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YIELD GAINS IN WHEAT BY THREE METHODS OF SELECTION

by

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A B S T R A C T

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by Josef F. Seitzer

Three crosses of spring wheat (Triticum aestivum L.), differing in degree of heterosis were chosen to compare the efficiency of three methods of selection for identifying high yielding late generation lines. The three methods compared were (1) a pedigree method where visual selection was practiced in F_3, (2) an early generation yield test where F_3 plots were compared to adjacent controls, and (3) an early generation yield test wherein replicated tests with hill plots were used to evaluate the yield potential of F_3 families.

The efficiency of these methods was evaluated in F_5. One hundred and eighty lines derived from 45, 6 and 3 selected F_3 lines in methods (1), (2) and (3) respectively, were grown at each of 2 locations. Comparisons among crosses were made for mean yield, variances among F_3 families and among F_5 lines within F_3 families, actual line yield and line yield relative to the control variety.

The methods did not differ significantly with regard to mean yield, variances and line yield. Significant differences between methods were obtained in two crosses when line yields were

compared to the control. In cross I, all three methods of selection were effective in recovering lines outyielding the control, but the control plot method retained the most. In cross II none of the methods was successful in identifying lines which exceeded the control. In cross III the hill plot method isolated significantly more lines than the pedigree method and was slightly better than the control plot method of selection. Both crosses I and III were more heterotic than cross II.

It was concluded that early testing may have an advantage when dealing with crosses of lower yield potential.

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INTRODUCTION

One ot the major goals in plant breeding is the production of high yielding varieties. With a growing human population and food shortages in many parts of the world, the need for varieties without a genetic ceiling to their yielding ability becomes even greater.

Yield is thought to be influenced by many genes and to be the endproduct in a long chain of reactions, interactions and compensatory effects. Because yield is very sensitive to environmental influences, it is difficult to manipulate. This fact is reflected in that methods of selection applied and population sizes vary greatly in breeding programs (Shebeski, 1967).

Few empirical studies comparing the efficiency of various selection methods are available. The more classical methods of selection, the pedigree and bulk method, rely heavily on visual selection which is generally believed to be of little value especially when dealing with yield differences of 10% or less. Because of this, early generation yield tests were used in developing the high yielding variety Glenlea (Evans et al., 1972).

The study reported herein compares the efficiency of three breeding methods; the classical pedigree method and two which use early generation yield testing. The early generation yield tests were the use of rod row plots compared to an adjacent control plot (Shebeski, 1967) and replicated hill plots (Jellum _et al_., 1963). The hill plot method allows for replicated tests on one or more locations. With replicated tests, the breeder could obtain information as to the adaptation and performance of a line at a very early stage. Such information should allow more effective selection in early generations (Shebeski and Evans, 1973).

The effectiveness of breeding methods can be evaluated by measuring the overall mean yield of selected lines or by the number of lines which exceed a certain minimum yield.

The study also compares three crosses; two of the crosses gave F_1 populations with much more heterosis than the third.

LITERATURE REVIEW

The plant breeder concerned with the improvement of varieties and their yielding ability faces three main problems.

(1) The choice of parents.

(2) The choice of the most promising crosses.

(3) The choice of a selection method.

Although the present study concentrates mainly on selection methods, the choice of parents and of crosses are given some consideration as they pertain to this research.

1. Choice of parents.

A common procedure among breeders in selecting parents for hybridisation is "to cross the best with the best and hope for the best", (Whitehouse, 1968). In practice, the actual number of crosses performed varies greatly. Some breeders prefer a few carefully planned whereas others (e.g. CIMMYT in Mexico) produce a great many almost at random. In barley, Smith and Lambert (1968) found that the yield of the parents was a good index of how many F_5 lines they would contribute to the class of high yielding lines. Working with soybeans, Shannon _et al._ (1972) observed that at least one high yielding parent was involved in all superior progenies. Whitehouse (1968) however points out that such an approach could misjudge the situation if the combining ability of parents can only be evaluated by testing their progenies.

2. Choice of the most promising crosses.

Cress (1966) showed that intralocus interactions may result in negative heterosis so that the performance of a F_1 would be of little value in evaluating crosses. Lupton (1961) and Whitehouse (1968) also concluded that the yield of advanced lines cannot always be predicted by the performance of the F_1, but that crosses which are superior in F_1 and F_2 produce a higher frequency of favorable lines in later generations. Smith and Lambert (1968) tested bulk populations from F_2 to F_5 and found the predictive values of the F_3 and F_4 generations to be good but that F_2 data was less reliable. They do propose however that early generation bulk tests can be used to eliminate 70 to 80% of the crosses with little probability of loosing superior genotypes.

3. Choice of selection methods.

After having decided what crosses should be dealt with, the breeder must chose a technique to handle his segregating populations. This decision obviously cannot be independent of the number of crosses to be handled.

In the pedigree method, visual selection is practiced in the early generations for the more simply inherited characters such as plant height, maturity and disease resistance as well as for plant characteristics supposedly related to productivity such as tillering, head size etc. Actual yield tests are delayed until F_5 or later when the material approaches homozygosity, (Allard, 1960).

St.Pierre et al. (1967) found a good association between yield components in early generations and yield in later generations and concluded that yield per spike was a good indicator of total yield. These findings are substantiated by the reports of Paroda and Joshi (1970), Walton (1971) and Sun et al.(1972). They found large additive variance for seed weight and high intercorrelations at the genotypic and phenotypic level for seed weight, weight per spike and total seed yield. Paroda and Joshi (1970) conclude that seed weight is the most heritable and genetically stable component of yield in wheat. Alessandroni and Scalfati (1973) found yield per head of F_2 plants highly correlated with the yield of their F_4 progenies and concluded that this should be a good trait for selection in segregating generations.

Other workers found yield components less efficient in improving the yield level. Lupton et al. (1963) and Monyo and Whittington (1971) state that the best component in selecting for higher productivity is yield itself. In a recent study under European conditions, Utz et al. (1973) conclude that efficient selection for yield by using yield components in the F_2 or F_3 seems unlikely.

The main feature of the pedigree method of breeding is that, in early generations (F_2 to F_4), visual methods are used to discriminate and eliminate plants and plant progenies. Working with oats, Frey (1961) found visual selection somewhat more efficient when based on progeny rows than on single plants. Knott (1972) demonstrated that visual selection resulted in a significant increase over random selection, but that selected lines showed a considerable range. McGinnis and Shebeski (1968) could not demonstrate any differences between random and visually selected lines. However, their "random" lines had to have a minimum of 750 seeds to be included in the test and thus were probably not truly random.

The relative inefficiency of visual selection was also demonstrated in cereals by Boys _et al_. (1947), McKenzie and Lambert (1961) and by Hanson _et al_. (1962) for soybeans. In a more recent study, Townley-Smith _et al_. (1973) reported on an experiment, wherein 9 selectors with various levels of experience failed to identify many of the highest yielding lines of wheat when selecting at the 25% retention level.

Briggs and Shebeski (1970) evaluated the efficiency of visual selection for the improvement of seed yield in wheat. They concluded that lines that were visibly very poor in yield could safely be discarded. They showed that some people were more efficient than others in visually discriminating between high and low yielders.

Shebeski (1967) has stressed the importance of the F_2 and F_3 generations when selecting for yield. He suggests that, if one considers two parents differing for a number of genes for yield, the progenies having most of the desirable genes will have their highest frequency in F_2. Recognizing the relative inefficiency of visual selection, Shebeski (1967) advocates yield testing of F_3 families to identify those with the highest mean yield. These families are the only ones exploited in subsequent generations. Whitehouse (1968) states that, although one selects from the fringe of the yield distribution, it will be evident that the nearer the mean of a family is to the ideal the greater is the probability of finding outstanding plants in that family. Frey (1954), also in recognition of the fact that the F_2 has the greatest genetic variability, suggested that selection in barley should start as early as possible. Selection within late generation families would give rapidly diminishing returns. Delaying selection to later generations also means a decrease in probability of recovering superior genotypes (Allard, 1960; Shebeski, 1967).

Early generation testing procedures are rationalized on the premise that a positive correlation exists between the yield in early generations and the yielding ability of later generations, e.i. that genetic variance in control of seed yield is mainly additive. Positive correlations between F_2, F_3 and later generations have been reported by Shebeski (1967) and DePauw and Shebeski (1973). Exceptions to these findings are given by Briggs and Shebeski (1971), who found that F_3 yields did not predict F_5 yield performance in 2 out of 3 years.

The control of yield by additive gene action was reported by Lonquist et al., 1961; Sprague, 1966; Brown et al., 1966; Whitehouse, 1968; Smith and Lambert, 1968; Sing et al., 1969; Bhatt, 1971; Walton, 1972 and Sampson, 1972. Robinson (1963) concludes that the additive genetic variance appears to be the most important component of genotypic variance in open pollinated species and probably even more so in selfpollinated species.

Dominance and epistatic effects for yield have been observed (Grafius, 1952; Lupton, 1961; Walton, 1972). Busch et al. (1971) analysed 3 crosses and found large dominance effects in the first two crosses and epistatic effects in the third. In all crosses, they were able to isolate lines which outyielded the better parent and F_1. They concluded: "This seems to invalidate the genetic analysis, since if overdominance and non-fixable types of epistasis were of major importance in these crosses, pure lines should yield less than F_1 hybrids." The effects of genotype can change in order and magnitude under changing environmental conditions (Chapmann and McNeal, 1971; Amaya et al., 1972; Kaltsikes and Lee, 1973). Thus it seems necessary to grow several tests and account for genotype-environment interactions in order to obtain unbiased estimates.

