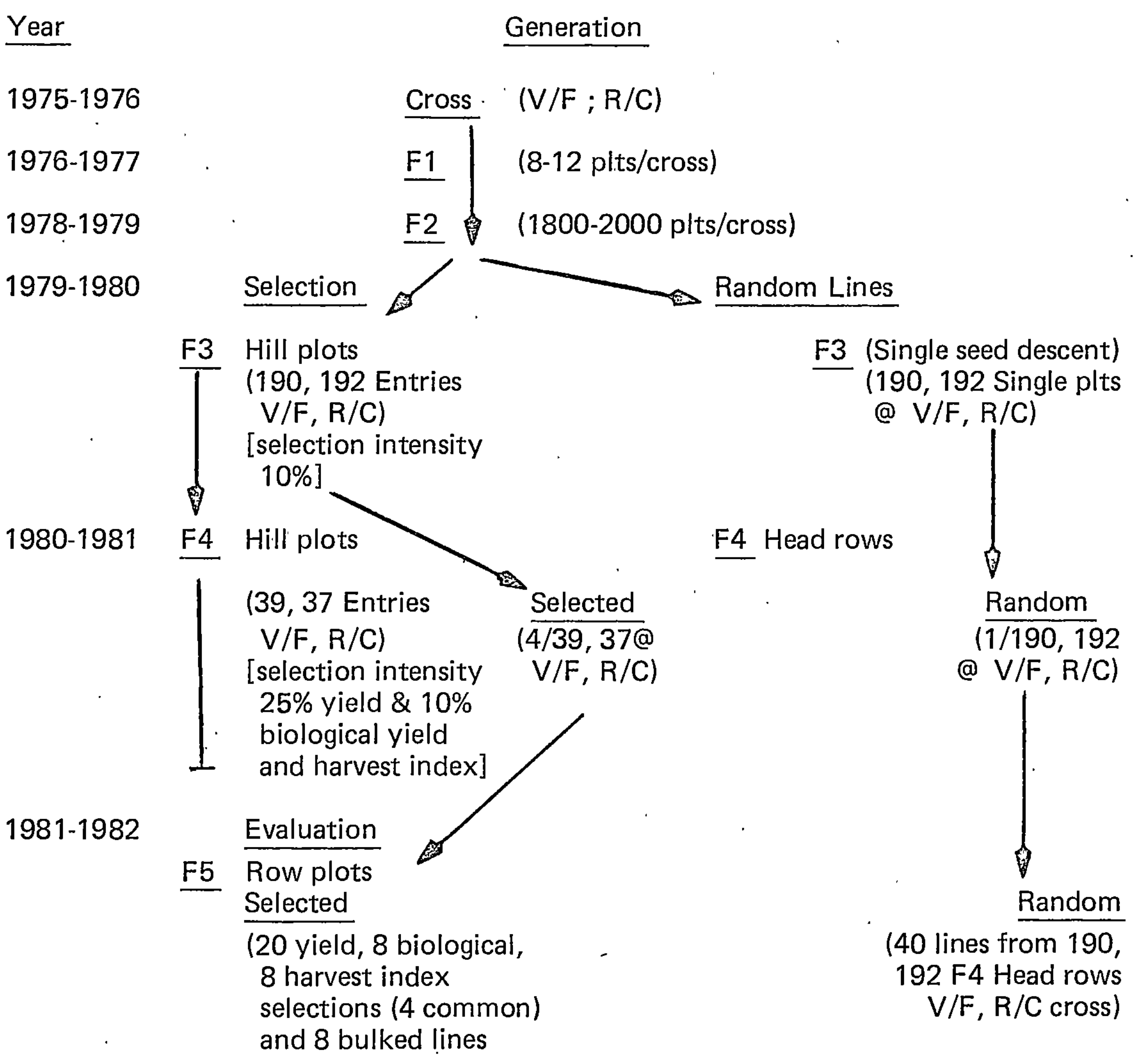

Figure 1. Generation procedures for selection and evaluation in both crosses.

index resulted in 2 families or a total of 8 F3-derived F5 lines and 2 bulked F3-derived F5 lines from each cross advanced to the F5 yield tests. A common family was selected for yield and biological yield in each cross. This gave a total of 8 selected families or 32 selected F5 lines and 8 selected F5 bulked lines per cross a total of 40 selected lines and bulked lines (Figure 1).

Random F3-derived F5 lines originated from a single seed of each F2 plant used to produce a F2-derived F3 entries (Figure 1). The single seeds were planted in the greenhouse during the 1979-1980 winter. One spike from each greenhouse F3 plant was harvested and the seed planted as F3-derived F4 head rows. Forty F3-derived F4 rows were randomly chosen to represent the original F3 population as random F3-derived F5 lines. The single seed method was employed to advance the F2 base population to F3-derived F5 lines.

Selection and Evaluation Methods

F3 and F4 Field Experiments

The F3 and F4 yield tests consisted of 2 experiments each having 10 replications. The F3 V/F cross experiment had 190 entries F3s with parents and the F3 R/C cross experiment had 192 entries F3s with parents. The F4 V/F cross experiment had 39 F4s entries with parents and the F4 R/C cross experiment had 37 F4s entries with parents. The F3 and F4 experiments were planted in a randomized complete block design. The experimental unit was a single hill plot placed on a 0.3 m grid spacing. Thirty seeds of a chosen F2 plant for the F3 experiments or a chosen F3 bulk for the F4 experiments were planted at each intersection of the grid (a single hill). Seeds were dropped in 3-4 cm deep holes dug with hoses. Seed generally was contained within a 3-5 cm diameter area. Each block was bordered by two hill rows of the lodging resistant cultivar 'Redwin', CI 17844. The F3 yield tests were planted October 1 and 2, 1979 (in field G-2) at the A. H. Post Field Research Laboratory located near Bozeman, Montana (Amsterdam silt, loamy, Typic Haploborall soil). The F3 yield tests received 42.57 cm of precipitation for the total crop year (September 1979 to August 1980). Eight replications were harvested for evaluation. The remaining two replications were used as the source of the head selections for the F4 head rows. The F4 yield tests were planted September 24, 1980 (in field G-3) at the Post Field Research Laboratory, Bozeman, Montana, employing the same general procedure as the F3 experiments. The F4 yield tests received 47.65 cm of precipitation for the crop year (September 1980 to August 1981). Ten replications were harvested for evaluation.

F5 Field Experiments

The F5 yield tests consisted of row plots for each cross, replicated three times and planted at three locations. Each field test experiment had 82 entries. Two locations were at the Post Field Research Laboratory near Bozeman (field Y-5 and field R-6). Environments were altered by distance separations of 250 m, field slopes, fertilizer applications and cropping history (Y-5 location followed spring wheat and R-6 location followed summer fallow). Both Bozeman locations were planted September 21, 1981. The third location was planted September 24, 1981 at the Southern Agriculture Research Center, Huntley, Montana. The two Bozeman locations had 0.3 to 0.5 m of snow cover from December to February. The first Bozeman location had slightly more (< 0.3 m) snow cover prior to November and after February, than the second Bozeman location.

Fertilizer was applied in mid-May at the Bozeman locations. The first location received 32.6 kg/ha nitrogen as NH_4NO_3 (34-0-0) and 48.9 kg/ha potassium as KCL (0-0-600. The first field reserves were 78.5 kg/ha nitrogen to 122 cm level, 30.3 kg/ha phosphorus and 321.7 kg/ha potassium for the 30 cm level based on a November 1981 soil test. The second location received 126.4 kg/ha nitrogen as NH_4NO_3 (34-0-0) and NH_4PO_4 (18-36-0), 64.6 kg/ha phosphorus as NH_4PO_4 (18-36-0), 48.9 kg/ha potassium as K_2SO_4 and 16.9 kg/ha sulfur (0-0-52-18). The second field reserves were 95.3 kg/ha nitrogen to 122 cm level, 25.8 kg/ha phosphorus, and 355.3 kg/ha potassium for the 30 cm level based on a November 1981 soil test.

Crop year total precipitation (September 1981 to August 1982) at Bozeman was 47.12 cm and at Huntley was 33.78 cm. Each row plot was two nonbordered rows (3.0 m lengths 0.3 m apart) machine planted at a seeding rate of 8 gms per 3.0 m row (approximately 240 seeds) at a depth of 0.03-0.04 m.

All row plot experiments used a randomized complete block design and had outside borders of the lodging resistant cultivar 'Redwin'.

One R/C replication was lost due to harvesting problems at the first Bozeman location. One V/F replication was lost due to water erosion and winter injury at the second Bozeman location. One R/C replication was lost due to chemical residue in the soil at the Huntley location.

Measurements

Heading date, plant height, and sheaf weight (biological yield) were recorded for each experimental unit. The heading date was the number of days from January 1 until 50% of the heads in a plot were fully out of the boot (beyond flag leaf collar). Plant height was a single measurement height in centimeters from the soil surface to tip of the majority of spikes within a plot, excluding awns. Sheaf weight was the weight of the bundle sheaf from a plot cut approximately 4 cm above the soil surface and allowed to dry down at the Bozeman locations before weighing. Biological yield was calculated as the total bundle sheaf weight. All hill plots were harvested by hand sickles. Rows trimmed to 2.4 m lengths were harvested by a two row cutter-binder. Vogel type plot threshers were used for both hill and row plots.

Grain yield, test weight, 1000 kernel weight, percentage grain protein and grain moisture were measured. Test weight, kg/hl, was measured only for row plots, since seed was inadequate from hill plots. One thousand kernel weight was determined for row plots and on combined seed of two hill plot replications. Protein and moisture percentages were determined on the 1000 kernel weight samples using a near infrared analyzer (Technicon 400). Straw weight was calculated by subtracting grain weight from biological yield. Harvest index was calculated by dividing grain yield by biological yield.

