THE UNIVERSITY OF MANITOBA

AN EVALUATION OF TILLERING, GRAIN PROTEIN, AND OTHER SELECTION CRITERIA AS EARLY GENERATION INDICATORS OF YIELD AND QUALITY IN HARD RED SPRING WHEAT

by

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ABSTRACT

Early generation selection in wheat was evaluated in two spring wheat crosses in duplicate nurseries at Winnipeg and Swift Current.

The effectiveness of F_2 single plant selection, based on tillering capacity, for increasing yields of subsequent generations was assessed. In both crosses, most of the highest yielding lines and families were derived from well-tillered F_2 plants.

The relationship of protein content of F_2 plants to that in derived lines was studied; and the relationship between protein and yield assessed. Significant positive correlations were obtained between protein levels in different years; and selections for high protein were somewhat effective in raising protein levels in a later generation. While the two locations differed for correlations of protein to yield, high yield selections resulted in generally slight reductions in protein levels. However, in some of the highest yielding lines protein content was also high.

The possibility of selecting for wide yield adaptability was investigated by selecting for high yield at both locations in the F_4 and testing in the F_6. Selecting the top few lines on the average of both locations, substantial yield increases were achieved over the population means in the F_6.

Visual selection for yield was assessed by numerous selectors at both locations. Visual selections were only slightly inferior to yield select

lines. Winnipeg selections were generally more effective than Swift Current selections in identifying high yielding lines. This can in part be explained by the greater variability for yield expressed at Winnipeg.

All F_4 and F_6 nursery plots were grown adjacent to a control plot in order to assess the value of frequent controls for yield evaluation. Correlations between control plots decreased with increasing distances. This indicated that considerable soil heterogeneity was present in the fields. Selecting top yielding F_4 lines for both yield per se and yield as percentage of an adjacent control plot resulted in substantial yield improvements in the F_6, over selections by either method alone.

The reliability of the relationship of certain agronomic characters to yield and of quality characters to protein and loaf volume were assessed by within-generation and inter-generation correlations; as well as a small selection study for the quality parameters. Aside from protein, none of the chosen characters was found to be a reliable indicator of future generation yield or quality, respectively.

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INTRODUCTION

The methodology of breeding for the quantitative characters of yield and quality in wheat has received some re-evaluation in recent years. Conventional breeding methods have been considered inadequate for detecting and utilizing the yield potential of superior lines. High quality has been maintained in Western Canada, but little or no improvement in yield resulted. As Hamilton (1959) pointed out:

> "--- plant breeding successes have contributed, in large measure, to our reputation as a high quality wheat country --- yet we have been unable to produce a variety that has appreciably more yield potential than Thatcher. This may mean that we have reached the limit in yield potential or it could mean that our methods are too cumbersome to detect small increments which, in total, would represent an advance."

In re-evaluating conventional breeding methods, Shebeski (1967) suggested modifications in the pedigree method. The basic premises of these modifications were that the F_3 generation is the critical generation in the selection process; and that in order to more effectively evaluate the potential of F_2 plants, interline competition should be minimized, a larger size F_3 plot should be grown, and an adequate control system should be utilized.

The present study was undertaken to evaluate early generation selection in wheat, especially the breeding system developed by Shebeski (1967), in the light of sometimes conflicting points raised by subsequent studies at the University of Manitoba. The effectiveness of single plant selection, based on tillering capacity, in the F_2, on yields of subsequent generations is to be examined. The relationship of protein content of F_2 plant kernels to that of subsequent generations was to be studied. The possibility of selecting for wide-range adaptability at the F_4 level was to be examined by growing the progenies of F_2 plants at two widely diverse locations. Winnipeg and Swift Current were chosen because of their differences in: latitude; altitude; soil type; average annual precipitation; stem rust severity; lodging conditions; and concomittant altered performance of genotypes in these differing environments (e.g. in respect to yield and protein levels). Swift Current is generally more representative of a larger area of Canada's wheat growing prairies than Winnipeg is. The yield and protein levels of lines were to be examined at the two locations in two generations. Visual selection for high plot yield was to be evaluated. Finally, the reliability of relationships of selected agronomic characters to yield and of quality characters to protein as well as loaf volume were to be assessed.

LITERATURE REVIEW

1. Breeding for yield

a) General

Yield increases in wheat have been largely due to improved agronomic practices (e.g. fertilization, seeding rates and seeding depths, irrigation) and to breeding for overcoming limiting factors (e.g. Frankel, 1947; Bell and Kirby, 1966). These limiting factors include: disease and insect resistance or tolerance, lodging tolerance, shatter resistance, maintenance of quality, as well as other specific agronomic and/or morphological requirements.

It is only in recent years that some wheat breeders have placed a major emphasis in their breeding programme on breeding for yield per se. Here the goal is to accumulate as many yield genes as possible into one variety (Whitehouse et al. 1958). The first Canadian variety derived from such a programme, Glenlea, a red spring wheat, which was developed by the Department of Plant Science at the University of Manitoba, was the result of a cross made in 1965 and licensed as a variety in 1972 (Seed Scoop, 1972).

While yield is inherited, it was in fact shown by Kuspira and Unrau (1957) that genes for yield are present on every chromosome.

The direct action of genes is on the processes of metabolism and development (Stebbins, 1950). Factors involved in yield include the physical organization and transmission of genetic material, the biochemistry of gene duplication, and of gene products influencing histogenesis, cell metabolism, morphogenesis, and physiology (Dickerson, 1963; Watson, 1952). Physiological responses of crops affecting yield can find their ultimate expression in the physical components of yield (Grafius, 1965). Thus the hereditary differences between mature plants in their yield and yield components are produced indirectly by a chain of interrelated complex physiological processes, which are sequentially integrated in time, and are gene-regulated at critical sites and times (Adams, 1967; Leng, 1963; Moll *et al*. 1962; Stebbins, 1950; and Watson, 1952). While under genetic control, these processes are subject to profound interactions with environmental factors (Adams, 1967; Leng, 1963; and Watson, 1952). Environmental influences are the greatest on components which take the longest to develop (Adams, 1967): e.g. tillers per meter row (Pollmer, 1957). According to Pollmer (1957) kernel weight was least influenced by environment. Yield, which involves a very large number of genes, shows considerable interaction with the environment, because, as pointed out by Gamble (1962), as the number of genes involved in the inheritance of an attribute becomes greater, the opportunity for influence by environment becomes greater. As pointed out by Lupton (1970), the rate at which carbohydrate (the main contributor to grain yield) is being stored in the grain at any time is determined by the product of: i) the rate of photosynthesis per unit area; ii) the photosynthetic area available; and iii) the proportion of photosynthate which is translocated to the grain.

To the extent that total dry matter production may be correlated to grain yield (i.e. dry matter production in the seeds) and to the different yield components, leaf area and net assimilation rate (NAR) are two complex functions affecting grain yield. NAR is a measure of the excess of the rate of photosynthesis over the rate of dry matter loss by respiration (Watson, 1952). While studies of Morley (1961) showed genetic differences in relative growth rate (and hence in total leaf area) and NAR, Watson (1952) cites earlier studies where it was shown that leaf area was largely under genetic control, but that NAR was wholly controlled by external factors. However, since cultural changes cause little change in NAR and since NAR is high even below full daylight intensity (Watson, 1952), the possibility of increasing yield by increasing NAR is small.

Individual polygenes have very small effects on the expression of the quantitative character yield (Falconer, 1960). The environmental variation contributes more to the phenotypic expression of yield, and thus masks the genetic values of individual polygenes (Palmer, 1952; Smith, 1936-37). But as Palmer (1952) indicated, closely linked polygenes may act as oligogenes and oligogenes for some yield components may be present and modified by polygenes. Genes interacting with other genes or with the environment may prevent increases in yield potential being observed if the environment limits development. By "limiting" is meant that for example, the cumulative increments of inorganic nutrients and synthesized materials which are produced in or transported to the yield component system are insufficient to support development of these yield components to their genetic maxima (Adams, 1967). Conversely, non-limiting environments permit a greater expression of genetic differences of yield, as shown by Johnson (1967) in the case of high soil-phosphorus levels on oats.

Adams (1967) and Johnson (1967) thus recommend that selection for genetic gain should be evaluated under physiological input conditions which will permit full expression of relevant genes, thus lowering environmental stress, as for example by raising the soil fertility. Adams and Grafius (1971) suggest that the major emphasis in breeding for higher yields should be directed towards increasing the flow of environmental resources throughout the period of greatest need by the individual yield components. Rassmusson (1968) recommends developing varieties for American agriculture which produce the highest mean yields and yield above average in all environments. Such a well buffered variety, which can adjust its genotype and phenotype to fluctuations in environment, that is, exhibits a low genotype-environment interaction, and gives high economic returns, is also recommended by Allard and Bradshaw (1964). However, in breeding specifically for drought resistance, Hurd (1971) emphasizes that it is more important to breed for maximum yield in the most adverse year rather than highest yield in a good year. Nickell and Grafius (1969) presented evidence in barley that certain optima exist in any given gene pool for the yield components and their interrelationships in order to obtain maximum yields in a particular environment; and further, that selection in one environment for these optima does not necessarily ensure comparable production performance in another environment. Obviously the area a variety is intended for, whether for a very narrow adaptation range or a wide one, as well as the annual climatic fluctuations are important criteria to influence selection practices. But as Johnson et al. (1968) showed on the basis of 238 winter wheat tests covering the period from 1937 to 1960, even at a single location, the environment cannot easily be identified with a particular set of environmental factors, thus general adaptation of a variety would be important even in a restricted area of production. On the basis of data from the Canadian Western Wheat Co-operative Tests over five years and at nine locations, Baker (1971) concluded that rust infection (both leaf rust and stem rust) accounts for a major portion of the genotype-environment interaction for yield. Thus he recommends that if the genotype-environment interaction for yield is due to such simply inherited but correlated traits as rust resistance, then research into problems other than genotype-environment interaction may be more important in improving the efficiency of plant breeding methods.

In selecting for increased yield, the breeder is concerned with selecting superior genotypes, but of necessity he must choose individuals on the basis of their phenotypic expression. Thus, as shown for corn by Robinson et al. (1951) it is important to ascertain how realistic an estimate the phenotypic value is of the genotype, by comparing the phenotypic and genotypic variances. Since in selecting directly for certain yield components one may unwittingly deselect other desirable traits, Trujillo-Figueroa (1968) employed the variability of yield components as his selection criterion in induced mutations of wheat: components with the highest variances having the greatest potential for selection. Another prerequisite to effective selection is additive genetic variances for yield and components used for selection. Only in this way can real progress be realized in self-pollinated species which approach homozygosity quickly on selfing after the F_2 generation. That yielding capacity is strongly influenced by additive effects was demonstrated for example for winter wheat by Brown, et al. (1966) and Kronstadt and Foote (1964) and for barley by Smith and Lambert (1968). Frey (1954) suggests selection to be in the earliest possible generations since selection within strains subsequent to F_2 would give rapidly diminishing returns, F_2 showing the greatest genetic variance among segregates. In later generations, the effect of segregation decreases.

b) Pedigree method

With some modifications, the pedigree method as described by Love (1927) has been used very extensively in hybridization improvement of self-fertilized crops in Canada, the U.S., Great Britain, Australia, amongst others. In Western Canada, the spring wheat varieties Pembina, Cypress, Park, and Neepawa have been produced by the pedigree method. It has also served as a source of valuable parental material for breeding programmes.