Early generation tests are performed on a line or family basis. Since the breeder has only the limited amount of seed from a single (F_2 or F_3) plant at his disposal, very few plots can be tested in early generations. In response, Shebeski (1967) proposed that a single 3-row plot of 5 m length be planted close to a control variety and evaluated as percent of this control. He was able to show that high yielding F_5 lines traced back to F_3 lines that yielded high relative to the adjacent control. This method was further evaluated by Briggs and Shebeski (1970), who found a positive relationship between F_3 plots and the mean yield of F_5 populations in only 1 year out of 3. For theoretical reasons and with the support of a 2 year study, Baker and McKenzie (1967) doubt wether the use of these systematic controls is of much value as a fertility index.

The use of a moving mean in evaluating early generations was proposed by Townley-Smith and Hurd (1973). This technique employs the mean yield of adjacent plots to evaluate soil fertility in the area of a particular plot. They found the moving mean superior to control plots and to analysis of covariance in reducing the experimental error in nonreplicated yield trials.

The use of hill plots was advocated by Jellum et al. (1963). Ross and Miller (1955) compared hill plots with row plots. They found that variability in hill plots was generally higher than in row plots. They also found that the method gave better relationship with oats than with barley and recommend hill plots only as a supplement to row plots. Frey (1965) evaluated 8 years of oat breeding data involving 300 000 hill plots and obtained genetic correlations between rows and hills of 0.98 for grain yield. In a review paper, Le Clerg (1966) provided evidence of similar ranking in rows and hill plots, which was confirmed by Fonseca and Patterson (1968b). In a study by Bonnett and Beaver (1947), correlations between yield in hills and in rod rows ranged from - 0.22 to 0.96 and they concluded that hills have a value in preliminary yield tests. In a study involving 10 spring wheat and 10 durum cultivars tested over 2 years, Baker and Leisle (1970) compared yields in both hills and plots. They found the correlation to be high in all cases and conclude that hills could be used in early testing methods. They also noted that the cultivars exhibited a greater range of yield in hills than in row plots. Johnson et al. (1966) and Fonseca and Patterson (1968a) found high heritabilities for grain yield when lines were tested in hill plots.

Few empirical studies comparing various selection techniques are available. Frey (1968) found that early testing produced greater yield gains than either of two modified pedigree methods. Breeding varieties for the dryer areas of Canada, Hurd (1969) gave data on lines originating from early tests. In 275 out of 465 comparisons, the selected lines significantly outyielded the control varieties. Seed yields significantly lower than the best control were recorded in only 5 comparisons. Fasoulas (1973) used a technique in which spaced plants were evaluated on a yield per plant basis from F_2 onwards. The method was effective in breeding the variety "Rhodes".

Actual comparisons between the pedigree method and early testing have been done with soybeans. Voigt and Weber (1960) reported that lines developed from early tests were superior to those from pedigree and bulk methods in yield and agronomic characters. Their findings were substantiated by Kwon and Torrie (1964), who calculated the expected genetic gain of visual selection to be 50% of that based on plot yield. They noted that selectors were able to classify lines correctly only when differences were large. These reports are in contrast to the findings of Boerma and Cooper (1973), who found no consistent yield differences between the pedigree, early testing and single seed descent methods. However, their early testing lines were consistently later in maturity.

MATERIALS AND METHODS

F_1

In 1971, F_1 populations from 21 spring wheat crosses were compared in a three replicate yield test at Winnipeg. Plots were a single row 1.5 m in length and 60 cm apart. A planting rate of 50 seeds per row (approximately 75% of normal rate) was used. Parents were grown on either side of each hybrid. Glenlea was the common parent in 19 of the crosses and Tobari 66 in two. Seed yield was expressed as percent of Glenlea. The crosses selected for this study yielded 119, 87 and 121% of Glenlea and were designated crosses I, II and III, respectively. A t-test (with 2 d.f.) showed that only the F_1 hybrid of cross III was significantly different from the control.

The parentage of the three crosses studied is given below, following Purdy *et al.*'s (1968) pedigree designation:

Cross I: Sonora 64/Ske/Aue 3/3/El Gaucho/Pitic 62/4/ x Glenlea

Cross II: Wisconsin Supremo/2*Frocor/A/3/2*African Mayo/4/ x Glenlea

Cross III: Hard Federation/Chinese Spring/Nero/3/3*purple Pitic/ 4/ x Glenlea.

To determine the gene action controlling the inheritance of seed yield, parents F_1, F_2 and backcross generations were planted in a randomized complete block design with 4 replicates. Each cross was tested in a separate experiment. Plots were a single row 1.80 m in length. Spacing between plots was 30 cm and seedrate 30 seeds per row. A short strawed wheat cultivar was planted on either side of each test plot to standardize competition. These tests were conducted in 1973 at Winnipeg. Seed yields per plot were recorded and means and variances calculated for individual generations. With these data, a weighted least square analysis (Hayman, 1958) was performed to estimate gene effects, employing the computer program of Lee and Kaltsikes (1971).

F_2

The F_2 was space planted in a winter nursery at CIANO, Obregon, Mexico. For each cross approximately 2000 plants were grown. At harvest time, 360 well tillered plants were selected from each cross for F_3 testing in hills and with control plots; an additional 1040 plants were selected from each cross for a total of 1400 to be included in the pedigree method.

Seed of each of the 360 plants from a cross was divided into 3 parts: 600 seeds for each of the two early testing methods and 30 seeds for the pedigree method. Hence a plant had to have at least 1230 seeds to be included in all 3 methods of selection. No minimum seed number was set for the additional 1040 plants to be tested by the pedigree method only.

$\underline{F_3}$

Early testing-adjacent control plots (ETC). Each of the 360 families per cross were tested in a single 2 row plot, 5.60 m in length and trimmed to 5.0 m at harvest. Seedrate was 300 seeds per row for all entries. Spacing between rows was 30 cm and between plots 60 cm. Every seventh plot was planted to Glenlea as a control plot. Individual F_3 plot yields were expressed as % of the nearest control plot.

Six F_3 families were selected in each cross. To be selected, a family had to have high actual yield as well as being high relative to the adjacent control plot.

Early testing - hill plots (ETH). 360 F_3 families were tested in replicated hill plot tests at 2 locations, Winnipeg and Glenlea. Hills were spaced 90 cm apart in each direction. Each hill measured 20 cm in diameter and was planted by hoe and stove pipe (Plates 1 and 2). Seeding rate was 50 seeds per hill. Six replicates (hills) were planted per F_3 family. Hence an equal number of seeds were used in both early generation tests.

The 360 families of a cross were divided randomly into groups of 36. Each group was treated as a complete randomized block with 6 replicates (a total of 216 hills). Each randomized group was surrounded by hill plots of the control variety Glenlea, planted at comparable spacing and density. A diagramatic representation of the field design is given below:

```
x o o o o o o x o o o o o o x
x o o o o o o x o o o o o o x
x o o o o o o x o o o o o o x      Rep.II
x o o o o o o x o o o o o o x
x o o o o o o x o o o o o o x
x o o o o o o x o o o o o o x
-----------------------------
x o o o o o o x o o o o o o x
x o o o o o o x o o o o o o x
x o o o o o o x o o o o o o x      Rep. I
x o o o o o o x o o o o o o x
x o o o o o o x o o o o o o x
x o o o o o o x o o o o o o x
```

Arrangement of a portion of the F_3 nursery indicating relationship of control (x) to hybrid hills (o).

An analysis of variance was performed on seed yields of each group of 36 families. The error variances of these analyses were tested for homogeneity and found to be highly heterogeneous. To obtain comparable values for all families tested, it was decided to transform the data. For this, mean yields for each F_3 family were transformed by substracting the mean of the 72 hills of Glenlea which surrounded the particular experiment. The difference was then divided by the standard error of that particular randomized block to account for the environmental variability. This transformation gives the mean yield of a F_3 family as a deviation from the mean of the control variety, measured in standard error units (Steel and Torrie, 1960). All families in a cross were then ranked on the basis of the transformed values and the best three families selected. A family mean was considered to yield significantly more than the control if its transformed yield was greater than 1.796 (t-value at P 0.05 and 11 degree of freedom).

P e d i g r e e   m e t h o d (P). The 1400 entries of each cross were planted at Glenlea in rows of 1.25 m length, 30 cm apart. Rows of Glenlea and parent 2 of cross I were planted at frequent intervals to aid visual selection. An entry consisted of either 30 seeds from each of the 360 plants tested in ETH and ETC or a selected head of the additional 1040 plants selected for this method only. No identity was kept as to the origin of the entries.

100 of the 1400 head rows were selected on the basis of visual observation. Then the 10 largest spikes in each of these rows were threshed and weighed. The yield of the 10 spikes of each selected F_3 family was compared to the yield of 10 spikes from the nearest row of Glenlea and the 72 F_3 families which had the highest yield per head relative to the control were retained.

A schematic outline of the generation sequence and family - line relationship is given below:

F_1 Yield test

F_2 2000 spaced plants from a selected cross

F_3 360 families tested in both early tests — 1040 heads + 360 fam. grown as "head rows" for the pedigree method

F_4
- 3 families x 100 spaced plants each for the hill plot method
- 6 families x 60 spaced plants each for the control plot method
- 72 families x 30 spaced plants for the pedigree method

F_5

Hill plot method	- 3 families	x	60 lines each	=	180 lines total
Control plot method	- 6 families	x	30 lines each	=	180 lines total
Pedigree method	-45 families	x	4 lines each	=	180 lines total

F_4

Seed samples of the selected F_3 families were space planted in the winter nursery in Mexico. The number of single F_4 plants per F_3 family was approximately 100, 60 and 30 for the hill plot test, adjacent control test and pedigree test, respectively. At harvest, 60 plants from each of the 3 families from hill plot testing, 30 from each of the 6 families for the adjacent control test and 8 from each of the 60 families for the pedigree method (reduced to 4 x 45 by selecting for plant yield and grain characters) were harvested to give a total of 180 plants per method in each cross.

F_5

Duplicate nurseries were planted at Winnipeg and Glenlea. Each method within a cross was represented by 180 F_5 lines and each line was grown in one plot at each location. Plate 3 gives a general view of the F_5 experiments. A plot consisted of 3 rows of 5.60 m length, which was trimmed to 5 m before harvest. Spacing was 15 cm between rows and 45 cm between plots. Seedrate was constant for each entry at 200 seeds per row.