Statistical Analyses

An analyses of variance was calculated for each F3 and F4 hill experiment and for each F5 experiment for each agronomic trait evaluated in this study. For the F5 experiments, which examined traits in more than one location (environment), a combined analysis of variance over locations was calculated to examine the interaction between environment and the other sources of variation. In the combined analyses of variance, the mean squares of each genotypic factor were tested using the pooled mean square error (McIntosh, 1983). The environment mean square was tested using the pooled environment by replication mean square error (McIntosh, 1983).

Mean comparison of each examined trait was accomplished with a t-test of phenotypic means using appropriate pooled degrees of freedom, error variances, standard errors of means weighted for unequal sample sizes and student's t-test distributions (Snedecor and Cochran, 1980). Formulas for the F3-F4 comparisons and F5 comparisons are in Appendix A.

Genetic variances and narrow sense heritability for yield, biological yield and harvest index were calculated for genotypes tested in the F3 and F4 generations. Standard errors for heritability estimates were calculated using procedure outlined by Hallauer and Miranda (1981). Predicted response to selection was estimated and standard errors calculated from procedures used by Pesek and Baker (1971). Formulas used are in Appendix A.

Phenotypic correlations were between traits computed from phenotypic means for each measured or calculated trait. Formulas used are in Appendix A.

RESULTS AND DISCUSSION

Early Generation Selection in Hill Plots

Direct Yield Selection

Significant differences for yield were detected among F3s and F4s in the 1980 Fs and 1981 F4 experiments of both crosses (Table 1). The replicated single hill plot technique detected differences among the F3s and F4s and corroborated the findings of other researchers (Frey, 1965; Jellum et al., 1963; LeClerg, 1966; Fonseca and Patterson, 1968; Jensen and Robson, 1969; Baker and Leisle, 1970; O'Brien et al., 1978 I & II).

Table 1. Mean Squares of Yield of F2-derived F3s and F4s for Two Winter Wheat Crosses Grown in 1980-1981 Hill Experiments.

	Means Square			
	Cross			
	VT159/Froid		Roughrider/Centurk	
	df		df	
F3s Source				
Replications	7	4.32**	7	5.80**
Genotypes	189	3.13**	191	3.44**
Errors	1323	0.92	1337	1.16
F4s Source				
Replications	9	0.43 ns	9	1.15 ns
Genotypes	38	2.95**	36	1.39*
Errors	342	0.98	324	0.93

*, **Significant at 5% and 1% levels of probability, respectively.
ns Not significant.

Genotypic differences for yield among the F3s and F4s in both crosses suggested selection for yield could be practiced. However, F4 genotypes consisted of plants selected from using three different selection criteria; yield, biological yield and harvest index. The analyses were done on the combined genotypes because of the common entries within these selection criteria groups. The F4 analysis of yield and estimates of F4 heritabilities were first calculated using combined genotypic data. These analyses indicated yield heritabilities were high enough for reselection for yield in each cross.

Comparisons between the F3s and mid-parent values in 1980, and the yield selected F4s and mid-parent values in 1981, indicated high yield potential in progeny of both crosses (Table 2). Certain selected F3s and reselected F4s outperformed their high parent (Tables 21-24, Appendix B).

Table 2. Yield Means of F2-derived F3s, Yield Selected F4s and Midparent Values for Two Winter Wheat Crosses Grown in 1980-1981 Hill Experiments.

	Yield Means (Mg/ha)	
	Crosses	
Generation	VT159/Froid	Roughrider/Centurk
F3s	5.23	5.65
Midparent	3.95	5.24
F3 vs midparent	1.28**	0.41 ns
F4s	5.35	5.00
Midparent	4.12	4.45
F4 vs midparent	1.23**	0.55 ns

** Significant at 1% levels of probability.
ns Not significant.

Several researchers suggested mid-parent analysis, not early generation testing, for predicting the origin of the best progeny (Grafius et al., 1952; Fowler and Heyne, 1955; Leffel and Hansen, 1961). The V/F cross would have been discarded if mid-parent analysis had been used to evaluate the two crosses being discussed (Table 2). Mid-parent analysis of unadapted material requires careful examination since the unadapted cultivar performance may unjustly bias the mid-parent values. Mid-parent evaluation, then, could result in the restricted introduction of important new germplasm into a breeding program.

Heritability estimates for F3 yield were similar in both crosses and had similar standard errors (Table 3). Yield heritabilities were high enough to suggest successful direct selection for yield. Yield heritabilities were similar to those reported for F3 bulks of four spring wheat crosses by O'Brien et al. (1979) using one location. As O'Brien et al. (1979) pointed out, heritability estimates for the F3 bulks are biased upward due to confounding of the estimate of genetic variances by its components; especially the environment by genotype interaction variance which could not be estimated from the single location F3 data. Progress in F4s is usually less than expected due to the biased estimates for F3s.

Table 3. Heritability estimate for Yields of F2-derived F3s and Yield Selected F4s for Two Winter Wheat Crosses Grown in 1980-1981 Hill Experiments.

	Heritabilities	
	Cross	
Generation	VT159/Froid	Roughrider/Centurk
F3s	70.5 ± 10.4	66.1 ± 10.3
F4s	34.3 ± 35.1	-1.06 ± 35.2

Selections were made for the top yielding 10 percent in F3s and 25 percent in the F4s. The planting of the yield selected F5s was completed before heritability estimates were calculated. Low heritability and high error suggested less reselection success in the V/F F4s and unwarranted reselection in the R/C F4s (Table 3).

The F3 relationship among yield and the other measured traits revealed by the F3 correlations gave little additional information and agree with the correlations reported by several researchers (Syme, 1970; Singh and Stoskopf, 1971; Chaudhary et al., 1977; Rosielle and Frey, 1975; Donald and Hamblin, 1976; Bhatt, 1976 & 1977; Bhatt and Derera, 1978; Frederickson, 1979; Nass, 1980; McVetty and Evans, 1980) (Table 4).

Correlations among yield selected F4s (Table 5) for yield, biological yield, harvest index, plant height, straw weight, heading date, percent protein, and 1000 kernel weight were similar to the F3 correlations (Table 4). The positive relationship of yield and plant height in the F3s was a major concern addressed by Rosielle and Frey (1975). They suggested restrictions for tallness be imposed for yield selection in hill plots. No other meaningful relationships were noted between F3 or F4 traits related to yield selection within early generations (Tables 4 and 5).

Table 4. Phenotypic Correlations for Measured Traits of the F3s for Two Winter Wheat Crosses Grown in 1980 Hill Experiments.

	Phenotypic Correlations													
Traits	Biological Yield		Harvest Index		Plant Height		Straw Weight		Heading Date		Percent Protein		1000 KWT	
Yield	.92 **	.96[†] **	.55 **	.46 **	.44 **	.47 **	.80 **	.90 **	-.03 ns	-.05 ns	-.14 ns	-.17 *	.36 **	.19 **
Biological Yield			.18 *	.21 **	.58 **	.54 **	.97 **	.99 **	.09 ns	-.05 ns	.06 ns	-.11 ns	.39 **	.24 **
Harvest Index					-.13 ns	-.06 ns	-.05 ns	.05 ns	-.27 **	-.02 ns	-.22 **	.03 ns	.09 ns	.08 ns
Plant Height							.62 **	.56 **	.27 **	.05 ns	.04 ns	-.06 ns	.33 **	.38 **
Straw Weight									.15 *	-.05 ns	.01 ns	-.08 ns	.38 **	.26 **
Heading Date											-.07 ns	-.02 ns	.07 ns	-.14 *
Percent Protein													.05 ns	.04 ns

*, **Significant at 5% and 1% levels of probability, respectively.
ns Not significant
[†]'r' values for VT159/Froid and Roughrider/Centurk, respectively.

Indirect Yield Selection

Significant differences were detected among genotypes for the indirect selection criteria (biological yield and harvest index) among F3s and F4s (Table 6). An exception was biological yield in the F4s of the R/C cross (Table 6). The inability to detect biological yield differences in the R/C cross F4s was not surprising since the parents were of similar genetic backgrounds (Table 6).

Table 5. Phenotypic Correlations for Measured Traits of Yield Selected F4s for Two Winter Wheat Crosses Grown in 1981 Hill Experiments.

Traits	Phenotypic Correlations													
	Biological Yield		Harvest Index		Plant Height		Straw Weight		Heading Date		Percent Protein		1000 KWT	
Yield	.80 **	.60† **	.53 *	.84 **	.07 ns	.02 ns	.63 **	.18 ns	.38 ns	-.22 ns	-.27 ns	-.63 **	.21 ns	.23 ns
Biological Yield			.08 ns	.10 ns	.32 ns	.33 ns	.97 **	.89 **	.15 ns	-.25 ns	-.25 ns	-.52 *	.11 ns	.01 ns
Harvest Index					-.37 ns	-.14 ns	-.32 ns	-.36 ns	.48 *	.21 ns	-.14 ns	-.46 *	.18 ns	.31 ns
Plant Height							.39 ns	.39 ns	-.50 *	-.57 *	.48 *	-.33 ns	-.05 ns	.61 ns
Straw Weight									.04 ns	-.18 ns	-.21 ns	-.29 ns	.06 ns	-.12 ns
Heading Date											-.49 *	-.35 ns	.26 ns	-.12 ns
Percent Protein													.18 ns	-.44 ns

*, **Significant at 5% and 1% levels of probability, respectively.
ns Not significant.
†'r' values for VT159/Froid and Roughrider/Centurk, respectively.