In the F_2, selection decisions have to be made on the basis of only the phenotype of individual plants because, as outlined by Alber (1969), F_2 plants: cannot be reproduced, thus there is no replication; are grown at only one location, thus experimental error, genotypic yield potential and genotype-environment interaction cannot be estimated. F_2 plant selection for yield has not been successful (e.g. Allard, 1960; Frankel, 1947; Petr and Frey, 1966; Shebeski, 1967). Thus it has been commonly suggested to mainly eliminate plants carrying undesirable genes and to retain the most vigorous plants showing a high intensity of the characteristics sought in the new variety (Allard, 1960; Briggs and Knowles, 1967).

Shebeski (1967) employing genetical and mathematical considerations presented tables for population sizes required in the different generations for varying gene differences among parents, for obtaining the most desirable genotype (the one with a maximum number of genes for a quantitative character under consideration).

Thus for parents in a cross differing by 25 important genes for yield, 1330 F_2 plants would be required for one plant that would contain all 25 desired genes. The most probable genotype of this one plant would be homozygous for 8 and heterozygous for 17 of the desired genes. Only one F_3 line out of 1330 would be expected to contain all the desired genes. For the chance presence of recovering in this one line one plant with all the remaining unfixed desirable alleles, 133 plants would have to be grown in the F_3. Thus the emphasis is on selecting many plants in a few (1-2%) lines to maximize the probability of including the highest genotypes in the selected group. Since the limiting factor in breeding for yield has been the ability to recognize superior F_3 lines, Shebeski (1967) has recommended the following practices for F_3 yield nurseries to provide a more reliable basis for predicting both yield and quality in subsequent generations:

i) increasing the sample size in the F_3 to at least 750 seeds;

ii) minimizing the effects of inter-plot competition by increasing the spacing between plots to two feet;

iii) providing an adequate number of controls by seeding a control plot adjacent to every test plot.

The results supported the considerations of the study in that the best yielding F_5's traced back to the best yielding F_3's. Briggs (1969) following the outlined procedure found F_3 yield performance so effective in predicting yield performance of related F_5 populations in the first year of his study, that selection in the subsequent two years was restricted mainly to the upper portion of the F_3 yield spectrum. Selection for yield between F_3 lines representing only the highest yielding portion of the F_3 population was ineffective as judged by F_5 yield performances. De Pauw (1970) however found that 9 selected F_3 families yielded 108.4% of adjacent control in F_5, which was significantly different ($P = 0.01$) from the mean of 99.6% of adjacent control for all F_3 lines. A factor to consider in this case is that the F_3 lines were grown in 1968 and compared to F_3 bulk controls while the selected F_5 lines were grown in 1969 and compared to Manitou controls.

2. Heritability and selection

Heritability is the proportion of observed total variance (phenotypic variance) for a defined reference unit for which difference in heredity (genotype) is responsible, hence which is expected to be transmitted to the progeny (Dudley and Moll, 1969; Frey and Horner, 1955; and Hanson, 1963). Thus, heritability is a measure of the ability to differentiate among genotypes (Pesek and Baker, 1971). This is also called "broad sense" heritability in contrast to "narrow sense" heritability which is the proportion of additive genetic variance to total variance (Robinson, 1963). Additive genetic variance, the heritable variation, represents the breeding value of a cross (Walker, 1969), i.e. the variation responsible for progress resulting from selection (Hazel, 1943; Robinson et al. 1951; and Sprague, 1966). The "broad sense" heritability can be represented by the equation given by Frey and Horner (1955): $\hat{H} = \hat{\sigma}^2_s / (\hat{\sigma}^2_s + \hat{\sigma}^2_e /r)$ where $\hat{H}$ is the estimated heritability; $\hat{\sigma}^2_s$ is the estimate of between-line variance; $\hat{\sigma}^2_e$ is the estimate of environmental variance and "r" is the number of replications used in the experiment. As pointed out by Fonseca and Patterson (1968) and Sprague (1966), heritability is not a stable population parameter but varies with the precision with which the environmental variance is estimated, and which generation is involved. The unit of evaluation may be a single plant, a plot, or a group of plots each grown under one or two or more sets of environmental conditions.

Frey and Horner (1955) considered the parent-offspring regression as the most realistic method of calculating heritabilities, since they feel that it more nearly represents what plant breeders practice when selecting in segregating populations rather than selecting from one set of environmental conditions by estimating heritability from components of variance. In order to remove some of the bias due to scale from genotype-environment interactions of year to year or location to location, Frey and Horner (1957) employed the standard units method for calculating heritabilities using the regression approach. In this way, the mean of each population becomes 0.0 and the standard deviation 1.0 and estimates of heritability can never exceed the theoretical maximum of 1.0. Standard unit heritability does not allow for altered gene effects with successive generations and is thus most reliable where additive effects predominate.

According to Hanson (1963), the use of heritability has value primarily as a method of quantifying the concept of whether progress from selection for certain plant characters is relatively easy or difficult to make in a breeding programme. As Dudley and Moll (1969) indicated, broad sense heritability estimates apply specifically to the germ plasm pool sampled. Thus, according to Dudley and Moll (1969), heritability estimates in the literature should not be compared among studies, even on the same crop, but mainly within the study if the same years, fields, plot sizes were used. In the case of estimates from one location in one year, the data do not strictly provide an estimate of heritability, but rather, as mentioned by Johnson et al. (1955), an estimate of the ratio of genetic variance plus interaction variances to phenotypic variances. The interactions involved will be: genotype - location, genotype - year, and genotype - location - year. Thus, to the extent that these interaction variances are significant, heritability estimates will be biased upwards. Aside from this bias, heritability of differences among means upon which selection is based increases with an increase in the number of replications, years, and locations used in estimating the means (Johnson *et al*. 1955). In itself, the heritability estimate is not an indication of the amount of genetic progress which might be made from selecting within the particular population (Dudley and Moll, 1969; Johnson *et al*. 1955). But, the utility of the heritability estimate is increased when it is multiplied by the selection differential to give the *expected genetic gain* (or predicted response) (Johnson *et al*. 1955; Pesek and Baker, 1971). The *selection differential* is the mean phenotypic superiority of the selected lines over the mean of the population from which they were chosen (Dickerson, 1963). Genetic progress increases with an increase in variance of a character. Frey and Horner (1955) indicated that segregating populations with the widest ranges tend to give the highest heritability estimates. Such estimates of genetic progress help the breeder to ascertain if the potential for gain is adequate in his breeding population to permit substantial improvement in the desired characters.

Frequently, a selection programme can be decided upon by examining the error variances in an analysis of variance. In such a case, as Robinson (1963) pointed out, estimates of heritability by components of variance can be of use in estimating expected progress from adopting that programme or method. As will be shown in this study, use of standard units can be used for comparing error variances and calculating heribilities by use of components of variance for methods employing different scales for the data (i.e. data per se vs. data as percent of adjacent control) as well as for comparing different characters. Frey (1968) used standard units for calculating genetic advance from realized heritability of F_3 selected compared to F_2 selected barley and oats for grain yield, plant height, and seed weight per volume.

Johnson et al. (1955) caution about the use of estimates of genetic advance. Since these estimates are made on the basis of the actual materials selected, they may not be descriptive of the effect of selection measured in terms of genotypes derived from sexual reproduction from those materials, particularly to the extent that segregation still occurs. What would be anticipated will depend on the nature of the genetic variances. In self-pollinated crops, as indicated by Sprague (1966), when homozygosity has been achieved, the variance remaining among lines within a family is entirely of the additive and additive epistatic types. Pesek and Baker (1971) testing over 5 years, at 3 to 6 locations, from 17 to 23 inbred families of wheat, found no significant differences between observed responses for yield and responses predicted from the preceding generation. This is indirect evidence of additive genetic variance and hence supports the considerations of both previously cited workers. Thus the major concern is with segregating generations.

In diallel crosses involving Mexican, a Canadian and U. S. varieties of spring wheats, Walton (1971) found marked additive genetic variance. However, since dominance was also present for grain yield and yield components, that worker recommends that selection for those characters could best be made in the more advanced generations of a cross, as homozygosity is approached. Bhatt (1972) and Whitehouse et al. (1958) were able to demonstrate essentially additive genetic control for yield components of wheat but some epistatic action for yield per se. Large amounts of additive genetic variance were found by Sun et al. (1972) for kernel weight of six spring wheat crosses. Chapman and McNeal (1971) also caution the breeder of spring wheat against possible epistatic sources of variation influencing the phenotypic expression, which might thus influence predicted gain in selection programmes. The fact that some yield components may have less non-additive genetic variances associated with them suggests that early generation selection for components which are highly correlated to yield may improve genetic gain for yield.

3. Yield components and related characters

a) Mature character relationships to yield

The primary yield components of wheat, in order of development are: fertile tillers per plant (or: per length of row, in the case of row plantings), number of kernels per tiller, and weight per kernel. Fonseca and Patterson (1968) showed by path coefficient analyses that all three components had direct effects on grain yield of winter wheat. Characters with a more indirect effect on yield which will be considered in this study are: height, days to maturity, and hectoliter weight of kernels. Johnson et al. (1966) demonstrated the influence of height on the primary components of yield as well as grain yield, while Grafius (1956) showed such relationships for earliness. The inheritance of yield and related characters, as adapted from Harrington et al. (1946) are:

Character	Manner of inheritance	Number of workers reporting
Yield	Multigenic	9
Tillers	Monogenic	2
Kernels/Spikelet	Digenic	1
Kernel weight	Trigenic	2
	Multigenic	2
Plant height	Digenic	2
	Multigenic	4
Date of ripening	Trigenic	1
	Multigenic	4
Test weight	Multigenic	3

It has been demonstrated by several workers (e.g. Robinson et al. 1951; Swamy Rao and Goud, 1971; Virk and Anand, 1970) that while genotypic correlations differed for most characters from phenotypic correlation, the former were generally greater. Thus greater increases in yield could be expected from selecting for a component with high phenotypic correlation to yield than predicted on the basis of that correlation.

Two yield components readily measured under field conditions are: fertile tillers per meter of row and kernel weight. Fertile tillers had positive to highly significant positive correlations to grain yield (Alber, 1969; Roy et al. 1969; Singh et al. 1970; and Virk and Anand, 1970). According to these workers, fertile tillers was not generally highly heritable. Alternatively, kernel weight, which has generally been shown to be the most highly heritable yield component (e.g. Lebsock and Amaya, 1969) was most inconsistent in correlations with grain yield: highly significant positive (Virk and Anand, 1970); positive (Alber, 1969; Roy et al. 1969); no correlation (Grant and McKenzie, 1970); to significant negative (Alber, 1969; Singh et al. 1970) correlations. As pointed out by Alber (1969), Schrimpf (1960), Shebeski (1966), and Walton (1970), the classes of wheats used, the specific genotypes and generations, the specific growing conditions and genotype - environment interactions, as well as the field plot and designs and sampling techniques used may all have affected the nature of the correlations obtained, affecting which component is most important to yield.

b) Developmental interdependence and component compensation

As was demonstrated by Leng (1963) for a corn hybrid, varying seeding rate resulted in drastically altered yield components without causing significant changes in total grain yield. In another corn hybrid, similar levels of expression of one component occurred at widely different levels of yield. Similar results have been reported for small grains including wheat by: Hsu and Walton (1971); Lashin and Schrimpf (1962); Matzinger (1963); and Nickell and Grafius (1969). Thus there appears to be no fixed relation between the level of expression of the yield components and the resulting level of total grain yield. While yields may be stabilized by compensation among yield components, Johnson et al. (1966), Knott and Talukdar (1971) showed that this compensation is not always complete. Thus a genetic increase in one component may well result in an increase in yield. For example, increase in seed weight of a spring wheat cross had a greater effect on yield than a decrease in the number of seeds did (Knott and Talukdar, 1971). As Matzinger (1963) and Rod and Weiling (1971) pointed out, this mechanism of adjustment of yield components may permit a genotype to perform well for yield in many different environments.

