EVALUATION OF F_3 SELECTION FOR YIELD

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by

Lindsay O'Brien

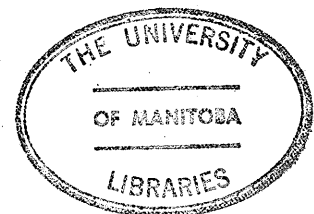In Partial Fulfillment of the

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EVALUATION OF F_3 SELECTION FOR YIELD

BY

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the University of Manitoba in partial fulfillment of the requirements
of the degree of

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

O'BRIEN, LINDSAY, Ph.D. The University of Manitoba, October, 1977.

Evaluation of F_3 Selection for Yield. Major Professor: L. E. Evans.

Four wheat crosses that involved the cv. Glenlea as a common
female parent, were used to evaluate the effectiveness of F_3 selection
for yield in its two components, the ability of the yield test to
identify high-yielding lines, and the persistence of their yield
performance into later generations. Seventy eight random large F_2
plants were evaluated as F_3 lines in a three replicate yield test
using three-row x 3 m length plots and a nine replicate hill plot
yield test where hill plots of 30 seeds per hill were planted on an
approximate 1 m grid. Ten high-yielding and ten low-yielding entries
were selected from each cross using the mean of the three-row plot
yields and the mean of four replicates of the hill plot yields.
F_4 and F_5 bulks and families of F_5 lines were derived from each of
the selected F_3 entries, and their performance in a subsequent season
in replicated tests of three-row x 3 m length plots used to verify
the results of the F_3 yield tests. The replicated F_3 yield tests
identified high-yielding lines. There were significant phenotypic
correlations (P = 0.01) for each cross between yield performance of
F_3 entries in hill plots and three-row plots. The genetic correlations

between hill plot and three-row plot performance indicated that the
genotypes were performing similarly in the two plot types. Hill plots
could be used for early generation testing if seed supply was limited.
Hill plots had increased error variation, they required more replications
to estimate yield differences between genotypes and they must be hand
planted and harvested compared with a totally mechanised operation
for three-row plots. The mean performance of the derived F_4 and F_5
bulks and the means of the families of F_5 lines confirmed the yield
classification based on F_3 performance in Crosses I and II and in some
instances in Crosses III and IV. Crosses I and II were characterised
by lower population mean yield than Crosses III and IV, but considerably
increased genetic variance compared with Crosses III and IV. Errors
of misclassification of yield potential based on F_3 yield performance
were detected. The observed responses to selection of the F_4 and F_5
bulks and the F_5 family means were less than the predicted responses
probably because the estimates of heritability obtained from the F_3
yield test were biased upwards due to the estimate of genetic variance
being confounded with components of variation resulting from genotype
x environment and genotype x year interaction effects. The strength
of intergeneration correlations between F_3, F_4 and F_5 bulk and F_5
family mean performance were influenced by the yield range and genetic
variance in the F_3 yield test. In all four crosses, replication resulted
in an improvement in the intergeneration correlations. Genotype x
year effects did not seem to be as important as the precision of
estimating the yield value of a genotype (i.e. the use of replication).
Adjustment of entries in single replicate yield tests to a percentage

of their adjacent control plot failed to improve the intergeneration correlations. The number of F_5 lines that can be evaluated per selected F_5 was shown to be determined by (1) the final objective of the breeding program (2) the variability of response to selection (3) the maximisation of response. Selection of spaced plants from the F_2 and F_4 generation winter nurseries in which the plants were grown in the absence of interplant competition, seemingly did not affect the performance of the randomly derived selections in the F_3 and F_5 yield tests in which there is interplant competition within the plot. The modification of the pedigree breeding system proposed by Shebeski (1967) has been modified to incorporate replicated F_3 and F_5 yield testing.

ERRATA

p35. Table 8. The single degree of freedom comparison for

Cross III was significant at the 5% level of probability.

p34. Alteration to text resulting from change in Table 8.

Last sentence of paragraph 1 now reads;

'The mean yield of the F_5 bulks derived from high-

yielding F_3 lines was significantly higher than the mean

of those derived from low-yielding F_3 lines for Crosses

I and II (P = 0.01) and Cross III (P = 0.05).'

p60. The new sentence beginning on line 11 should read;

'The adjustment procedure adjusted the F_4 and F_5 yield

values such that a negative correlation coefficient

resulted. For Cross IV, the correlation between the

replicated values was significant, whereas that based on

the unreplicated values was not significant. Furthermore,

the.....'

p72. The new sentence on line 19 should read;

'The total operating cost, C, can be expressed as, ...'

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performance of their progeny in later generations. It is generally

agreed that one cannot select high yielding genotypes on the basis of

single plant performance. In order to distinguish high yielding genotypes,

Shebeski (1967) proposed a method whereby the seed of harvested F_2 plants could be planted as single replicate entries in three-row plot trials with a control plot adjacent to every breeding entry; the control plot serving as a covariate, adjusting for soil heterogeneity. Yields of the breeding entries could be expressed as a percentage of their adjacent control plot.

Briggs and Shebeski (1971) conducted a study using the F_3 nursery design proposed by Shebeski. They reported a significant intergeneration correlation between F_3 and derived F_4 bulk yields, obtained in different seasons, only when they sampled the complete yield range of the F_3 population. De Pauw and Shebeski (1973) reported significant intergeneration rank correlations between yields expressed as a percentage of their adjacent control plot for F_3 lines and F_4 bulks, and F_3 lines and F_5 family means. De Pauw and Shebeski sampled the whole F_3 yield range to derive the F_4 bulks and the upper 30% of the F_3 yield range to derive the F_5 families. Although De Pauw and Shebeski's intergeneration correlations were significant, the F_3 yield values only predicted 34.8 and 31.4% of the total variability in F_4 bulk and F_5 family mean yields respectively. Knott and Kumar (1975) reported significant (P = 0.01) F_3 and derived F_5 line intergeneration correlations (r = 0.29 and r = 0.14 for the two crosses studied) but stated that the correlations were so low that they were of doubtful value. The strength of the intergeneration correlations between F_3 line yield and the yield of derived F_4 bulks, or F_4 lines, or F_5 lines has been used by some researchers (for example, Briggs and Shebeski, 1971; De Pauw and Shebeski, 1973; Knott and Kumar, 1975) to measure the value of F_3 yield testing.

Low intergeneration correlations suggest that F_3 line performance is not a good predictor of performance of derived bulks or lines. A number of factors can effect the expectations of intergeneration correlations. The precision of the yield estimates in each generation affect the correlations. Reduced precision of the estimates are reflected in reduced heritability estimates. The range of the yield values and the genetic variance in each generation are reflected in the heritability estimates for each generation. The yields in different generations can be considered as separate traits within the same genotype. The phenotypic correlation between two traits within the same genotype has been shown to be due to genetic and environmental causes of correlation (Falconer, 1960). Genotype x environment and genotype x year interactions affect the expectations of intergeneration correlations by reducing the genetic correlation. Using the relationship of correlated response-direct response to selection of Falconer (1960), the effects of reduced heritability estimates and genetic correlation on the expectations of intergeneration correlations are evident.

This dissertation reports the results of a study conducted to:

- evaluate two methods of replicated F_3 yield testing, three-row plots and hill plots, for their ability to identify true genetic differences, and to measure response to selection on the basis of yield in three-row plots.

- assess the relative importance of the precision of yield estimates and genotype x environment interactions by comparing intergeneration correlations measured with different amounts of replication in the same or different years.

LITERATURE REVIEW

Early Generation Selection for Yield

Shebeski (1967) and Sneep (1977) have shown that, for a character controlled by many genes (for example yield), a genotype with all the more desirable genes in either the homozygous or heterozygous condition for any given number of genes, occurs with the greatest frequency in the F_2 generation and its frequency decreases rapidly in subsequent generations. They conclude therefore that selection should commence in the earliest possible generation while the genotypes with all the more desirable genes are present at their greatest frequencies.

In the F_2 generation selection is based on single plants. McGinnis and Shebeski (1968) and Knott (1972) reported that visual selection resulted in an increase in the mean of the selected population compared with random selection. McGinnis and Shebeski concluded that selection of well-tillered, vigorous F_2 plants would be advantageous to a breeding program, whereas Knott concluded that the increase due to visual selection was of little use to the plant breeder. The ineffectiveness of single plant selection has been reported by Bell (1963), and Hamblin and Donald (1974) working with barley, MacKey (1963), and De Pauw and Shebeski (1973) working with wheat and Coyne (1968) working with field beans.

Knott (1972) examined the regressions of F_3 line yields on the yield of their parent F_2 plants and found the size of the regressions to be of little plant breeding value. Fasoulus (1973) proposed the

honeycomb method for selecting plants in the absence of interplant
competition in the early generations of a breeding program. Selected
high-yielding F_2 plants gave rise to high-yielding F_3 progeny when
yield in both generations was measured using single plants planted in
the honeycomb design. Skorda (1973) reported a study in which the
seeds of two F_2 families and their parental cultivars were sown in
a randomised complete block experiment with six replications at a seeding
rate approaching commercial planting density. From each replication
(of crosses and parents) the twenty highest yielding F_2 plants (first
selection) and the next twenty highest yielding F_2 plants (second
selection) were selected and grown in replicated F_3 yield tests. The
correlations between F_3 plot and F_2 plant yield for each cross were
nonsignificant within both the first and second selections. However,
when the two groups of selections were combined within each cross highly
significant correlations ($r = 0.848$ and $r = 0.871$) were obtained.
Skorda concluded that the selection was effective as the crosses which
generated the higher mean and larger genetic variances of F_3 lines were
derived from the higher yielding F_2 plants.

Allard (1960) summarised the studies of selection in the F_2 as
follows: "The effect of environment on single-plant yields is so large
that selection for heritable high yield in the F_2 is virtually futile.
On the other hand, effective selection among spaced F_2 plants for disease
resistance and other characters of high heritability is frequently pos-
sible. Since selection in the F_2 must be based on performance in a
single season, effectiveness of selection in that generation for char-
acters moderately subject to seasonal fluctuations (e.g., plant height,

maturity date) is often small. The effectiveness of selection among individual plants is therefore seen to be highly sensitive to the magnitude of the heritable variability <u>relative to</u> environmental variability".

The F_3 generation is the earliest possible generation in which plot yield trials can be conducted. A major factor in F_3 yield testing has been the availability of seed. Because of the failure to select for yield on a single plant basis in the F_2, and reports of interplant competition within plots, plant breeders have moved away from the use of F_2 nursery designs that result in the production of large F_2 plants. As a result, the restricted seed quantity produced by the F_2 plants has dictated the design of F_3 yield nurseries. Mostly, small, single replicate plots have been used in F_3 yield testing.

Shebeski (1967) proposed a single replicate nursery design where each entry was planted adjacent to a control plot and the yield of breeding entries expressed as a percentage of their adjacent control plot. The control plot acts as a covariate for adjusting for soil heterogeneity. The covariate adjustment relies upon the premise that the yield of two plots are more likely to agree the closer they are together. Wiebe (1935) and Briggs and Shebeski (1968) reported significant correlations between contiguous control plots that decreased to non-significance as the distance between plot entries increased. Townley-Smith and Hurd (1973) compared the moving mean method of adjusting plot yields with the percentage of adjacent control plot and the analysis of covariance and concluded that several types of adjustment may be needed to obtain the most reliable results. Baker

and McKenzie (1967) considered both theoretical grounds and plot data before concluding that systematic controls were of doubtful value as a soil fertility index. Baker (1968) reported that the use of control plots, on average, reduced error variance by only two percent, and Seif *et al.* (1974) reported increases in efficiency with the use of systematically arranged control plots, however, both reports doubted the increase in efficiency worth the inclusion of the extra plots.

Briggs and Shebeski (1971) using a single replicate F_3 nursery and adjusting yields to a percentage of the adjacent control plot, reported a significant rank $F_3 - F_5$ intergeneration correlation (r = 0.71, P = 0.01) only when they sampled the whole F_3 yield range for the purpose of developing F_5 lines. They concluded that adjustment to a percentage of the adjacent control plot yield was effective in adjusting for environmental variability. Furthemore, the "best yielding" F_5 populations were derived from F_3 plots from the upper area of the F_3 population, both for yield per plot and yield as a percentage of the adjacent control plot.

De Pauw and Shebeski (1973) used the same nursery design as Briggs and Shebeski to test F_3, F_4 bulk and F_5 families. They reported significant intergeneration rank correlations between F_3 and F_4 bulk (r = 0.59, P = 0.01) and F_3 and F_5 family mean (r = 0.56, P = 0.01). They concluded that the F_3 yield test was effective because the highest yielding F_4 bulks and F_5 families originated from F_3 lines that had high yield relative to the yield of their adjacent control plot.

Seitzer (1974) conducted a study in which a replicated F_3 yield test (hill plots planted at two locations) was compared with a F_3 yield

test where the entries were compared with their adjacent control plot and a pedigree method where visual selection was practised in the F_3. Early yield tests seemed to have a slight advantage over the pedigree method when dealing with crosses of lower yield potential.

Boerma and Cooper (1975) compared early generation testing with pedigree selection and the single seed descent breeding method. They concluded that the single seed descent method was the most efficient because it required less selection effort, allowed rapid advance of early generation segregating populations and did not use expensive yield testing until later generations.

Knott and Kumar (1975) compared early generation yield testing with the single seed descent procedure. The yield tests consisted of replicated 3.3 m length single row plots planted 0.3 m apart. One F_5 line was derived from each F_3 entry and yield tested. Material developed by single seed descent was F_6 generation when yield tested. The intergeneration correlations between F_3 and F_5 performance of the early generation test material were significant (P = 0.01), but sufficiently low to be of doubtful value (r = 0.29 and r = 0.14 for the two crosses studied). Further yield testing of the best 20% of F_5 lines developed by early generation testing and F_6 lines developed by single seed descent revealed that the single seed descent lines were at least as good as the early generation test lines. The authors concluded that it was doubtful whether early generation testing was worth the effort.

Different plot designs are often used at different stages of the breeding cycle because of restrictions of seed quantity, land and labour.