Table 6. Mean Squares of Biological Yield and Harvest Index of F2-derived F3 and F4s for Two Winter Wheat Crosses Grown in 1980-1981 Hill Experiments.

	Mean Squares					
	Cross					
		VT159/Froid			Roughrider/Centurk	
		Biological Yield	Harvest Index (x10-4)		Biological Yield	Harvest Index (x10-4)
F3s Source						
Replication	7	9.32**	454 **	7	157 **	378 **
Genotypes	189	20.9 **	21.2**	191	23.9**	11.1**
Errors	1323	7.66	7.57	1337	8.77	5.11
F4s Source						
Replications	9	11.7 ns	30.2**	9	19.2*	87.5**
Genotypes	38	28.7**	21.4**	36	10.9 ns	19.6*
Errors	342	11.4	3.73	324	8.50	12.2

*, **Significant at 5% and 1% levels of probability, respectively.
ns Not significant.

Genotypic differences among F3s and F4s were also detected for the five other measured traits (plant height, straw weight, heading date, percent protein and 1000 kernel weight) (Tables 26 and 27, Appendix B). The exception was F4 straw weight in the R/C cross. This resulted from close association of straw weight and biological yield, and, similar percentage (Table 26, Appendix B).

Biological yield and harvest index comparisons between F3s or F4s and mid-parent values indicated the high biological yield or harvest index potential of progeny in each cross (Table 7) and that certain selected F3s and reselected F4s equalled or outperformed the high parents (Tables 21, 22, 27-30, Appendix B).

Table 7. Means of Biological Yield and Harvest Index of F2-derived F3s and Biological Yield and Harvest Index Selected F4s and Mid-parent Values for Two Winter Wheat Crosses Grown in 1980-1981 Hill Experiments.

	Means			
	Crosses			
	VT159/Froid		Roughrider/Centurk	
Generation	Biological Yield (Mg/ha)	Harvest Index	Biological Yield (Mg/ha)	Harvest Index
F3	16.0	.328	16.3	.350
Midparent	13.2	.304	16.2	.326
F3 vs midparent	2.8**	.024**	0.1 ns	.024**
F4	20.0	.274	19.0	.270
Midparent	16.3	.257	18.2	.245
F4 vs midparent	3.7**	.017 ns	0.8 ns	.025 ns

**Significant at 1% levels of probability; ns Not significant.

Heritability estimates of F3s for biological yield and harvest index were similar in both crosses and had similar standard error (Table 8). Heritabilities of biological yield or harvest index were high enough to suggest successful indirect selection for yield. Reselections were made and planted before heritability estimates were calculated. Low heritabilities indicated little progress would be expected for biological yield selection in either cross (Table 9). However, harvest index selection could be expected to succeed in the V/F cross and have limited success in the R/C cross (Table 9). Furthermore, the F4 yield heritabilities of the indirect selection groups were equivalent or greater than the F4 direct selection groups yield heritabilities (Tables 3 and 9).

Table 8. Heritability Estimates for Biological Yields and Harvest Indices for F2-derived F3s for Two Winter Wheat Crosses Grown in 1980 Hill Experiments.

	Heritabilities	
	Crosses	
Generation	VT159/Froid	Roughrider/Centurk
F3		
Biological yield	63.3 ± 10.4	63.2 ± 10.3
Harvest index	64.2 ± 10.4	53.7 ± 10.4

Table 9. Heritability Estimates for Indirect Selection Criteria and Yield of F2-derived F4s of the Biological Yield and Harvest Index Selection Groups for Two Winter Wheat Crosses Grown in 1981 Hill Experiments.

	Heritabilities	
	Crosses	
Generation	VT159/Froid	Roughrider/Centurk
F4		
Biological Yield Selected		
Yield	52.0 ± 33.8	−2.3 ± 35.2
Biological yield	27.8 ± 34.3	−102 ± 40.2
Harvest Index Selected		
Yield	80.2 ± 35.4	50.2 ± 34.8
Harvest index	82.3 ± 35.4	43.7 ± 34.9

The F3 and F4 relationships between biological yield and harvest index with all other measured traits are in general agreement with the results of several researchers (Syme, 1970; Singh and Stoskopf, 1975; Chaudhary et al., 1977; Rosielle and Frey, 1975; Donald and Hamblin, 1976; Bhatt, 1976 & 1977; Bhatt and Derera, 1978; Frederickson, 1979; Nass, 1980; McVetty and Evans, 1980) (Tables 4, 10 and 11). The positive F3 correlation between biological yield and harvest index, and the nonsignificant F4 relationship

Table 10. Phenotypic Correlations for Measured Traits of Biological Yield Selected F4s for Two Winter Wheat Crosses Grown in 1981 Hill Experiments.

	Phenotypic Correlations													
Traits	Biological Yield		Harvest Index		Plant Height		Straw Weight		Heading Date		Percent Protein		1000 KWT	
Biological Yield Selected F4s														
Yield	.73 **	.60† **	.64 **	.90 **	.24 ns	-.05 ns	.49 *	.07 ns	.40 ns	-.23 ns	-.12 ns	-.60 **	-.08 ns	.14 ns
Biological Yield			-.70 ns	.22 ns	.50 *	.21 ns	.95 **	.84 **	.24 ns	-.30 ns	-.05 ns	-.39 ns	.03 ns	.08 ns
Harvest Index					-.21 ns	-.11 ns	-.36 ns	-.34 ns	.34 ns	-.22 ns	-.10 ns	-.56 **	-.15 ns	.24 ns
Plant Height							.53 *	.30 ns	-.22 ns	-.58 **	.39 ns	-.25 ns	.12 ns	.15 ns
Straw Weight									.13 ns	-.22 ns	.01 ns	-.09 ns	.07 ns	-.19 ns
Heading Date											-.19 ns	-.39 ns	.02 ns	-.08 ns
Percent Protein													.16 ns	-.41 ns

*, **Significant at 5% and 1% levels of probability, respectively.
ns Not significant.
†'r' values for VT159/Froid and Roughrider/Centurk, respectively.

were contradictory to the negative correlation reported by Singh and Stoskopf (1971) and Chaudhary et al. (1977).

The lower 'r' values between yield and biological yield in the biological yield-selected F4s versus F3s may be the response of F3 selection (Tables 4 and 10). Lower 'r' values were not found between the yield and harvest index in the harvest index selected F4s versus the F3s (Tables 4 and 11).

The positive relationship of biological yield with plant height as seen in the F3s (Table 4) was a major concern addressed by previous researchers. Rosielle and Frey (1975) suggested restrictions for tallness and maturity when selecting for biological yield. Donald and Hamblin (1976) advised biological yield selection be adjusted for tallness. McVetty and Evans (1980, II) suggested biological yield worked only when selecting within tall

Table 11. Phenotypic Correlations for Measured Traits of Harvest Index Selected F4s for Two Winter Wheat Crosses Grown in 1981 Hill Experiments.

	Phenotypic Correlations													
Traits	Biological Yield		Harvest Index		Plant Height		Straw Weight		Heading Date		Percent Protein		1000 KWT	
Harvest Index Selected F4s														
Yield	.90 **	.80† **	.58 *	.59 **	.09 ns	.66 **	.79 **	.62 **	.10 ns	-.31 ns	-.25 ns	-.53 *	.16 ns	.47 *
Biological Yield			.18 ns	.01 ns	.37 ns	.73 **	.98 **	.97 **	.07 ns	-.26 ns	-.04 ns	-.44 ns	.28 ns	.23 ns
Harvest Index					-.49 *	.10 ns	-.03 ns	-.25 ns	.14 ns	-.20 ns	-.63 **	-.35 ns	-.14 ns	.46 ns
Plant Height							.47 ns	.67 **	.08 ns	-.22 ns	.67 **	-.17 ns	.31 ns	.37 ns
Straw Weight									.05 ns	-.21 ns	.17 ns	-.35 ns	.31 ns	.10 ns
Heading Date											.06 ns	-.12 ns	.32 ns	.38 ns
Percent Protein													.19 ns	-.19 ns

*, **Significant at 5% and 1% levels of probability, respectively.
ns Not significant.
†'r' values for VT159/Froid and Roughrider/Centurk, respctively.

progeny. My F3 data for both crosses and the F4 V/F cross data suggest unrestricted selection for biological yield could result in increased plant height. However, harvest index showed no association with increased height in either cross and in the V/F cross F3s was associated with earliness.

The other phenotypic correlations among plant height, straw weight, heading date, percent protein and 1000 kernel weight offer little practical information (Tables 10 and 11). Selection for biological yield met criteria suggested by researchers (Searle, 1965; Fischer and Kertesz, 1976) for indirect selection of yield since: (1) measurements of biological yield (sheaf or bundle weight) are easier than grain yield measurements; (2) biological yield was highly correlated with yield (Table 4); (3) the heritability of biological yield and yield were similar (Table 3). Such repetitious results suggest selection for biological yield has merit as a method for indirect selection for high yielding progeny in a winter wheat breeding program.

Harvest index would be less desirable than biological yield as an indirect selection method if we considered its measurement difficulties and lower correlations with yield. However, the heritabilities of harvest index are as high as yields in F3 and was the only selection group in the F4s having a large enough heritability to continue successful reselection in both crosses (Table 9). Harvest index's slightly negative association with tallness and late heading dates in the F3 and F4, while maintaining higher yields, retains its attractiveness as an indirect selection criteria for identifying high yielding F3 and F4 especially if shorter, earlier wheats are desirable.