Different lines yielding the same or the same line grown under different environmental conditions, negative correlations are to be expected among the components. For example, Hsu and Walton (1971) found negative correlations between ear number and kernel weight in a 5x5 diallel cross of five spring wheat varieties. As has been demonstrated by Adams (1967), Adams and Grafius (1971), Grafius (1972) and Watson (1952) inverse correlations among yield components arise from the sequential pattern of their development in drawing on limited resources: hence their developmental interdependence, which results in component compensation. As pointed out by McKey (1966), the ability to compensate is possible because there generally exists an overproduction of primordia at each growth phase. As the first component in such a time sequence uses up more or less of the available metabolic input, the component next in the developmental sequence will tend to vary in a compensating direction. Thus, as demonstrated by Adams (1967) for bush field beans, if the first component draws on the input so that it may approach its genetic potential, the next component in the sequence may not be able to obtain enough input for its optimum development. Components which are differentiated and developed during the most advantageous part of the growing period would be favoured (McKey, 1966). Thus a negative correlation would arise, unless strong genetic linkage existed (e.g. Rasmusson and Cannell, 1970). For such quantitative characters as are under discussion, linkage is apparently not the source of some of the larger and more consistent correlations (Adams 1967; Johnson et al. 1955). Kernel weight being the last component to be developed, should not result in compensation by the other components (Rasmusson and Cannell, 1970). Genes affecting the common physiological, metabolic or developmental processes thus indirectly affect the different yield components (Leng, 1963; Stebbins, 1950). Grafius (1972) was able to demonstrate in 36 oat varieties that while components shared a pool of environmental resources, certain resources are also trait-specific. Competition within the trait-specific pool was more intense than in the shared pools. The extreme compensation between yield components and the effect of environment in the genetic processes has been postulated by Nickell and Grafius (1969) to cause low year to year correlations of components.

Allard and Adams (1969) demonstrated how not only the direct contributions of genes to yield components of individual plants but also the associate effects of other plants in field conditions are included in compensatory variation. As Adams (1967) exemplified with field beans, when they were grown in non-competitive wide spacings (45 cm apart) correlations of zero were obtained among yield components; versus significant negative correlations in highly competitive stands (plants 7.5 cm. apart). If these correlations were genetic correlations due to direct gene effects, they should have appeared also under the less crowded conditions. Thus, measurement of components of yield of individual plants in field plantings may not only be impossible, but becomes meaningless. As Morley (1961) therefore concluded, measurements of groups in competition, comprising intra-component, intra-plant, and inter-plant competition and compensation, alone is meaningful.

c) Tillering

The production of tillers, being ontogenetically the first of the yield components, forms the basis for yield with which other later components interact; particularly under unfavourable growing conditions with concommittant limited nutrient or water supplies (Alber, 1969; Pollmer, 1957). As Donald (1968), Hurd, (1969) and Hurd (1971) stated, many tillers established in spring will under dry conditions use up nutrients and moisture rapidly and cause the plant to suffer from moisture stress later in the season. Lupton (1970) reported on work with radiotracers demonstrating that translocation may take place freely between tillers of young plants in the vegetative phase. However, as stems begin to elongate and the reproductive phase commences, translocation between tillers ceases almost completely. Thus sterile tillers contribute almost nothing to those which do form seeds. However, McKey (1966) pointed out that pronounced tillering, also including non-fertile shoots will assist in building up a well-branched root system. Thus a photosynthetically more ideal type with maximum emphasis on the reproductive phase, with few tillers, will conflict with a demand for an extensive root system for supplying water and nutrients. Furthermore, McKey (1966) outlined that under arid or semi-arid conditions, where drought and heat gradually decrease assimilation but increase respiration and transpiration, tillering, the earliest yield component will gain in importance. Under moister conditions, Thorne (1966) found the production of fewer tillers, most of them fertile, associated with higher yield. Highest yielding winter and spring wheats (28 varieties tested) in Germany had 98% as many fertile tillers as the mean yielding ones (Pollmer, 1961). McKey (1966) explains the lower tillering under moister conditions on the basis of NAR being at its maximum later in the season, thus the ontogenetically later yield components would be more advantageous for grain production. In developing his uniculm wheat ideotype, Donald (1968) pointed out that there would be no internal competition between developing ears and young tillers, but only a uni-directional organization towards head and grain formation. However, in drier areas and at low seed rates, an obligatorily uniculm variety cannot show phenotypic adaptation to more favourable moister seasons by tillering. Thus Donald (1968) proposes that the uniculm habit may first prove of value under irrigation or high rainfall conditions.

d) Selecting components

Rasmusson and Cannell (1970) outline two prerequisites to obtaining higher yields by selecting for components:

i) effective selection for the components;

ii) a positive association between yield and the component selected.

Selecting for high tiller number resulted in decreased kernels per tiller in winter wheat (Fonseca and Patterson, 1968) and barley and oats (Stoskopf and Reinbergs, 1966). Selecting for increased seed weight in a spring wheat cross resulted in a decreased number of seeds per plot but not enough to decrease yield (Knott and Talukdar, 1971). On the basis of phenotypic correlations in a barley population, Rasmusson and Cannell (1970) found a lower correlation for kernel weight to yield than for number of heads to yield; yet selection for the former resulted in a much larger yield response. The above workers therefore conclude that phenotypic correlations do not provide a satisfactory basis for drawing conclusions about selection for yield components in order to increase yield. On the basis of heritability estimates and/or correlations, Lebsock and Amaya (1969), Reddi et al. (1969) and Virk and Anand (1970) found selection for kernel weight to be very effective and even more effective for selecting highest yielding lines in the following generation than by selecting for yield itself. Virk and Anand (1970) showed that kernel weight and yield had the highest correlations and coheritability (ratio of the genetic covariance of two characters to the product of their phenotypic standard deviations). Showing high coheritability, the component is not much affected by environment, and selection for yield based on this character should be more effective than based on others. The same authors concluded however that selection for both, fertile tiller number and kernel weight together provided the maximum improvement possible by selection. Thus, some of the above cited studies showed that certain components could be better predictors of future generation yield than early generation yield itself.

4. Plant and plot selection for future generation yield

a) F_2 Plant selection

As outlined in the standard plant breeding texts by Allard (1960) and Briggs and Knowles (1967), the first criterion for selection in the F_2 is the elimination of all plants carrying undesirable major genes. Next, the most vigorous plants showing the characteristics sought in the new variety are selected.

Several studies have in recent years been carried out at the University of Manitoba as to the effectiveness of F_2 plant selection for increasing yield in subsequent generations. Shebeski (1967) reported on a study in which four plant breeders each selected about 1% of F_2 plants on the basis of vigour. The progeny of these selected lines yielded about 50% above and 50% below control plots of unselected plants adjacent to each test plot. Thus selection for yield was ineffective in the F_2.

A follow-up study by McGinnis and Shebeski (1968) tried to overcome some of the weaknesses in the previous study. F_2 interplant competition was reduced by spacing plants 45 cm x 45 cm in double rows 90 cm from the next pair. Three breeders selected over 100 plants each (out of 8000) on a visual basis of what they believed to be high yielding plants with superior qualitative agronomic characters. A random sample of plants was also selected. However, since 750 seeds were required for the F_3 plot, poorly tillered and very low yielding plants were not included in the "random sample." In F_3, every third plot was a control, constituted of seed from a single head of each F_2. The F_3 lines outyielded the control on the average by 8%. There was no difference between the selected samples and the "random sample." Thus, the conclusion drawn was that selection for F_2 plants with a reasonable level of tillering was as effective as selecting those with more profuse tillering, as far as F_3 yield was concerned. In either case, the general yielding capacity of F_3 lines was increased above the adjacent bulk controls. A parallel study was reported in an M.Sc. Thesis by DePauw (1970) in which case three breeders selected 278 out of 10,000 F_2 plants. Neither the visually selected plants nor the "random sample" gave rise to F_3 progenies exceeding the control.

Alber (1969) studied F_2 plant characters in two winter wheat crosses in relation to their bulk progenies. Simple correlations which he found were the following:

F_2 character	F_5 yield	
	Cross 1	Cross 2
Plant Yield	.23	.11
Fertile tiller number	.14	.08
Yield per tiller	.37**	.28**
Kernel weight	.21	.01

The non-significant correlations of F_2 plant yield to future generation plot yield agrees with the findings of McGinnis and Shebeski (1968) and DePauw (1970). Of the four F_2 plant characters measured, only yield per tiller was highly significantly correlated to F_5 yield.

b) F_3 plot selection

Because large F_3 yield nurseries would entail considerable manpower and hence cost input to harvest, thresh and weigh all lines, visual selection for yield, if effective, could reduce the cost of handling material considerably. Boyce et al. (1947) in a study of 200 F_3 winter wheat lines concluded that visual selection for yield was as successful as plot yield determination for increasing future generation yield. In a study of 828 F_3 plots of spring wheats at the University of Manitoba (Briggs and Shebeski, 1970), 14 individuals selected visually for yield: top 10, next 20, next 20, next 30 and lowest 10. For positive visual selection, each group was significantly higher yielding than four random selections. However, since numerous of the highest yielding plots were not identified by any of the selectors in their top groups, success in increasing yield visually could only be considered limited. Thus the conclusion was that when visual selection is used as a means of screening lines, the intensity of selection should be relatively low.

5. Use of frequent control plots

A few years ago, Shebeski (1967) outlined a procedure employed at the University of Manitoba in its wheat breeding programme for evaluating large numbers of F_3 lines with limited seed supplies in yield nurseries. One of the key features of this procedure is the use of controls in every third plot. The American Society of Agronomy (ASA, 1921) in its first standardization of U.S. field experiments prefered adequate replication to the use of control plots. If however such check plots are to be used, the ASA (1921) recommends using these every third or fifth plot. With controls every third plot each line to be tested is adjacent to such a control. As Briggs and Shebeski (1968) indicated, the main assumption for this approach is that the yield of the control plot provides a good measure of the soil fertility of the adjacent plot on which a test line is grown. Thus, they concluded that frequent controls are essential for efficient selection for yield. This is an agreement with Yates (1936). Hayes and Garber (1927) calculated correlation of yielding ability of nearby plots of single rod rows of spring wheat. Their results indicated a drop from a correlation coefficient of 0.618 for adjacent plots to one of 0.383 for plots separated by three others. Briggs and Shebeski (1968) found correlation coefficients to rapidly decrease from 0.63, 0.88 and 0.87 for control plots 2.7 m apart in three fields respectively, such that non-significance was reached at plots 19.2 m apart in the first two nurseries and at 35.7 m in the third. Smith (1938) cautioned that errors of observation such as errors in technique (sowing, harvesting, threshing and weighing) would tend to lower correlations of adjacent areas.

Melton and Finkner (1967) indicated that use of systematic controls of a standard variety has the added advantage of enabling the plant breeder to make sounder judgement decisions concerning qualitative observations. The ASA (1921) also recommended use of a standard, well adapted variety as control. Baker (1968) using barley quality data demonstrated that for per cent nitrogen error variances were reduced from 11% to 44% in 5 of six tests, but increased in one by 14%, by using control plots for adjustments. However, as an average over four quality characteristics, three tests, and two varieties each, error variances by the use of control plots were reduced by only 2%. Baker and McKenzie (1967) employing controls in alternate plots of a 20 variety oat test and one of 27 varieties concluded that a control variety may provide inadequate representation of environmental variability. Their analyses showed a maximum gain in efficiency (by error variance reduction) of 14% by the use of control plots. They thus recommended that such control plots should not be used in place of replication. This is in agreement with recommendations made by the ASA standards committees (ASA, 1921; ASA, 1933), which considered replication as the most effective means of reducing the effects of soil heterogeneity and other random factors.