The use of different plot designs depends on their ability to predict performance in the plot type used in final evaluation. Hill plots were suggested by Bonnett and Bever (1947) as a means for removing off-types in pure seed production and for selection of disease resistant genotypes. Since then a number of workers (Jellum *et al.*, 1963; Frey, 1965; Baker and Leisle, 1970; Bliss, 1976) have reported that hill plots are useful for early generation selection and genetic studies because of their ability to predict performance in row plots. Frey (1965) reported almost perfect genetic correlations for yield, plant height and maturity in hills and rod row plots, in oats, while Baker and Leisle (1970) reported highly significant genetic correlations in common and durum wheat. Torrie (1962) found the relative performance of soybean cultivars in hill and row plots to be similar but concluded that more replicates would be needed using hill plots to estimate the yield differences between cultivars. Frey (1965) and Baker and Leisle (1970) also reported the need for increased replication with hill plots. Ross and Miller (1955) found that yield variability in hill plots was generally greater than that in row plots and recommended hill plots only as a supplement to row plots. The spatial arrangement of plants in hill plots leads to a different type of interplant competition to that in row plots. Schutz and Brim (1967) reported large competitive effects in soybean hill plots. Jensen and Robson (1969) proposed the use of linear hill plots in an attempt to correct for the interplant competitive effects of hill plots.

Estimation of Heritability and Response to Selection

Falconer (1960) defined heritability as the ratio of the additive genetic variance to the phenotypic variance. This relationship is often termed the narrow sense heritability because it considers only the additive genetic variance. Broad sense heritability is the ratio of total genetic variance to phenotypic variance, where the total genetic variance includes additive, dominance and epistatic variation. With inbred lines, Hanson (1963) and Pesek and Baker (1971) point out that genetic variance includes additive, and additive x additive epistatic types of genetic variation which are fixable by selection, with negligible variability due to dominance. The distinction between narrow and broad sense heritability has little meaning when considering inbred lines.

One of the most common methods of estimating heritability in self-pollinating crops was described by Comstock and Moll (1963) and is based on the estimation of variance components. Comstock and Moll describe heritability as the ratio of genetic variance to phenotypic variance, where genetic variance is the component of variance due to genotypes and phenotypic variance depends on the number of locations, years and degree of replication. Some confusion exists on the meaning of heritability in self-pollinating crops. Heritability can be estimated on the basis of means or on a single-plot basis. As the number of replications, locations and years used to estimate the means increases, phenotypic variance decreases and the estimate of heritability increases (Comstock and Moll, 1963).

Hanson (1963) discussed the estimation of heritability using the regression of offspring on parents. For the progeny from an open-pollinated plant, heritability is twice the regression coefficient of offspring on parent. For progeny from self-pollinated individuals the covariance estimates additive genetic variance, a dominance bias, additive x additive epistatic variance and a negligible epistatic component involving dominance. When selection is practised on advanced progeny rows (after F_3) the variability due to dominance can be ignored, and the regression of offspring on parents estimates heritability.

Many authors have estimated the heritability of yield. Generally the estimates have been low. Shebeski (1967) suggested that many of the estimates reflected the procedures used, in that inadequate provisions were taken to minimise the effects of soil heterogeneity and interline competition, and insufficient sample sizes were used to prevent gross sampling errors. Rasmusson and Glass (1967) reported heritability for yield of 0.65 when three replications, two locations and two years of testing were used, whereas a single-plot basis heritability was only 0.17. Baker *et al.* (1968) reported heritability for yield on a single-plot basis of 0.28, which increased to 0.74 when three replications, two locations and two years were used to obtain the estimate. These two reports illustrate that as the number of replications, locations and years increased, sampling errors and phenotypic variance decreased, and heritability increased as suggested it would by Comstock and Moll (1963).

Pesek and Baker (1971) suggested that "as with any estimate, the components of variance are subject to sampling errors". Consequently

estimates of heritability are subject to error and are of little worth without an estimate of sampling error. They described a simple method for computing the standard errors of heritability estimates.

Heritability and total phenotypic variability are important in determining expected response to selection. Falconer (1960) showed that the response to selection was equal to the selection differential multiplied by the heritability of the trait. The selection differential, which is the mean of the group selected as parents minus the mean of the whole population is not a suitable unit for predicting response as its magnitude is not known until selection within the parental generation has taken place. Falconer showed that the selection differential could be generalised, if both response and the selection differential were considered in terms of the phenotypic standard deviation. Then response is the product of the intensity of selection (determined by the proportion of the total population that is selected), the phenotypic standard deviation and the heritability of the trait.

Knott and Kumar (1975) compared actual and expected genetic advance measured as a percentage increase above the population mean in two wheat crosses. They found reasonable agreement between predicted advance based on an F_3 yield test and observed advance based on a yield test of an F_5 line derived from each F_3 line, at a range of selection intensities. Selection efficiency declined when more than 20% of the lines were saved. Pesek and Baker (1971) reported no significant differences between observed responses to selection and responses predicted by multiplying the estimate of heritability by the selection differential. On the other hand, Nickell and Grafius (1969) in a study with F_5 derived

lines of winter barley, reported significant discrepencies between predicted and observed responses to selection.

Baker (1966, 1971, 1975) and Hill (1974) considered the theoretical variance of response to selection and found that response is expected to be more variable with higher selection intensity or greater genetic variance and less variable with larger population size. The variance of expected response to selection is critical in selection programs where the selected proportion is subject to further evaluation, if the effects of sampling variability are to be reduced. Baker (1966, 1971) and Soller and Genizi (1967) have shown that the coefficient of variation of expected response is minimised when the proportion selected is between 10 and 30% of the total population. Expected response to selection is important in considering choice of breeding methods. Methods must be chosen such that the expected response to selection is maximised.

GENERAL EXPERIMENTAL DETAILS

A series of experiments were conducted using material generated from four crosses that involved the cultivar Glenlea as a common female parent. Two of the male parents were cultivars and two were breeding lines. The term variety shall be used to describe the parents. The pedigree and origin of the five parent varieties is given in Table 1.

A schematic outline of the generation and year sequence used for each cross is shown in Figure 1. F_2 plants of each cross were space planted in the winter nursery at Ciudad Obregon, Mexico in 1974. Each F_2 progeny, an F_3 line, was yield tested at Winnipeg in replicated hill plot and three-row plot yield tests in 1975. A random sample of F_4 seed from each of ten high- and ten low-yielding F_3 lines was space-planted in the winter nursery in the 1975-76 season. Residual F_4 seed from each selected F_3 line was yield tested in replicated experiments at Winnipeg and Glenlea, and in unreplicated experiments at Winnipeg in 1976.

Eight random large F_4 plants were selected from the winter nursery and planted as F_5 lines in a replicated yield test at Winnipeg in 1976. A group of eight F_5 lines having a common F_3 line progenitor constituted an F_5 family. Single heads from each F_4 plant in the winter nursery were composited to form an F_5 bulk. The F_5 bulks were yield tested in replicated experiments at Winnipeg and Glenlea and in unreplicated

TABLE 1.   Pedigree and origin of the varieties used as parents

Variety	Origin	Pedigree
Glenlea	University of Manitoba	Pembina / 2 / Bage / CB 100 CB 100 = Sonora 64 // Tezanos Pintos Precos // Nainari 60
Norquay	University of Manitoba	Lerma Rojo / Sonora 64 // Justin
Yecora 70	Centro Internacionale Mejoriamento de Maiz y Trigo, Mexico City, Mexico	Ciano 'S' / 3 / Sonora 64 // Klein Rendidor // 8156
NB 116	University of Manitoba	Glenlea sib // Sonora 64 / Tezanos Pintos Precos
J 34	University of Manitoba	Hard Federation / Chinese Spring // Nero / 3 / 3* purple Pitic / 4 / Glenlea

FIGURE 1. Schematic outline of the generation and year sequence for each cross

Year	Winter Nursery Ciudad Obregon, Mexico	Summer Nursery Manitoba, Canada

1974-75 F_2 Two thousand spaced plants

↓

Seventy-eight
Random large plants
Selected

1975 F_3 lines

Ten high- and ten low-
yielding lines selected

1975-76 F_4 Two hundred spaced plants

Composite of single head
from each plant

Eight
Random large plants
Selected

1976 F_4 bulk

F_5 bulk

F_5 family of eight F_5 lines
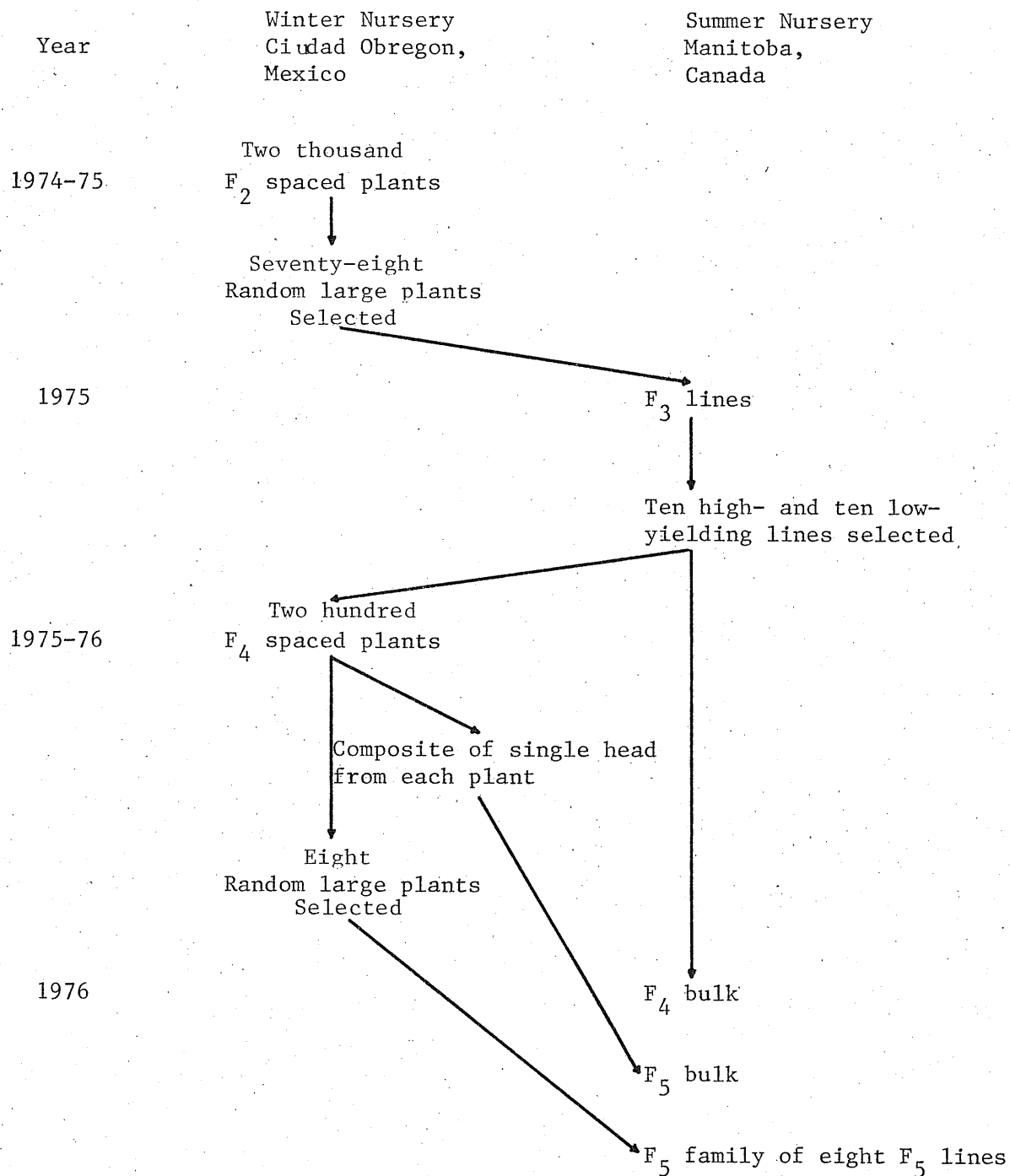
experiments at Winnipeg, in 1976.

Material grown in the winter nursery was space-planted 0.3-0.4m apart in pairs of rows 11 m long and 0.3m apart with 0.6m between pairs. Growth conditions and planting density were both conducive to tillering and large plants constituted most of the nursery. Selection of random large F_2 plants in Mexico was affected by maturity; late-maturing plants were ignored.

Hill plots were hand cut and threshed using a stationary Hege 125 plot combine. All three-row plots were trimmed to 3 m length and direct harvested with a Hege 125 plot combine. Plot weights were recorded from the harvested samples. Plots grown at the Winnipeg location were planted on Riverdale clay at the University of Manitoba, while plots at the Glenlea location were planted on Red River clay at the University of Manitoba's Glenlea Research Station.

Growing season rainfall (April 1 - September 1) at the University of Manitoba for 1975 was 364 mm, with 215 mm being recorded in June. In 1976, 224 mm was recorded for the growing season, with 137 mm being recorded in June. The six year average (1971-76) for the same period was 313 mm. Sprinkle irrigation, sufficient to ensure even germination and plant stand was applied to all plots at the University of Manitoba in 1976.

EXPERIMENT I

Response to early generation yield testing depends on the ability of the early generation test to identify true genetic differences between genotypes, and on the existence of a high correlation between the performance of selected genotypes and the performance of their progeny in later generations. The objective of this experiment was to determine if a replicated F_3 yield test identifies high yielding lines. Two types of replicated yield testing procedure were to be evaluated, three-row plots and hill plots. The performance of F_4 and F_5 bulk samples derived from selected F_3 lines together with the mean yield of eight random F_5 lines derived from each selected F_3 line (F_5 family mean) were to be used to verify the results of the F_3 yield tests.

Materials and Methods

The seed from random large F_2 spaced-plants grown in the winter nursery was grown in two replicated yield tests at the University of Manitoba in 1975. In yield test 1, three-row x 3 m length plots were evaluated using a partially balanced lattice design with three replications. The plots were planted with 0.15m between the rows and 0.9m between the center rows. Seeding rate was 50 seeds per metre of row. In yield test 2, hill plots planted approximately on a one metre grid with 30 seeds scattered in a 0.2m diameter hill were evaluated using a randomised complete block design with nine replications. In both yield tests the same 81 entries were evaluated, 78 F_3 lines plus three entries of cv.