Selection among F3s was made equally at 10 percent selection intensity for biological yield and harvest index each and selections were advanced to F4 hill plot experiments. Reselection for biological yield and harvest index remained 10 percent for F4 in both crosses a result of first treating all selection groups as a single yield selection group. The F4 reselections identified the families to be evaluated in the F5 row plot experiments.

Evaluation of Early Generation Selections

Yield Response to Selection in F5s

F3-derived F5 lines resulted from direct and indirect selection for yield, in the F3 and F4 generations from two winter wheat crosses. The selected F5s of the two crosses, VT159/Froid and Roughrider/Centurk, were yield tested with the random F3-derived F5s from each cross population. Row plot experiments were conducted with the F5s at three locations in 1982 to examine the effectiveness of early generation selection.

Significant differences for F5 yields occurred in the combined 1982 yield data of the V/F and R/C cross experiments (Table 12). Significant yield differences were found among the three test environments and among F5 genotypes in all experiments. Furthermore,

Table 12. Mean Square for Yield of F3-derived F5s for Two Winter Wheat Crosses in Row Plot Experiments over Three Environments in 1982.

	Mean Squares					
	Crosses					
	VT159/Froid			Roughrider/Centurk		
Source	df			df		
Environments	2	133	**	2	98.7	**
Env/Replication (pooled)	5	5.85	**	4	1.08	**
Genotypes	78	1.54	**	79	.454	**
Random	38	1.72	**	39	.587	**
Selected and Bulked Lines	39	1.23	**	39	.266	ns
Bulked Lines	7	.720	**	7	.364	ns
Selected Lines	31	1.34	**	31	.251	ns
Selected Line Families	7	3.15	**	7	.126	ns
Within Families	24	.813	**	24	.288	ns
Line vs Bulked Line	1	1.36	*	1	.022	ns
Random vs Line Selection	1	8.26	**	1	2.48	**
Environment X Genotypes	156	.437	**	158	.269	ns
Environment X Random	76	.508	**	78	.284	ns
Environment X Selected & Bulked Lines	78	.354	ns	78	.243	ns
Environment X Bulked Lines	14	.222	ns	14	.156	ns
Environment X Line	62	.371	ns	62	.265	ns
Environment X Line Families	14	.380	ns	14	.334	ns
Environment X Within Families	48	.369	ns	48	.245	ns
Environment vs Line vs Bulked Line	2	.725	ns	2	.173	ns
Environment vs Random vs Line Selected	2	.809	ns	2	.395	ns
Pooled Error	390	.317		316	.223	
Mean		4.36			4.84	
Range		3.34-5.39			4.27-5.67	
C.V.		12.6			9.76	
LSD .05		0.55			0.50	
LSD .01		0.73			0.65	

*, **Significant at 5 or 1% level of probability, respectively.
ns Not significant.

yields differed between the random and selected F5 lines of both crosses. Partitioning the sources of variation among genotypic groups showed significant yield differences among all F5 genotypic groups of the V/F cross. The R/C cross partitioned genotypic groups had significant yield differences only among the random lines.

A significant genotype by environment interaction for yield occurred in the V/F cross (Table 12). Significant environment by random F5 lines interaction was observed for the V/F experiments.

If the large genotype by environment interaction variance is not separated from the total estimated genetic variance (i.e., the F3 and F4 genetic variance estimates did not have genotype by environment variance separated) the effectiveness of early generation selection can be reduced if the estimated genetic variance is biased upward. O'Brien et al. II (1978) suggest the absolute amount of genotype by environment variance is not critical, but the amount of environment by genotype variance relative to the total genetic variance is critical to the estimate of genetic variance in a cross. The genotype by environment interaction variance partitioned for each genotypic group generally accounted for only half of the total estimated genetic variance in my experiments (Table 12). Based on the 1982 F5 data for the genotype by environment estimated variances, the influence of the interaction would have had a large effect on early generation selection in F4 bulks for the yield and biological yield selections in both crosses and possibly harvest index selections in the R/C cross (Tables 3, 8 and 9).

The differences among F5 genotype groups suggest the selection criteria groups identified F5 lines or bulked lines which differed in their yield performance in the V/F cross. No yield differences among the selected F5s were detected in the R/C cross. Furthermore, the important significant yield differences were between the selected and random F5 lines for both crosses. In the R/C cross experiments the error mean square for the experiments are homogeneous between crosses. The amount of detectable yield difference (LSDs) was nearly equal in both crosses (Table 12) (Mean squares and means of other traits measured and their phenotypic correlations are in Tables 31-37, Appendix B).

The bulks of the four selected lines per family (see Materials and Methods) were included as entries along with the selected lines of each selected family in the 1982 F5 yield experiments. The 1982 combined F5 yield analyses of variance indicated yields differed among selected lines and bulked lines in the V/F cross (Table 12). A comparison between selection criteria group yields for F5 families and bulked lines of families indicate the yield difference was between one yield-biological yield selected F5 family (No. 2) the V/F cross (Table 13). Early generation selection based on bulked line yield performance could be used. Decreased degrees of freedom in any analyses might be a primary reason for deficiencies in evaluations of early generation selection by F5 bulked lines.

Table 13. Mean Yield Comparisons Between F3-derived F5 Selected Families and Their Bulked Lines of the Selection Groups for Two Winter Wheat Crosses Row Experiments over Three Environments in 1982.

	Mean Yield (Mg/ha)				
	Cross				
Families	VT159/Froïd		Families	Roughrider/Centurk	
No.	Lines	Bulks	No.	Lines	Bulks
Yield Selected					
5	4.31 ns	4.07	3	5.02 ns	5.39
6	4.93 ns	4.60	4	5.01 ns	4.92
8	4.81 ns	4.53	5	4.86 ns	4.71
10	4.11 ns	4.28	6	4.93 ns	4.98
Biological Yield Selected					
2†	4.42 **	3.95	8†	5.09 ns	5.14
3	4.47 ns	4.68	9	4.98 ns	4.81
Harvest Index Selected					
1	4.83 ns	4.65	1	4.97 ns	4.72
7	4.94 ns	4.75	2	4.96 ns	4.97

†Yield and biological yield selected.
**Significant 1% level of probability.
ns Not significant.

The analyses of variance of the combined 1982 F5 biological yield and harvest index data indicated differences for biological yield and harvest index in experiments of the V/F and R/C crosses (Tables 31 and 32, Appendix B). Significant differences between selected and random F5s were found for biological yield in the V/F cross and for harvest index in the R/C cross. Significant differences were noted for plant height, straw weight, heading date, percent protein, 1000 kernel weight and test weight among environments and genotypes. Environment by genotype interactions varied for significance (Tables 33 and 34, Appendix B).

The analyses of variance for the combined 1982 F5 yield data indicated early generation direct selection for yield and indirect selection for yield, through biological yield or harvest index, was effective in the two winter wheat crosses. Furthermore, the effectiveness of the early generation selection was demonstrated by F5 yield performance row plot experiments.

Direct Yield Selection

Early generation yield selected lines outyielded the random F5s in both crosses and were greater than the mid-parent value in the V/F cross (Table 14). Although the R/C cross yield selections were not greater than the mid-parent value, early generation selected F5 lines had yields superior to the random unselected population. The yields of the yield selected families provided better evidence of this success. Selected families no. 6 and no. 8 in the V/F cross had higher yields than random lines and in addition to selected families no. 5 and no. 2 outyielded the mid-parent (Table 14). Family no. 8 of the R/C cross outyielded the random lines. No other R/C family differed with the random lines nor were any R/C families different from the midparent for yield (Table 14). In the V/C cross two families (nos. 6 and 8) were superior in yield to the other three families, while in the R/C cross no differences were detected among families (Table 14).

The random F3-derived F5 lines represent the original F3 population (see Materials and Methods). The F2 plants used to develop the random lines were restricted to having stem rust resistance and producing an excess of 360 seeds (at least nine well developed heads per plant) for each F2 plant selected. Therefore, yield selected F5s equaling the random line yields does not constitute a deficiency in early generation selection, but more likely reflects some selection for yield in the F2s (Table 14). The lack of significant yield

Table 14. Mean Yield Comparisons for Random Lines, Yield Selected Lines Means, Yield Selected Families and Mid-parent of Two Winter Wheat Crosses in Row Experiments over Three Environments in 1982.

	Mean Yield (Mg/ha)				
	Crosses				
	VT159/Froid			Roughrider/Centurk	
Groups	vs RL	vs MP	Groups	vs RL	vs MP
Random F5 Lines (39)	4.36		Random F5 Lines (40)	4.84	
Mid-parent Value (2)		3.82	Mid-parent Value (2)		5.03
Yield Selected F5 Lines (20)	4.52 **	**	Yield Selected F5 Lines (20)	4.98 **	ns
Yield Selected Family (4)			Yield Selected Family (4)		
#5	4.31 ns	**	#3	5.02 ns	ns
#6	4.93 **	**	#4	5.01 ns	ns
#8	4.81 **	**	#5	4.86 ns	ns
#10	4.11 ns	ns	#6	4.93 ns	ns
#2†	4.42 ns	**	#8†	5.09 **	ns
LSD .05	.28			.25	
LSD .01	.36			.33	

( ) # of entries.
† Selected for Yield and Biological Yield.
*, ** Significant at 5 or 1% level of probability, respectively.
ns Not significant.
RL Random Line.
MP Mid-parent.

differences between the yield selected F5 lines and midparent in the R/C cross may be the result of reduced genetic variability within the cross, not a deficiency in early generation selection.