Different workers have employed different methods of correcting yield on the basis of control plots. The method suggested by the ASA (1921) was to assume that differences of soil fertility and moisture between check plots are uniformly progressive. Hayes and Garber (1927) outlined direct methods of correcting yields on the basis of the relative distance to each of two nearest control plots directly or as percentage of the mean of all control plots in the test. Methods based on partial correlations between nearby plots and also employing the mean of all control plots gave lower error variances ("average deviations") than the direct methods (Hayes and Garber, 1927). Sugar beet breeding programmes of the Kleinwanzlebener Saatzucht employed two controls after every 8 test lines (Haufe, 1969). By their programme, the mean yield of two adjacent controls is used for fitting a soil curve across the field. Plot values are adjusted upwards (or downwards) by the same amount as the soil/curve based on controls falls below (or above) the mean of all controls in the test. DePauw (1970) subtracted yields of adjacent controls from test lines. Baker and McKenzie (1967) employed subtracting yield of control, subtracting mean of two adjacent controls, and using the same indices as a covariant in an analysis of variance (ANOCOVA). Yates (1936) mentioned the use of yields as percent of controls, but found an ANOCOVA, using the yield of the controls as covariates, to be more effective for correcting yields. Shebeski (1967), and McGinnis and Shebeski (1968), as well as DePauw (1970), using a control every third plot, corrected yields by calculating them as percentage of the adjacent control. Melton and Finkner (1967) testing alfalfa over eight years, with controls on each side, used the average of two adjacent control plots as covariate. In every case, the coefficient of variation was lower by using this ANOCOVA than by using a straight ANOVA of the randomized blocks. The increased relative efficiency of using ANOCOVA was calculated as being 38% to 528%. It must be borne in mind that for such ANOCOVA's, not only are the frequent control plots required, but also replication. Thus seed must not be limiting.

As Hayes and Garber (1927) pointed out, any direct method of yield correction based on the performance of nearby checks requires the assumption that all varieties respond in the same relative manner to the various environmental influences. Salmon (1914) presented two hypothetical cases of varieties as controls in fields with a soil moisture gradient across the field. Firstly, a variety with minimum water requirement is exemplified. This variety would give relatively uniform yields across the field thus the field plots would be considered uniform. Secondly, a variety requiring maximum amounts of water is described. In this instance, yields across the field would vary greatly and hence, corrections made on the basis of such a variety would on the average result in overadjustments. Thus, considerable caution would seem essential in choice of the control variety. Furthermore where at all possible, seed supplies being adequate, frequent controls should not be used in place of replication but rather to supplement it.

6. Quality considerations

a) Protein and yield

Protein quantity and quality being to a large extent responsible for bread making quality of wheat, have been of prime importance in wheat breeding programmes in Western Canada. Bread making quality and yield are the result of correlated responses between the genetic potential of a variety and the biological-physical interaction with the existing environment (Brandenburger, 1970). According to McKey (1966), proteins are transmitted to the grains earlier than the carbohydrates. As Bingham (1968) outlined, high yield is largely based on the synthesis and translocation to the seed of a large quantity of carbohydrates. Thus, to the extent that specific metabolites are scarce at critical times or physiological pathways are in common, an inverse relation could be expected between protein and yield. A developmental interdependence would result.

Negative correlations of yield and protein have frequently been ascertained. Referring to the physiological negative correlation, Hänsel (1969) obtained a mean intervarietal coefficient of -0.573. Platzer (1971) in four crosses, as a mean over three years, obtained correlations averaging from -0.049 which was non-significant to -0.780 which was highly significant. In a study involving Manitou wheat, Bushuk et al. (1969) found a negative between year relationship of yield to protein. In the first test year mean protein was higher than in the second; the reverse was true for yield.

Significant positive correlations between yield and protein have also been reported. In F_1 hybrid wheat, Shebeski (1966) obtained a correlation coefficient of 0.684. Briggs et al. (1969) and Bushuk et al. (1969) obtained positive within year correlations. Briggs et al. (1969) explained this result on the basis of both yield and protein level being adversely affected by the lack of soil fertility in areas of the field deficient in nitrogen. Platzer (1971) explained his result of non-significant correlation in one cross as due to lack of a close relationship among the parents. He obtained individual F_2 families whose protein decreased only very slightly with increasing yield.

Some workers thus concluded that high yielding ability and low protein content need not be closely linked: i.e. selecting for high yield need not adversely affect quality (Platzer, 1971; Shebeski, 1966). As Brandenburger (1970) explained: the "dilution effect" (Verdünnungseffekt) of decreasing protein content with increasing yield does not exist. Instead, the negative correlation frequently obtained is only manifested when at a particular crucial period of nutrient requirement, these metabolites are not optimally available. Bingham (1968) and Plarre (1971) pointed out what is decisive for the success of a breeding programme is not so much the percentage of protein of total kernel dry matter but rather the grain protein yield per unit of field area. These European workers relate to different technological and hence rheological requirements in their milling and baking trade than do breeders of hard red spring wheats in North America. Here the demands of industry dictate high kernel protein.

b) Protein stability

That protein quantity in the wheat kernel is strongly influenced by the environment, especially soil nitrogen levels and climatic conditions during maturation, has been well documented (e.g. Bingham, 1968; Brandenburger, 1970; Plarre, 1971; and Platzer, 1971). Bingham (1968) while demonstrating large varietal differences in the nitrogen content of the kernel (hence, in protein per cent), found these differences to be considerably smaller than those from location to location or year to year. Protein heritability is intermediate to high in relation to other quality traits (Baker et al. 1968; and Baker et al. 1971). Protein content, nevertheless being largely governed by additive genetic variance (Bains et al. 1972; Bingham, 1968; and Chapman and McNeal, 1970), has potential for improvement by selection. For example, Briggs (1969) found F_3 protein content to be a good predictor of mean protein content of derived F_5 populations.

c) Protein and other quality parameters

Bushuk *et al.* (1969) found significant positive correlations of protein over two years' testing of Manitou wheat to most other quality parameters. In that study flour yield showed nonsignificant correlations to protein. In one of the two years, nonsignificant correlations to grain protein were also obtained for dough development time, mixing tolerance index, and the sedimentation value. McNeal *et al.* (1964) finding protein content associated with dough strength, as measured by farinograph data, suggested that selection for peak and stability indirectly increased protein content. An additive genetic association and a high degree of co-inheritance between grain protein and the Pelshenke value suggested to Bains *et al.* (1972) that simultaneous improvement in both these traits is possible. Platzer (1971) stressed the importance of gluten, the dough-forming proteins, for good baking quality.

d) Loaf volume and other quality parameters

Highly significant ($p=0.01$) positive correlations of Zeleny sedimentation value, residue protein (the insoluble protein in a flour), and dough development time caused Orth et al. (1972) to suggest the use of any one of these three parameters in a regression equation for predicting loaf volume. Furthermore, these workers concluded that the use of any one parameter precludes the use of the other two. Baker and Campbell (1971) found in three years' data of 23 to 25 cultivars tested across Western Canada, that the three parameters nitrogen content (i.e. protein), sedimentation value, and centrifuge absorption contain all the information about loaf volume that was available from a set of eight tests. Heyne and Finney (1965) concluded that early generation (F_3 and F_4) selection for mixing time increases loaf volume to some extent.

Early generation selection for quality parameters has been variously stressed. McNeal et al. (1964) found that delaying selection for farinograph data from F_3 to F_4 resulted in decreased advance in breeding for quality. Shebeski (1967) found F_3 loaf volume and farinograph absorption to be good predictors of the performance of F_5 lines derived from the F_3's. McNeal et al. (1969) concluded that there are probably many genes with small individual effects involved in baking quality performance, and that selection must thus be practiced in early generations to avoid losing some of the genes which govern quality.

MATERIALS AND METHODS

In this study, two crosses were selected which were the top two yielders in a replicated F_1 yield test grown in 1968 at the University of Manitoba campus. The one cross, UM953A x Manitou, referred to as cross A, averaged 137% of the yield of Manitou controls; the other cross, UM401B x UM739A, referred to as cross B, averaged 132% of Manitou controls. Brief descriptions and backgrounds of the parents used in the crosses are presented in Appendix I.

1. Field and laboratory methods

F_2 Generation: Several thousand single plants were grown on the University of Manitoba campus in 1969, in paired rows 30.5 cm apart, 61 cm from adjacent pairs, 30.5 cm between plants in rows. Just before harvest, plants were selected to cover the total range of tillering. Tiller groups were established with increments of five tillers per plant: Group 1 $\leq$ 5; Group 2 = 6-10; Group 3 = 11-15; --- to Group 9 = 41-45; and Group 10 = 46-50 tillers per plant. While more than ten plants per tiller group were pulled where possible, these were reduced to ten by selecting only plants with the highest grain yield and preferred agronomic characters. Thus 84 plants were selected for cross A in nine tiller groups ranging from 2 to 45 tillers per plant. Cross B had 92 plants in ten tiller groups ranging from 3 to 50 tillers per plant. Prior to harvest, one head was removed from all F_2 plants in each of the crosses for a bulk seed sample, to be advanced through the F_3 into the F_4 to serve as bulk control. The selected F_2 plants were individually threshed and the seed weighed. In order to adequately sample the genetic variability of each F_2 plant, 50 seeds were retained of each plant for the F_3.

<u>F_3 Generation:</u> Seeds were hand sown at Ciudad Obregon, Mexico (CIMMYT) in the fall of 1969. In order to obtain enough seed for duplicate F_4 plots, for yield testing lines derived from the lowest to the highest F_2 tillering plants, seed from each F_2 plant was space-planted into paired 11 m long rows at 25 seeds per row. Pairs of rows were 30 cm apart and 60 cm from adjacent pairs. Pairs of rows of a line were randomized in the nursery. The two bulks were solid seeded (35 gm seed per row) into twelve 11 m rows each, 30 cm apart.

The material segregated for daylength sensitivity into insensitive, segregating, and sensitive lines. Daylength sensitive lines would not mature in the required time and hence were discontinued, as were daylength sensitive plants in segregating lines. Effective tillers were counted on all plants of daylength insensitive lines six weeks prior to harvest. In addition, at harvest time, tillers of light insensitive plants in segregating lines were also counted.

In order to reduce the F_3 generation to manageable proportions and at the same time to evaluate the relationship between F_2 and F_3 for tillering, the two highest and the two lowest tillering plants of each of the utilizable lines were harvested. A few plants had 12 or fewer tillers. These were not included as seed would have been inadequate for duplicate F_4 plots. Since a heavy irrigation subsequent to tiller counts of plants in light insensitive lines had resulted in heavy late tillering, tillers on all selected plants were counted at harvest. Single plant threshing was carried out by machine. The two bulks were harvested and threshed separately.

F_4 Generation: Following the general considerations of Shebeski (1967) for an F_3 yield nursery, as diagrammed by Briggs and Shebeski (1968), duplicate nurseries were planted at Winnipeg (University of Manitoba campus) on May 8th, 1970, and at Swift Current (Canada Department of Agriculture, South Farm) on May 22nd, 1970. However, to be able to include the maximum number of lines, with seed adequate for the two locations, single two-row plots were used, omitting the centre row. Plot dimensions were dictated by the methods followed at each of the two stations. Thus, rows were 30.5 cm apart at Winnipeg and 22.9 cm apart at Swift Current. Plots were 61 cm and 45.7 cm apart at Winnipeg and Swift Current respectively. Net row length, after trimming ends just prior to harvest, was 5.03 m at both locations. The seeding rate was approximately 300 seeds per row, as obtained from a counted volume sample. The bulk F_4 control was planted every third plot. The lines derived from each F_2 plant were kept together but randomized among themselves and lines derived from different F_2 plants were randomized throughout the nursery. The type of field data recorded during the growing period is outlined in Appendix II. Visual selections for yield were also made by two selectors at each location. Plots were harvested manually, dried, threshed and weighed. The types of laboratory data that were obtained are also outlined in Appendix II. In addition to these, selected lines (of good yield potential and covering the protein spectrum) were tested for quality. Quality tests included flour tests, dough tests, and baking tests by methods outlined by Briggs et al. (1969).