Glenlea. In each yield test, every tenth plot was seeded with cultivar Glenlea.

The three-row plot yield test was planted on summer fallowed, Riverdale clay. Four replications of the hill plot yield test were planted on the same block of land and five replications on land that had been cropped with corn the previous summer. An application of 55 kg./ha. of elemental nitrogen, applied as urea and ammonium sulphate, was broadcast on the cropped land the autumn preceding planting.

In both the three-row plot yield test and the hill plot yield test the crosses were planted and harvested in the order, Cross I, Cross II, Cross III and Cross IV. Ten high-yielding and ten low-yielding lines were selected from each cross for the development of F_4 and F_5 bulks, and families of F_5 lines. The lines were selected on the basis of mean performance in the three-row plot yield test and four replicates of the hill plot yield test. The F_4 bulk sample from each selected F_3 line was a random sample taken from a composite of the three replicates of the three-row plot yield test. The F_5 bulk sample of each selected F_3 line was a composite of a single head from each F_4 spaced plant in the 1975-76 winter nursery (see Figure 1). The F_4 and F_5 bulk yield tests for each crosses were planted at each of two two locations, the University of Manitoba (Winnipeg) on May 3rd (Crosses II and III) and May 4th (Crosses I and IV), and the Glenlea Research Station (Glenlea) on April 28th, 1976. Eight separate, three replicate, randomised complete block experiments were planted at each location. The selected entries for each cross for each generation

together with the cv. Glenlea formed the entries for each experiment. Data from the two locations was initially considered separately and later combined after testing for homogeneity of the variances using Bartlett's test.

From each of the selected ten high- and ten low-yielding lines planted as F_4 spaced plants in the winter nursery, eight random large plants were selected. The eight random selections constituted an F_5 family of F_5 lines. The cv. Glenlea was also considered as a family. The selections were randomised within families and families randomised within blocks. The entries were planted as three-row x 3 m length plots on land that had been cropped the previous summer with a faba bean (*Vicia faba* L. var Minor) seed increase. Crosses II and III were planted on May 3rd and Crosses I and IV on May 4th, 1976. A two-way analysis of variance was run for each cross using the F_5 family means. Sources due to variation among F_5 families rated as high- and low-yielding by the F_3 yield test, and the contrast of Glenlea versus the remaining F_5 families were separated from the total variation due to F_5 families. Separate analyses of variance were run for the F_5 lines within each F_5 family and the sums of squares pooled over families. The error variances were tested for homogeneity with Bartlett's test.

Heritabilities were estimated by two methods. For each generation of each cross, the variance component method described by Comstock and Moll (1963) was used. For the F_3 yield tests, with n replicates of each genotype the phenotypic variance, σ_p^2, is

$$\sigma_p^2 = \sigma_g^2 + \frac{1}{n} \sigma_e^2$$

where σ^2_g and σ^2_e are the genetic and error variances, respectively.

For the F_4 and F_5 bulk yield tests, with n replicates in each of b

environments, the phenotypic variance, σ^2_p, is

$$\sigma^2_p = \sigma^2_g + \frac{1}{b}\sigma^2_{ge} + \frac{1}{nb}\sigma^2_e$$

where σ^2_g, σ^2_{ge} and σ^2_e are the genetic, genotype x environment interaction

and error variance components, respectively. The corresponding heri-

tabilities, h^2, would be

$$h^2 = \frac{\sigma^2_g}{\sigma^2_p}$$

Standard errors of the heritability estimates were obtained following

the method described by Pesek and Baker (1971).

Using the combined locations mean yields of the F_4 and F_5 bulks,

the offspring-parent regression (F_5 on F_4) was calculated. The standard

error of the heritability estimate was the standard error of the regres-

sion coefficient.

Correlation matrices were constructed between, the F_3 three-row

plot mean yields that were adjusted using the intra-block error in

the partially balanced lattice analysis of variance, the unadjusted

F_3 three-row plot mean yields, the F_3 hill plot mean yields, the F_4

bulk mean yields for the Winnipeg and Glenlea locations and the mean

of the combined locations, the F_5 bulk mean yields for the Winnipeg

and Glenlea locations and the mean of the combined locations, and the

mean of the family of F_5 lines.

Results and Discussion

The analysis of variance for the F_3 three-row plot yield test for each cross is summarised in Table 2. The unadjusted treatments mean square was tested for significance using the randomised complete block error term and was significant ($P = 0.01$) for each cross. Adjustment of the unadjusted treatments sum of squares and testing with the intra-block error mean square is a more sensitive procedure (Cochran and Cox, 1950) but was unnecessary, because significance was obtained using the randomised complete block error mean square.

The yield range (maximum and minimum plot yields) and the mean of all entries tested in the F_3 three-row plot yield test are given in Table 2. The higher population mean yield of Crosses III and IV suggest these crosses may have more breeding potential than Crosses I and II if F_3 yield performance is a good predictor of performance in subsequent generations. The coefficients of variability for each cross (Table 2) are reasonable for the level of replication used in the yield test.

The analysis of variance of the F_3 hill plot yield test for each cross is summarised in Table 3. Significant treatment and block effects ($P = 0.01$) were obtained for each cross. The yield range and the mean of all entries tested is given in Table 3. Crosses III and IV had the highest population means. The coefficients of variation for the hill plot test (Table 3) were quite high for the level of replication used in the yield test. Comparison of the coefficients of variation for the three-row plot (Table 2) and hill plot (Table 3) yield tests suggests that more replications of hill plots than three-row

TABLE 2.. Means squares with their associated degrees of freedom, the coefficient of variation, the population mean (g/plot), and the yield range (g/plot) for each cross for the three-row plot, F_3 yield test.

Source	df	Cross I	Cross II	Cross III	Cross IV
Replications	2	147264.00	5360.00	113792.00	59968.00
Blocks within replications (Adj)	24	32669.71	10106.29	23807.85	20349.95
Treatments (Unadj.)	80	60311.80**	59772.00**	23676.80**	15219.40**
Intra Block Error	136	6312.82	6244.76	5598.53	4359.48
Randomised complete block error	160	10266.35	6823.99	8329.93	6758.05
Total	242	27942.51	24315.36	14274.86	9994.94
Coefficient of Variation %		8.69	8.96	7.11	6.83
Population mean (g/plot)		914.3	921.5	1051.9	966.6
Yield range (g/plot):					
Maximum		1212.3	1191.3	1225.3	1144.3
Minimum		615.7	511.7	773.0	820.0

** Significant at the 1% probability level

TABLE 3.   Mean squares with their associated degrees of freedom, the
coefficient of variation, the population mean (g/plot), and the
yield range (g/plot) for each cross for the hill plot F_3 yield test.

Source	df	Cross I	Cross II	Cross III	Cross IV
Treatments	80	2831.66**	3068.21**	2084.27**	1272.14**
Blocks	8	27358.16**	6065.10**	6777.61**	20046.94**
Error	640	340.21	469.58	672.94	635.33
Total	728	910.90	816.63	895.12	918.63
Coefficient of Variation %		18.5	23.8	20.1	20.5
Population mean (g/plot)		100.0	91.1	129.4	122.9
Yield range (g/plot):					
Maximum		147.3	128.3	168.3	146.4
Minimum		61.0	48.7	82.4	98.2

** Significant at the 1% probability level

plots would be required to estimate differences between genotypes with equal precision.

The selection of the ten high- and ten low-yielding F_3 lines from each cross was based on the combined performance of the lines in three-row plots (means unadjusted for intra-block error) and the mean of four replicates of hill plots (Figure 2). The regression of mean three-row plot yield on mean yield of four replicates of hill plots is given in Figure 2. The regressions were significant for each cross (P = 0.05 for Cross IV and P = 0.01 for Crosses I, II and III).

Simple product-moment correlation coefficients between the mean three-row plot yields (unadjusted) and the mean of four replicates of hill plots for each cross are given in Table 4. The relationships are all significant. However, hill plots explain only a small part of the variability in three-row plot yields in Crosses III and IV. In each cross, increased replication within the hill plots improved the correlation with three-row plot performance.

It is important to note that the relationships between three-row and hill plot yields are based on phenotypic values. Falconer (1960) points out that a phenotypic correlation, r_p, is composed of two components, the genetic correlation, r_A, and the environmental correlation, r_E, with the relationship between them being given by,

$$r_p = h_x h_y r_A + e_x e_y r_E$$

where in the case of three-row and hill plots, h_x is the square root of the heritability of three-row plot means, h_y is the square root of
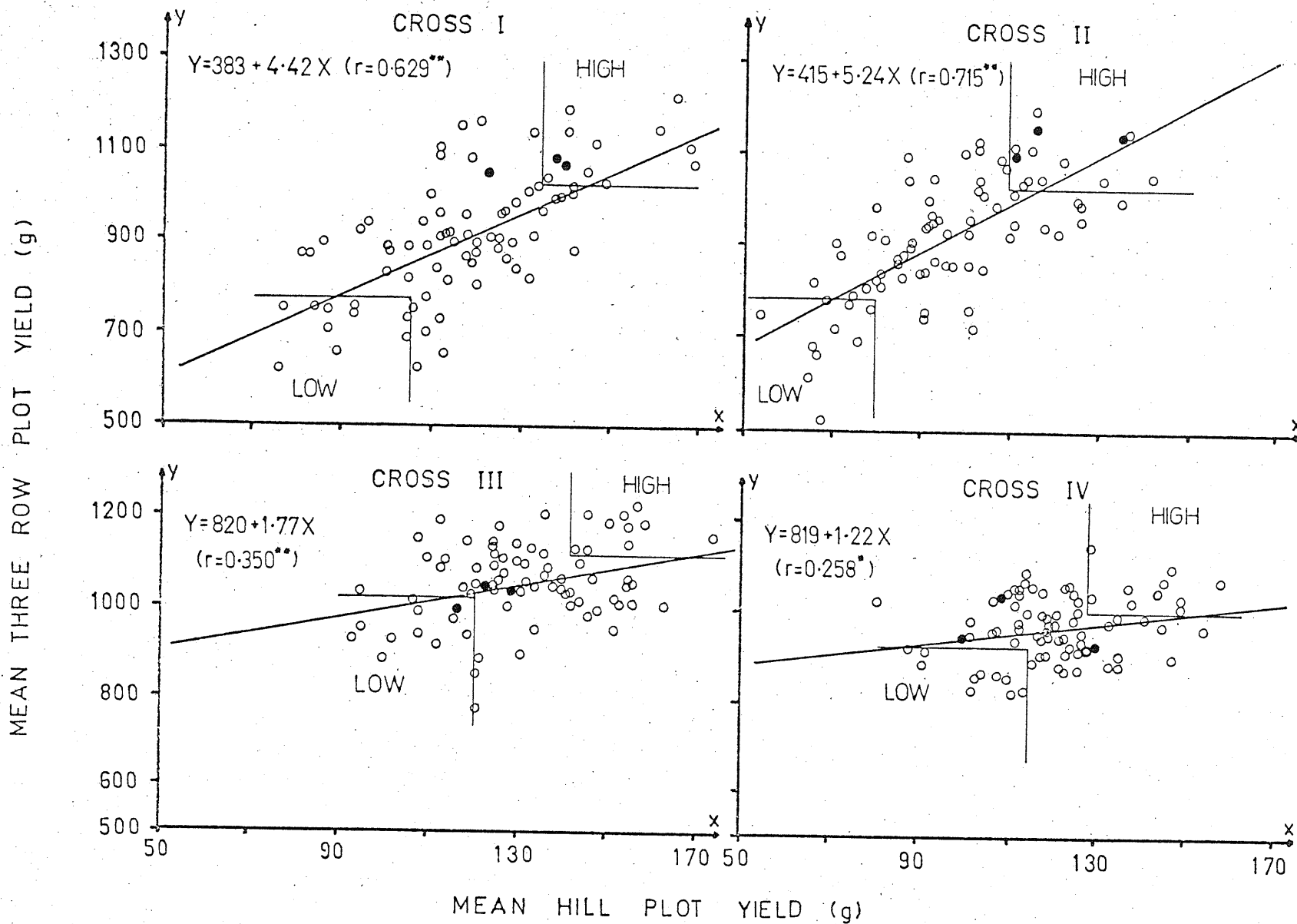
FIGURE 2. The regressions of mean three-row plot yield (unadjusted means) on mean hill plot yield (four replicates) for the F_3 yield tests for each cross. (Note: The selected high- and low-yielding F_3 entries are within the right-angled brackets. The solid circles are cv. Glenlea).

TABLE 4. Simple product-moment correlation matrix for each cross for the different F_3 plot procedures

Variables	3-row (adjusted)	3-row (unadjusted)	Hills (9 replicates)	Hills (4 replicates)
Cross I				
3-row (adjusted)	1.000	0.973**	0.758**	0.698**
3-row (unadjusted)		1.000	0.749**	0.685**
Hills (9 replicates)			1.000	0.926**
Hills (4 replicates)				1.000
Cross II				
3-row (adjusted)	1.000	1.000**	0.786**	0.715**
3-row (unadjusted)		1.000	0.786**	0.715**
Hills (9 replicates)			1.000	0.905**
Hills (4 replicates)				1.000
Cross III				
3-row (adjusted)	1.000	0.957**	0.508**	0.420**
3-row (unadjusted)		1.000	0.402**	0.350**
Hills (9 replicates)			1.000	0.794**
Hills (4 replicates)				1.000
Cross IV				
3-row (adjusted)	1.000	0.937**	0.506**	0.294**
3-row (unadjusted)		1.000	0.443**	0.258*
Hills (9 replicates)			1.000	0.744**
Hills (4 replicates)				1.000

*, **, Significant at the 5% and 1% probability levels, respectively

the heritability of hill plot means, and e is the square root of one minus the heritability, with e_x and e_y corresponding to three-row plots and hill plots, respectively. It can be assumed that r_E is zero, since there is no reason to suspect the environmental effects in one randomised experiment (three-row plots) are correlated with those of another randomised experiment (hill plots). The genetic correlations can then be calculated from phenotypic correlations between three-row and hill plot yields and the heritabilities of three-row plot and hill plot means are known.