Several yield selected F5 lines yielded more than the random F5s in both crosses, but only surpassed the high parent in V/F cross (Table 15). Although several R/C cross yields were greater than the high yielding parent, Centurk, none were significant. Early generation direct yield selection successfully identified F3 and F4 bulks which were the source of superior yielding F5 lines in both winter wheat crosses studied.

Table 15. Mean Yield for Individual Yield Selected F5 Lines in Families Compared to Random F5 Line Yields or High Parent Yields of Two Winter Wheat Crosses over Three Environments in 1982.

		Mean Yield (Mg/ha) Crosses					
		VT159/Froid				Roughrider/Centurk	
Groups		vs RL	vs HP	Groups		vs RL	vs HP
Random F5 Lines (39)		4.36		Random F5 Lines (40)		4.84	
High Parent (1)			3.93	High Parent (1)			5.16
Yield Selected				Yield Selected			
Family # 5	Line # 8	5.15 **	**	Family # 3	Line # 1	4.88 ns	ns
	12	3.72 **	ns		35	5.11 ns	ns
	70	4.46 ns	*		36	5.27 *	ns
	88	3.93 *	ns		54	4.80 ns	ns
Family # 6	Line #24	4.88 **	**	Family # 4	Line # 10	5.30 **	ns
	51	5.00 **	**		27	4.89 ns	ns
	55	4.71 ns	**		53	5.01 ns	ns
	96	5.13 **	**		96	4.83 ns	ns
Family # 8	Line # 9	4.66 ns	**	Family # 5	Line # 13	4.79 ns	ns
	23	4.89 **	**		14	5.17 ns	ns
	28	4.65 ns	**		31	4.47 *	ns
	53	5.03 **	**		58	5.01 ns	ns
Family #10	Line # 15	3.84 *	ns	Family # 6	Line # 46	5.04 ns	ns
	68	4.36 ns	ns		49	5.13 ns	ns
	84	4.09 ns	ns		75	4.63 ns	ns
	95	4.14 ns	ns		82	4.93 ns	ns
Family #2†	Line # 6	4.46 ns	*	Family #8†	Line # 32	5.08 ns	ns
	10	4.14 ns	ns		65	5.08 ns	ns
	48	4.34 ns	ns		89	5.18 ns	ns
	85	4.74 ns	*		98	5.08 ns	ns

( ) # of entries.
† Selected for Yield and Biological Yield.
*, ** Significant at 5 or 1% level of probability, respectively.
ns Not significant.
RL Random Line.
HP High Parent.

Indirect Yield Selection

Indirect selection (i.e., for biological yield and harvest index) for yield was successful in both crosses (Table 16). In the V/F cross both groups of indirect selected F5s had yields greater than the mid-parent values. Only harvest index selected F5s had yields greater than random F5s. The indirect selected F5 had greater yields than the random F5s in the R/C cross (Table 16). The lack of yield difference between the indirect selected F5s and mid-parent in the R/C cross reflects the low genetic variability of that cross.

Table 16. Mean Yield Comparisons for Random Lines, Biological Yield and Harvest Index Selected Lines Means, Indirect Yield Selected Families and Mid-parent of Two Winter Wheat Crosses in Row Experiments over Three Environments in 1982.

	Mean Yield (Mg/ha) Crosses				
	VT159/Froid			Roughrider/Centurk	
Groups	vs RL	vs MP	Groups	vs RL	vs MP
Random F5 Lines (39)	4.36		Random F5 Lines (40)	4.84	
Mid-parent Value (2)		3.82	Mid-parent Value (2)		5.03
Biological Selected F5 Lines (8)	4.45 ns	**	Biological Selected F5 Lines (8)	5.03 **	ns
Harvest Index Selected F5 Lines (8)	4.88 **	**	Harvest Index Selected F5 Lines (8)	4.97 *	ns
Biological Yield Selected Family (4)			Biological Yield Selected Family (4)		
#2†	4.42 ns	**	#8†	5.09 **	ns
#3	4.47 ns	**	#9	4.98 ns	ns
Harvest Index Selected Family (4)			Harvest Index Selected Family (4)		
#1	4.83 **	**	#1	4.97 ns	ns
#7	4.94 **	**	#2	4.96 ns	ns
LSD .05	.28			.25	
LSD .01	.36			.33	

( ) # of entries.
† Selected for Yield and Biological Yield.
*, ** Significant at 5 or 1% level of probability, respectively.
ns Not significant.
RL Random Line.
MP Mid-parent.

In the V/F cross the harvest index selected families nos. 1 and 7 had higher yields than the biological yield selected families and greater yields than the random F5s (Table 16). All V/F cross families had greater yields than the midparent (Table 16). Family no. 8

had superior yield over the R/C random F5s and was commonly selected for yield and biological yield. The lack of significant yield differences between R/C F5s and the mid-parent, and, among R/C families may be the result of reduced genetic variability in the cross. The low genetic variability for yield makes any method of detecting yield differences difficult, but does not indicate a deficiency in early generation selection.

Indirect selected individual F5 line yields further indicated the success of early generation indirect selection (Table 17). In both crosses both indirect selection criteria identified at least one F5 superior yielding line compared to the random F5 line yields. In the V/F cross several individual F5 lines beat the high parent. In the R/C cross at least one high yielding selected F5 was in each of the selection groups and equaled the high parent. Early generation biological yield and harvest index selection successfully identified high yielding F5 sources in F3 and F4 of both crosses.

Predicted and Observed Response

Predicted responses to F3 yields, for yield, biological yield or harvest index selections, were greater than the observed responses except for yields of the harvest index selections (Table 18). Pesek and Baker (1971) point out the predicted response calculations are assumed to be derived from yield tests grown over several environments. Despite the fact the predicted responses are based only on one location-year data, the magnitude in differences between the predicted and observed for yield and biological yield selections (Table 18) were about as extreme as those reported by O'Brien et al. (1979).

Early generation selection for yield would be most successful in the crosses having the greatest amount of genetic variation. However, actual yield of selected lines marks success rather than observed versus predicted response. Early generation selection for yield either directly or indirectly was successful in both the winter wheat crosses examined in this

Table 17. Mean Yield for Individual Indirect Yield Selected F5 Lines in Families Compared to Random F5 Line Yields or High Parent Yields of Two Winter Wheat Crosses over Three Environments in 1982.

	Mean Yield (Mg/ha) Crosses					
	VT159/Froid				Roughrider/Centurk	
Groups	vs RL	vs HP	Groups		vs RL	vs HP
Random F5 Lines (39)	4.36		Random F5 Lines (40)		4.84	
High Parent (1)		3.93	High Parent (1)			5.16
Biological Yield Selected			Biological Yield Selected			
Family #2 Line # 6	4.46 ns	ns	Family #8	Line # 32	5.08 ns	ns
10	4.14 ns	ns		65	5.08 ns	ns
48	4.34 ns	ns		89	5.18 ns	ns
85	4.74 ns	**		98	5.08 ns	ns
Family #3 Line #11	3.99 ns	ns	Family #9	Line # 19	5.30 *	ns
39	4.19 ns	ns		47	4.99 ns	ns
80	4.82 *	**		51	4.96 ns	ns
93	4.88 **	**		66	4.76 ns	ns
Harvest Index Selected			Harvest Index Selected			
Family #1 Line # 4	4.84 *	**	Family #1	Line #22	5.29 *	ns
54	4.85 *	**		38	4.73 ns	ns
57	4.88 **	**		55	4.85 ns	ns
61	4.75 ns	**		76	5.02 ns	ns
Family #7 Line #37	4.91 **	**	Family #1	Line # 8	4.90 ns	ns
41	4.84 *	**		15	4.91 ns	ns
45	5.20 **	**		42	5.04 ns	ns
71	4.79 *	**		69	5.00 ns	ns

( ) # of entries.
† Selected for Yield and Biological Yield.
*, ** Significant at 5 or 1% level of probability, respectively.
ns Not significant.
RL Random Line.
HP High Parent.

study. High yielding F5 lines were identified which originated from early generation selected F3 and F4 bulks.

Single Seed Descent

The single seed descent method was employed to maintain and advance a random sample of the original F3 populations to the F5 generation for each cross (see Materials and Methods). Heritabilities for yield, biological yield and harvest index in the random F5

Table 18. Estimates of Predicted and Observed Responses to F3 Direct and Indirect Selections for Yield in Two Winter Wheat Crosses in Row Plot Experiments over Three Environments in 1982.

	Yield (Mg/ha)		
	Field	Biological Yield	Harvest Index
VT159/Froid			
Predicted Response F3 Data in Hills	0.84 ± 0.12	0.73 ± 0.11	0.35 ± 0.05
Selected F5 Lines			
Observed F5 Response in Rows	0.16 ± 0.28	0.09 ± 0.28	0.52 ± 0.28
Roughrider/Centurk			
Predicted Response F3 Data in Hills	0.75 ± 0.12	0.74 ± 0.12	0.20 ± 0.04
Selected F5 Lines			
Observed F5 Response in Rows	0.14 ± 0.25	0.19 ± 0.25	0.13 ± 0.25

lines indicated the genetic variability was maintained compared to the F3 estimates for each of the selection criteria (Table 19). The F5 estimates for each selection criteria were similar or higher than the F3 estimates.

The selection potential of the random F5s can be illustrated by comparing yield of the selected F5s for each selection criteria group to the high yielding random F5 lines selected at equal intensities directly and indirectly for yield (Table 20) as those used for the selected F5s. The lack of yield differences between the selected F5s and this selected groups of random F5s suggested that the random F5 lines could be a source of direct or indirect selection for yield.