F_5 Generation: Thirty-five grams of seed was seeded into each of two F_5 rows grown in pairs at Ciudad Obregon, Mexico, from each F_4 line grown at Winnipeg. The two 11 m rows were 30 cm apart and 60 cm from the next pair of rows. The whole row was harvested, threshed and weighed. All lines were brought back to Canada to be planted as bulk F_6.

F_6 Generation: The planting design was similar to that of the F_4. Two replications were grown at each of Winnipeg and Swift Current in a randomized block design. Seeding rates were adjusted on the basis of germination tests to be approximately equal to 250 seeds per row of Neepawa, which was used as a control variety in every third plot. At Winnipeg, cross A was seeded on May 6th, 1971, on the campus. Cross B was planted on May 12th, 1971, at the University of Manitoba Farm at Glenlea, about 12 miles south of the University. The Swift Current nurseries were planted on May 10th and May 11th, 1971. Net row length was reduced to 2.75 m at Swift Current. Cross A rows at Winnipeg were again trimmed to 5.03 m; while those of cross B, at Glenlea, with generally low vigour, were harvested untrimmed, at 5.64 m length. Data taken and methods of handling the F_6 lines was similar as for the F_4 (see Appendix II for field and laboratory data and Briggs et al. (1969) for quality parameters ascertained for selected lines). While kernel protein was analyzed for each plot, other quality data were taken on composite samples of both replicates of a line at one location. Several selectors attempted visual selection for the highest yielding lines. The Swift Current nurseries were harvested and threshed mechanically by a Hege experimental plot combine.

The F_4 and F_6 yield nurseries grown at the University of Manitoba campus site were grown on Riverdale silty clay loam. Cross B F_6 at Glenlea was grown in Red River clay. These locations are at an altitude between 750 and 800 feet above sea level.

The Swift Current F_4 and F_6 nurseries were grown on Haverville clay loam. The altitude of these fields was approximately 2600 feet above sea level.

Monthly temperature and precipitation summaries for the yield nursery areas are presented in Appendix III, for the growing periods of 1970 and 1971. April data are included mainly as guide to moisture available at time of seeding in May. The most striking single entry is the June 1970 rainfall at Swift Current of 185.9 mm; which contrasts with an average June figure of 65 to 70 mm.

2. Statistical and selection methods

a) Reliability tests

One of the main emphases in the present study is on the reliability of results obtained by different methods. In particular this refers to yield expressed per se (Kg/ha) or expressed as percentage of adjacent control plot yield. If control plot yields at increasing distances result in decreased correlations, this would be direct evidence as to the effectiveness of frequent control plots in accounting for field environmental variation. This has been demonstrated for yield by Briggs and Shebeski (1968) and for protein and six other quality characteristics by Briggs et al. (1969). Consequently, such sequential autocorrelations were obtained for yield and protein of control plots of all F_4 and F_6 nurseries.

The F_6 yield data were analyzed by an analysis of variance (ANOVA). The same data were also analyzed by an analysis of covariance (ANOCOVA) using the adjacent check plot yield as covariate for the yield of each line. The increase in precision due to the use of covariance was estimated by comparing the "effective error mean square" after adjustment for the covariate with the unadjusted mean square by the method outlined by Steel and Torrie (1960, p. 317). A decreased error mean square is an indication of more reliable results.

In order to be able to directly compare error mean squares of ANOVAs of data per se and of data expressed as percentage of adjacent controls, all F_6 data were converted to the standard unit scale (i.e. Z scale):

$$Z = (X - \bar{X}) / SD$$

$$SD = \sqrt{(X - \bar{X})^2 / n - 1}$$

where Z is the value in standard units; X is the value for a particular line in original units; $\bar{X}$ is the mean of the population in original units; SD is the standard deviation based on original units; n is the number of lines. On this Z scale, the mean is zero and the standard deviation is one. Using this scale, error variances, based on the same data, can be compared directly since the differences in scale of expressing the data in different ways has been removed. Error variances for ANOVAs of yield per se, as percent of adjacent control, and as percentage of nearest control with every second control plot being ignored, were compared. Similarly, ANOVAs were obtained on the standard unit scale, for the data per se and as percentage of adjacent control for: protein percentage, kernel weight, test weight, days to maturity, and height.

For the same six characters, heritability as outlined by Frey and Horner (1955) (See Literature Review) was calculated on the basis of the components of variance. This measure being for one cross at one location in one year in each case is, as Johnson et al. (1955) pointed out, the ratio of genetic variance and interaction variances to phenotypic variance. Nevertheless, this measure, to the extent that large interactions between the different characters under altered environmental conditions do not occur, enables the breeder to assess which parameter is the most stable, the most predictable.

Simple correlation coefficients were obtained within the F_4 and F_6 generations among the various characters measured. This is an average descriptive statistic for the degree of association of the different characters measured for each particular population. The genetic and environmental influences are both included in this measure. Spearman's coefficient of rank correlation (Steel and Torrie, 1960 p. 409) was calculated for between generation and location associations. This was estimated for F_4 to F_6 yield; F_4 characters to the F_6 character; F_4 character to F_6 yield; F_2 tiller number to each of F_4 and F_6 yields. This rank correlation was considered of greater importance than an intergeneration simple correlation. Effective selection requires a character which will result in very little relative rank change in whichever character is measured in the following generation.

b). Effectiveness of selection tests

Testing the effectiveness of selection requires at least two generations: one to select and one to test the performance of selected lines in relation to the mean population performance. Selection for yield was done on the basis of F_2 plant tillering, F_4 yield per se, F_4 yield as percentage of adjacent control plot yield and F_4 visual selection for yield. The test generation was the F_6. Means of selected lines averaged over replications were used. For visual selection, the selection intensities varied with selector: depending in large measure on what each considered to be the required population size to effect a gain in yield. For the other selection criteria the selection intensity was approximately 10% of the population, or 20 lines. Also 1% (2 lines) and the top line was followed through to F_6 in each case, excepting visual selection. In order to be able to compare selections based on different scales, yield means were expressed as percentage of each population mean. Thus the means of selected lines in F_6 could be compared directly.

In order to test for adaptability of high yielding lines, those selected in F_4 at one location were followed through F_6 at the other. This method of selection also reduces the effect of phenotype. However, the genotype - environment interactions, to the extent that these are important, would tend to confound results.

Selections for high F_4 protein as well as for protein as percentage of adjacent control plot were followed to F_6. Three high and three low lines for the respective character in F_4 at Winnipeg were followed into F_6 at both locations for: loaf volume, Zeleny sedimentation value, farinograph absorption and farinograph dough development time.

RESULTS AND DISCUSSION

A basic assumption required for analyses of variance and covariance as well as for correlations and regressions is that the data are normally distributed about the mean. Field data are not necessarily normally distributed. Finlay and Wilkinson (1963) used log transformations to attain normality. Appendix IV presents the two tests of normality, skewness and kurtosis, for untransformed and log transformed yield data expressed as percentage of adjacent control plot. The untransformed data were generally normally distributed. Log transformations tended to increase skewness and kurtosis. Consequently only untransformed data were used for all the analyses of this study.

1. Relationship of tillering to yield

The number of fertile tillers of single plants was significantly (p=.01) correlated to total plant yield in F_2 (Table 1.1). The same table shows non-significant correlations between F_2 plant tillering and yield per tiller. Thus high yield of spaced individual plants was associated with tillering rather than with the weight of seeds per tiller.

Tillering of the spaced F_2 plants grown at Winnipeg was significantly (p = .05 or .01) correlated to the tillering of the spaced F_3 plants (Table 1.1) grown under the vastly different growing conditions of Obregon, Mexico (irrigated, short daylengths). The level of tillering was considerably higher in the F_3 at Obregon than in the F_2 at Winnipeg.

Fertile tillers per meter row in F_4 did not show the same general relationship to F_2 spaced plant tillering as F_3 plant tillering did (Table 1.1). Cross A showed positive correlations of F_2 plant tillering for both Winnipeg (non-significant) and Swift Current (significant); cross B, however, showed a highly significant negative correlation for Winnipeg and a highly significant positive correlation for Swift Current. These results can be better visualized by looking at Table 1.2, in which tillering of groups of spaced F_2 plants is compared to the tillering of meter rows of derived F_4 lines. The difference of tillering response of the two crosses at the two locations is at once apparent. In cross A, F_4 tillering was relatively high at both locations. In cross B however, F_4 tillering at Winnipeg was much higher than that at Swift Current.

TABLE 1.1

SIMPLE CORRELATIONS TO F_2 PLANT TILLERING (X)

Y Variable	Cross A		Cross B	
	N	r	N	r
F_2 yield	63	.92**	64	.95**
F_2 yield/tiller	63	.01	64	.13
F_3 tillers (mean)				
(i) light insens. lines	17	.53*	35	.49**
(ii) segregating lines	43	.32**	34	.34*
F_4 tillers (per meter)				
(i) Winnipeg	193	.13	215	-.29**
(ii) Swift Current	193	.15*	215	.31**

TABLE 1.2

TILLERING OF SPACED F_2 PLANTS

COMPARED TO TILLERING IN F_4 ROWS

F_2 Tiller Group	F_2 Tiller Number	Number of Lines	F_4 tillers per meter row			
			Winnipeg		Swift Current	
			Mean	Rank	Mean	Rank
Cross A						
1	2 - 5	29	141.5	6	127.9	3
2	6 - 10	19	127.9	7	116.0	8
3	11 - 15	28	126.1	8	123.0	5
4	16 - 20	28	169.9	1	125.9	4
5	21 - 25	26	151.1	4	119.1	7
6	26 - 30	15	151.6	3	112.7	9
7	31 - 35	19	160.3	2	139.0	2
8	36 - 40	18	124.6	9	120.2	6
9	41 - 45	11	149.7	5	143.3	1
Cross B						
1	2 - 5	27	136.4	3	76.6	7
2	6 - 10	23	143.7	1	77.4	6
3	11 - 15	26	132.7	5	72.8	9
4	16 - 20	28	134.4	4	76.4	8
5	21 - 25	30	126.8	6	78.6	5
6	26 - 30	23	120.2	7	72.5	10
7	31 - 35	22	139.9	2	79.3	4
8	36 - 40	12	102.6	10	85.3	2
9	41 - 45	20	114.8	9	86.7	1
10	46 - 50	4	117.3	8	85.0	3

The low tillering of cross B at Swift Current permitted the highest F_2 tiller groups to tiller the highest: thus to express their genetic potential for tillering above that of the lower F_2 tillering plants. At Winnipeg however, cross B F_4 lines of the highest F_2 tillering groups had in fact the lowest numbers of fertile tillers per meter row. This could possibly be explained by the generally good growing conditions for the cross B genotypes at Winnipeg, permitting the lower F_2 tillering groups to tiller relatively profusely in the F_4, and even reach a maximum possible for the row plantings: a tiller "saturation". The highest F_2 tiller groups, in producing many tiller initials during a relatively moist spring, may have ended by producing many partially or totally sterile tillers due to a dry June (Appendix III), which prevented many tiller initials from heading. Thus intra- as well as interplant competition may have limited the number of fertile tillers produced. This could help to explain the significant negative correlation obtained in Table 1.1 for F_2 plant tillering to F_4 row tillering in cross B at Winnipeg.