The genetic correlations between three-row plot and hill plot yields for each cross are given in Table 5. The high genetic correlations for Crosses I, II and IV suggest that in these crosses the lines were performing similarly in three-row plots and hill plots. This result agrees with reports by Frey (1965) and Baker and Leisle (1970) on the suitability of hill plots for early generation selection, and illustrates the danger of considering only phenotypic correlations.

Comparison of the F ratio values for the three-row plot and hill plot yield tests (Table 5) shows that hill plots were more effective in distinguishing lines (higher F ratios) in Crosses I and III than three-row plots. Baker and Leisle (1970) reported a similar result with common and durum wheat in comparisons of performance in rod row and hill plots. Comparison of the coefficients of variation for the three-row plot yield test (Table 2) and the hill plot yield test (Table 3) reveals that error variation was considerably greater in hill plot yield tests, which agrees with the findings of Ross and Miller (1955), Torrie (1962), Frey (1965) and Baker and Leisle (1970 who reported increased error variation associated with hill plots

TABLE 5. Summary statistics for the comparison of F_3 genotype performance
in hill plots and three-row plots for each cross

Statistic	Cross I	Cross II	Cross III	Cross IV
Genetic correlation between hill plots and three-row plots	0.887	0.908	0.767	0.959
F ratios: Hill plots	8.32	6.53	3.10	2.00
Three-row plots	5.87	8.76	2.84	2.25
Heritability on a single-plot basis: Hill plots	0.459	0.381	0.189	0.100
Three-row plots	0.619	0.722	0.407	0.295
Efficiency ratio	0.755	0.660	0.523	0.558
The number of replicates of hill plots to give equivalent information to one three-row plot	1.2	2.4	1.4	3.6

compared with row plots.

Frey (1965) used the relationship between correlated response and direct response to selection described by Falconer (1960) to measure the selection efficiency of hill plots relative to row plots. When selecting in hill plots for performance in three-row plots, the effectiveness of selection is estimated by the product of the square root of the heritability of yield in hill plots, h_H, and the genetic correlation between hill and row plots, r_A. The square root of the heritability estimated for three-row plots, h_R, is a measure of the efficiency of selection in such plots. The ratio of the former to the latter, i.e. $h_H r_A / h_R$, measures the efficiency of selection in hill plots relative to selection in three-row plots. The efficiency ratio for each cross is given in Table 5, and indicates that hill plots are only half to three-quarters as efficient as three-row plots.

Frey (1965) also described a procedure whereby the number of replicates of hill plots required to give equivalent information to one replicate of three-row plots could be computed. The values for each cross are given in Table 5, and indicate that more replicates of hill plots are required to give equivalent information to one three-row plot. This result encompasses the range of replicates of hill plots required to give equivalent information to one rod row plot reported by Frey (1965) and Baker and Leisle (1970).

The effectiveness of hill plots relative to three-row plots depends on the genetic correlations between hill plot and three-row plot yields. In all four crosses the genetic correlation between performance in the two plot types exceeded the heritability of hill plot yield. Hill

plots are a valid alternative to three-row plots for early generation

selection. Hill plots have the advantage that they require less seed

and land than three-row plots. However, they possess the disadvantages

of:

    - the need for increased replication to give the equivalent

information of one three-row plot

    - hand planting and harvesting compared with a totally mechanised

operation for three-row plots.

The mean yield (g/plot) of the selected F_3 entries in three-row plots

(adjusted treatment means from the partially balanced lattice analysis

of variance) and hill plots, together with the averaged yield for the

three entries of cv. Glenlea for each cross is given in Table 6.

Using the least significant difference (P = 0.05) as a guide to the

level required for significance between treatment means it can be seen

from Table 6 that only Crosses III and IV produced entries that were

superior to cv. Glenlea. Crosses III and IV could be considered as

the only crosses with breeding potential if F_3 line performance is

a reliable predictor of performance in subsequent generations.

The analyses of variance for the F_4 bulks of each cross are given

in Table 7. In all four crosses differences between locations and

environments were significant (P = 0.01). In Crosses I, II and IV,

differences among genotypes were significant (P = 0.01). In Crosses

I and II, significant genotype x environment interactions were recorded.

The mean yield of the F_4 bulks derived from high-yielding F_3 lines

was significantly higher (P = 0.01) than the mean of those derived

from low-yielding F_3 lines for Crosses I, II and IV, further substantiating

TABLE 6. Mean yield (g/plot) of selected entries for each cross for the three row plot yield test (adjusted means) and the hill-plot test, together with the average of the entries of cv. Glenlea.

Yield rating	Entry	Cross I 3-row	Cross I Hill	Entry	Cross II 3-row	Cross II Hill	Entry	Cross III 3-row	Cross III Hill	Entry	Cross IV 3-row	Cross IV Hill
	38	1203	147	81	1191	109	62	1209	159	61	1155	132
	4	1169	139	72	1145	123	57	1195	142	77	1101	145
	59	1116	120	48	1112	110	8	1194	137	1	1078	146
	58	1106	124	67	1107	117	69	1189	143	12	1072	139
High	28	1105	124	79	1085	117	7	1183	152	62	1041	141
	71	1090	114	17	1070	97	9	1177	137	67	1027	129
	21	1086	147	26	1048	127	11	1166	144	38	1021	133
	57	1079	131	29	1047	125	17	1163	168	4	1016	140
	6	1034	114	11	1044	112	32	1124	136	36	1009	142
	47	989	111	76	1035	107	48	1104	138	34	999	146
	Mean	1098	127		1088	114		1170	146		1052	139
	69	803	74	34	777	67	81	1017	101	79	922	98
	35	761	61	13	766	62	43	1005	126	44	906	116
	17	751	78	62	753	71	20	986	115	58	890	109
	77	737	85	56	744	56	1	967	115	45	884	108
Low	65	731	78	10	712	69	73	957	94	51	882	103
	60	699	78	73	687	78	56	932	119	80	867	110
	1	694	72	46	673	60	72	901	106	66	859	105
	76	672	92	35	657	64	46	899	112	14	853	116
	11	658	69	61	607	56	51	872	104	40	843	99
	61	624	61	31	512	49	23	836	82	55	830	112
	Mean	713	75		689	63		937	108		874	108
cv. Glenlea		1080	120		1129	117		1039	121		959	111
LSD (P = 0.05)		127	23		132	23		120	27		106	27

TABLE 7. Mean squares with their associated degrees of freedom for the combined locations analysis of variance of the F_4 bulks for each cross

Source	df	Cross I	Cross II	Cross III	Cross IV
Genotypes	20	84444.99**	97555.22**	13635.79	28111.14**
High-Low F_3 rating	1	1319222.70**	1450680.30**	29956.80	106207.50**
Environments	1	8495774.00**	5627384.00**	4071607.14**	14249098.29**
Replications in Environments	4	26086.25**	30392.82*	101954.94**	55037.75**
Genotypes x Environments	20	20968.55**	29060.45**	23800.29	12248.04
Error	80	6721.76	9496.36	19731.70	11626.10
Total	125	90117.30	72327.82	54453.48	129652.17

*, ** Significant at the 5% and 1% probability levels, respectively.

the classification based on the F_3 yield test (Table 7).

The analyses of variance for the F_5 bulks of each cross are given in Table 8. The difference between environments was significant (P = 0.01) for all four crosses. There were significant (P = 0.01) differences between genotypes in Crosses I, II and III, and for Crosses I and IV, there were significant genotype x environment interactions (P = 0.05 and P = 0.01, respectively). The mean yield of the F_5 bulks derived from high-yielding F_3 lines was significantly higher (P = 0.01) than the mean of those derived from low-yielding F_3 lines only for Crosses I and II.

The occurrence of significant differences between the bulks derived from high- and low-yielding F_3 lines for Crosses I, II and IV for the F_4 bulks and only Crosses I and II for the F_5 bulks indicates that Crosses I and II possessed greater genetic variance in the F_3 generation. Although Crosses III and IV exhibit the least genetic variance of the four crosses, they possess the greatest potential from a breeding point of view. Estimates of genetic variance ($\hat{\sigma}_g^2$) for each cross, estimated from the analysis of variance of the F_3 three-row plot yield test were:

Cross I	$\hat{\sigma}_g^2 =$	16681.8
Cross II	$\hat{\sigma}_g^2 =$	17649.3
Cross III	$\hat{\sigma}_g^2 =$	5115.6
Cross IV	$\hat{\sigma}_g^2 =$	2820.5

The decreased genetic variance makes it more difficult to obtain and verify significant differences based on F_3 yield performance. As the generation number increased the absolute yield difference between the selected entries decreased. These factors combined with year effects,

TABLE 8.   Mean squares with their associated degrees of freedom for the combined locations analysis of variance of the F_5 bulks for each cross

Source	df	Cross I	Cross II	Cross III	Cross IV
Genotypes	20	95758.44**	72992.44**	83205.46**	14814.49
High-Low F_3 rating	1	1532280.00**	903967.50**	40186.80	21870.00
Environments	1	8500448.64**	12224194.57**	3214866.67**	16071428.57**
Replication in Environments	4	69003.31**	45438.44**	160167.17**	16716.52
Genotypes x Environments	20	11580.54*	14440.42	12569.75	37656.62**
Error	80	6447.39	8671.72	10049.90	14693.25
Total	125	91512.27	118786.81	52600.25	147078.21

*, ** Significant at the 5% and 1% probability levels, respectively.

sampling variability and possible inadequate levels of replication
are possible reasons for the lack of significant differences between
the F_4 and F_5 bulks derived from high- and low-yielding F_3 lines in
Crosses III and IV.

The estimates of heritability for each generation of each cross
are given in Table 9. It should be remembered that these estimates
are based on means, in the case of the F_3 yield tests, the mean of
three replicates of three-row plots and the mean of nine replicates
of hill plots. With the F_4 and F_5 bulks, the estimates are based on
the mean of genotypes replicated three times at each of two locations.
The effect of using mean values to estimate heritability can be seen
by comparing the estimates based on the means of the genotypes tested
in the two F_3 yield tests, three-row plots and hill plots (Table 9)
with those estimated on a single plot basis using the same genotypes
(Table 5). The estimates of heritability based on plot means are
generally high (Table 9). The heritability estimates in F_3 were based
on 78 genotypes whereas those in the F_4 and F_5 were based on twenty
genotypes. Test conditions were conducive to high heritability esti-
mates because of

- the levels of replication used in the F_3 yield tests

- the use of replication and two test locations for the F_4 and
F_5 bulk yield tests

- the selection of genotypes for the F_4 and F_5 bulk yield tests
from the extreme ends of the yield range of the F_3 yield tests

- the use of a random effects model in the analysis of variance
of the F_4 and F_5 bulk yield tests.

TABLE 9. Percent heritability, estimated by two different methods for each cross for different generations and plot-types

	Heritability				
	Variance Component Method				Offspring-Parent Regression
	F_3 hill plots	F_3 three-row plots	F_4 bulks	F_5 bulks	F_5-F_4 bulks
Cross I	88.0 ± 2.0	83.0 ± 3.5	75.2 ± 10.6	87.9 ± 5.2	95.5 ± 10.7
Cross II	84.7 ± 2.6	88.6 ± 2.3	70.2 ± 12.7	80.2 ± 8.5	70.5 ± 11.5
Cross III	67.7 ± 5.4	64.9 ± 6.7	-74.5 ± 74.4	84.9 ± 6.4	19.9 ± 23.7
Cross IV	50.1 ± 8.3	55.7 ± 8.5	56.4 ± 18.6	-154.2 ± 108.4	44.6 ± 13.1

The heritability estimates suggest that expected response to selection for grain yield would be greater in Crosses I and II than in Crosses III and IV. However, it is Crosses III and IV that possess the greater breeding potential, by virtue of their absolute yield values relative to the control, cv. Glenlea. The population means, the means of the selected groups and the predicted and observed responses to selection for each cross are given in Table 10. The ten high-yielding entries from each cross formed the selected group. Predicted response was estimated by multiplying the selection differential (the mean of the selected group minus the mean of all entries) by the estimate of heritability. The difference between the mean yield of the selected entries and the mean of all entries was used as the measure of observed response. With the F_4 and F_5 bulks, the combined locations mean yields were used to measure the observed responses. The standard errors of predicted and observed responses were derived by the method used by Pesek and Baker (1971).

The predicted response to selection in Crosses I and II were much greater than those for Crosses III and IV. However, the higher mean yields obtained in the F_3 yield tests for Crosses III and IV show that less response was required from these crosses to obtain lines with high yield. The greatest response to selection can be achieved from those crosses with low population mean yield. However, they are not necessarily the crosses of interest to the breeder. As the absolute yield value of the population to be selected is increased by the breeder, the closer it gets to the upper genetic limit, consequently genetic variance and heritability decrease. As a result the expected response

TABLE 10. Means and predicted and observed responses to selection for yield in each cross (g/plot)

Cross and Generation	Mean of population	Mean of selected high yield group	Predicted response	Observed response
Cross I				
F_3	914.3	1105.9	159.1 ± 5.6	
F_4 bulk	913.3	1018.1		104.9 ± 10.6
F_5 bulk	869.7	982.7		113.0 ± 10.4
F_5 family	818.9	899.9		81.0 ± 45.0
Cross II				
F_3	921.5	1088.5	147.9 ± 3.9	
F_4 bulk	824.7	934.6		110.0 ± 12.6
F_5 bulk	803.8	890.5		86.7 ± 12.0
F_5 family	911.4	969.7		58.3 ± 31.1
Cross III				
F_3	1051.9	1172.0	77.9 ± 8.0	
F_4 bulk	885.8	901.6		15.8 ± 18.1
F_5 bulk	920.1	938.4		18.3 ± 12.9
F_5 family	1032.1	1065.3		33.4 ± 35.3
Cross IV				
F_3	966.6	1056.5	50.1 ± 7.6	
F_4 bulk	898.2	927.9		29.8 ± 13.9
F_5 bulk	874.2	887.7		13.5 ± 15.6
F_5 family	955.0	958.4		3.4 ± 32.2

to selection would be less from a population of greater breeding potential than that from a population of lower absolute yield value.