A random group of 18 lines per cross and method was planted on either side of the control variety Glenlea. These groups were planted each 3 plots wide and 6 plots deep across the block. Every 7th plot then was planted to the control. A diagramatic representation

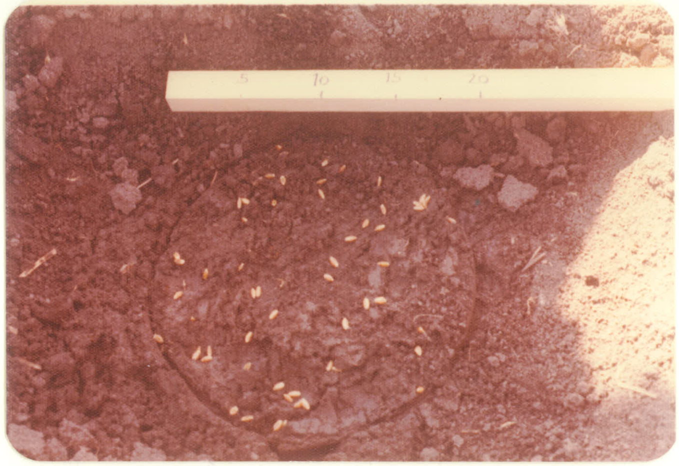

Plate 1.
Planting hill plots by stove pipe; diameter of plots approximately 20 cm.

Plate 2.
F_3 hill plots in heading stage.

Plate 3.
F_5 - test plots at Winnipeg in 1973. The 6 plots in the center are framed on either side by the control.

of the F_5 nursery is given below:

X 0 0 0 0 0 0 X 0 0 0 0 0 0 X	Range 6	
X 0 0 0 0 0 0 X 0 0 0 0 0 0 X	Range 5	
X 0 0 0 0 0 0 X 0 0 0 0 0 0 X	Range 4	
X 0 0 0 0 0 0 X 0 0 0 0 0 0 X	Range 3	Block
X 0 0 0 0 0 0 X 0 0 0 0 0 0 X	Range 2	
X 0 0 0 0 0 0 X 0 0 0 0 0 0 X	Range 1	

Diagramatic representation of arrangements of line plots (0) and control plots (X) in the F_5 nursery.

An analysis of variance was performed individually for each cross and method combination with locations as replicates. Differences between lines were tested for significance by an LSD-test. In addition, lines were compared individually to the control. For this purpose the yield of each line was transformed to standard deviates (Z) by subtracting the mean of the six plots of Glenlea closest to the line and then dividing the difference by the standard deviation of that particular group of 18 lines. A line yield was considered to yield significantly more than the control variety if its transformed value was greater than 1.10 or 1.65 (tabulated values at P 0.10, P 0.05, respectively for the normal distribution; Snedecor and Cochran, 1969).

The standard deviates so computed were also pooled over locations and means were calculated for each line.

The test sites involved were the experimental fields at the University of Manitoba Campus (Winnipeg) and at the Glenlea Research Station (15 miles South of Winnipeg). The soil type at Winnipeg is Riverdale silty clay loam and at Glenlea Red River clay.

The yield tests were performed in 1972 for F_3 and in 1973 for F_5. In 1972, rainfall recorded during the critical months of April to July was 5.52 inches at Winnipeg and 5.25 inches at Glenlea. The respective rainfall for 1973 was 11.7 and 10.7 inches. The longtime expectation of rainfall at Winnipeg is 9.5 inches for this period.

At Winnipeg, the test received 100 lbsN/acre in 1972 and 60 lbs N/acre in 1973. No fertilizer was applied in either year at Glenlea.

The tests in 1972 at Glenlea suffered throughout the year from drought. In 1973, leaf rust was noticed in some lines of cross II at both locations. Harvesting delays caused by rainy weather in 1973 resulted in some shattering at Glenlea in all three crosses. No attempt was made to correct for these losses.

RESULTS AND DISCUSSION

1. EVALUATION OF CROSSES AND INHERITANCE OF SEED YIELD

1.1 Seed yield of parents, F_1 hybrids and backcrosses

Seed yields of parents, F_1 hybrids and the two backcrosses ($F_1 \times P_1$; $F_1 \times P_2$) are given in Table 1. This test was conducted primarily to identify gene action controlling yield. As indicated the F_1 yield of crosses I and III was significantly higher than either the mid parent or high parent value. The F_1 of cross II was significantly above the mid parent value but not different from the high parent. These data are in agreement with the data initially obtained in the testing of the 21 F_1 hybrids in that the F_1 of crosses I and III show more heterosis than the F_1 of cross II.

In the absence of epistasis, the expectation of a F_2 mean yield is $1/4\ \bar{P}_1 + 1/4\ \bar{P}_2 + 1/2\ \bar{F}_1$. The observed values closely fit the expected. As shown in Table 1, there is a considerable decrease in yield from F_1 to F_2 in crosses I and III, while little difference existed between the F_1 and F_2 of cross II.

Table 1. Seed yields (g/plot) and standard errors of parents, F_1, F_2 and backcross generations of crosses I, II and III.

Designation	Cross I		Cross II		Cross III	
	Yield	SE	Yield	SE	Yield	SE
P_1	339	17	347	4	357	29
P_2	301	6	185	10	301	5
F_1	460	11	357	7	429	4
F_2	338	33	286	18	374	21
$F_1 \times P_1$	431	9	361	14	428	24
$F_1 \times P_2$	326	13	263	9	335	18
Mean	374		300		371	
LSD (P 0.05)	64		34		61	
(P 0.01)	89		47		85	

1.2 Inheritance of seed yield

Gene effects were estimated by a least square analysis (Hayman, 1958) of parental, F_1, F_2 and backcross data for each cross. Results are given in Table 2. As indicated by the chi-square test, a 3 parameter model fits all crosses. The inheritance of seed yield was strongly influenced by dominant genes in crosses I and III where additive effects were nonsignificant. On the other hand, cross II exhibits significant additive gene action as well as dominant gene action.

This analysis shows that, in these crosses, dominance plays a major part in the inheritance of yield. Dominance variance diminishes by 1/2 for each generation of selfing and is thus not fixable. However, as Falconer (1960) points out, dominant genes can have a considerable masking effect on additive genes.

Table 2. Estimates of genetic effects for seed yield based on parents, F_1, F_2 and backcross generations.

Cross	Genetic Parameters			X^2
	Mean (m)	Additive (d)	Dominance (h)	
I	394.3	38.3	120.1*	5.9 NS
II	309.4	83.4**	91.4*	0.7 NS
III	382.5	36.9	92.1*	1.1 NS

*, **, estimated effects significantly different from zero at P 0.05, P 0.01, respectively.

2. EARLY TESTING IN F_3

2.1 The control plot method (ETC).

The results of the test plots grown at Winnipeg in 1972 are given in Table 3. On the basis of mean yield performance, crosses I and III outyielded cross II by 10 and 4%, respectively. Of special interest is the lower range in yield obtained in cross II than in the other crosses.

Table 3. F_3 population mean yields and range of yield for three crosses, as tested by the control plot method at Winnipeg.

Cross	N	Mean Yield		Range of Yield	
		g/plot	% of Glenlea	g/plot	% of Glenlea
I	360	1425	99.2	779 - 2001	47.4 - 190.9
II	360	1284	89.3	689 - 1876	40.7 - 167.9
III	360	1340	93.2	725 - 1970	54.6 - 209.8
Control		1437	100.0		

The selection intensity applied was approximately 2% with 6 families selected per cross from a total of 360. A selected family had to have high absolute yield as well as a high ranking in percent of control. The lines selected and their performance is given in Table 4. In all crosses except cross I, the families ranking first in actual and relative yield were included in the selected portion.

Table 4. The seed yields and ranks of F_3 families selected by the control plot method.

Cross/Line No.	Seed Yield g/plot	Seed Yield % of control	Ranking % of control
I-72- 76	1493	191	1
88	1853	165	4
91	1891	155	5
243	1926	137	11
319	1910	128	19
352	1950	121	29
$\bar{x}$	1837 ± 70		
II-72- 4	1740	116	19
16	1702	113	27
22	1738	117	16
58	1511	168	1
64	1734	121	13
262	1870	112	30
$\bar{x}$	1716 ± 47		
III-72-55	1888	210	1
155	1732	121	22
161	1882	120	23
168	1841	137	4
274	1804	134	10
279	1970	112	53
$\bar{x}$	1853 ± 33		

2.2 The hill plot method (ETH).

The mean performance of the crosses at Winnipeg and Glenlea are presented in Table 5. Again, ranking of crosses is identical to the ranking obtained in the control plot method. When lines are compared relative to the control, it can be seen that cross I has an abundance of lines exceeding the control, cross II had only one and cross III had eleven F_3 families which were considered to be higher yielding than the control. Although both crosses I and III have similar means, cross I shows a wider range of variability (Figure I). The inferiority of cross II is indicated by its lower mean and the few lines exceeding the control.

Table 5. F_3 population mean yields and No. of lines exceeding the control for each of the three crosses as tested by the hill plot method at Winnipeg and Glenlea.