Table 1.3 presents Spearman's Rank Correlation Coefficients of single plant tillering (in F_2 and F_3) and fertile tillers in a meter of F_4 row to F_4 and F_6 yields. All correlations to F_3 tiller number were non-significant. The F_3 generation was grown in Mexico. Thus, the very different growing conditions (shorter daylengths, irrigation) make F_3 plant tillering of no value as a criterion for predicting subsequent yield. Both crosses had highly significant positive correlations between

TABLE 1.3

SPEARMAN'S RANK CORRELATIONS OF TILLERING TO YIELD

	F_2 tiller number (per plant)		F_3 tiller number (per plant)		F_4 tiller number (per meter row)	
	Winnipeg	Swift Current	Winnipeg	Swift Current	Winnipeg	Swift Current
Cross A (N = 193)						
F_4 yield	.18**	.08	.06	.08	.31**	.27**
F_6 yield	-.02	.01	-.07	.05	-.01	.10
Cross B (N = 215)						
F_4 yield	-.06	.50**	-.07	.08	.49**	.25**
F_6 yield	.21**	.25**	.02	.00	-.16**	.04

* Significant at 5% level
** Significant at 1% level

F_4 tillers and F_4 yield. Correlation of F_4 tiller number was non-significant to F_6 yield except for cross B at Winnipeg (Glenlea), in which case it was negative. In cross A, a highly significant positive correlation of F_2 tillering was only obtained to F_4 yield at Winnipeg. In cross B, only F_4 yield at Winnipeg did not have a significant positive correlation to F_2 tillering.

Table 1.4 corroborates the finding of highly significant positive correlations of F_4 tillering per meter row to F_4 yield presented in Table 1.3. In both crosses and at both Winnipeg and Swift Current, the highest tillering groups of F_4 lines tended to be associated with the highest yields, while the lowest tillering groups of F_4 lines tended to have the lowest yields.

In cross A (Table 1.5 (a)) at both Winnipeg and Swift Current, the highest yielding F_6 group of lines was derived from the highest tillering F_2 group of plants. However, the second highest yielding F_6 group was derived from the lowest tillering F_2 group. In cross B (Table 1.5 (b)), the top F_2 tillering groups of plants tended to produce the highest yielding groups of both F_4 and F_6 lines at Swift Current and F_6 lines at Winnipeg. In the F_4 of cross B at Winnipeg, the top three F_2 tillering groups were the lowest yielding groups. In view of the highly significant positive correlation of F_4 tillering to F_4 yield for cross B at Winnipeg (Table 1.3), the discussion presented above concerning the finding of lower fertile tillers per meter row for the highest F_2 tiller groups

TABLE 1.4

FERTILE TILLERS PER METER COMPARED TO YIELD IN F_4

		Winnipeg				Swift Current			
F_4 Tiller Group	Number of lines	Tiller Number Range	Lines in top 20 for yield	Yield % of Mean	Yield Rank	Tiller Number Range	Lines in top 20 for yield	Yield % of Mean	Yield Rank
				Cross A					
1	20	73 - 109	0	86.2	10	86 - 102	3	98.6	8
2	20	111 - 123	1	95.5	9	103 - 110	1	98.8	7
3	20	124 - 131	3	97.3	6	111 - 115	1	94.6	10
4	20	132 - 137	0	96.7	7	116 - 120	1	95.8	9
5	20	139 - 144	1	95.8	8	121 - 125	1	99.1	6
6	13	145 - 151	3	109.7	2	126 - 128	2	99.9	3
7	20	152 - 158	5	100.2	5	129 - 132	0	99.6	4
8	20	159 - 164	1	103.6	3	133 - 136	1	99.5	5
9	20	165 - 175	1	103.2	4	137 - 147	4	103.6	2
10	20	176 - 235	5	111.0	1	148 - 180	6	110.5	1
				Cross B					
1	20	51 - 94	1	79.0	11	58 - 65	1	93.2	10
2	20	95 - 104	0	80.9	10	66 - 68	1	96.5	6
3	20	105 - 114	0	95.5	9	69 - 70	1	81.4	11
4	20	115 - 123	0	100.2	6	71 - 73	2	101.6	5
5	20	124 - 127	0	97.3	7	74 - 75	1	95.8	8
6	15	128 - 132	1	101.8	5	76 - 77	1	96.1	7
7	20	133 - 138	4	110.3	3	78 - 81	4	105.0	3
8	20	139 - 145	1	96.7	8	82 - 84	1	96.0	9
9	20	146 - 150	3	107.6	4	85 - 86	2	101.9	4
10	20	152 - 162	4	113.5	2	87 - 90	4	111.4	1
11	20	164 - 201	6	120.0	1	91 - 101	2	110.1	2

TABLE 1.5 (a)

SUMMARY OF F_2 TILLERING TO: F_4 YIELD AND F_6 YIELD: CROSS A

			Winnipeg				Swift Current			
			F_4 yield		F_6 yield		F_4 yield		F_6 yield	
F_2 Tiller Group	F_2 Tiller Number	Number of lines	Mean (Kg/ha)	Rank	Mean (Kg/ha)	Rank	Mean (Kg/ha)	Rank	Mean (Kg/ha)	Rank
1	2 - 5	29	1824.4	8	3552.9	2	2366.5	6	2291.9	2
2	6 - 10	19	2045.5	6	3426.2	7	2214.3	9	2162.9	9
3	11 - 15	28	1839.6	7	3526.2	3	2372.8	5	2231.5	7
4	16 - 20	28	2073.4	4	3480.9	5	2412.5	4	2254.1	5
5	21 - 25	26	2356.3	1	3521.2	4	2430.6	3	2255.0	4
6	26 - 30	15	2053.3	5	3379.7	8	2240.9	8	2279.6	3
7	31 - 35	19	2166.3	2	3362.6	9	2440.9	2	2191.1	8
8	36 - 40	18	1823.7	9	3448.5	6	2320.5	7	2244.8	6
9	41 - 45	11	2077.8	3	3765.0	1	2521.3	1	2310.9	1

TABLE 1.5 (b)

SUMMARY OF F_2 TILLERING TO: F_4 YIELD AND F_6 YIELD: CROSS B

F_2 Tiller Group	F_2 Tiller Number	Number of lines	Winnipeg				Swift Current			
			F_4 yield		F_6 yield		F_4 yield		F_6 yield	
			Mean (Kg/ha)	Rank	Mean (Kg/ha)	Rank	Mean (Kg/ha)	Rank	Mean (Kg/ha)	Rank
1	2 - 5	27	1900.6	7	1609.4	7	1800.7	9	2023.8	5
2	6 - 10	23	2095	4	1619.7	5	1683.0	10	1763.0	10
3	11 - 15	26	2254.1	2	1556.4	10	1822.0	8	2019.9	7
4	16 - 20	28	1968.2	5	1584.1	9	2062.9	5	1932.6	9
5	21 - 25	30	2169.2	3	1592.3	8	2048.4	6	2022.0	6
6	26 - 30	23	1968.0	6	1614.4	6	2004.6	7	2183.0	1
7	31 - 35	22	2435.6	1	1654.1	4	2109.1	4	2006.1	8
8	36 - 40	12	1740.6	9	1763.3	2	2328.9	2	2100.2	4
9	41 - 45	20	1710.5	10	1750.4	3	2442.8	1	2178.1	2
10	46 - 50	4	1740.8	8	2105.5	1	2286.5	3	2162.8	3

(Table 1.2) as a result of intraplant competition pertains.

Table 1.6 compares the effectiveness of selecting on the basis of F_2 plant criteria to selecting on the basis of F_4 line yield. The test generation was the F_6. High and low F_2 tillering, high F_2 yield, and high F_2 yield per tiller are compared. On the average, 3 to 4 lines were derived from an F_2 plant. Therefore, lines from approximately 5 to 7 F_2 plants comprised the 19 to 21 lines included in the 10% selected lines. When the intensity of selection was 10%, in both crosses at Winnipeg and in cross B at Swift Current, highest F_2 tillering resulted in higher mean yields than F_4 yield selection (Table 1.6 (a) and (b)). Increasing the intensity of selection to the three or four (about 2%) lines derived from an extreme F_2 plant, high F_2 tillering was inferior to the top four F_4 yielding lines as a selection criterion for cross A (Table 1.6 (a)). However in cross B, lines from highest F_2 tillering plants showed a substantial yield increase over those yielding the highest in F_4 (Table 1.6 (b)).

Table 1.7 presents the top six F_2 families (approximately 10%) for yield. Yield of all lines in the family was averaged over the two generations (F_4 and F_6) and over both locations (Winnipeg and Swift Current). Twenty tillers per F_2 plant was the approximate average. In cross A, four of the six families were from F_2's of above average tillering; whereas in cross B all of the top six families were derived from F_2 plants of greater than average tillering. Thus ten of the top yielding twelve F_2 families were above average for F_2 plant tillering. Therefore, the re-

TABLE 1.6 (a)

YIELD OF F_6 LINES FROM F_2 TILLER AND YIELD SELECTIONS

COMPARED TO F_4 YIELD SELECTIONS: CROSS A

	Winnipeg					Swift Current				
	Lowest F_2 tillering	Highest F_2 tillering	Highest F_2 yield	Highest F_2 yield/tiller	Highest F_4 yield	Lowest F_2 tillering	Highest F_2 tillering	Highest F_2 yield	Highest F_2 yield/tiller	Highest F_4 yield
	Ten percent of lines									
Yield (Kg/ha)	3515.1	3652.5	3560.9	3646.3	3512.1	2302.3	2332.5	2183.8	2298.4	2362.4
Percentage of population mean	100.6	104.6	102.0	104.4	100.5	102.5	103.9	97.3	102.4	105.2
	Lines from extreme F_2 plant				Four highest F_4 lines	Lines from extreme F_2 plant				Four highest F_4 lines
Yield (Kg/ha)	3482.8	3759.3	3465.0	3657.4	3842.1	2393.8	2314.9	2074.5	2248.0	2402.8
Percentage of population mean	99.7	107.6	99.2	104.7	110.0	106.6	103.1	92.4	100.1	107.0
Test line numbers	1, 2, 3	234, 235, 236, 237	216, 217 218	31, 32, 33, 34	139, 142 143, 144	1, 2, 3	234, 235 236, 237	216, 217 218	31, 32 33, 34	95, 133, 143, 230

TABLE 1.6 (b)

YIELD OF F_6 LINES FROM F_2 TILLER AND YIELD SELECTIONS

COMPARED TO F_4 YIELD SELECTIONS: CROSS B

	Winnipeg					Swift Current				
	Lowest F_2 tillering	Highest F_2 tillering	Highest F_2 yield	Highest F_2 yield/tiller	Highest F_4 yield	Lowest F_2 tillering	Highest F_2 tillering	Highest F_2 yield	Highest F_2 yield/tiller	Highest F_4 yield
	Ten percent of lines									
Yield (Kg/ha)	1628.0	1784.9	1840.1	1706.3	1718.6	2032.9	2176.2	2049.3	1916.7	2158.3
Percentage of population mean	99.6	109.2	112.6	104.4	105.1	100.6	107.7	101.5	94.9	106.9
	Lines from extreme F_2 plant				Four highest F_4 lines	Lines from extreme F_2 plant				Four highest F_4 lines
Yield (Kg/ha)	1595.4	2105.5	2105.5	1846.3	1729.9	1913.6	2162.8	2162.8	1938.0	2014.0
Percentage of population mean	97.6	128.8	128.8	112.9	105.8	94.7	107.1	107.1	96.0	99.7
Test line numbers	1, 2, 3, 4	240, 241 242, 243	240, 241 242, 243	72, 73, 74, 75	78, 132, 133, 196	1, 2, 3, 4	240, 241 242, 243	240, 241, 242, 243	72, 73, 74, 75	209, 228, 238, 239

TABLE 1.7

AVERAGE TOP YIELDING FAMILIES IN F_4 AND F_6 AT WINNIPEG AND SWIFT CURRENT

	Cross A				Cross B			
Family yield rank	F_2 plant number	F_2 tiller number	Number of entries	Mean yield (% of population mean)	F_2 plant number	F_2 tiller number	Number of entries	Mean yield (% of population mean)
1	42	21	24	121.6	45	22	24	115.6
2	28	14	18	111.7	61	31	24	114.5
3	45	23	6	111.0	66	33	24	112.5
4	82	42	18	105.5	84	42	18	112.1
5	80	40	12	105.5	82	41	18	109.9
6	30	14	18	104.1	92	50	24	107.6

sults presented indicate that above average F_2 tillering was a useful selection criterion for future generation yield.