Comparison of the predicted and observed responses (Table 10) reveals that in no case did observed response approach predicted response. The failure of observed response to approach the predicted values may be due to assumptions involved in computing predicted and observed responses. Pesek and Baker (1971) point out that the theory of computing predicted response assumes that the estimates of heritability are derived from yield tests in an adequate sample of the reference set of environments. Significant discrepancies between predicted and observed responses suggests that this assumption was unsound. The estimates of predicted response were probably too high. This could result from genotype x year and genotype x environment interaction components being confounded with the estimate of genetic variance obtained from the F_3 yield test. The estimates of heritability based on the plot means of genotypes in the F_3 three-row plot yield test were all high (Table 9). Also the comparison of predicted and observed responses assumes that observed responses have been measured in an adequate sample of environments. The discrepancies obtained between predicted and observed responses were most likely due to combined effects of the factors suggested above.

Simple product-moment correlations relating yield of the selected F_3 entries in three-row plots (both adjusted and unadjusted treatment means) and in hill plots to performance of derived F_4 and F_5 bulks and F_5 family means for each cross are given in Tables 11 to 14.

The intergeneration correlations of F_3 with the derived F_4 and

F_5 bulks for the selected entries in Cross I (Table 11) were all highly significant (P = 0.01). The correlations between the adjusted three-row plot mean yield and the yield of the derived bulks averaged over locations were, r = 0.880 between F_3 and derived F_4 bulk, r = 0.913 between the F_3 and derived F_5 bulk and r = 0.905 between the derived F_4 and F_5 bulks.

The intergeneration correlations among the selected entries for Cross II (Table 12) were generally significant. The correlations between the adjusted three-row plot mean yield and the yield of the derived bulks averaged over locations were, r = 0.856 between the F_3 and derived F_4 bulk, r = 0.771 between the F_3 and the derived F_5 bulk, and r = 0.816 between the derived F_4 and F_5 bulks.

The intergeneration correlations among the selected F_3 entries and their derived F_4 and F_5 bulks for Cross III were mostly nonsignificant (Table 13). There was no significant correlation between the yield of the selected F_3 entries and the yield of the derived F_4 and F_5 bulks averaged over locations. The correlation between the yield averaged over two locations of the derived F_4 and F_5 bulks was not significant.

The intergeneration correlations among the selected F_3 entries in Cross IV and their derived F_4 and F_5 bulk yields averaged over two locations are given in Table 14. The correlations between F_3 yield and derived F_4 and F_5 bulk yields were not significant. The correlation between the two location average yield of the derived F_4 and F_5 bulks (r = 0.650) was significant (P = 0.01).

The lack of significant intergeneration correlations in Crosses

TABLE 11. Correlation matrix between F_3 performance and performance of derived F_4 and F_5 bulks and F_5 family mean for the selected entries of Cross I

Variable	1	2	3	4	5	6	7	8	9	10
1. Three-row plots (adjusted)	1.000	0.987	0.936	0.818	0.774	0.880	0.845	0.897	0.913	0.712
2. Three-row plots (unadjusted)		1.000	0.928	0.794	0.783	0.873	0.824	0.906	0.909	0.715
3. Hill plots			1.000	0.801	0.750	0.857	0.818	0.881	0.892	0.657
4. F_4 bulk Winnipeg				1.000	0.620	0.870	0.904	0.783	0.871	0.687
5. F_4 bulk Glenlea					1.000	0.926	0.574	0.867	0.774	0.683
6. F_4 bulk combined locations						1.000	0.795	0.921	0.905	0.759
7. F_5 bulk Winnipeg							1.000	0.832	0.944	0.521*
8. F_5 bulk Glenlea								1.000	0.969	0.657
9. F_5 bulk combined locations									1.000	0.625
10. F_5 family mean										1.000

*, Significant at the 5% probability level, the remaining coefficients all significant at the 1% probability level

TABLE 12. Correlation matrix between F_3 performance and performance of derived F_4 and F_5 bulks and F_5 family mean for the selected entries of Cross II

Variable	1	2	3	4	5	6	7	8	9	10
1. Three-row plots (adjusted)	1.000	1.000	0.933	0.703	0.795	0.856	0.724	0.688	0.771	0.660
2. Three-row plots (unadjusted)		1.000	0.933	0.703	0.795	0.856	0.724	0.688	0.771	0.660
3. Hill plots			1.000	0.709	0.821	0.875	0.774	0.651	0.775	0.570
4. F_4 bulk Winnipeg				1.000	0.550*	0.842	0.692	0.444*	0.611	0.649
5. F_4 bulk Glenlea					1.000	0.914	0.698	0.767	0.803	0.449*
6. F_4 bulk combined locations						1.000	0.788	0.711	0.816	0.605
7. F_5 bulk Winnipeg							1.000	0.680	0.901	0.426†
8. F_5 bulk Glenlea								1.000	0.931	0.469*
9. F_5 bulk combined locations									1.000	0.491*
10. F_5 family mean										1.000

*Significant at the 5% probability level, the remaining coefficients significant at the 1% probability level.

†Coefficient not significant.

TABLE 13. Correlation matrix between F_3 performance and performance of derived F_4 and F_5 bulks and F_5 family mean for the selected entries of Cross III

Variable	1	2	3	4	5	6	7	8	9	10
1. Three-row plots (adjusted)	1.000	0.978**	0.886**	0.180	0.104	0.239	0.338	0.317	0.441	0.490*
2. Three-row plots (unadjusted)		1.000	0.858**	0.197	0.095	0.247	0.381	0.270	0.439	0.482*
3. Hill plots			1.000	0.224	0.142	0.306	0.406	0.294	0.471*	0.388
4. F_4 bulk Winnipeg				1.000	-0.273	0.661**	0.418	0.192	0.411	0.531*
5. F_4 bulk Glenlea					1.000	0.542*	-0.304	0.020	-0.194	0.092
6. F_4 bulk combined locations						1.000	0.129	0.184	0.210	0.535*
7. F_5 bulk Winnipeg							1.000	0.110	0.756**	0.006
8. F_5 bulk Glenlea								1.000	0.734**	0.286
9. F_5 bulk combined locations									1.000	0.193
10. F_5 family mean										1.000

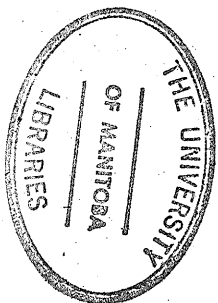*, ** Significant at the 5% and 1% probability levels respectively.

TABLE 14. Correlation matrix between F_3 performance and performance of derived F_4 and F_5 bulks and F_5 family mean for the selected entries of Cross IV

Variable	1	2	3	4	5	6	7	8	9	10
1. Three-row plots (adjusted	1.000	0.972**	0.842**	0.474*	0.250	0.442	0.535*	-0.151	0.440	0.186
2. Three-row plots (unadjusted)		1.000	0.859**	0.435	0.262	0.424	0.478*	-0.122	0.403	0.165
3. Hill plots			1.000	0.363	0.269	0.383	0.248	-0.199	0.100	-0.096
4. F_4 bulk Winnipeg				1.000	0.393	0.853**	0.730**	-0.150	0.645**	0.406
5. F_4 bulk Glenlea					1.000	0.815**	0.249	0.217	0.431	0.098
6. F_4 bulk combined locations						1.000	0.602**	0.027	0.650**	0.311
7. F_5 bulk Winnipeg							1.000	-0.436	0.700**	0.432
8. F_5 bulk Glenlea								1.000	0.337	0.269
9. F_5 bulk combined locations									1.000	0.665**
10. F_5 family mean										1.000

*, ** Significant at the 5% and 1% probability levels, respectively.

III and IV compared with Crosses I and II may be due to:

- the smaller yield range of the F_3 entries in three-row plots of Crosses III and IV compared with Crosses I and II

- reduced genetic variance in Crosses III and IV compared with Crosses I and II

- the precision of estimating the F_3 yield value and the yield values of F_4 and F_5 generations

- the precision of the various estimates would also be effected by genotype x environment and genotype x year interactions.

The method of selecting the F_3 entries, meant that the expectations for the intergeneration correlations would be high, as selection from the extreme ends of the range of the independent variable tends to reduce the variance of the regression coefficient, resulting in an improved correlation. The intergeneration correlation in Crosses I and II, where there was a wide yield range, were all highly significant ($P = 0.01$). In Crosses III and IV, where the yield range was much reduced, the strength of the intergeneration correlations declined, in some instances to non-significance. Error associated with estimating yield value of genotypes becomes increasingly important in determining the strength of intergeneration correlations as the yield range and genetic variance of the material being investigated decreases. The relative values of the genetic and environmental variances in these crosses results in lower heritability estimates. The effect of the reduced heritability on the intergeneration correlations can be seen using the relationship given by Falconer (1960), viz.

$$r_p = h_x h_y r_A$$

where r_p is the phenotypic correlation (in this instance the inter-generation correlation), h_x and h_y the heritability in the two generations and r_A the genetic correlation.

The yield performance of selected F_3 entries as derived F_4 and F_5 bulks was repeatable although conducted in a different season and sample of environments. Although the intergeneration correlations for two out of the four crosses investigated were generally not significant, reasons for the lack of correlation have been suggested. Given sufficient range and genetic variance the replicated yield tests conducted in the F_3 generation, the three-row plot yield test and the hill plot yield test, identified high yielding lines, and the performance of those lines was repeatable as derived F_4 and F_5 bulks grown in a different year and sample of environments.

The analysis of variance of the F_5 family means for each cross is summarised in Table 15. Significant differences (P = 0.01) between F_5 family means were obtained only for Crosses I and II. In Cross II there was significant variability between F_5 family means among those families rated high-yielding (P = 0.05) and low-yielding (P = 0.01) by the F_3 yield test. In Crosses I and II the difference between F_5 family means was due to the difference between families derived from high- and low-yielding F_3's (Table 15). F_5 families derived from high-yielding F_3's were significantly different from those derived from low-yielding F_3's in Crosses I, II and III (significant P = 0.01, P = 0.01 and P = 0.05, respectively), indicating that there was response to selection among F_5 families based on F_3 yield performance. In Cross IV there was no difference between F_5 families derived from

TABLE 15. Mean squares and their associated degrees of freedom of the F_5 family means for each cross

Source	Degrees of freedom	Cross I	Cross II	Cross III	Cross IV
F_5 families	20	317427.81**	278622.71**	108282.01	47993.65
Among F_5 families derived from high-yielding F_3's	9	254288.65	139498.81*	132355.40	43030.59
Among F_5 families derived from low-yielding F_3's	9	100749.61	212555.52**	37869.48	62289.18
Glenlea versus remaining F_5 families	1	1177.38	775411.83**	96453.85	107447.23
F_5 families derived from high-yielding F_3's versus those derived from low-yielding F_3's	1	3152034.60**	1628553.50**	536070.17*	5603.33
Blocks	2	1408766.42**	1742748.54**	266459.44*	80261.86
F_5 families x Blocks	40	121225.71	57930.09	74605.64	62181.85
Total	62	226050.28	183470.24	91657.82	58188.24

*, **, Significant at the 5% and 1% probability levels, respectively.

high- and low-yielding F_3's. The differences between F_5 family means in Cross II suggests that the F_5 lines should be tested within their F_3 derived family groups and between family selection prior to within family selection would be effective. In Crosses III and IV, the F_5 lines derived from different selected F_3's could have been grouped and tested in a common yield test. Although only four crosses were studied, it appears that as the estimate of genetic variance based on the F_3 yield test decreases differences between F_5 family means are no longer distinguishable. This apparent trend is of consequence in practical breeding programs, as it has a bearing on how the F_5 lines should be evaluated.

The pooled analysis of variance of the F_5 lines for each cross is summarised in Table 16. Significant differences ($P = 0.01$) existed between F_5 lines in F_5 families for each cross, suggesting there exists considerable variability between F_5 lines developed at random from selected F_3's. Cross II was the only cross in which the error variances were homogeneous, and the effect of the heterogeneity of the error variances on the differences between F_5 lines is unknown. The variability between F_5 lines is of consequence in a practical breeding program where an optimum number of F_5 lines to be derived from each selected F_3 must exist such that response to selection is maximised. Shebeski (1967) has stated that most plant breeders limit progress in their programs by evaluating too few F_5 lines. On theoretical considerations, Shebeski suggested that 80-100 lines should be evaluated to give a high probability of selecting the best line. The choice of the number of F_5 lines from each selected F_3 depends on the proportion of additive

TABLE 16. Mean squares and their associated degrees of freedom for
the pooled analysis of variance of the F_5 lines for each cross

Source	df	Cross I	Cross II	Cross III	Cross IV
F_5 lines in F_5 families	140	483240.72^{**}	511089.84^{**}	630874.37^{**}	378977.91^{**}
Error	280	247552.35	196989.18	141191.33	183504.78

**, Significant at the 1% probability level

genetic variance that is fixable by selection at that stage, the total

resources available to the breeder, the final objective of the program,

the maximisation of response to selection and the minimisation of the

coefficient of variation of expected response. The factors effecting

F_5 family size will be considered in the general discussion.

Intergeneration correlations between the F_3 yield test value and

F_5 family mean for each cross are given in Tables 11 to 14. The

intergeneration correlations between adjusted three-row plot yield

and F_5 family mean yield were significant for Crosses I, II (P = 0.01)

and III (P = 0.05). There was no significant correlation for Cross IV.

Least significant differences at the 0.05, 0.10 and 0.20 probability

levels for the mean of the cv. Glenlea family of entries were calculated

and used to determine the lines better than cv. Glenlea within each

cross. The number of lines for each cross superior to each least

significant difference are given in Table 17. In Crosses II and III,

all of the entries with mean yield greater than the upper confidence

intervals of cv. Glenlea were derived from high-yielding F_3 lines.