The ease of maintaining the single seed descent populations by use of greenhouse and field facilities suggests this method might reduce labor, land and seed requirements similar to early generation selection employing hill plots. Additionally, the hill techniques may be incorporated with the single seed method and allow testing of advanced generations of a cross with further saving of limited resources. The single seed descent method, therefore, showed some important advantages over the early generation selection procedures studied. These included easier handling of materials and evaluation of selections at advanced generations with greater degrees of homozygosity. These conclusions are similar to Knott and

Kumar (1975) study comparing single seed descent to early generation selection. If combined with the use of hill plots this method could increase a breeders ability to handle an increased number of selections while saving in labor, land and seed.

Table 19. Heritability Estimates for Yield, Biological Yield, and Harvest Index of the Random F5 Lines Compared to F3s for Two Winter Wheat Crosses.

		Heritabilities Cross	
		VT159/Froid	Roughrider/Centurk
Yield of Random	F5	81.6 ± 3.1	62.0 ± 2.8
	F3	70.5 ± 10.4	66.1 ± 10.3
Biological Yield of Random	F5	68.1 ± 4.1	68.7 ± 2.7
	F3	63.3 ± 10.4	63.2 ± 10.3
Harvest Index of Random	F5	73.7 ± 2.4	72.5 ± 1.3
	F3	64.2 ± 10.4	53.7 ± 10.4

Table 20. Mean Yield of the Selected F5 Lines Versus a Comparable Number of Random F5 Lines Selected Directly or Indirectly for Yield in Two Winter Wheat Crosses.

	Mean Yield (Mg/ha) Cross	
Selected for	VT159/Froid vs RL	Roughrider/Centurk vs RL
Yield (20)	4.52 ns 4.72	4.98 ns 5.06
Biological Yield (8)	4.45 ns 4.82	5.03 ns 5.09
Harvest Index (8)	4.88 ns 4.69	4.97 ns 5.07

SUMMARY

Early Generations Selection Employing Hill Plots

The single, 30 cm equally-spaced, 30-seed-per-hill technique adequately distinguished differences for yield, biological yield, harvest index and five other traits among F3 and F4 early generation progeny of the two winter wheat crosses. This plot size and seeding rate provide a unique environment for the examination of genotypic differences for selection purposes.

The economics of hill plots consists of less seed required, less land area needed and a greater ease of maintenance, all of which contribute to the evaluation of more breeding lines. The planting and harvesting of hill plots requires less labor than other plot types. Mechanization of the planting and harvesting procedures would increase efficiency and possibility reduce the high coefficient of variability associated with hill plots. The blocking of wheats by height should enhance the use of hill plots in evaluating yield of cultivars differing in height.

Direct Selection for Yield in Winter Wheat

Yield selection in the F3 and F4 generations in the two winter wheat crosses was successful in distinguishing F2-derived F3 and F2-derived F4 bulks which produced F5 progeny with superior yield. The theory that the best progeny come from the best early generation selection was reinforced by this study. The evaluation of the early generation yield, selections as F5 lines or F5 line bulks suggested adequate sampling of the selected bulks was necessary to account for continued segregation and represent the yields of any selected family. Early generation yield selection through replicated field tests offers a unique opportunity to evaluate new crosses. Yield potential is evaluated earlier than in conventional selection methods and allows calculation of genetic variance and heritability. Replicated tests in at least two diverse environments should enhance the reliability of the genetic variance and heritability estimates and allow the calculation of genotype by environment interaction variance. These calculations would allow examination of crosses and indicate possibilities of successful early generation yield selection. Continued similar treatment of selected early generation populations would provide needed information as to which populations would lend themselves to more than one generation of selection.

Indirect Yield Selection in Winter Wheat

Indirect yield selection (using biological yield or harvest index) distinguished high yielding F3s and F4s in both crosses.

In the V/F cross the two harvest index selected F5 families accounted for most of the high yielding F5 lines (Tables 16 and 17). In the R/C row experiments, though several selected families contained more than one F5 with high yield, the commonly selected yield-biological yield family accounted for more high yielding progeny (Tables 16 and 17).

High yielding F5 progeny resulted from both selection criteria. Therefore, the usefulness of a given indirect selection criteria depends on other advantages it possesses. Biological yield is attractive for its ease of measurement. Harvest index showed an ability to incorporate yield efficiency, even in selecting among the standard height progeny of the two crosses studied.

Single Seed Descent

The single seed descent method showed advantages in using limited labor, land and seed. This method may be as efficient as any technique or procedure to maintain genetic variability in a cross until the progeny can be evaluated and selection made on homozygous genotypes in a later generation.

Overall Summary

Early generation selection for yield was successful in two winter wheat crosses employing the replicated single hill plot technique in F3 and F4 populations in one environment. A number of the early generation selections in both crosses produced F5 progeny with yield performances greater than the highest yielding parent.

The selection critera were direct yield selection, and, indirect selection for yield using biological yield and harvest index. Selected families of each selection criteria in both crosses produced high yield F5 lines.

Four important conclusions can be made from this study. First, early generation selection for yield in winter wheat was successful. The employment of early generation yield selection is warranted for reducing the number of progeny from any one cross until yield testing in conventional breeding methods. Second, indirect selection for yield, using biological yield selection in winter wheat could be an efficient method of identifying high yielding progeny when combined with restrictions on plant height. Third, harvest index selection as an indirect selection criteria for yield selection proved to be as effective as yield or biological yield selection. Fourth, the single seed descent method affords an efficient and inexpensive way to advance generations while maintaining genetic variability, thus allowing selection to be implemented when the progeny have reached the desired homozygosity.

Single seed descent combined with the hill technique could increase the efficient use of limited resources and allow an increased number of progeny to be evaluated in a winter wheat breeding project. Lines derived by single seed descent through the F4 or F5 could be evaluated for yield in replicated hill experiments in at least two environments. The resulting selections would be evaluated in row plots.

The results from this study were very encouraging for employing early generation selection on the quantitative characteristic yield, and, for the employment of the replicated single hill plot. These results suggest indirect selection of yield using biological yield or harvest index warrants additional examination and preliminary implementation into winter wheat breeding schemes. Finally, this study demonstrated the usefulness of the single seed descent technique to advance the generation of progeny and maintain the genetic variance in winter wheat.

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APPENDICES

APPENDIX A

FORMULAS USED FOR CALCULATIONS

F3-4 Comparisons

$$t = \frac{(\bar{X}p1 + \bar{X}p2)/2 - Fx}{(\frac{1}{4}s^2/n_{p1} + \frac{1}{4}s^2/n_{p2} - s^2/n_{fx})^{1/2}}$$

F5 Comparison

$$t = \frac{\bar{X}_s - \bar{X}_r}{[s^2(1/n_s + 1/n_r)]^{1/2}}$$

Genetic Variance for F3-F4 and F5

$$\sigma^2_g = (mst - mse)/r \qquad \sigma^2_g = (mst - mstx2 - mse)/r$$

$$\sigma^2_p = \sigma^2_g + \sigma^2/r \qquad \sigma^2_p = \sigma^2_g + \sigma^2_{gxe} + \sigma^2_{e/r}$$

$$= \sigma^2_g + \sigma^2_{e/r}$$

Heritability (broad sense)

$$h^2 = \sigma^2_g/\sigma^2_p$$

Genetic Variance SE

F3-F4

$$SE(\sigma^2_g) = [2/r^2 (mst^2/df + mse^2/df)^{1/2}$$

F5

$$SE(\sigma^2_g) = [2/r^2 (mst^2/df + mstxe^2/df + mse^2/df)^{1/2}$$

$$SE(h^2) = SE(\sigma^2_g)/\sigma^2_p$$

Genetic Gain

$$\Delta g = (\bar{X}_{sel'n} - \bar{X}_{unsel'n}) \times h^2$$

$$SE(\Delta g) = (\bar{X}_{sel'n} - \bar{X}_{unsel'n}) \times SE\ h^2$$

Phenotypic Correlations

$$r_p = mst_{xy}/(mst_x\ mst_y)^{1/2}$$

APPENDIX B

Table 21. Eight Trait Means of F3s Selected and Nonselected for Yield, Biological Yield and Harvest Index and Parents for VT159/Froid Cross Grown in 1980 Hill Experiment.

	Means								
Groups	F3 Bulk	Yield		Biological Yield		Harvest Index		Parents	
Traits		Selected	Nonselected	Selected	Nonselected	Selected	Nonselected	VT159	Froid
Yield (Mg/ha)	5.23	6.30	5.11	6.16	5.12	5.67	5.18	3.43	4.46
Biological Yield (Mg/ha)	16.0	18.7	15.7	18.9	15.7	16.1	16.0	11.0	15.3
Harvest Index	.328	.337	.327	.327	.328	.355	.325	.312	.297
Plant Height (cm)	128	133	128	135	128	125	129	109	140
Straw Weight (Mg/ha)	10.8	12.4	10.6	12.7	10.5	10.4	10.8	7.59	10.8
Heading Date (days)	177	178	177	178	177	177	177	178	178
Percent Protein	14.8	14.9	14.8	14.9	14.8	14.7	14.8	16.7	15.1
1000 Kernel Weight (gm)	32.7	34	32.8	34.1	32.8	32.8	33.0	30.9	27.2
No. Entries	188	18	169	19	170	17	170	1	1

Table 22. Eight Trait Means of F3s Selected and Nonselected for Yield, Biological Yield and Harvest Index and Parents for Roughrider/Centurk Cross Grown in 1980 Hill Experiment.