Thus, while the genetic differences of crosses, concerning the influence of single plant tillering on future yield in row stand need to be considered, the general conclusion of McGinnis and Shebeski (1968) can be concurred with: that well-tillered vigorous F_2 plants will increase the general yielding capacity of lines in subsequent generations.

2. Grain Protein

(a). Selecting for high kernel protein

To obtain an estimation of the uniformity of performance for grain protein over generations, rank correlations between F_2 single plant protein and each of F_4 and F_6 are presented in Table 2.1 (top). The F_2 generation was only grown at Winnipeg. All these intergeneration correlations were significant ($p = 0.05$ or 0.01). Correlations of protein content of plants or plots in generations closer together (F_2 to F_4; F_4 to F_6) were generally higher than those from F_2 to F_6. All cross B correlations were higher than the corresponding cross A correlations, which could be explained by a lower genotype-year interaction for cross B than for cross A.

Selecting for high protein among F_2 single plants was effective in increasing the protein content of F_4 lines derived from these plants (Table 2.1, bottom). The F_6 protein contents of the same lines from the top F_2 plants resulted in protein levels 6.6 and 5.8% above the population mean at Winnipeg and Swift Current respectively for cross A. For cross B, selection for high protein in the F_2 appeared to be less effective than in cross A for increasing the F_6 protein level (Table 2.1, bottom), in spite of the higher F_2 to F_6 rank correlations for cross B (Table 2.1, top). The same table shows that while for cross B, F_4 selections were more effective than F_2 selections for increasing F_6 protein,

TABLE 2.1

PROTEIN: INTERGENERATION RELATIONSHIPS

Generation	Cross A Sample size	Cross A Winnipeg	Cross A Swift Current	Cross B Sample size	Cross B Winnipeg	Cross B Swift Current
Rank correlations over generations						
F_2 to F_4	184	.14*	.22**	199	.45**	.45**
F_2 to F_6	184	.17*	.16*	199	.28**	.29**
F_4 to F_6	184	.33**	.39**	199	.42**	.51**
Selections for high protein in one generation tested in a subsequent generation (expressed in percentage of population mean)						
F_2 selections in F_4	19	104.9	106.5	15	105.3	102.3
F_2 selections in F_6	19	106.6	105.8	15	102.8	100.3
F_4 selections in F_6	20	102.5	101.3	20	105.7	103.7
F_4 selections at Swift Current in F_6 at Winnipeg	20	102.5	-	20	108.1	-
F_4 selections at Winnipeg in F_6 at Swift Current	20	-	101.2	20	-	102.6

* Significant at 5% level
** Significant at 1% level

for cross A, F_2 selections appeared to be more effective. These apparent discrepancies of selections for protein compared to the intergeneration rank correlations could have resulted from differential sampling errors: unrepresentative samples involved to some extent in the selected lines. This possibility definitely exists because only one gram of the seed was used for determining protein of an F_6 line.

Selecting for high F_4 protein at one location and testing in F_6 at the other, was no more effective in increasing the protein level of cross A as selecting in F_4 and testing in F_6 at the same location (Table 2.1, bottom). The same table shows a protein increase for F_4 protein selection at Swift Current and F_6 testing at Winnipeg (Glenlea) for cross B. Selection in cross B for high F_4 protein at Swift Current was also slightly more effective for increasing F_6 protein at that location than F_4 selection at Winnipeg was (Table 2.1, bottom).

Heritability estimates for protein based on the F_6 data, were 69 and 51% for Winnipeg and Swift Current respectively of cross A and 53 and 65% for the respective locations of cross B. The significant intergeneration rank correlations presented in Table 2.1 (top) are further indicators of the relatively good heritability for protein. Thus, in spite of possible sampling errors, it appears from the two crosses dealt with, that progress can be made by starting selection for high protein in the F_2, irrespective of location.

(b). Relationship between grain protein and yield

As shown in Table 2.2 simple correlations for both crosses of F_2 plant protein to each of tiller number, yield, and yield per tiller were negative.

TABLE 2.2

SIMPLE CORRELATIONS OF F_2 SINGLE PLANT PROTEIN TO YIELD, TILLERS, AND YIELD/TILLER

Cross	Number of Plants	Tiller Number	Yield	Yield/Tiller
A	80	-0.15	-0.22*	-0.24*
B	87	-0.59**	-0.62**	-0.26*

* Significant at 5% level
** Significant at 1% level

Cross B differed from cross A in that in the former, the negative correlations of protein to tiller number and protein to yield were highly significant ($p = 0.01$).

Simple correlations of protein content to yield of corresponding plots were: non-significant positive for both crosses in F_4 at Winnipeg; highly significant positive for both crosses in F_6 at Winnipeg; highly significant negative for both crosses in F_4 and for cross A in F_6 at Swift Current; and non-significant negative for cross B in F_6 at Swift Current (Table 2.3, top). It becomes strikingly apparent when comparing the correlations ob-

TABLE 2.3

RELATIONSHIPS BETWEEN PROTEIN AND YIELD IN F_4 AND F_6

Generation	Cross A			Cross B		
	Sample size	Winnipeg	Swift Current	Sample size	Winnipeg	Swift Current
Simple correlation coefficients						
	N	r		N	r	
F_4 protein to F_4 yield	193	.01	-.42**	215	.13	-.27**
F_6 protein to F_6 yield	386	.24**	-.20**	430	.31**	-.11
F_4 protein to F_6 yield	184	-.36**	-.39**	199	-.13	-.42**
Protein levels (as percentage of population mean) of top 20 lines for yield in F_4						
F_4		98.43	96.84		102.17	96.44
F_6		100.25	97.75		99.34	99.32

* Significant at 5% level
** Significant at 1% level

tained for the same genetic material (all lines were grown at both locations) that there need not be an inherent negative correlation between protein and yield. It is possible that at Swift Current during particular crucial periods of nutrient requirement, essential metabolites were not optimally available. This could result in negative correlations between yield and protein, as suggested by Brandenburger (1970). Alternatively, the positive correlations obtained at Winnipeg may have been due to both protein and yield being adversely affected by the lack of soil fertility in certain areas of the field deficient in nitrogen, as suggested by Briggs et al. (1969). The negative correlations between F_4 protein and F_6 yield (Table 2.3) can be explained on the basis of differential response of protein and yield to the environments pertaining in the two different years.

Selecting for high yield in the F_4 resulted in somewhat reduced protein content in that generation for both crosses at Swift Current and for cross A at Winnipeg (Table 2.3, bottom). In the case of cross B, the protein content of lines selected for yield in F_4 averaged slightly above the population mean. For both crosses, the protein reduction associated with yield selections was greater at Swift Current than at Winnipeg. In the F_6, the protein level of the lines selected for yield in F_4 was lowest in cross A at Swift Current (Table 2.3, bottom). The other protein levels were very close to the population mean. As can be seen from Table 2.4, some of the top yielding lines were also in the top protein group. None of these lines was represented at both locations or in both generations.

TABLE 2.4

NUMBER OF LINES IN COMMON TO TOP
20 FOR YIELD AND TOP 20 FOR PROTEIN

	Cross A		Cross B	
Generation	Winnipeg	Swift Current	Winnipeg	Swift Current
F_4	1	1	1	0
F_6	1	1	4	2

Of the average top yielding 10% (six) F_2 families the lowest in protein were 8.6 and 3.8% below the population means for crosses A and B respectively (Table 2.5). These families had 11.7 and 7.6% higher yields than the population means of crosses A and B respectively (Table 1.7, page 60). Cross A had lower relative protein levels compared to the respective population mean than cross B for these top yielding families. In cross B, family 66 had a protein level of 104.8% of the population mean (Table 2.5) with a yield level of 112.5% of the population mean (Table 1.7). It is possible that the generally slight decrease in protein with increasing yield, and the one increase in protein pointed out above, are due to a lack of a close relationship among the parents, as has been suggested by Platzer (1971).

The possibility of only slight decreases, if any, in protein when selecting for high yield in the two crosses dealt with are indicated by the data.

TABLE 2.5

PROTEIN LEVEL OF AVERAGE TOP YIELDING FAMILIES IN F_4 AND F_6 AT WINNIPEG AND SWIFT CURRENT

Yield Rank	Cross A		Cross B	
	F_2 Plant No.	Protein (% of popul. mean)	F_2 Plant No.	Protein (% of popul. mean)
1	42	94.1	45	98.5
2	28	91.4	61	99.4
3	45	97.1	66	104.8
4	82	94.3	84	97.9
5	80	91.9	82	98.7
6	39	94.0	92	96.2

(c). Selecting for high protein per area

Table 2.6 shows very clearly that high protein per unit area was more closely related to high yield than to high protein. For both crosses, in both the F_4 and F_6 generations at both Winnipeg and Swift Current, more than half of the top 20 lines for protein per area were also in the top 20 lines for yield; while substantially less than half were also in the top 20 for kernel protein.

TABLE 2.6

RELATIONSHIP OF HIGH PROTEIN PER AREA TO YIELD AND KERNEL PROTEIN

Top 20 Line Selection Basis	Number of lines in top 20 for protein/ha							
	Cross A				Cross B			
	Winnipeg		Swift Current		Winnipeg		Swift Current	
	F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6
Yield	14	12	14	16	12	15	14	17
Kernel protein	4	5	6	2	4	7	3	3

These results are of importance to breeding programmes for feed wheats and for wheats for human use in which a primary concern is the quantity of protein produced and not the breadmaking quality of the wheat per se. The above data (Table 2.6) would suggest that selecting for high yield in these crosses would be more advantageous than selecting for grain protein, if the breeding goal includes high protein per area as a criterion. Thus in fact, lines can be selected giving high yield as well as high protein per area.