In CrossI, one of the high-yielding F_5 lines was derived from a low-

yielding F_3. In Cross IV, with the 5% least significant difference

of cv. Glenlea, three out of four of the high-yielding lines were from

low-yielding F_3's, with the 10% least significant difference, four

out of five were from low-yielding F_3's, and at the 20% least significant

difference, five out of eight were from low-yielding F_3's. Most of the

high-yielding lines derived from low-yielding F_3's belonged to the

one family (F_3 line number 40, see Table 6), which could have been

misclassified by the F_3 yield test. One of the high-yielding F_5 lines

TABLE 17. The number of lines superior in mean yield performance to
the least significant difference of cv. Glenlea for each cross

Percent probability level of the least significant difference	Cross I	Cross II	Cross III	Cross IV
5	21	4	4	4
10	25	6	5	5
20	37	6	8	8
Glenlea Mean Yield (g)	826	1096	1097	1027

derived from a low-yielding F_3 had one replicate with a spuriously high plot yield (almost twice the value of the other two replicates).

Crosses III and IV did not produce as many high-yielding lines as was expected, considering the F_3 yield test data (see Table 6). Sampling variability associated with the precision of estimating the true genotypic value for yield, genotype x environment and genotype x year interactions may be responsible for the relatively low number of high-yielding lines in these two crosses.

The number of lines better than cv. Glenlea realised from Cross I is surprising considering the F_3 performance of this Cross. Most likely the number is a reflection of the low mean yield of the cv. Glenlea family of entries. However, the number could result from, segregation in the F_4 generation, genotype x environment and genotype x year interactions, or a combination of all four of the above reasons. Only further testing of lines in an attempt to determine their true genetic value would elucidate the reason for the high number of lines superior to cv. Glenlea.

At the 5% least significant difference of the mean of cv. Glenlea, considering all four crosses, four lines out of thirty three originated from low-yielding F_3 lines. If only high-yielding F_3 lines were being retained, this would result in a loss of 12.1% of the highest yielding lines from the four crosses. At the 10% least significant difference, five lines out of forty one originated from low-yielding F_3 lines, which would result in a loss of 12.2% of the highest yielding lines if only the high-yielding F_3 lines were retained. At the 20% least significant difference, six lines out of fifty nine originated from

low-yielding lines, which would represent a loss of 10.2% of the highest-yielding lines, if only high-yielding F_3's were retained. Most of the high-yielding lines derived from low-yielding F_3's were derived from Cross IV. The performance of the F_5 bulks and F_5 family means did not substantiate the selection based on F_3 yield performance in Cross IV, and reasons have already been suggested for the results observed with this cross. It should be noted that lines superior to the 20% least significant difference of cv. Glenlea, represent yield advances over cv. Glenlea of at least, 13.6%, 4.2%, 10.4% and 6.4% for Crosses I to IV, respectively.

EXPERIMENT II

The objective of this experiment was to assess the relative importance of the precision of the estimate of yield and genotype x year interactions on the strength of intergeneration correlations by comparing intergeneration correlations obtained from replicated yield tests conducted in separate years with those obtained from unreplicated yield tests conducted in the same year.

Materials and Methods

Residual F_3 seed of the F_3 yield test, and seed of the derived F_4 and F_5 bulks of each of the ten high- and ten low-yielding entries selected from each cross in Experiment I were grown as single replicate entries in a completely randomised experiment, one for each cross, with a control plot of cv. Glenlea adjacent to each entry. Each completely randomised experiment contained sixty entries, the ten high- and low-yielding selections for each of the F_3, F_4 and F_5 generations. The three-row x 3 m length plots were planted on summer fallowed land at the University of Manitoba on May 3rd (CrossesII and III) and May 4th (Crosses I and IV),1976. Replicated yield data of the same entries was obtained from the replicated F_3 three-row yield test grown in 1975 (means adjusted for intra-block error), and from the F_4 and F_5 bulk yield tests grown in 1976. The replicated F_4 and F_5 bulk yield tests were planted adjacent to the single replicate tests.

Yield values considered were (a) the mean of the three replicates from the replicated tests, (b) the single replicate yield value and (c) the single replicate yield value adjusted to a percentage of its adjacent control plot as suggested by Shebeski (1967) and Briggs and Shebeski (1968).

Simple product-moment correlation matrices between the replicated, unreplicated and adjusted unreplicated yield values were constructed for each cross. Significance between correlation coefficients were tested using the "t" distribution test statistic based on Fisher's Z-transformation.

Results and Discussion

The single replicate yield test was conducted in a nursery identical to that used by Briggs and Shebeski (1968). Correlations between the control plots at varying distances apart were calculated serially along a range using each plot in turn as a dependent and then as an independent variable. The correlations between the control plots were 0.635, 0.558, 0.379, 0.241, 0.131 and -0.023 at distances of 0.9, 2.7, 5.4, 8.1, 10.8 and 13.5 m apart, respectively. The relationship agrees with that reported by other researchers (for example Wiebe, 1935; Briggs and Shebeski, 1968). The correlations depend on the assumption that adjacent or contiguous plots are more likely to be alike in yield than plots further apart. Adjustment of single replicate yield values to a percentage of their adjacent control plot is done to adjust for soil heterogeneity (Briggs and Shebeski, 1968). The correlation between the adjacent control plots (r = 0.635, significant P = 0.01) suggests that improved response to selection could be expected by adjusting

the yields of entries to a percentage of their adjacent control plot.

The intergeneration correlations for each cross are given in Table 18. In Cross I there was no difference between the intergeneration correlations based on the unreplicated and adjusted unreplicated yield values for F_3-F_4, F_3-F_5 or F_4-F_5. However, in the case of the F_3-F_5 comparison, the adjustment produced a significant intergeneration correlation. In Cross II, the adjustment procedure produced a significant F_3-F_4 intergeneration correlation that was significantly different from the coefficient based on the unreplicated yield values. In the remaining comparisons, F_3-F_5, and F_4-F_5, the adjustment procedure was ineffective. In Cross III, the adjustment procedure was ineffective. In Cross IV, the adjustment procedure produced a significant negative correlation between the F_4 and F_5 yield values.

In the situation examined, where all plots of the different generations were grown in the same season, adjustment to a percentage of the adjacent control plot was generally ineffective, as the adjustment failed to improve the intergeneration correlations in fifteen of sixteen cases. This is contrary to the findings of De Pauw and Shebeski (1973) who found that adjustment to a percentage of the adjacent control resulted in significantly higher F_3 line-F_5 family mean correlations. When the adjustment procedure is ineffective it cannot be expected to improve response to selection.

The F_4-F_5 intergeneration correlations (Table 19) are an indicator of the role of replication in increasing the precision of the estimate of genotypic value for yield. Both the replicated and unreplicated tests were planted on the same field on the same days. For

TABLE 18. Intergeneration correlations for each cross based on unreplicated and adjusted unreplicated yield values

Basis of comparison	Cross I	Cross II	Cross III	Cross IV
Unreplicated F_3 - Unreplicated F_4	0.775**	-0.199 a†	0.254	0.306
Unreplicated F_3, % control plot - Unreplicated F_4, % control plot	0.628**	0.531*b	0.034	0.417
Unreplicated F_3 - Unreplicated F_5	0.354	0.541*	0.384	0.101
Unreplicated F_3, % control plot - Unreplicated F_5, % control plot	0.504*	0.499*	-0.037	0.001
Unreplicated F_4 - Unreplicated F_5	0.312	0.077	-0.057	-0.047
Unreplicated F_4, % control plot - Unreplicated F_5, % control plot	0.248	0.404	-0.232	-0.526*

*, **, Correlation coefficients significant at the 5% and 1% probability levels, respectively.

† The pair of correlation coefficients followed by different letters are significantly different at the 5% probability level. The remaining pairs of coefficients are not significantly different.

TABLE 19. F_4-F_5 intergeneration correlations for each cross based on replicated, unreplicated and adjusted unreplicated yield values

Basis of comparison	Cross I	Cross II	Cross III	Cross IV
Replicated F_4 - Replicated F_5	0.904**a†	0.692**a	0.418 a	0.730**a
Unreplicated F_4 - Unreplicated F_5	0.312 b	0.077 b	-0.057 ab	-0.047 b
Unreplicated F_4, % control plot - Unreplicated F_5, % control plot	0.248 b	0.404 ab	-0.232 b	-0.526* b

*,**, Correlation coefficients significant at the 5% and 1% probability levels, respectively.

† Correlation coefficients followed by different letters are significantly different at the 5% probability level.

Cross I the intergeneration correlation based on replicated yield values was significantly different from those based on the unreplicated and adjusted unreplicated yield values. For Cross II, the correlation based on the replicated values was different from the coefficient for the unreplicated values, but not different from that for the adjusted unreplicated values. The adjustment procedure improved the correlation but not sufficiently for significance to be obtained. For Cross III, none of the intergeneration correlations were significant. However, adjustment of the unreplicated yield values resulted in the correlations between the replicated and adjusted unreplicated comparisons being significantly different. The adjustment procedure adjusted the F_4 and F_5 yield values such that a negative correlation between the replicated values was significant, whereas that based on the unreplicated values was not significant. Furthermore, the two coefficients were significantly different. Adjustment of the unreplicated yield values resulted in the production of a significant negative intergeneration correlation. The correlation coefficients for the replicated and adjusted unreplicated comparisons were significantly different, but there was no difference between the coefficients of the unreplicated and adjusted unreplicated comparisons. In this case, the adjustment of the F_4 and F_5 yield values resulted in the production of a negative intergeneration correlation that was significantly different from that obtained with replicated testing. Clearly, the adjustment was producing spurious yield results.

The F_3-F_4 and F_3-F_5 intergeneration correlations based on replicated yield values obtained in different growing seasons is given in

Table 20. The correlations were significant for Crosses I and II

(P = 0.01) and Cross IV (P = 0.05). In the crosses which exhibited

a wide yield range and genetic variance in the replicated F_3 yield

test (Crosses I and II), the intergeneration correlations between

the replicated yield values were highly significant (P = 0.01). As

the yield range and genetic variance declined so did the strength of

the intergeneration correlations.

The general lack of significant F_3-F_4 and F_3-F_5 intergeneration

correlations between the yield values of unreplicated entries obtained

in the same growing season (Table 18) compared with significant corre-

lations between the replicated yield values obtained in different

growing seasons suggests that the error associated with estimating

the yield value of a genotype with a single replicate may be more

important in determining the strength of intergeneration correlations

than genotype x year effects.

Observation of the intergeneration correlations, especially the

F_4-F_5 intergeneration comparisons in which there is no year effect to

take into account, shows clearly the importance of replication in

increasing the precision of the estimate of genotypic yield value.

In all cases the correlations based on the replicated yield values were

stronger than those based on unreplicated and adjusted unreplicated

yield values, and in some instances the difference between correlation

coefficients is significant. The failure of De Pauw and Shebeski (1973)

to obtain intergeneration correlations in which the regression relation-

ship explained at least 50% of the variability in the dependent variable

can in part be attributed to the lack of precision associated with

TABLE 20. F_3-F_4 and F_3-F_5 intergeneration correlations for each cross based on replicated yield values obtained in different growing seasons.

Basis of comparison	Cross I	Cross II	Cross III	Cross IV
Replicated F_3-Replicated F_4	0.818**	0.703**	0.180	0.474*
Replicated F_3-Replicated F_5	0.845**	0.724**	0.338	0.535*

*,**, Significant at the 5% and 1% probability levels, respectively.

determining the yield values in unreplicated tests in which the yield of each entry was adjusted based on the performance of its adjacent control plot.

Adjustment procedures could only be considered as a replacement for replication if they give the same information as to the yield value of a genotype or give improved intergeneration correlations. Clearly, this is not always the case for the adjustment procedure considered in this study. Adjustment to a percentage of an adjacent control plot requires that one-third of the total nursery area be occupied by control plots. Replication increases the precision of the estimate of the yield value of a genotype, and provides a standard error of the estimate. In a practical breeding situation where the total number of plots in the nursery is fixed by available resources, it would be logical to replicate fewer entries than to utilise one-third of the nursery with control plots.

GENERAL DISCUSSION

The effectiveness of a breeding method is measured by the performance of lines derived by the method. The effectiveness of F_3 yield testing was measured by the performance of F_4 and F_5 bulks or lines derived from selected F_3's. The correlations between the yield values or rankings in the different generations form the basis of evaluation of the worthiness of the F_3 yield test. High intergeneration correlations imply that performance of selected lines will persist into subsequent generations. It is the degree of certainty with which the performance of derived lines can be predicted that is basic to the application of early generation testing. In addition, resource requirements must be considered in judging the effectiveness of early generation yield testing. Some researchers have suggested that costly yield evaluation should be delayed until the F_5 or F_6 generations when the lines to be evaluated are homozygous or near homozygous.

A number of factors can affect the comparison of different breeding methods. The magnitude of the phenotypic and genetic variances, which are a characteristic of the starting population can have a considerable effect on the effectiveness of early generation selection. Greater response to selection can be expected from selection in populations having greater phenotypic and genetic variance. In the present study, significant responses to selection were observed in Crosses I and II

which had greater genetic variance than either Crosses III or IV.

Although response to selection will be greater in populations with larger genetic variance, the highest yielding lines may be derived from populations having less genetic variance but a higher mean yield to start with. As populations approach the upper genetic limit for yield, genetic variance decreases as does heritability and response to selection. Nevertheless, these populations possess the greatest potential from the breeding standpoint. Perhaps the absolute yield values of lines developed by different breeding methods may provide the single most effective criterion for determining the effectiveness of different methods. In this study, the F_5 lines of highest yield were from Cross III, which had the highest yielding F_3 lines and the highest F_3 population mean yield of the four crosses.

The fact that the highest yielding lines of the four crosses were derived from a cross with low genetic variance but a high mean yield has implications to the debate over the use of wide and narrow crosses. In terms of short-term breeding programs, it may be more important to choose populations whose mean is closest to the desired goal rather than concentrating on populations with large genetic variances. Within limits, a cross of high x high may be expected to be more productive than a cross of high x low.

In comparing selection methods it should be remembered that the results of selection experiments will vary even if the same material and procedures are used (Falconer, 1960). Variability can result from random sampling of the F_3 lines to be tested, from conditional sampling of the F_3 lines during the actual selection phase and from random

sampling of the environmental and genotype x environment interaction effects during the F_3 test and in the final evaluation of selected lines.