Cross/ Location	N	Mean Seed Yield g/hill Wpg.	Mean Seed Yield g/hill Gl.	Mean Seed Yield % of control Wpg.	Mean Seed Yield % of control Gl.	No. of lines exceeding the control
I	360	172	104	96	96	40
II	360	147	88	82	80	1
III	360	164	94	91	86	11
Control	-	180	109	100	100	

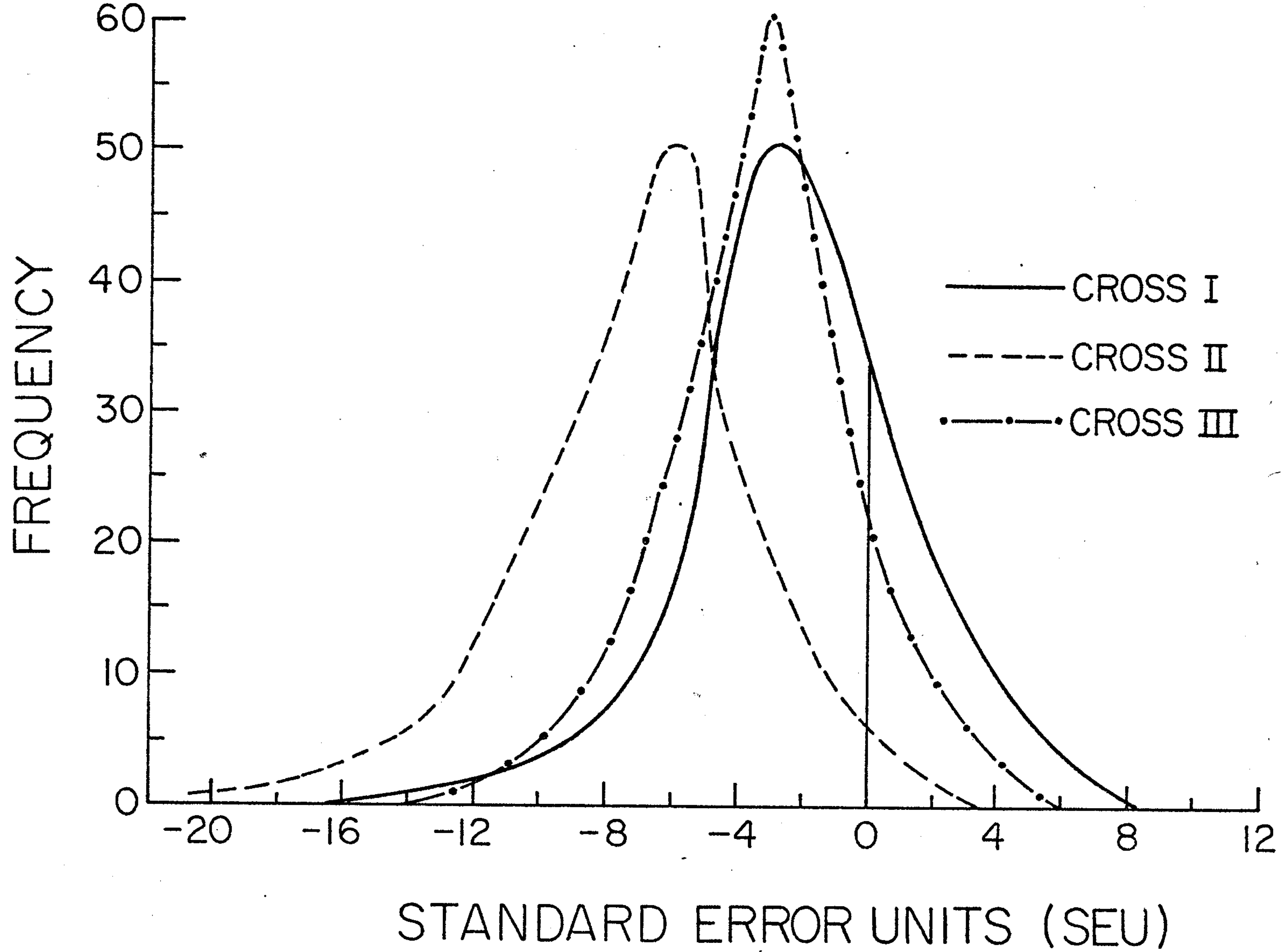

Fig. 1: Yield distribution of F_3 families from three crosses (N = 360), tested at two locations by the replicated hill plot method (ETH).

The performance of the 3 families selected in each cross is given in Table 6. With the exception of cross II, the families selected include the highest yielding ones in each cross; the highest yielder in cross II was accidentally omitted due to harvesting delays.

Table 6. The seed yields (means of 2 locations) and ranks of F_3 families selected by the hill plot method.

Cross/Line No.	Seed Yield		Ranking			
			S E U		Seed yields	
	g/hill	% of control	Winnipeg	Glenlea	Winnipeg	Glenlea
I-72- 4	192*	122	7	7	3	20
66	200*	124	5	1	6	1
77	190*	120	1	4	14	3
II-72- 84	158*	105	3	10	5	22
130	133	95	78	3	98	69
230	110	90	223	1	243	200
III-72-68	181*	110	17	2	9	1
94	156*	111	7	6	15	78
333	145	102	84	1	125	43

*, considered to yield significantly higher than the control by test criterion outlined in text.

Ideally, the families to be selected should outyield the control significantly at both locations. With a preponderance of high yielding lines in cross I, 3 families of similar potential were selected (Table 6). In cross II only 1 family outyielded the control significantly. The other 2 families selected in this cross were evaluated on only their Glenlea performance, Winnipeg not being harvested at that time. From the 3 families selected in cross III, 2 were superior to the control while the third was not. Line III-333 was selected on data from one location only.

Having tested genetically identical material in both early generation tests it is of interest to compare the ranking of mean yields of lines selected by the two methods (Tables 7 and 8). With few exceptions, there seems to be no common ranking between methods; families I-72-243 and III-72-68, which later proved to be outstanding, ranked well in both tests.

The poor agreement in ranks might be due to one or both of two possible causes. The first possibility is that one or both methods do not accurately measure the true yield potential. Obviously, with 6 replicates at each of 2 locations for the hill plot method as compared to one plot for the control plot method, one would give more reliance to results obtained by the former. Besides, yield estimates of the hill plot method contain with 2 locations one additional variance component, namely genotype - location interactions. For these last reasons, one would expect lines from the hill plots to show wider adaptation to various conditions of testing.

Table 7. Comparisons of seed yield ranks of F_3 families selected by the hill plot method (ETH) and their ranking in the control plot method (ETC).

Cross I			Cross II			Cross III		
Family No.	Rank ETH	Rank ETC	Family No.	Rank ETH	Rank ETC	Family No.	Rank ETH	Rank ETC
72- 4	6	192	72- 84	2	294	72- 68	1	19
66	1	128	130	30	14	94	4	308
77	2	14	230	40	69	333	24	244

Table 8. Comparisons of seed yield ranks of F_3 families selected by the control plot method (ETC) and their ranking in the hill plot method (ETH).

Cross I			Cross II			Cross III		
Family No.	Rank ETH	Rank ETC	Family No.	Rank ETH	Rank ETC	Family No.	Rank ETH	Rank ETC
72- 76	268	1	72- 4	51	19	72- 55	201	1
88	56	4	16	306	27	155	69	22
91	348	5	22	142	16	161	344	23
243	37	11	58	19	1	168	232	4
319	143	19	64	22	13	274	90	10
352	150	29	262	90	30	279	86	53
			(130	164	14	68	1	19)*

*, see text for explanation.

A second explanation is that in the two testing methods, yield in one is a genetically different trait from yield in the other. It is not possible to separate the two possibilities in this experiment.

When the initial selection was made with control plots and compared to those selected by hill plots, 2 families were found to be in common. No. II-72-130 was then omitted from the control method since other equally good material was available. No.III-72-68 was carried to F_4 in both methods but was omitted at harvesting time from the control plot method due to late maturity.

It must be emphasized that selections made in both early tests were based purely on yield performance; no consideration was given to such agronomic characters as maturity and lodging. However, only disease free plants were selected in F_2 and F_4 to be included in the tests.

2.3 Pedigree method (P).

The mean yields of the initial 100 head rows selected visually and the 72 finally retained is given in Table 9. Visual selection was exercised for agronomically desirable traits but size and filling of the spike was given first priority.

The ranking of crosses, with crosses I and III outyielding cross II by approximately 10%, was similar to the early tests. However, on a g/spike basis no difference existed between cross I and cross III.

Table 9. Mean yields of heads of initial and final selection from F_3 head rows of the pedigree method.

Designation		Seed Yield		
		g/10 spikes	SE	% of control
Cross I	- initial selection	17.46	0.18	103
	final selection	17.93	0.19	106
Cross II	- Initial selection	15.20	0.17	88
	final selection	15.65	0.21	91
Cross III	- initial selection	17.26	0.16	100
	final selection	17.64	0.18	102

3. RESULTS IN F_5

3.1 Means and Variances.

To evaluate the effectiveness of the 3 methods under investigation an analysis of variance was performed for each method in each cross. Locations were considered as replicates. Therefore each analysis comprised 180 lines of 2 entries each. The mean square expectations for this analysis are given in Table 10 and relevant results in Table 11. The F-test reveals significant differences between families under all methods of selection. Significant variability among lines within families is also present among all three methods in cross I but is inconsistent in crosses II and III.

Table 10. Mean square expectations for methods of selection within crosses, pooled over locations.*

Source of variation	DF	E M S
Locations	1	$S_e^2 + 2S_w^2 + 2nS_b^2 + mnS_1^2$
Families	m - 1	$S_e^2 + 2S_w^2 + 2nS_b^2$
Lines in families	m(n-1)	$S_e^2 + 2S_w^2$
Error	mn-1	S_e^2

* n F_5 lines in each of m F_3 families tested at each of 2 locations.

Table 11. Mean squares (x 10^{-3}) of families, lines within families and error mean squares for the hill plot method, the control plot method and the pedigree method of selection from F_3 derived F_5 families.

Cross/Method	Families	Lines within families	Error mean squares
I - Hill plot method	3,922.9**	81.7**	49.2
Control plot method	331.4**	84.8**	53.8
Pedigree method	237.1**	81.4**	48.8
II - Hill plot method	353.5**	60.7**	32.1
Control plot method	463.6**	51.4	64.5
Pedigree method	213.8**	61.4	47.8
III - Hill plot method	441.2**	55.7	56.9
Control plot method	770.6**	52.0	45.9
Pedigree method	157.8**	72.6**	51.7

**, significant at $P<0.01$.

Components of variance are presented in Table 12. The variance among F_5 lines within F_3 families (S_w^2) do not differ significantly for the three methods of selection, e.i. variability present within families is of similar magnitude for all methods. Two components are considered to be significantly different if this difference exceeds twice the square root of the sum of squares of their standard deviations.