Groups	Means								
	F3 Bulk	Yield		Biological Yield		Harvest Index		Parents	
Traits		Selected	Nonselected	Selected	Nonselected	Selected	Nonselected	Rough-rider	Cen-turk
Yield (Mg/ha)	5.65	6.68	5.54	6.68	5.56	5.92	5.62	4.77	5.72
Biological Yield (Mg/ha)	16.3	19.1	16.0	19.2	15.9	16.2	16.3	15.6	16.9
Harvest Index	.348	.351	.347	.350	.347	.367	.346	.306	.345
Plant Height (cm)	116	121	116	121	116	116	117	131	116
Straw Weight (Mg/ha)	10.6	12.4	10.4	12.5	10.4	10.3	10.7	11.2	10.8
Heading Date (days)	173	173	173	173	173	173	173	175	172
Percent Protein	14.7	14.6	14.7	14.6	14.7	14.6	14.7	15.0	14.5
1000 Kernel Weight (gm)	30.7	31.4	30.6	31.6	30.6	29.9	30.8	28.7	30.9
No. Entries	190	19	171	18	172	18	172	1	1

Table 23. Eight Trait Means of F4s Selected for Yield, Reselected and Non-reselected for Yield and Parents for VT159/Froid Cross Grown in 1981 Hill Experiment.

	Means				
F4 Bulk Groups	Selected	Reselected	Non-reselected	Parents	
Traits				VT159	Froid
Yield (Mg/ha)	5.35	5.84	5.17	4.04	4.20
Biological Yield (Mg/ha)	19.8	21.0	19.3	15.3	16.7
Harvest Index	.271	.278	.268	.264	.250
Plant Height (cm)	134	134	134	108	134
Straw Weight (Mg/ha)	14.4	15.1	14.1	11.3	12.5
Heading Date (days)	178	179	178	181	177
Percent Protein	16.8	16.6	16.9	15.9	17.4
1000 Kernel Weight (gm)	31.5	31.6	31.5	35.3	28.2
No. Entries	19	5	14	1	1

Table 24. Eight Trait Means of F4s Selected for Yield, Reselected and Non-reselected for Yield and Parents for Roughrider/Centurk Cross Grown in 1981 Hill Experiment.

F4 Bulk Groups	Means				
	Selected	Reselected	Non-reselected	Parents	
Traits				Roughrider	Centurk
Yield (Mg/ha)	5.00	5.38	4.87	4.32	4.57
Biological Yield (Mg/ha)	18.9	19.1	18.8	17.1	19.3
Harvest Index	.265	.282	.260	.251	.239
Plant Height (cm)	122	120	122	126	119
Straw Weight (Mg/ha)	13.9	13.8	13.9	12.8	14.7
Heading Date (days)	174	174	174	175	173
Percent Protein	15.9	15.4	16.0	16.7	16.8
1000 Kernel Weight (gm)	28.9	29.3	28.7	29.7	28.1
No. Entries	19	5	14	1	1

Table 25. Mean Squares of Plant Height, Straw Weight, and Heading Date of F2-derived F3s and F4s for Two Winter Wheat Crosses Grown in 1980-1981 Hill Experiments.

	Mean Squares							
	Cross							
	VT159/Froid				Roughrider/Centurk			
	df	Plant Height (cm)	Straw Weight (Mg/ha)	Heading Date (days)	df	Plant Height (cm)	Straw Weight (Mg/ha)	Heading Date (days)
F3s Source								
Replications	7	381 **	88.0 **	37.5 **	7	1400 **	124 **	46.7 **
Genotypes	189	297 **	9.17**	10.9 **	191	121 **	990 **	12.5 **
Errors	1323	28.1	3.80	1.26	1337	20.6	3.89	2.00
F4s Source								
Replications	9	957 **	11.2 ns	2.28**	9	82.0 **	20.7 **	2.84**
Genotypes	38	235 **	16.1 **	24.1 **	36	129 **	6.61ns	21.1 **
Errors	342	24.4	6.20	0.46	324	14.7	5.06	0.45

*, **Significant at 5% and 1% levels of probability, respectively.
ns Not significant.

Table 26. Mean Squares of Percent Protein and 1000 Kernel Weight of F2-derived F3s and F4s for Two Winter Wheat Crosses Grown in 1980-1981 Hill Experiments.

		Mean Squares				
		Cross				
		VT159/Froid			Roughrider/Centurk	
	df	Percent Protein (X 10-4)	1000 Kernel Weight (gm)	df	Percent Protein (X 10-4)	1000 Kernel Weight (gm)
F3s Source						
Replications	3	372 **	82.7 **	3	127 **	20.2 **
Genotypes	189	9.04**	19.2 **	191	12.6 **	11.0 **
Errors	567	3.50	1.21	573	6.48	1.26
F4s Source						
Replications	2	0.64ns	8.90**	2	3.68**	4.57ns
Genotypes	38	0.87**	9.67**	36	0.69**	6.12**
Errors	76	0.30	1.29	72	8.29	3.17

*, **Significant at 5% and 1% levels of probability, respectively.
ns Not significant.

Table 27. Eight Trait Means of F4s Selected for Biological Yield, Reselected, and Non-reselected for Biological Yield and Parent for VT159/Froid Cross Grown in 1981 Hill Experiment.

F4 Bulk Groups	Means				
	Selected	Reselected	Non-reselected	Parents	
Traits				VT159	Froid
Yield (Mg/ha)	5.32	6.12	5.23	4.04	4.20
Biological Yield (Mg/ha)	20.0	22.3	19.7	15.3	16.7
Harvest Index	.267	.276	.266	.264	.250
Plant Height (cm)	135	141	134	108	134
Straw Weight (Mg/ha)	14.6	16.0	14.5	11.3	12.5
Heading Date (days)	179	181	178	181	177
Percent Protein	16.7	16.8	16.7	15.9	17.4
1000 Kernel Weight (gm)	31.1	30.7	31.1	35.3	28.2
No. Entries	19	2	17	1	1

Table 28. Eight Trait Means of F4s Selected for Biological Yield, Reselected, and Non-reselected for Biological Yield and Parent for Roughrider/Centurk Cross Grown in 1981 Hill Experiment.

F4 Bulk Groups	Means				
	Selected	Reselected	Non-reselected	Parents	
Traits				Roughrider	Centurk
Yield (Mg/ha)	5.01	5.27	4.97	4.32	4.57
Biological Yield (Mg/ha)	19.0	19.7	18.9	17.1	19.3
Harvest Index	.265	.269	.264	.251	.239
Plant Height (cm)	122	121	122	126	119
Straw Weight (Mg/ha)	14.0	14.4	13.9	12.8	14.7
Heading Date (days)	174	173	174	175	173
Percent Protein	15.8	15.4	15.9	16.7	16.8
1000 Kernel Weight (gm)	29.0	29.4	29.0	29.7	28.1
No. Entries	19	2	17	1	1

Table 29. Eight Trait Means of F4s Selected for Harvest Index, Reselected, and Non-reselected for Harvest Index and of Parents for VT159/Froid Cross Grown in 1981 Hill Experiment.

F4 Bulk Groups	Means				
	Selected	Reselected	Non-reselected	Parents	
Traits				VT159	Froid
Yield (Mg/ha)	5.15	6.12	5.02	4.04	4.20
Biological Yield (Mg/ha)	18.8	20.4	18.6	15.3	16.7
Harvest Index	.274	.300	.270	.264	.250
Plant Height (cm)	128	125	129	108	134
Straw Weight (Mg/ha)	13.7	14.3	13.6	11.3	12.5
Heading Date (days)	178	178	178	181	177
Percent Protein	16.6	15.9	16.7	15.9	17.4
1000 Kernel Weight (gm)	31.5	32.6	31.3	35.3	28.2
No. Entries	17	2	15	1	1

Table 30. Eight Trait Means of F4s Selected for Harvest Index, Reselected, and Non-reselected for Harvest Index and of Parents for Roughrider/Centurk Cross Grown in 1981 Hill Experiment.

	Means				
F4 Bulk Groups	Selected	Reselected	Non-reselected	Parents	
Traits				Roughrider	Centurk
Yield (Mg/ha)	5.00	6.05	4.86	4.32	4.57
Biological Yield (Mg/ha)	18.5	21.4	18.2	17.1	19.3
Harvest Index	.270	.287	.268	.251	.239
Plant Height (cm)	118	125	118	126	119
Straw Weight (Mg/ha)	13.5	15.3	13.3	12.8	14.7
Heading Date (days)	175	173	175	175	173
Percent Protein	15.8	15.4	15.8	16.7	16.8
1000 Kernel Weight (gm)	28.8	30.5	28.6	29.7	28.1
No. Entries	18	2	16	1	1

Table 31. Mean Squares of Biological Yield of F3-derived F5 Lines for Two Winter Wheat Crosses over Three Environments in 1982.

	Mean Squares			
	Crosses			
	VT159/Froid		Roughrider/Centurk	
Source	df		df	
Environments	2	1402 **	2	1052 **
Env/Replication (pooled)	5	496.8 **	4	24.30 **
Genotypes	78	8.00**	79	2.91 **
Random	38	8.06**	39	3.96 **
Selected and Bulked Lines	39	6.11**	39	1.85 *
Bulked Lines	7	4.08ns	7	1.89 ns
Selected Lines	31	5.52*	31	1.89 *
Selected Line Families	7	10.2 *	7	1.23 ns
Within Families	24	4.15*	24	2.08 *
Line X Bulked Line	1	10.8 *	1	0.162ns
Random X Line Selection	1	89.9 **	1	2.19 ns
Environment X Genotypes	156	2.57ns	158	1.01 ns
Environment X Random	76	2.38ns	78	1.40 ns
Environment X Selected and Bulked Lines	78	2.74ns	78	1.09 ns
Environment X Bulked Lines	14	1.13ns	14	1.93 ns
Environment X Line	62	3.52*	62	0.926ns
Environment X Line Families	14	2.85ns	14	0.720ns
Environment X Within Families	48	3.72*	48	0.986ns
Environment X Line X Bulked Line	2	3.42ns	2	0.173ns
Environment X Random X Line Selection	2	5.24ns	2	2.139ns
Pooled Error	390	2.57	316	1.24
Mean		13.7		14.3
Range		11.1-16.9		12.8-16.2
C.V.		11.7		7.78
LSD .05		1.57		1.17
LSD .01		2.06		1.54

*, **Significant at 5 or 1% level of probability, respectively; ns Not significant.