In this study the selection intensity applied to the F_3 populations was within the range suggested by Baker (1966, 1971) and Soller and Genizi (1967) to minimise the coefficient of variation of response to selection. Previous studies, Briggs and Shebeski (1971), (their 1966 and 1967 F_3 yield nurseries), De Pauw and Shebeski (1973) and Seitzer (1974) have been conducted with very high selection intensities, so the variability of response would be expected to be quite high. To avoid this problem, selection intensity was set at 13% in the present study.

In this study response to early generation selection was analysed in its two components - the selection of high-yielding genotypes in early generations and the persistence of their yield performance into later generations. Results confirmed that replicated testing of F_3 lines was capable of identifying F_3 lines that differ in yielding ability. However, these differences persisted over generations in only two of the four crosses. Differences observed in the F_3 yield test would be due in part to genetic differences that will persist over generations and in part to genetic differences that are expressed only under the environmental conditions peculiar to the F_3 yield test. It would appear in this study that differences of the latter type accounted for most of the differences among F_3 lines in Crosses III and IV. This raises the question of whether or not genotype x environment interaction becomes such an important masking effect in crosses

showing little genetic variation that early generation selection will have little or any effect in such populations.

The performance of the derived F_4 and F_5 bulks and the mean of the family of F_5 lines verified the yield classifications (high or low) based on the F_3 yield tests in Crosses I and II. In some cases, the differences persisted in Crosses III and IV. In general, the highest-yielding F_5 lines were derived from high-yielding F_3's, which is in agreement with the findings of Briggs and Shebeski (1971). In Cross IV, there is a real possibility that the F_3 yield test misclassified one F_3 line. Cross IV had the narrowest yield range and least genetic variance of the four crosses examined. The effect of reduced yield range and genetic variance combined with errors of determination of yield value, genotype x environment and genotype x year effects were probably responsible for the observations within Cross IV.

The observed response to selection among F_3 lines was significantly less than predicted on the basis of the F_3 yield data in all four crosses. This probably resulted from the estimates of heritability obtained from the F_3 yield data being too high, due to components of variation due to genotype x environment and genotype x year effects being confounded with the estimate of genetic variance. To overcome this, replicated F_3 yield testing at a number of locations within and over years would be required. This would be possible utilizing hill plots for the F_3 yield tests. However, it may be more practical and beneficial to the plant breeder to acknowledge that the heritability estimates and the predicted response are biased upwards and divert the resources to evaluation of more F_3 and F_5 lines.

The role of replication in improving the strength of intergeneration correlations was evident. The comparison of single replicate yield tests where the F_3 line, F_4 and F_5 bulks were grown in the one season, with the replicated tests where the F_3 test was grown in a different season to the F_4 and F_5 bulks revealed that errors associated with determining the yield value of a genotype using a single replicate value have a profound effect on the values of intergeneration correlations. The use of a control plot adjacent to each entry to adjust for the effects of soil heterogeneity as suggested by Shebeski (1967) and practised by Briggs and Shebeski (1971), De Pauw and Shebeski (1973) and Seitzer (1974) did not significantly improve the intergeneration correlations. The lower values for intergeneration correlations reported by Briggs and Shebeski (1971) for the lines derived from the 1966 and 1967 yield tests, and De Pauw and Shebeski (1973) are in part a result of the use of only one replicate to estimate genotypic yield value and the effect of yield range and genetic variance on the expectations of the intergeneration correlations.

Two methods of replicated F_3 yield testing (three-row plots and hill plots) were evaluated for their ability to distinguish differences between genotypes. Hill plots would be suitable for early generation yield testing where seed or land availability were limited. Three-row plots were considered superior to hill plots because they required fewer replications to estimate yield differences between genotypes and they could be handled with a totally mechanised field operation compared with hand planting and harvesting of hill plots.

The modification of the pedigree breeding system used in this study is essentially a two-stage selection program where lines selected

in the first stage, F_3 lines, segregate in the F_4 generation and are available for further evaluation in the second stage as F_5 lines. Shebeski (1967) suggested that most plant breeders limited progress in their programs by developing too few F_5 lines from each selected F_3, and suggested therefore, that as many as 100 F_5 lines should be evaluated from each selected F_3 in order to give the breeders a chance of recovering the "best" lines. This proposal requires that relatively few F_3 lines be selected in the first stage of selection. Shebeski (1967) proposed that the best 10 F_3 lines be selected from 1000 tested, a selection intensity of 0.1 percent. The choice of a much lower selection intensity in the present study was made for two reasons. On a theoretical basis Baker (1966, 1971) and Hill (1974) have shown that response to selection will be more variable under more intense selection. Furthermore, Soller and Genizi (1967) and Baker (1971) have shown that variability of response, when expressed as a percent of average response, is least when selection intensities are between 10 and 20 percent.

On a more practical basis, it was felt that the experiment should be designed with maximum probability of detecting response, if early generation selection was indeed effective. Only 78 F_3 lines were studied in each cross in order that they could be replicated. Of these, ten high-yielding and ten low-yielding were selected. In this way, 19 degrees of freedom were available for any test of differences among F_4 and F_5 bulks and F_5 family means. With more intense selection, fewer degrees of freedom would be available and a larger F ratio would be required to establish significance.

Shebeski (1967) suggested that 100 F_5 lines should be sampled in order to obtain a representative sample of all possible F_5 lines that could be derived from a single F_3 line. While it is true that sampling variation will result in the exclusion of good F_5 lines in some families and poor F_5 lines in others, there is no reason to suspect that the sampling process will be biased towards the exclusion of one type or the other. Certainly, if each F_3 family produced F_5 lines distributed with a mean and variance common to all families, the distribution of one F_5 line from each of 100 families would be very nearly the same as the distribution of 100 F_5 lines taken from one such family. The more limited sampling of a greater number of F_3 lines seems necessary to minimise the undesirable effects of unavoidable misclassification of F_3 yield potential as appears to have occurred with Cross IV in the present study.

Most plant breeding programs operate on fixed resources, and it is resource availability that determines the amount of material that can be evaluated. With fixed resources, the cost of growing, maintaining and harvesting each plot determines the total number of plots that can be grown. The breeder must decide how many lines, and at what level of replication should be assigned to each stage of a two-stage selection program so that total response to selection and response per unit cost are maximised. In most cases the objective of the breeding program is selection of a number of lines for further evaluation at different locations over seasons, leading to eventual variety release.

In trying to develop a strategy for the optimum allocation of resources in a two-stage selection program, the idea that the coefficient

of variability of response to selection should be minimised in both

stages, and the idea that for a given amount of resource, there is an

optimum amount of replication that maximises response to selection

have both been accepted. Baker (1966, 1971) considered the coefficient

of variation of response to single trait selection and concluded that

it was minimum when the proportion selected was between 10 and 30

percent. Similarly, Soller and Genizi (1967) found that estimates

of realised heritability were expected to have the smallest sampling

variances when the selected proportion was about 10 percent. Minimi-

sation of the coefficient of variation of expected response is critical

in two-stage selection where the consequences of sampling error in

the first stage are manifested in the second stage. The proportion

of lines selected at each stage needs to be sufficiently large that

the selected group has a "high" probability of containing the "best"

lines. This probability will depend on the degree of replication,

the percent difference in the trait that is required and the number

of lines being evaluated (Sokal and Rohlf, 1969). Sampling variability

obviously affects the probability that the best lines selected at

the end of the second stage are in fact the best lines. Consequently,

the proportion of lines selected in each stage must be in the range

that minimises the coefficient of variation of expected response.

When the breeder sets the number of lines to be selected in the second

stage for further evaluation over locations and seasons, the number

of lines to be tested in the second stage is set in order to minimise

the coefficient of variation of expected response.

Baker (see Townley-Smith *et al.*, 1973) has determined the number

of plots (replicates) of each genotype required to maximise the

performance of a given number of selected lines. Results depend on the heritability of the trait being considered and on the total number of plots that can be handled. For example, if 1000 plots can be grown, and ten lines are to be selected, then the proportion selected of the total number of plots grown is 0.01. If the heritability on a single plot basis for the trait is 0.3, then four replications of each of 250 lines should be grown if the performance of the lines to be selected is to be maximised. That an optimum amount of replication exists relates to the fact that increasing replication increases heritability (and hence response to selection) but necessitates a reduction in the number of lines that can be tested with fixed resources. This reduction in number of lines tested results in a diminished selection differential and consequently less response to selection.

In a two-stage program where l_o F_3 lines and l_1 F_5 lines are replicated n_o and n_1 times in each of the first and second stages, respectively, then the breeders' total operating cost, C, depends on the number of lines and replications in each stage, the cost of creating lines for the second stage and the cost, c, of growing, maintaining and harvesting each plot in the program. The total operating, C, can be expressed as,

$$C = cn_o l_o + cp_o l_o + cn_1 l_1$$

where p_o is the proportion of lines selected in the first stage. It can be readily seen that the total number of plots that can be handled in any program is determined by the total resources, C, and the cost per plot, c. The number of plots that have to be grown to produce material for the second stage is $p_o l_o$, and $l_1 = kp_o l_o$, where k is the number of selections, F_5 lines, developed from each of the $p_o l_o$ lines,

the selected F_3 lines.

Utilising the above relationship, values for the number of F_5 lines from each selected F_3 line have been computed for a hypothetical case where the maximum number of plots, C/c, that the breeder can grow is 1000 plots, and after the two stages of selection the best 10 lines are required for further evaluation over locations and seasons (Table 21). The actual numerical value of C/c is immaterial as the proportionate allocation of lines to each stage is determined by the values of l_0, p_0, n_0 and n_1, and the factors determining their values have already been considered. It can be seen from Table 21 that the number of F_5 lines developed from each selected F_3 in this study, eight F_5 lines, was adequate to maximise expected response to selection and to minimise the coefficient of variation of expected response to selection.

It can be generally concluded that the results obtained in this study testify to the effectiveness of early generation testing and indicate that replication should be an integral part of any early generation testing procedure. Alternatives to replication largely resulted from studies that indicated the general ineffectiveness of selection for yield in the F_2 generation, consideration of the problems of intra- and intergenotypic competition and limitations of seed quantity. However, there is no evidence to suggest that an F_3 yield test of a random sample of large F_2 plants would be detrimental to progress in selecting for yield. In fact the results of this study indicate that in those crosses with considerable genetic variance in the F_3 generation considerable progress in yield was made, and in

TABLE 21. The number of lines in the first stage of selection (l_o), for varying levels of replication, n_o and n_1 in each of the two stages respectively when $l_1 = 100$ and the proportion selected in each stage is 10% ($p_o = p_1 = 0.10$). The number of selections, k, from each of the $p_o l_o$ lines selected in stage I is given for the corresponding n_1, n_o, l_o and l_1 values

n_1	$n_o = 1$		$n_o = 2$		$n_o = 3$		$n_o = 4$		$n_o = 5$	
	l_o	k	l_o	k	l_o	k	l_o	k	l_o	k
1	818	1	428	2	290	3	219	5	176	6
2	727	1	380	3	258	4	195	5	156	6
3	636	1	333	3	225	4	170	6	137	7
4	545	2	285	3	193	5	146	7	117	8
5	454	2	238	4	161	6	121	8	98	10

those crosses with less genetic variance high-yielding F_5 lines were recovered, utilising a random sample of only seventy-eight F_2 plants. It is critical to remember, however, that no a priori knowledge of F_3 population mean yield or estimate of genetic variance exists. This information can only be obtained from a replicated F_3 yield test.

To make best use of replicated early generation yield testing in plant breeding practice, the plant breeder requires the facilities to produce large F_2 and F_4 plants, so that seed quantity will not restrict the design of the F_3 yield test. Use of irrigation and high-fertility conditions would ensure that seed quantity would not be a limitation. Such conditions would also facilitate disease screening, so that undesirable susceptible genotypes could be discarded. A random sample of the remaining agronomically acceptable genotypes would form the basis of the entries for the replicated yield tests. The breeding method proposed by Shebeski (1967), can be modified to reflect the results of this study. Shebeski's original proposal incorporating the results of this study is outlined below.

Modification of the pedigree breeding method for breeding for yield. (Modified* from Shebeski, 1967).

Year 1 (Spring)   –   Sufficient crosses of the parents possessing between them the desired qualitative factors are made in the greenhouse.

Year 1 (Summer) –   The F_1's are grown under field or greenhouse conditions. If sufficient crossed seed has been produced to permit a replicated yield trial of

*Any modifications from Shebeski's original proposal are in italics.

F_1's and their parents only the crosses with the best yield and quality characteristics should be retained.

Year 1-2 (Winter) — Sufficiently large numbers of F_2 plants to permit selection for stem and leaf rust resistant, stronger-strawed plants are grown in Mexico. *The plants are spaced 30-40 cm apart in pairs of rows 11 m long and 30 cm apart with 60 cm between pairs. A random sample of 80-100 resistant, stronger-strawed plants selected for each cross.*

Year 2 (Summer) — *Yield test the selected F_2 plants in replicated trials using either hill plots or three metre length three-row plots.* Rows are spaced 15 cm apart and 50 seeds are planted per metre of row. Plots are planted with 90-100 cm between the centre rows to minimise interplot competition. *All plots are harvested for the estimation of yield. The lines are ranked in order of their mean yields and compared with the yield of the control cultivar. Select the top-yielding 10% of lines only from crosses that produce F_3 lines superior to the control cultivar.*

Year 2-3 (Winter) — *Random F_4 populations from each of the selected 10% of F_3 lines are grown in Mexico as described for the F_2. Eight to ten random selections*

*(F$_5$ lines) derived from among the rust resistant,
stronger-strawed plants for each selected F$_3$
line.*

Year 3 (Summer)   –   *Replicated F$_5$ yield trials of the 8-10 random
selections derived from each selected F$_3$ line.
Rank F$_5$ lines on their mean yields. Select the
top-yielding 10% of lines superior to the yield
of the control cultivar.* If the top yielding
lines are not sufficiently uniform to be bulked
as a potential new strain their respective F$_6$
populations could be grown in Mexico as described
for the F$_4$.

Year 3-4 (Winter)   –   Each superior F$_5$ line that was considered uniform
could be increased in Mexico.

Year 4 (Summer)   –   Extensive regional trials to verify yielding
potential and select for wide range adaptability.

Year 5 (Summer)   –   The top lines from the previous year's test
entered in the Co-operative tests.