Although there is a tendency for the pedigree method to show a larger between family component of variance in crosses II and III, there are no significant differences between the three methods.

Heritability estimates were computed on a line basis as the ratio $(S_w^2 + S_b^2) / (S_w^2 + S_b^2 + S_e^2/2)$. With nearly homozygous lines in F_5, this represents additive and additive x additive epistatic types of genetic variance divided by the phenotypic variance of F_5 line means (over 2 locations). Heritability as computed here would draw from both sources of variability, S_w^2 and S_b^2. With the exception of crosses II and III for the control plot and hill plot method respectively, the heritabilities obtained are high and differences are insignificant between methods within crosses. Negative estimates were obtained for the control plot method in cross II and for the hill plot method in cross III. These negative variances resulted in extremely low estimates of heritability for these methods. Only in cross II is this estimate significantly lower than the other two.

Table 12. Variance components ($\times 10^{-3}$) among F_5 lines within F_3 families (s_w^2), between F_3 families (s_b^2) and heritability (H) for the hill plot method, the control plot method and the pedigree method of selection for each of three crosses.

Cross / Method	s_w^2	s_b^2	H
I - Hill plot method	16.3±5.0	32.0±21.1	.66±.11
Control plot method	15.5±5.3	4.1±2.9	.42±.08
Pedigree method	16.3±5.5	19.4±6.3	.59±.06
II - Hill plot method	14.3±3.6	2.4±2.1	.51±.07
Control plot method	-6.5±4.3	6.9±4.4	.01±.18
Pedigree method	6.8±4.5	19.1±5.6	.52±.07
III - Hill plot method	-0.6±4.2	3.2±2.6	.08±.15
Control plot method	3.0±3.7	12.0±6.9	.39±.13
Pedigree method	10.4±5.2	10.6±4.3	.45±.08

In evaluating different methods of selection, the method mean yields are of considerable interest. These means are averaged over the 180 lines for each method. Their variances contain within and between family variances as given in Table 12. Therefore, only an approximate test for differences can be applied (Snedecor and Cochran, p.279, 1969). According to these tests, method means within crosses do not differ significantly (Table 13).

Table 13. Seed yield means (g/plot) and standard errors for the hill plot method (ETH), the control plot method (ETC) and the pedigree method of selection for each of three crosses. (Means of 180 F_5 lines each, tested at two locations).

Cross	Seed Yield					
	ETH	SE	ETC	SE	PEDIGREE	SE
I	1594	104	1609	28	1548	23
II	1293	30	1285	33	1224	21
III	1513	33	1479	45	1478	17

In addition to these analyses performed on original data, identical analyses were conducted with the transformed data (Z - values). Results are presented in Appendix I to III.

With respect to variances and variance components, similar results were obtained. The overall method mean yields from transformed data however do suggest that, in cross III, the hill plot method was superior to the pedigree method of selection ; their difference exceeds the probability at the 5 percent level.

3.2 Family evaluation in F_5.

The means of the F_3 derived families, their variances and standard errors were computed on their respective F_5 lines (Tables 14 to 16). These family means can be tested for significance of differences by t-tests within methods and unpaired t-tests between methods (Steel and Torrie, p. 81, 1960).

The families derived by visual selection in the pedigree method fluctuate greatly and significant differences exist. This would suggest that visual selection was less effective with respect to yield.

No differences existed between 5 of the 6 families derived by the control plot method in cross I, but family I-72-91 was significantly below the others. Inferior families were also obtained in crosses II (72-16) and III (72-155, 168, 274, 279), which by a t-test were all significantly different from the high yielding families.

Significant differences also exist between the families derived by the hill plot method. Families I-72-4 and III-72-68 were superior to their sibs.

It is of interest here to compare family performance in F_5 with their rankings obtained in F_3 (Tables 14 to 16). This comparison is possible only for the early test methods. As to the control plot method, little relation seems to exist in cross I. In cross II and cross III the top yielders rank identical in both generations. Similar results are obtained when families from the hill plot method are compared.

Table 14. Cross I: Seed yield means (g/plot) and standard errors of F_3 derived families tested in F_5 and their yield ranks in F_3 for the pedigree method, the control plot method and the hill plot method of selection.

Pedigree method			Control plot method				Hill plot method			
Fam.	Yield	SE	Fam.	Yield	SE	Rank F_3	Fam.	Yield	SE	Rank F_3
72- 1	1747	114	72-76	1581	51	1	72- 4	1783	29	6
2	1097	94	88	1638	51	4	66	1580	29	1
3	1543	72	91	1471	37	5	77	1422	32	2
4	1917	90	243	1671	47	11				
5	1581	151	319	1656	46	19				
6	1636	75	352	1640	41	29				
7	1474	186								
8	1633	93								
9	1659	83								
10	1645	116								
11	1508	122								
12	1405	129								
13	1679	106								
14	1814	105								
15	1272	118								
16	1713	114								
17	1293	138								
18	1741	92								
19	1697	86								
20	1659	121								
21	1613	92								
22	1394	158								
23	1568	103								
24	1832	61								
25	1493	183								
26	1497	108								
27	1372	136								
28	1518	135								
29	1635	61								
30	1572	138								
31	1661	57								
32	1271	153								
33	1445	88								
34	1419	100								
35	1601	169								
36	1481	119								
37	1271	132								
38	1666	119								
39	1565	114								
40	1752	143								
41	1592	93								
42	1265	136								
43	1596	157								
44	1371	59								
45	1482	91								
$\bar{x}$	1584	66		1609	28			1594	23	

Table 15. Cross II: Seed yield means (g/plot) and standard errors of F_3 derived families tested in F_5 and their yield ranks in F_3 for the pedigree method, the control plot method and the hill plot method of selection.

Pedigree method			Control plot method				Hill plot method			
Fam.	Yield	SE	Fam.	Yield	SE	Rank F_3	Fam.	Yield	SE	Rank F_3
72- 1	1313	79	72- 4	1344	34	19	72-84	1345	27	2
2	1028	93	16	1152	24	27	130	1237	24	30
3	1145	88	22	1203	32	16	230	1298	23	40
4	1173	100	58	1341	45	1				
5	1376	65	64	1334	39	13				
6	1269	111	262	1359	51	30				
7	956	119								
8	1040	85								
9	1114	77								
10	1364	45								
11	1148	87								
12	983	109								
13	907	70								
14	1211	60								
15	1531	45								
16	1499	93								
17	1166	118								
18	1278	97								
19	1397	97								
20	1264	122								
21	1100	50								
22	1255	140								
23	1393	100								
24	1176	79								
25	1254	37								
26	1394	67								
27	1291	159								
28	1312	113								
29	1425	73								
30	1426	50								
31	1392	105								
32	1321	129								
33	1162	60								
34	997	101								
35	1210	88								
36	1066	52								
37	1045	109								
38	1143	61								
39	1183	86								
40	1473	63								
41	1018	42								
42	1266	129								
43	1399	74								
44	886	91								
45	1332	55								
$\bar{x}$	1224	44		1285	12			1293	20	

Table 16. Cross III: Seed yield means (g/plot) and standard errors of F_3 derived families tested in F_5 and their yield ranks in F_3 for the pedigree method, the control plot method and the hill plot method of selection.

Pedigree method			Control plot method				Hill plot method			
Fam.	Yield	SE	Fam.	Yield	SE	Rank F_3	Fam.	Yield	SE	Rank F_3
72- 1	1731	90	72-55	1634	37	1	72-68	1582	28	1
2	1450	119	155	1428	36	22	94	1466	23	4
3	1639	135	161	1595	38	23	333	1491	28	24
4	1409	170	168	1348	44	4				
5	1441	96	274	1416	38	10				
6	1434	132	279	1442	31	53				
7	1640	145								
8	1283	106								
9	1550	102								
10	1322	73								
11	1510	100								
12	1523	103								
13	1598	113								
14	1294	115								
15	1309	129								
16	1612	131								
17	1317	64								
18	1696	102								
19	1309	101								
20	1449	138								
21	1197	123								
22	1786	95								
23	1506	114								
24	1354	140								
25	1628	135								
26	1402	73								
27	1636	74								
28	1536	109								
29	1597	143								
30	1614	152								
31	1713	90								
32	1356	61								
33	1585	118								
34	1506	161								
35	1453	153								
36	1273	102								
37	1594	71								
38	1373	79								
39	1399	149								
40	1354	174								
41	1373	72								
42	1424	97								
43	1470	81								
44	1377	158								
45	1493	167								
$\bar{x}$	1478	54		1479	19			1513	17	

3.3 Line evaluation.

Finally, methods of selection were evaluated on the basis of a single F_5 line. For this purpose, means were calculated from the 2 locations and results are given for the top 15% of the lines in Tables 17 to 19. To test for differences between line means, an analysis of variance was performed separately for each cross but including all 3 methods. On this basis, all 3 methods resulted in equally high yielding lines; there were no significant differences among the top 15% of the lines.

Actual line yields can be related to the performance of a standard variety by dividing the difference by a standard deviation as outlined in Material and Methods. Computations were performed individually and on pooled data. Those lines whose transformed yields exceeded the 5 percent level, were considered to be significantly higher yielding than Glenlea and are marked by asterisks in Tables 17 to 19. At Winnipeg, 37 and 16 lines exceeded Glenlea in crosses I and III when summed over methods. In cross II only one line was recovered which outyielded Glenlea. Similar results were noted at the Glenlea test site. It appears then that crosses I and III are superior to cross II.