Table 32. Mean Squares of Harvest Index of F3-derived F5 Lines for Two Winter Wheat Crosses over Three Environments in 1982.

	Mean Squares			
	Crosses			
	VT159/Froid		Roughrider/Centurk	
Source	df		df	
Environments	2	3.326 **	2	10.29 **
Env/Replication (pooled)	5	1.386 **	4	2.019 **
Genotypes	78	.5868**	79	.1285**
Random	38	.4855**	39	.1824**
Selected and Bulked Lines	39	.6997**	39	.0656ns
Bulked Lines	7	.7840**	7	.0514ns
Selected Lines	31	.6761**	31	.0707ns
Selected Line Families	7	1.943 **	7	.0299ns
Within Families	24	.3067**	24	.0826*
Line X Bulked Lines	1	.006742ns	1	.0086ns
Random X Line Selection	1	.03275 ns	1	.4671**
Environment X Genotypes	156	.1792**	156	.0562ns
Environment X Random	76	.1815*	78	.0638ns
Environment X Selected and Bulked Lines	78	.1602ns	78	.0625ns
Environment X Bulked Lines	14	.1793ns	14	.0894*
Environment X Line	62	.1794*	62	.0574ns
Environment X Line Families	14	.2174ns	14	.0814ns
Environment X Within Families	48	.1683ns	48	.0505ns
Environment X Line X Bulked Line	2	.08775ns	2	.1096ns
Environment X Random X Line Selection	2	.4321*	2	.0965ns
Pooled Error	390	.1277	316	.0500
Mean	**	.3277	**	.3442
Range	**	.2625-3846	**	.3109-.372
C.V.		10.90		6.496
LSD .05		.035		.023
LSD .01		.046		.030

*, **Significant at 5 or 1% level of probability, respectively; ns Not significant.

Table 33. Mean Squares of Plant Height, Straw Weight, and Heading Date of F3-derived F5 for Two Winter Wheat Crosses over Three Environments in 1982.

	Mean Squares			
	V/F Cross		R/C Cross	
	df		df	
Plant Height (source)				
Environment	2	7.82 **	2	277 ns
Replication (pooled)	5	.420 **	4	539 **
Genotypes	78	.500 **	79	111 **
Environment X Genotypes	156	.0292ns	158	25.0 ns
Error	390	.0270	316	22.0
Straw Weight (source)				
Environment	2	697.0 **	2	569.0 **
Replication (pooled)	5	32.48 **	4	21.38 **
Genotypes	78	5.536 **	79	1.862 **
Environment X Genotypes	156	1.786 ns	158	.6908ns
Error	390	1.608	316	.6147
Heading Date (source)				
Environment	2	739 **	2	394 **
Replication (pooled)	5	24.4 **	4	.716 ns
Genotypes	78	17.5 **	79	11.6 **
Environment X Genotypes	156	1.29 ns	158	2.43 **
Error	390	1.23	316	.685

*, **Significant at 5 or 1% level of probability, respectively.
ns Not significant.

Table 34. Mean Squares of Percent Protein, 1000 Kernel Weight, Test Weight of F3-derived F5 Lines for Two Winter Wheat Crosses over Three Environments in 1982.

	Mean Squares			
	V/F Cross		R/C Cross	
	df		df	
Percent Protein (source)				
Environment	2	151 **	2	310 **
Replication (pooled)	5	60.0 **	4	69.1 **
Genotypes	78	1.91 **	79	1.14 **
Environment X Genotypes	156	.859 ns	79	.993 **
Error	390	.824	316	.353
1000 Kernel Weight (source)				
Environment	2	1654 **	2	688.0 **
Replication (pooled)	5	31.63 **	4	46.04 **
Genotypes	78	50.17 **	79	25.18 **
Environment X Genotypes	156	3.686 **	158	2.294 *
Error	390	1.735	316	1.764
Test Weight (source)				
Environment	2	1648 **	2	298.7 **
Replication (pooled)	5	13.23 **	4	12.30 **
Genotypes	78	13.00 **	79	3.378 **
Environment X Genotypes	156	2.171 **	158	.7118**
Error	390	.8182	316	.4748

*, **Significant at 5 or 1% level of probability, respectively.
ns Not significant.

Table 35. Means for Nine Measured Traits of All Groups in V/F Cross over Three Environments in 1982.

Traits	Groups									
	Total	Random Lines	Bulk Yield Selected	Bulk Bio-Yield Selected	Bulk Harvest Index Selected	Lines Yield Selected	Lines Bio-Yield Selected	Lines Harvest Index Selected	Mid-Parent	Checks
Yield (Mg/ha)	4.50	4.36	4.29	4.32	4.70	4.52	4.45	4.88	3.82	5.08
Biological Yield (Mg/ha)	13.8	13.4	13.7	14.4	13.0	14.2	14.8	13.6	12.3	14.9
Harvest Index	.327	.327	.313	.301	.372	.321	.307	.361	.316	.343
Plant Height (cm)	127	120	131	133	122	130	133	119	113	120
Straw Weight (Mg/ha)	9.33	9.00	9.40	10.1	8.27	9.69	10.3	8.68	8.48	9.80
Heading Date (days)	180	180	181	181	180	181	181	79	181	177
Percent Protein	13.5	13.5	13.5	13.7	13.1	13.6	13.7	13.1	13.7	13.3
1000 Kernel Weight (gm)	36.71	35.77	37.72	38.21	36.43	37.49	38.05	36.80	35.27	34.61
Test Weight	80.42	80.80	80.10	79.25	80.10	80.02	79.18	80.11	75.70	83.35
Totals	792	312	35	14	14	160	64	64	16	24
Entries	99	39	5	2	2	20	8	8	2	3

Table 36. Means for Nine Measured Traits of All Groups in R/C Cross over Three Environments in 1982.

	Groups									
Traits	Total	Random Lines	Bulk Yield Selected	Bulk Bio-Yield Selected	Bulk Harvest Index Selected	Lines Yield Selected	Lines Bio-Yield Selected	Lines Harvest Index Selected	Mid-Parent	Checks
Yield (Mg/ha)	4.92	4.84	5.03	4.97	4.85	4.98	5.03	4.97	5.03	4.80
Biological Yield (Mg/ha)	14.4	14.3	14.6	14.7	14.1	14.4	14.5	14.4	15.3	15.5
Harvest Index	.343	.341	.349	.343	.344	.348	.349	.347	.332	.313
Plant Height (cm)	114	113	115	113	115	114	114	115	118	125
Straw Weight (Mg/ha)	9.49	9.41	9.56	9.77	9.30	9.39	9.43	9.42	10.3	10.7
Heading Date (days)	177	177	177	177	176	177	177	176	177	179
Percent Protein	12.8	12.9	12.8	12.6	12.5	12.8	12.4	12.7	13.0	13.3
1000 Kernel Weight (gm)	33.41	32.81	33.92	33.97	33.20	33.53	33.67	33.76	32.05	35.87
Test Weight (Kg/ha)	83.18	83.27	83.29	83.14	83.37	83.03	83.03	83.28	83.42	83.53
Totals	700	280	35	14	14	140	56	56	14	14
Entries	100	40	5	2	2	20	8	8	2	2

Table 37. Phenotypic Correlations for the Eight Measured Traits of F3-derived F5 Lines in Two Winter Wheat Crosses over Three Environments in 1982.

Traits	Phenotypic Correlations															
	Biological Yield		Harvest Index		Plant Height		Straw Weight		Heading Date		Percent Protein		1000 Kernel Weight		Test Weight	
Yield	.57 **	.65† **	.67 **	.54 **	-.12 ns	.10 ns	.16 ns	.32 **	.01 ns	-.25 **	-.51 **	-.25 *	.15 ns	.14 ns	.12 ns	-.12 ns
Biological Yield			-.20 ns	-.28 *	.51 **	.43 **	.90 **	.93 **	.36 **	.00 ns	-.02 ns	.04 ns	.44 **	.17 ns	-.04 ns	-.05 ns
Harvest Index					-.55 **	-.33 **	-.60 **	-.61 **	-.34 **	.30 **	-.59 **	-.35 **	-.18 ns	.01 ns	.16 ns	.07 ns
Plant Height							.68 **	.48 **	.36 **	.06 ns	.24 *	-.13 ns	.36 **	.39 **	-.07 ns	-.03 ns
Straw Weight									.43 **	.13 ns	.24 *	.17 n ns	.45 **	.15 ns	-.12 ns	.00 ns
Heading Date											.31 **	.15 ns	.33 **	-.13 ns	-.37 **	.12 ns
Percent Protein													.11 ns	.00 ns	-.11 ns	.19 ns
1000 Kernel Weight															-.12 ns	.06 ns

*, **Significant at 5 or 1% level of probability, respectively.
ns Not significant.
†'r' values for VT159/Froid and Roughrider/Centurk, respectively.

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