CONCLUSIONS

1. Replicated F_3 yield testing with three-row plots and hill plots identifies high yielding lines.

2. Considerable genetic variance for yield was detected in the F_3 generation from a sample of 78 random large F_2 plants.

3. Significant genetic correlations were obtained between F_3 line performance in hill plots and three-row plots. Three-row plots were preferable to hill plots because:

    - they were more efficient for selection

    - less replication was required to estimate yield differences between genotypes

    - they had lower coefficients of variability

    - they could be machine planted and harvested compared with a hand-planting and harvesting operation for hill plots

    Hill plots were suitable for early generation selection and require less seed and land than three-row plots.

4. F_4 and F_5 bulks derived from selected F_3's showed that the F_3 performance rating is repeatable within the limits of:

    - sampling variability

    - the precision of estimating the yield value in each generation

    - the range of yield and genetic variance for yield of the cross

5. The mean performance of F_5 families developed from selected F_3's indicated that the selection in the F_3 yield test was effective in Crosses I and II (intergeneration correlations significant $P = 0.01$) and in Cross III (intergeneration correlation significant $P = 0.05$).

6. In Crosses II and III, all of the F_5 lines superior to the cv. Glenlea in yield were derived from high-yielding F_3's. In Cross I, one high-yielding F_5 line was derived from a low-yielding F_3. In Cross IV, most of the high-yielding F_5 lines were derived from one of the low-yielding F_3's.

7. Errors of misclassification based on F_3 performance occur. Of those lines superior to the 20% least significant difference of cv. Glenlea, only 10.2% were derived from low-yielding F_3's. At this level, the F_5 lines were at least 13.6%, 4.2%, 10.4% and 6.4% superior to cv. Glenlea for Crosses I to IV, respectively.

8. In general, high estimates of heritability were obtained. Reasons for the high estimates were:

   - the wide yield range and genetic variance in Crosses I and II

   - the use of replication

   - the use of two test locations for the F_4 and F_5 bulks

   - the method of selection of the genotypes

9. Observed responses to selection of the F_4 and F_5 bulks and the F_5 family means were less than the predicted responses.

10. Yield range and genetic variance were important in determining the strength of intergeneration correlations.

11. Replication improved the strength of intergeneration correlations.

12. Genotype x year effects may not be as important in determining the strength of intergeneration correlations as the precision of the estimate of yield value (i.e. the level of replication).

13. Adjustment of the yield of entries in single replicate yield tests to a percentage of their adjacent control plot failed to improve intergeneration correlations.

14. Growing spaced plants in the F_2 and F_4 winter nurseries in the absence of competition seemingly did not affect the performance of the randomly derived selections in the F_3 and F_5 yield tests where there is interplant competition between plants within the plot.

15. The modified pedigree breeding method described by Shebeski (1967) was modified to allow for replicated yield testing in the F_3 and F_5 generations.

LITERATURE CITED

Allard, R.W. 1960. Principles of Plant Breeding. John Wiley and
Sons, New York.

Baker, R.J. 1960. Predicted variance of response to selection.
Ph.D. Thesis, University of Minnesota, St. Paul, Minn.

Baker, R.J. 1968. Effectiveness of control plots. Cereal News
(Research Branch, Agriculture Canada). 13: 26-27.

Baker, R.J. 1971. Theoretical variance of response to modified
pedigree selection. Can. J. Pl. Sci. 51: 463-468.

Baker, R.J. 1975. Letter to the Editor, Can. J. Pl. Sci. 55: 355.

Baker, R.J., Bendelow, V.M. and Kaufmann,M.L. 1968. Inheritance
of and interrelationships among yield and several quality traits
in common wheat. Crop Sci. 8: 725-729.

Baker, R.J. and Leisle, D. 1970. Comparison of hill and rod row
plots in common and durum wheats. Crop Sci. 10: 581-583.

Baker, R.J. and McKenzie, R.I.H. 1967. Use of control plots in
yield trials. Crop Sci. 7: 335-337.

Bell, G.D.M. 1963. Breeding techniques - general techniques. In
Barley Genetics I, Proc. 1st Int. Barley Gen. Symp. Wageningen,
pp. 285-302.

Bliss, F.A. 1976. Use of hill plots for genetic and breeding
studies of bean. J. Amer. Soc. Hort. Sci. 101: 77-80.

Boerma, H.R. and Cooper, R.L. 1975. Comparison of three selection
procedures for yield in soybeans. Crop Sci. 15: 225-229.

Bonnett, O.T. and Bever, W.M. 1947. Head-hill method of planting
head selections in small grains. J. Am. Soc. Agron. 39: 442-445.

Borlaug, N.E. 1968. Wheat breeding and its impact on world food
supply. In, Finlay, K.W. and Shepherd, K.W. (ed), Proc. 3rd
Int. Wheat Genet. Symp. (Aust. Acad. Sci, Canberra): 1-36.

Briggs, F.N. and Knowles, P.F. 1967. Introduction to Plant Breeding.
Reinhold Publishing Corporation, New York.

Briggs, K.G. and Shebeski, L.H. 1968. Implications concerning the frequency of control plots in wheat breeding nurseries. Can. J. Pl. Sci. 48: 149-153.

Briggs, K.G. and Shebeski, L.H. 1971. Early generation selection for yield and breadmaking quality of hard red spring wheat (*Triticum aestivum* L. em Thell.). Euphytica 20: 453-463.

Cochran, W.G. and Cox, Gertrude M. 1950. Experimental Designs. John Wiley and Sons, Inc., New York.

Comstock, R.E. and Moll, R.H. 1963. Genotype – environment interactions. pp. 164-196. In, Hanson, W.D. and Robinson, H.F. (ed). Statistical Genetics and Plant Breeding. NAS-NRC 982, Washington, D.C.

Coyne, D.P. 1968. Correlation, heritability and selection of yield components in field beans, *Phaseolus vulgaris* L. Proc. Am. Soc. hort. Sci. 93: 388-396.

Davis, W.H., Middleton, G.K. and Hebert, T.T. 1961. Inheritance of protein, texture and yield in wheat. Crop Sci. 1: 235-238.

De Pauw, R.M. and Shebeski, L.H. 1973. An evaluation of an early generation yield testing procedure in *Triticum aestivum*. Can. J. Pl. Sci. 53: 465-470.

Falconer, D.S. 1960. Introduction to Quantitative Genetics. The Ronald Press Co., New York.

Fasoulas, A. 1973. A new approach to breeding superior yielding varieties. Dept. of Genetics and Plant Breeding, Aristotelian Univ. of Thessaloniki, Greece. Publ. No. 3.

Fasoulas, A. 1976. Principles and methods of plant breeding. Dept. of Genetics and Plant Breeding, Aristotelian University of Thessaloniki, Greece. Publ. No. 6.

Fasoulas, A. and Tsaftaris, A. 1975. An integrated approach to plant breeing and field experimentation. Dept. of Genetics and Plant Breeding, Aristotelian University of Thessaloniki, Greece. Publ. No. 5.

Frey, K.J. 1965. The utility of hill plots in oat research. Euphytica 14: 196-208.

Hafez, A.G., Khadr, F.H. and Kassem , A.A. 1976. Effect of replication, year and location on quantitative statistics of wheat. Cereal Research Communications 4: 347-354.

Hamblin, J. and Donald, C.M. 1974. The relationships between plant form, competitive ability and grain yield in a barley crop. Euphytica 23: 535-542.

Hanson, W.D. 1963. Heritability. pp. 125-140. In, Hanson, W.D. and Robinson, H.F. (ed). Statistical Genetics and Plant Breeding. NAS-NRC 982, Washington, D.C.

Hill, W.G. 1974. Variability of response to selection in genetic experiments. Biometrics 30: 363-366.

Jellum, M.D., Brown, C.M. and Seif, R.D. 1963. Hill and row plot comparison for yield of oats. Crop Sci. 3: 194-196.

Jensen, N.F. and Robson, D.S. 1969. Miniature plots for cereal testing. Crop Sci. 9: 288-289.

Knott, D.R. 1972. Effects of selection for F_2 plant yield on subsequent generations in wheat. Can. J. Pl. Sci. 52: 721-726.

Knott, D.R. and Kumar, J. 1975. Comparison of early generation yield testing and a single seed descent procedure in wheat breeding. Crop Sci. 15: 295-299.

McGinnis, R.C. and Shebeski, L.H. 1968. The reliability of single plant selection for yield in the F_2. In, Finlay, K.W. and Shepherd, K.W. (ed). Proc. 3rd Int. Wheat Genet Symp. (Aust. Acad. Sci., Canberra): 410-415.

MacKey, J. 1963. Autogamous plant breeding based on already highbred material. In, Åkerberg, E. and Hagberg, A. (ed). Recent Plant Breeding Research, Svalof 1946-1961, Stockholm.

Nickell, C.D. and Grafius, J.E. 1969. Analysis of a negative response to selection for high yield in winter barley, Hordeum vulgare L. Crop Sci. 9: 447-451.

Pesek, J. and Baker, R.J. 1971. Comparison of predicted and observed responses to selection for yield in wheat. Can. J. Pl. Sci. 51: 187-192.

Rasmusson, D.C. and Glass, R.L. 1967. Estimates of genetic and environmental variability in barley. Crop Sci. 7: 185-188.

Ross, W.M. and Miller, J.D. 1955. A comparison of hill and conventional yield tests using oats and spring barley. Agron. J. 47: 253-255.

Schutz, W.M. and Brim, C.A. 1967. Inter-genotypic competition in soybeans. I. Evaluation of effects and proposed field plot design. Crop Sci. 7: 371-376.

Seif, E., Lind, Bronwyn, L. and Martin, R.H. 1974. An evaluation of control plot technique for testing cereal yields in Central and Southern New South Wales. J. Aust. Inst. agric. Sci. 40: 69-71.

Seitzer, J.F.   1974.   Yield gains in wheat by three methods of selection.
    Ph.D. Thesis, University of Manitoba.

Shebeski, L.H.   1967.   Wheat and Breeding.   In, K.F. Nielsen (ed)
    Proc. Can. Centennial Wheat Symp.   Modern Press, Saskatoon.
    pp. 253-272.

Skorda, E.A.   1973.   Increasing the efficiency of selection for F_2
    plant yield by reducing environmental variability, In, Sears, E.R.
    and Sears, L.M.S. (ed).   Proc. 4th Int. Wheat Genet. Symp.
    Agric. Expt. Station, Univ. of Missouri: pp. 595-600.

Sneep, J.   1977.   Selection for yield in early generation of self-
    fertilising crops.   Euphytica 26: 27-30.

Sokal, R.R. and Rohlf, F.J.   1969.   Biometry.   W.H. Freeman and
    Co.   San Francisco.

Soller, M. and Genizi, A.   1967.   Optimum experimental design for
    realised heritability estimates.   Biometrics 23: 361-365.

Stuber, C.W., Johnson, V.A. and Schmidt, J.W.   1962.   Grain protein
    content and its relationship to other plant and seed characters
    in the parents and progeny of a cross of *Triticum aestivum* L.
    Crop Sci.   2: 506-508.

Torrie, J.H.   1962.   Comparison of hills and rows for evaluating
    soybean strains.   Crop Sci.   2: 47-49.

Townley-Smith, T.F. and Hurd, E.A.   1973.   Use of moving means in
    wheat yield trials.   Can. J. Pl. Sci.   53: 447-450.

Townley-Smith, T.F., Hurd, E.A. and McBean, D.S.   1973.   Techniques
    of selection for yield in wheat.   In, Sears, E.R. and Sears, L.M.S.
    (ed).   Proc. 4th Int. Wheat Genet. Symp.   Agric Expt. Station,
    Univ. of Missouri: pp. 605-609.

Wiebe, G.A.   1935.   Variation and correlation in grain yield among
    1500 wheat nursery plots.   J. agric. Res.   50: 331-357.

APPENDIX I. Yield (g/plot) of the F_4 and F_5 bulks averaged over locations (Winnipeg and Glenlea, 1976) and the F_5 families (Winnipeg, 1976) of the selected high- and low-yielding entries, for each cross

F_3 Yield Rating	Cross I				Cross II				Cross III				Cross IV			
	Entry	F_4 Bulk	F_5 Bulk	F_5 Family	Entry	F_4 Bulk	F_5 Bulk	F_5 Family	Entry	F_4 Bulk	F_5 Bulk	F_5 Family	Entry	F_4 Bulk	F_5 Bulk	F_5 Family
High	38	1129	1100	911	81	892	851	979	62	905	959	1071	61	964	931	1015
	4	963	977	811	72	1032	842	1027	57	850	977	1077	77	952	956	1016
	59	1056	931	1030	48	989	925	1067	8	823	853	1092	1	910	851	892
	58	1024	976	1031	67	864	967	911	69	895	905	1092	12	859	893	979
	28	973	999	835	79	1016	1063	910	7	960	907	1079	62	994	896	998
	71	1050	930	987	17	859	801	1040	9	874	956	968	67	932	908	970
	21	1079	1044	934	26	872	796	1047	11	948	935	1173	38	934	914	956
	57	940	941	852	29	963	874	836	17	880	1024	1027	4	996	916	971
	6	1013	970	905	11	912	879	908	32	975	981	1146	36	905	847	948
	47	954	959	705	76	947	907	974	48	906	887	929	34	833	765	874
Low	69	826	747	822	34	760	811	885	81	899	989	992	79	924	940	948
	35	818	778	740	13	701	687	868	43	847	902	989	44	948	895	961
	17	737	793	657	62	742	770	1046	20	868	844	994	58	867	850	938
	77	741	653	713	56	727	628	825	1	939	913	1047	45	788	859	948
	65	868	780	615	10	593	664	763	73	797	924	1008	51	842	818	988
	60	738	737	800	73	789	690	858	56	830	913	912	80	777	814	882
	1	865	761	727	46	676	776	915	72	818	906	963	66	829	847	962
	76	865	736	798	35	700	721	760	46	904	886	1026	14	819	813	949
	11	815	817	768	61	790	758	894	51	916	920	1041	40	877	910	1058
	61	811	765	738	31	669	665	719	23	882	821	1016	55	1013	861	917
Glenlea		973	1015	826		945	857	1096		905	880	1097		857	926	1027