Methods were compared within crosses. In cross I at Winnipeg, hill plots and pedigree each yielded 19 lines exceeding Glenlea and both methods were thus equally effective, but less so than control

Table 17. Mean yield of 2 locations (kg/ha) of the top 15% of F_5 lines from cross I for the hill plot, the control plot and the pedigree method of selection, and lines exceeding the control at Winnipeg (W), Glenlea (G) and pooled (P).

Hill plot method					Control plot method					Pedigree method				
Line	Yield	W	G	P	Line	Yield	W	G	P	Line	Yield	W	G	P
14	7223	xx	xx	xx	240	6600		xx		375	7207	xx	x	xx
28	6973	x	xx	xx	288	6593	xx	xx	xx	415	6893	xx		
6	6850				223	6573	xx		xx	421	6723			
35	6800	xx	xx	xx	209	6560				373	6727	xx	x	
43	6790	xx			341	6490				455	6687			
18	6670	x	x		299	6480		xx		517	6613			
56	6657				344	6480	xx	xx		361	6447			
49	6550	x			238	6460				362	6433			
33	6537		xx		312	6450				529	6303	x	x	
3	6537				271	6427				422	6300			
51	6537	x			273	6427				388	6283			
1	6513				313	6413	xx			393	6280			
26	6453				199	6403	xx	x		431	6250	xx	xx	xx
50	6443	x			302	6400				410	6170			
45	6433				213	6383				387	6153		xx	
17	6430				221	6380				376	6150			
2	6403				301	6363				454	6133			
20	6393				287	6350	xx	xx	xx	377	6120			
118	6343				272	6350				497	6110			
74	6347				310	6317				389	6090			
27	6340		xx		332	6313				481	6067			
19	6330		xx		342	6310				413	6057			
125	6303				277	6290	xx			453	6047			
88	6250				283	6290	xx			509	6037			
24	6250				239	6290				435	6033			
112	6243				289	6260	x	x		502	6000			
54	6220				320	6240		xx		398	5980			
$\bar{x}$	6512±47					6403±20					6307±60			
12	6190	xx	x		308	6110	xx			372	5910	x	xx	
123	6083	x			226	6081	xx			432	5870	xx	x	
7	6031	xx	x		197	5940	xx			472	5783	xx		
37	6020	xx	xx	xx	335	5926		xx		512	5700	x	x	
173	5780	x			187	5910	xx			412	5563	xx		
70	5290	xx			300	5800		xx		444	5386	xx		
42	5170	xx			314	5763	xx			532	4943	xx		
128	5150	x			334	5690		xx						
130	5100	xx			316	5650	xx							
40	4673	x			348	5560	xx							
68	4623	x			228	5540	xx							
					236	5083	xx							
					235	4810	xx	xx	xx					
					206	4276	xx							

x, xx, exceeds P 0.10, P 0.05, respectively.

LSD (0.05) within and between methods 2640 kg/ha.

Table 18. Mean yield of 2 locations (kg/ha) of the top 15% of F_5 lines from cross II for the hill plot, the control plot and the pedigree method of selection, and lines exceeding the control at Winnipeg (W), Glenlea (G) and pooled (P).

Hill plot method					Control plot method					Pedigree method				
Line	Yield	W	G	P	Line	Yield	W	G	P	Line	Yield	W	G	P
541	5583				744	5810		xx		969	5663			
670	5520				847	5607				1059	5530			
543	5423				877	5503				963	5450		x	
550	5393				874	5447				988	5440			
694	5377				832	5443				979	5437			
702	5350				831	5287				957	5410			
667	5323				861	5270				1069	5383			
691	5287				863	5243				990	5250			
546	5277				817	5223				1020	5247			
566	5283				733	5203				1060	5230			
551	5213	x			749	5150				1028	5227			
669	5203				818	5137				1014	5223			
575	5177				741	5110				1023	5113			
582	5130				883	5103				962	5100			
697	5127				855	5097				1068	5100			
579	5117				890	5097				958	5090			
599	5090				736	5073				1027	5077			
574	5070				893	5067				1007	5050			
674	5057				740	5063				959	5020			
592	5023				879	5060				961	5017			
715	4993				840	5057				1021	5000			
571	4967				864	5017				973	4987			
719	4963				842	5013				1002	4970			
687	4963				829	5013				917	4970			
696	4930				860	5010				989	4947			
672	4920				726	4993				940	4913			
598	4920				734	4990				939	4897			
$\bar{x}$	5173±37					5188±40					5176±40			
548	4783	x			815	4733		x						
					724	4163		x						

x, xx, exceeds P 0.10, P 0.05, respectively.

LSD (0.05) within and between methods 2099 kg/ha.

Table 19. Mean yield of 2 locations (kg/ha) of the top 15% of F_5 lines from cross III for the hill plot, the control plot and the pedigree method of selection, and lines exceeding the control at Winnipeg (W), Glenlea (G) and pooled (P).

Hill plot method					Control plot method					Pedigree method				
Line	Yield	W	G	P	Line	Yield	W	G	P	Line	Yield	W	G	P
1120	6473		xx		1271	6430				1560	6557	xx		
1112	6307		xx	xx	1280	6307				1527	6410			
1212	6200	xx	xx		1288	6247				1562	6203			
1134	6137	xx			1343	6237				1525	6150		xx	
1128	6083				1266	6213	xx		xx	1540	6143			
1217	6077		xx		1309	6183				1442	6140			
1192	6070				1402	6163				1489	6023			
1097	6060	x	xx		1429	6140				1468	5987			
1123	5987				1322	6137				1587	5983			
1107	5987				1405	5963				1554	5973			
1081	5940	xx			1346	5947				1620	5930			
1087	5900		xx		1321	5893				1474	5920			
1096	5897	xx			1350	5887				1613	5920			
1116	5877		xx		1269	5847				1452	5897			
1119	5847				1285	5843				1509	5883			
1126	5840				1342	5833				1539	5867			
1227	5837				1399	5787				1444	5840			
1251	5810				1264	5770				1462	5837			
1117	5803				1404	5757				1501	5830			
1206	5797				1284	5743				1448	5817			
1098	5793				1340	5743				1564	5817			
1218	5767				1326	5740	xx			1502	5760			
1111	5760				1345	5720				1510	5747			
1170	5747				1262	5707				1551	5743			
1108	5713				1276	5700	x	xx		1553	5733			
1178	5693				1349	5693				1545	5730			
1106	5650				1287	5683				1546	5720			
$\bar{x}$	5927$\pm$38					5938$\pm$44					5947$\pm$40			
1101	5650	xx	x		1275	5390	xx			1473	5713		xx	
1174	5560		xx		1295	5187	xx			1537	5123	x	x	
1113	5550		xx		1265	5150	xx							
1092	5407		xx											
1234	5400		xx											
1129	5390	xx												
1172	5247		xx											
1083	5233	xx												
1151	5230		xx											
1103	5187	xx												
1099	5107	xx												
1198	4597	xx												

x, xx, exceeds P 0.10, P 0.05, respectively.

LSD (0.05) within and between methods, 2102 kg/ha.

plots which gave 19 (Table 20). At Glenlea, similar relative differences were observed. When locations were pooled, all three methods retained a similar number of lines. Due to possible genotype-environment interactions, pooling resulted in a decrease of superior lines and may thus mask the efficacy of a selection method.

None of the methods was successful in isolating good lines from cross II. Only one line was recovered by the pedigree method, which comes close to random chance.

In cross III, at Winnipeg hills yield 10, control plots five and the pedigree method one line which exceed the control. A X^2-test indicated hill plots to be significantly different from the pedigree method ($P < 0.01$) but equal to control plots. The results for Glenlea are 13, 1 and 2 for hill plots, control plots and pedigree method, respectively, hill plots being statistically different ($P < 0.01$) from both the other methods. Pooled over locations, hills recovered three lines and control plots one line; none of the lines from the pedigree method exceeded the control. When data were pooled, differences between methods were no longer significantly different.

Of interest are the lines with actual low yield but still exceeding the control, which are listed below the line of the top 15% of the lines (Tables 17 to 19). Whether or not one considers these lines, the overall outcome as to the relative efficiency of the selection methods remains unchanged. Table 20 summarizes these results and gives the number of lines exceeding the control for each cross and method combination.

Table 20. Number of lines exceeding the control in seed yield ($P<0.05$) for the hill plot (ETH), the control plot (ETC) and the pedigree (P) method of selection at Winnipeg, Glenlea and pooled over locations.

Location	Cross I			Cross II			Cross III		
	ETH	ETC	P	ETH	ETC	P	ETH	ETC	P
Winnipeg	9	19*	9	0	0	0	10***	5	1
Glenlea	7	10*	3	0	1	0	13***	1	2
Pooled	4	4	2	0	0	0	1	1	0

*, ***, indicates significance at $P<0.10$, $P<0.01$, respectively by a X^2 test.

Table 21 gives the distribution of all lines and their ranking in standard deviations. Standard deviates have a mean of zero and a standard deviation of one. To test for normal distribution of values, skewness and kurtosis was calculated as given by Snedecor and Cochran (1969). A normal distribution has a kurtosis of 3. Values below 3 indicate a flatter top of the curve and increasing flanks, and vice versa. With regard to skewness, a normal distribution has the value of ± 0; negative skewness indicates an extension of the lower tail. With few exceptions, all methods show a kurtosis value below 3 and slightly negative skewness. Differences between methods are inconsistent and not significant.

Table 22 gives the lines which exceed the control and their family origin. For the hill plot method approximately 70% of the superior lines originated in the family with the highest mean yield. A similar tendency is observed for the control plots in cross III, but families of cross I contributed more equally to the overall result.

For the pedigree method, most of the lines exceeding the control originated also from families with high mean yields. A t-test was performed to test for significance of differences between families resulting in lines exceeding the control vs. the rest. For both crosses I and III these tests were significant ($p < 0.05$).

Table 21. Seed yields of F_5 lines in standard deviates for the hill plot, the control plot and the pedigree method of selection, their frequency distribution, mean, skewness and kurtosis.

Cross/Method	Seed Yield in Standard Deviates									$\bar{x}$	Skew-ness	Kur-to-sis
	-5	-4	-3	-2	-1	0	1	2	3			
W I N N I P E G												
I - Hill plot method				26	40	58	46	10		-0.16	-0.22	2.37
Control plot method				20	39	50	49	19	3	0.11	-0.07	2.36
Pedigree method			10	19	52	63	27	7	2	-0.37	-0.07	3.01
II - Hill plot method		12	32	46	51	28	11			-1.52	-0.08	2.52
Control plot method		1	26	47	53	49	4			-1.23	-0.20	2.12
Pedigree method	1	12	33	38	73	21	2			-1.69	-0.30	2.46
III - Hill plot method			5	15	44	68	35	12	1	-0.12	-0.32	3.14
Control plot method		1	7	24	59	55	27	5	2	-0.53	0.01	2.90
Pedigree method		1	8	38	64	50	17	2		-0.81	-0.05	2.73
G L E N L E A												
I - Hill plot method			1	21	48	58	43	9		-0.17	-0.20	2.40
Control plot method		1	5	21	62	48	33	10		-0.42	-0.16	2.85
Pedigree method			1	28	46	60	42	3		-0.31	-0.03	2.23
II - Hill plot method	1	11	37	65	41	20	5			-1.79	-0.01	2.83
Control plot method		13	25	54	51	23	13	1		-1.50	0.19	2.58
Pedigree method		11	30	54	61	23	1			-1.69	-0.10	2.54
III - Hill plot method			3	26	55	46	35	12	3	-0.27	0.24	2.74
Control plot method		1	7	38	57	59	17	1		-0.76	-0.22	2.86
Pedigree method		2	12	35	60	46	23	2		-0.81	-0.12	2.65

Table 22. Mean seed yields (g/plot) of F_5 families for the hill plot, the control plot and the pedigree method of selection, and number of lines exceeding the control at Winnipeg and Glenlea.

Cross I			Cross II			Cross III		
Fam.No.	Yield	No.of Lines	Fam.No.	Yield	No.of Lines	Fam.No.	Yield	No.of Lines
			Hill plot method					
72- 4	1783	14	72-84	1345	0	72-68	1582	15
66	1580	1	130	1237	0	94	1466	4
77	1422	1	230	1298	0	333	1491	4
			Control plot method					
72-76	1581	4	72- 4	1344	1	72-55	1634	4
88	1638	7	16	1152	0	155	1428	1
91	1471	0	22	1203	0	161	1595	1
243	1671	8	58	1341	0	168	1348	0
319	1656	5	64	1334	0	274	1416	0
352	1640	5	262	1359	0	279	1442	0
			Pedigree method					
72- 3	1543	1				72- 9	1550	1
4	1917	2				25	1628	1
7	1474	1				30	1614	1
14	1814	2						
18	1741	3						
21	1613	1						
28	1518	1						
43	1596	1						

4. GENERAL DISCUSSION

The effectiveness of various selection methods can be compared in many ways. Recognizing the fact that a plant breeder employing the pedigree method can work with many crosses in early generations while early yield tests can be performed on a few hybrids only, comparisons could be done on a unit acreage basis. More legitimate yet, methods could be compared on units of input. Comparisons such as those would allow inferences about the total gain in a plant breeding program employing different genetic material in the various methods.

Our study was performed on identical genetic material. For final evaluation, an equal number of lines were tested in F_5 for each method. Efficiency of methods was judged by comparing method means and variances, family and line means, and finally by the number of lines exceeding the control.

Overall means and variance components have revealed small and insignificant differences between methods. Greater variability existed between methods with regard to their F_3 derived families in F_5. But again, families of similar performance were obtained from all methods.

The methods differed only in their ability to isolate superior genotypes when lines were evaluated relative to the control variety. This method admittedly is the least precise evaluation employed so far. The standard deviates (Z) used for these comparisons of line yield to control yield were computed for individual locations and pooled over the two locations. The fact that they do detect more lines exceeding the control on individual locations than pooled might be explained by a genotype - location interaction.

All methods seem effective in recovering lines of high yield potential in cross I but the control plot method seems to be superior. As was demonstrated in F_3, cross I exhibits great variability with an abundancy of good lines; any method of selection could be effective here. In cross II none of the methods was successful in identifying lines which exceeded the control. In cross III both early tests outyielded the pedigree method in their abilities to isolate lines of high yield potential.

At this point one might ask why the selection methods differ in their ability to identify superior lines on the basis of transformed yield, but fail to do so on actual yields. In this transformation the control variety serves as a fertility index, which brings all yields to a different scale. However, the efficiency of this transformation in reducing the experimental error and thus allowing a more accurate evaluation of the three methods cannot be tested in this experiment. Similar transformation procedures (percent of control) employed in absence of replications have been critisized by Baker and McKenzie (1967) and Townley-Smith and Hurd (1973). Both transformations employed here - standard error units and standard deviates - are recognized statistical tests. The validity of standard error units as calculated here can be questioned on grounds that instead of the population mean the mean of the control was employed. This introduces a second variable which does not have a t-distribution. Similar problems arise in the transformation of line yields to standard deviates.

Commonly, the effectiveness of the pedigree method or, more precisely, the ability to select visually, is tested in yield trials by comparing visual rating with plot yields actually obtained (Briggs and Shebeski, 1970; Townley-Smith et al.,1973). This might be a test for the effectiveness of visual selection but it is not a legitimate comparison of breeding methods; such comparisons would neglect the fact that population sizes and selection intensities employed differ considerably among methods.

In a study on oats, Frey (1962) found the yield response to visual selection was better when based on progeny rows than on single plants, but generally inconsistent and not very effective.

Has the pedigree method been given a real chance in these experiments? Briggs and Shebeski (1970) point out that for visual selection to be effective selection intensity should be between 10 and 20%. The intensity applied here was 3%. The percentage might be slightly misleading here, if one considers the fact that the number of families selected in F_3 was 3, 6 and 45 for hills, controls and the pedigree method, respectively. Thus the pedigree method tested approximately 7 and 15 times as many families as the early testing methods. In our choice of 180 lines to be tested in F_5 we felt that for the pedigree method the combination of 4 lines from each of 45 families was optimal. Furthermore, it was thought to be an improvement not normally applied in the pedigree method when in F_3 weights of 10 spikes of selected families were compared to the adjacent control.

We hypothesized that a precise estimate of the yielding potential of a given set of families would allow for selection and further propagation of only the best ones. Assuming this be true and knowing that genetic advance then would depend only on selection intensity, one can predict a corresponding increase in efficiency with increasing selection intensity. As given by their mean yields (Table 22), there were considerable differences among families in both early tests. This could point to non-additive inheritance as established for crosses I and III and, consequently, the loss of vigor due to inbreeding. The high frequency of superior lines in some families however, seems to contradict the genetic analysis. Of more importance is the fact that the yielding estimate in F_3 was not so precise and/or a high sampling error was introduced by applying 1 and 2% selection intensity. Falconer (1960) points out that such high selection intensities can have negative effects due to a correlated response (plant height and lodging) and may thus severely limit progress in selection (Dempster, 1963).

The more intensive testing in F_3 by the hill plot method has resulted in the isolation of a few families of high potential. But by selecting only 3 out of the 40 families greater than the control in cross I (11 in cross III), the random error introduced was considerable. This could explain the presence of mediocre families in this method.

With selection pressure relaxed by testing 6 families for the control plot method, the random error is relatively reduced by 1/2. Miss-classified families will thus not have as devastating an effect as by the hill plots: missing either I-72-4 or III-72-68 by chance would have resulted in a total loss of this method. Furthermore, family III-72-68 was initially included in both early tests but was omitted from the control plot method in F_4 for maturity reasons; this could be done here only since this family was planted in excess of the 6 families actually needed. This family alone accounts for the superiority of the hill plots over control plots in cross III. Consequently, with similar results to be expected for both early tests also in cross III, these methods did not differ significantly in their ability to identify superior genotypes.

For these and other reasons, one might ask how repeatable these results are, or, is the response obtained merely a manifestation of sampling variability. In a theoretical approach, Baker (1971) has demonstrated that for a given heritability, repeatability is best when the selected portion is between 10 and 30 percent. With near optimum conditions for the pedigree and control plot method it would appear that the extreme selection pressure exercised has resulted in underestimating the potentiality of the hill plot method. The fact that the analysis of data of F_3 families was incomplete at the time of selection would add to this underestimation. The potential of the hill plot method is indicated in the selection of an outstanding family, I-72-4, which yielded 70% of the lines exceeding the control in cross I. This potential is also expressed in a relative increase of superior lines at Glenlea (Table 20), indicative of successful selection for wide range adaptibility.

Early tests were found to yield a superior number of good lines in soybeans (Voigt and Weber, 1960) and oats (Frey, 1968). Luedders _et al._ (1973) compared bulk, pedigree and early generation testing and found that the complete bulk and early testing retained a few more good lines than the other methods. This is in contrast to the results obtained by Raeber and Weber (1953), who compared early testing and visual selection in soybeans and found that both methods were equally successful.

By analysing the F_3 derived F_5 families it was demonstrated that all methods yielded equally good families. However, with only 4 lines per family tested in the pedigree method, the potential of a high yielding family was not sampled adequately. Hence the superiority of the early tests in cross III can be attributed to the more intensive sampling of F_3 families. In other words, if equal sampling of F_3 families for all methods would have been possible the pedigree method would also have retained a comparable number of lines exceeding the control in cross III. The basic facts this study brings out are that success in selection depended on the F_3 family (the F_2 plant) and the number of lines extracted and tested in F_5. Hence it would appear that testing in F_3 should be given first priority in a breeding program; a family possessing desirable genotypes not identified in F_3 will be irretrievably lost. The testing of lines in F_5 thus seems to be of secondary importance. Frey (1954) also suggests that selection be made as early as possible, since selection within families would yield rapidly diminishing returns.

From the considerations of Van der Kley (1955), Allard (1960), Shebeski (1967) and others, recognizing the fact that the more desirable genotypes show their highest frequency in the F_2, this logically would point to early testing, omission of most of the undesirable types and sufficient sampling of families in F_5; rather than the testing of many families with few lines each in F_5 as derived by the pedigree method. With visual selection being unreliable for yield, the probability of missing the most valuable families in F_3 would be greater here than with any of the early tests.

It appears then that in this study progress in selection depended on a particular F_3 family and the testing of an "adequate" number of lines sampled from that family. How many lines per F_3 family are adequate? Obviously, 4 lines per family as tested in the pedigree method were not sufficient. Superior families such as I-72-4, I-72-14 and III-72-25 (Table 22) being sampled more adequately, would undoubtely have resulted in many more good lines. On the other hand, even a representation of 60 lines per family in the hill plot method was unable to identify a significant number of superior lines in families such as I-72-66 and III-72-333. The question then becomes how many "good" lines does a plant breeder actually need. Ultimately, only one line is required, the best one. To arrive at this line pedigree selection seems to be too haphazard a method to identify the genotype with the most desirable genes.

A theoretical approach to this question is given by Shebeski (1967). Based on the assumption that each wheat chromosome carries at least one gene for yield, he indicated that approximately 100 lines should be tested in F_5 from a F_3 family in order to include the most desirable genotype. In view of the considerable error connected with F_3 family evaluation it would appear that sampling of 20 to 30 lines per family in F_5 and testing more families instead would seem to be more promising.

Recent studies by Simchen and Stamberg (1969) and Clegg _et al._ (1972) indicate that breakup of linkage groups and recombination is not a random event but under genetic control. Characters conferring a high degree of fitness to the populations are kept together. Jana (1972) concluded from a 2 locus - 2 allelle study that so-called continuous variation needs not be caused by many genes, but instead by a few major genes. These studies would indicate that we might be dealing with less variability than calculated on the assumption of at least one gene for yield per chromosome.

For the present study we had selected 3 crosses expressing low and high heterosis. These populations cannot be considered a random sample allowing general inferences but it brings out another question: how meaningful is a yield test in F_1 relative to the future worth of a population? Early testing as executed in this research is a time and input demanding procedure, to be performed only on the most "promising" crosses.

An estimation of genes effective in the inheritance of seed yield revealed mainly dominant variation in the successful crosses I and III but additive variance in the unsuccessful cross II. (Other forms of epistasis could not be detected). These results are based on one test in one environment and their limitations are obvious.

The fact that the crosses exhibiting dominance variation yielded the best lines is in conflict with the usual interpretation of dominance variation. However, Mather and Jinks (p. 354, 1971) suggest transformation of data to various scales, shown to be able to reverse direction and magnitude of effects, until such values are obtained "on which interpretation is most fruitful". No such scaling attempt has been made on the present data. More important, how could either variance be interpreted with regard to the heterosis exhibited in crosses I and III and the high yielding lines obtained?

Interpretation of the terms "additive" and "dominance" is not without ambiguity. Additive variance can be attributed to genes either dominant or recessive in a Mendelian sense and, upon selfing and fixation, this variation can be effectively used in a breeding program. In biometrical genetics "additivity" is defined as 1/2 the difference between the parental values, the mid parent $(1/2\,(A_1A_1 + A_2A_2))$ and hence excludes heterotic effects.

Dominance variation signifies a form of interaction or non-additivity between alleles at the same locus, unfixable on inbreeding

(Mather and Jinks, 1971). It follows, that additive variance cannot be held responsible for heterosis and the presence of dominance variance cannot explain the high yielding lines isolated.

The most widely accepted explanation of heterosis is the dominance hypothesis by Jones (1917), e.i. by virtue of a particular combination of dominant and recessive genes. Giving each recessive allele a value of 1 and each dominant allele a value of 2, assuming complete dominance and the absence of epistasis, it can be shown that 2 parents differing by any number of gene pairs can yield a "heterotic" F_1, viz.

$$P_1 \ : AA + BB + cc + DD = 7,$$
$$P_2 \ : aa + bb + CC + DD = 6,$$
$$F_1 \ : Aa + Bb + Cc + DD = 8.$$

By recombination and segregation this "heterosis" could be fixed. Those genotypes possessing all the more desirable genes will however occur in low frequencies, which necessitates the growing and testing of larger populations than are commonly handled in breeding programs (Shebeski, 1967).

On these grounds one could explain the existence of high yielding inbred lines in crosses I and III; one could also defend the choice of heterotic crosses as being the only ones worth exploiting in subsequent selection work.

The isolation of superior inbred lines in heterotic crosses of wheat was also reported by Lupton (1961), Whitehouse (1968) and Busch et al. (1971). Similar results were obtained in tobacco (Smith, 1952) and tomatoes (Williams, 1959). If over-dominance or non-fixable types of epistasis were of major importance in these crosses, pure lines should yield less than the F_1 hybrids which have maximum heterozygosity. Lee (1973) recommends the use of crosses exhibiting "a moderate amount" of specific combining ability, for in these crosses the likelihood of transgressive segregation seems to be greater.

By analogous reasoning, the degree of heterosis could be an indication of parental gene differences. Consequently, heterotic crosses would offer more combinations than would non-heterotic crosses. Although few experimental results obtained (see above) would support this hypothesis, such an approach could be criticised on theoretical grounds. Crow (1948) for example concluded that "it would not require very many loci in which the heterozygote is superior to give a considerable selective advantage to a hybrid" (cited by Allard, 1960).

To test F_1 hybrids adequately, many time-consuming crosses have to be made. An alternative approach to cross evaluation would be the calculation of mid-parental values, as defined above. For crosses I, II and III these are 320, 266 and 329, respectively. Thus with respect to heterosis, the order of crosses changes from I, III, II to III, I, II but would still indicate the low potential of cross II.

5. CONCLUSION

The purpose of this research was to see if three methods of wheat breeding differ significantly in their ability to isolate superior genotypes and if so, which is most effective. One could refer to the statement by Dudley and Moll (1969), saying that a critical evaluation between selection methods has to consider the input of time and money. We have no exact figures as to the relative costs of the three methods studied, but indications are that at our present level of mechanization control plots involve 5 times and hill plots 10 times the manhour inputof the pedigree method of selection. On the other hand, could one not say that the most expensive method is the one which yields the least number of good lines? For an overall evaluation of the methods compared, the following facts were established:

(1) Method mean yields:

- actual data: no significant differences among method means;
- transformed data: in cross III, the hill plot method was superior to the pedigree method.

(2) Family means:

- all methods were equal; high yielding families were obtained by all methods.

(3) Variance components and heritability estimates:

- no significant differences between methods could be established. Material derived by the pedigree method exhibited slightly greater variability but differences were insignificant and inconsistent.

(4) Line means, absolute yields:

- all methods were equal, no significant differences could be detected among the top 15% of the lines.

(5) Line means, relative yields:

- the hill plot method was below the control plot method in one comparison, equal in two comparisons and superior in one, out of a total of four comparisons; the hill plot method was equal to the pedigree method in two and superior to the pedigree method in two, out of a total of four comparisons

- the control plot method was superior to the pedigree method in two and equal to the pedigree method in two, out of a total of four comparisons.

These findings are based on one years results. Obviously, conclusions drawn are tentative. The methods did not differ in their efficiency in most aspects. Thus we could not prove that early testing is superior to the pedigree method. However, there are indications that early tests seemed to have a slight advantage over the pedigree method when dealing with crosses of lower yield potential.

These findings agree with results published by some workers but are at variance with others.

The evidence relating to the worthiness of the three crosses indicates that only the more heterotic crosses yielded lines exceeding the control. However, data based on three crosses only are not sufficient to draw a general conclusion.

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Appendix I. Families, lines within families and error mean squares of transformed data for the hill plot method, the control plot method and the pedigree method of selection from F_3 derived F_5 families.

Cross/Method	Families	Lines within families	Error mean squares
I - Hill plot method	58.66**	0.78	0.81
Control plot method	7.20**	1.16	1.34
Pedigree method	3.78**	0.83	0.98
II - Hill plot method	11.35**	1.74**	0.96
Control plot method	7.58**	1.13	1.35
Pedigree method	3.11**	1.11	0.78
III - Hill plot method	13.53**	1.07	1.59
Control plot method	17.11**	1.12	0.87
Pedigree method	2.99**	0.91	0.99

**, significant at P 0.01

Appendix II. Variance components of transformed data among F_5 lines within F_3 families (S_w^2), between F_3 families (S_b^2) and heritability (H) for the hill plot method, the control plot method and the pedigree method of selection for each of three crosses.

Cross / Method	S_w^2	S_b^2	H
I - Hill plot method	-0.014± .060	0.482± .346	0.534± .188
Control plot method	-0.086± .094	0.101± .064	0.021± .163
Pedigree method	-0.075± .071	0.370± .099	0.376± .100
II - Hill plot method	0.387± .105	0.080± .067	0.493± .071
Control plot method	-0.109± .093	0.107± .068	-0.003± .171
Pedigree method	0.167± .079	0.249± .083	0.515± .073
III - Hill plot method	-0.259± .101	0.104± .080	-0.242± .252
Control plot method	0.125± .075	0.266± .152	0.472± .111
Pedigree method	-0.043± .076	0.260± .079	0.303± .109

Appendix III. Seed yield means and standard errors of transformed data for the hill plot (ETH), the control plot (ETC) and the pedigree method of selection for each of three crosses. (Means of 180 F_5 lines each, tested on 2 locations).

Cross	Seed Yield					
	ETH	SE	ETC	SE	PEDIGREE	SE
I	-0.156	0.404	-0.173	0.141	-0.331	0.102
II	-1.657	0.178	-1.367	0.145	-1.685	0.093
III	-0.195	0.194	-0.647	0.218	-0.809	0.091