(d). Protein per se and as percentage of adjacent control plot

The correlation of protein content of control plots of decreasing contiguity in both years, 1970 and 1971, and at both locations, Winnipeg and Swift Current, showed an initial drop from high to low (Fig. 2.1). Correlations of the closest distance between control plots (i.e. separated by two test line plots) varied considerably as follows: 0.76 and 0.68 for A and B Bulk F_4's respectively at Winnipeg (Fig. 2.1 (a)); 0.53 and 0.39 for A and B Bulk F_4's respectively at Swift Current (Fig. 2.1 (b)); 0.47 and 0.77 for Neepawa in 1971 at the University of Manitoba Campus and Glenlea respectively (Fig. 2.1 (c)); and 0.63 and 0.78 for Neepawa in 1971 in cross A and B respectively at Swift Current (Fig. 2.1 (d)). These initial correlations were all highly significant. The most consistent decrease in correlations with decreasing contiguity among control plots was obtained for Neepawa in 1971 at Winnipeg (Glenlea) (Fig. 2.1 (a)), indicating a strong degree of soil heterogeneity with non-uniform gradients. All the test sites indicate a considerable degree of soil heterogeneity as judged by this criterion of control plot correlations for protein of plots with decreasing contiguity. These results thus emphasize the utility of employing frequent controls as indicators

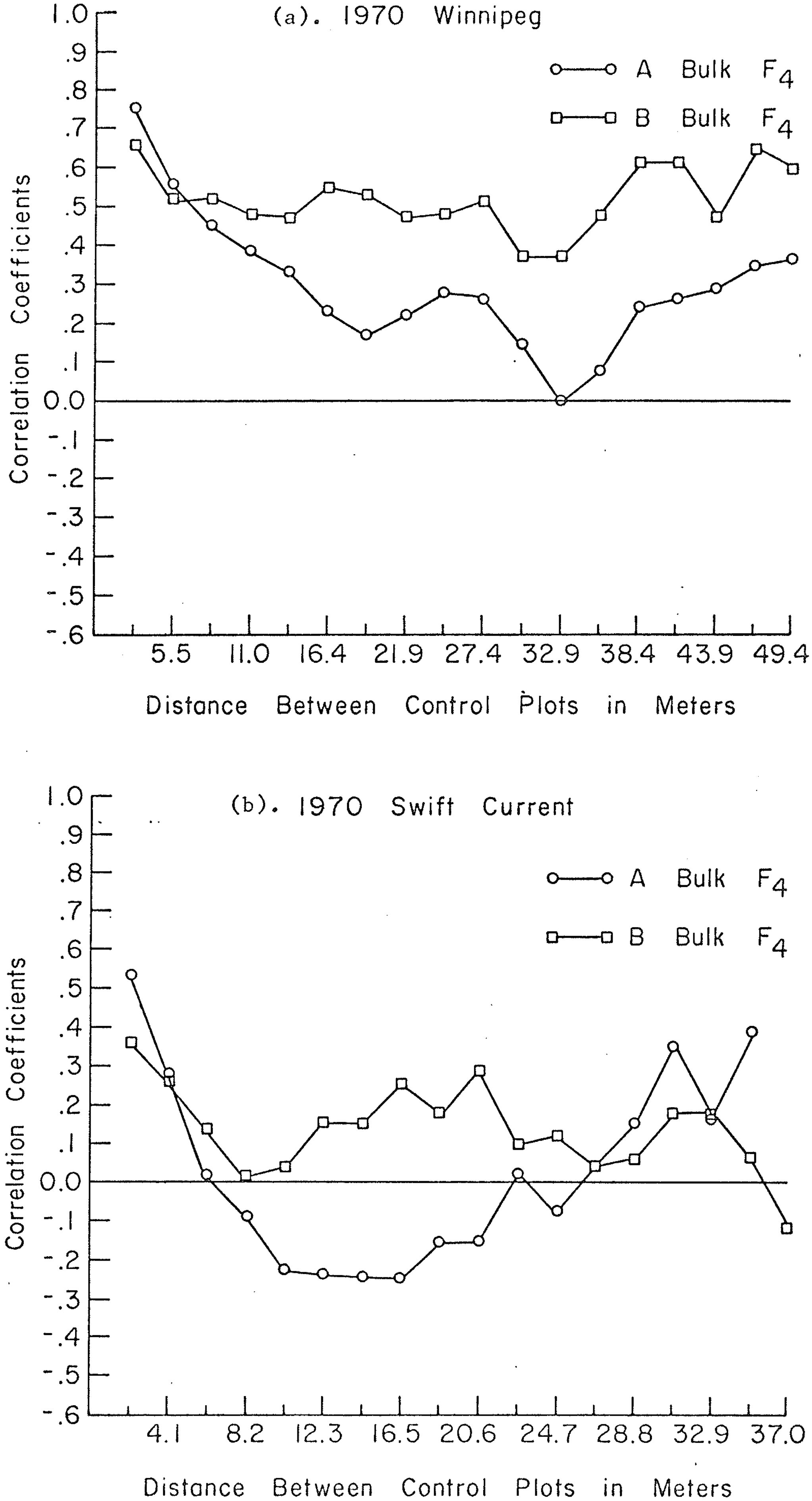
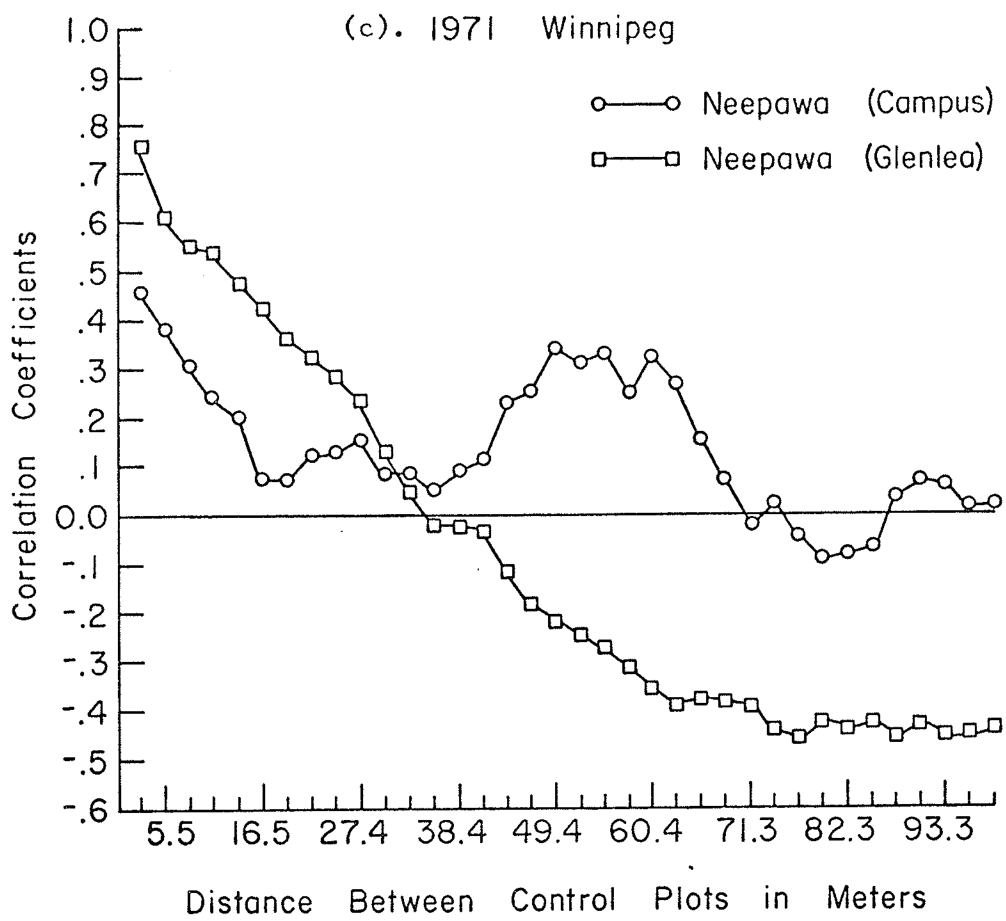


Fig. 2.1. Correlation between grain protein of control plots of decreasing contiquity



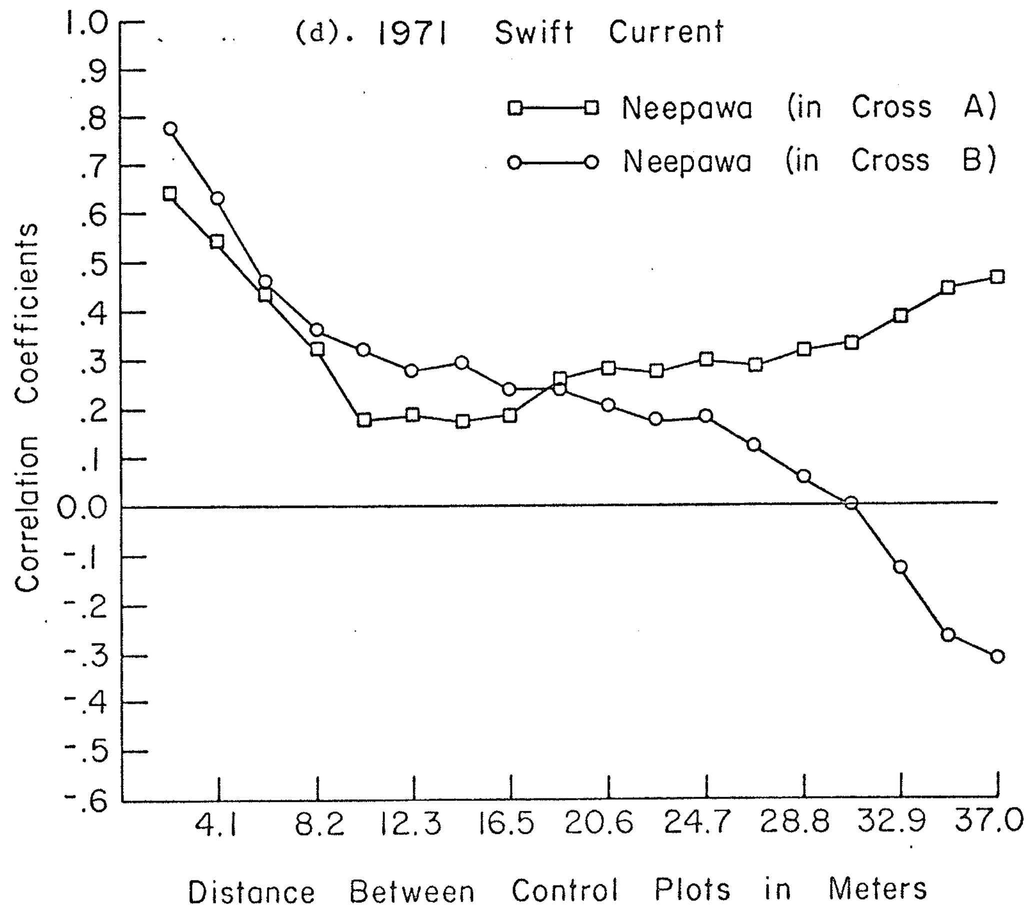


Fig. 2.1 (Continued). Correlation between grain protein of control plots of decreasing contiguity

of plot-location-effects on grain protein content.

Selecting the top 20 lines for protein in F_4 and F_6 by each method, per se and as "percentage of adjacent control plot," resulted in selecting less than half the lines in common, on the average (Table 2.7, top section).

The number of lines of the top 20 F_4 lines for protein which had above average protein contents in F_6 was almost identical for the two methods of selecting for cross A (Table 2.7, centre section). The mean F_6 protein content of the 20 F_4 selected lines of cross A was virtually identical by both methods, at both locations. In cross B at Winnipeg, adjustment resulted in more F_4 selected lines which were above the mean in F_6. The 20 F_4 selected lines had a slightly higher F_6 mean protein content than lines selected in F_4 without adjustment. The same section of Table 2.7 shows that for cross B at Swift Current the reverse occurred: unadjusted protein content resulted in more F_4 selected lines with above average F_6 means and the 20 F_4 selected lines had a higher F_6 mean protein content than lines selected in F_4 without adjustment for adjacent control plot.

Error variances in the F_6, of data analyzed in standard units, show the greatest difference between the two methods for cross B at Winnipeg (Glenlea) (Table 2.7, bottom section). However, none of the error variance differences were significant ($p=.05$).

The bottom section of Table 2.7 also shows the heritability estimates for the F_6 protein data. There was very little difference among methods

TABLE 2.7

PROTEIN IN F_4 AND F_6: COMPARING VALUES PER SE AND AS PERCENTAGE OF ADJACENT CONTROLS

	Cross A		Cross B	
	Winnipeg	Swift Current	Winnipeg	Swift Current
Number of lines of top 20 for each of protein per se and protein as percentage of adjacent control in common to both methods				
F_4	9	11	7	8
F_6	6	7	10	5
Values for each of the methods of selecting				
Lines of top 20 F_4 selections above F_6 mean				
(a) per se	14	13	14	19
(b) % control	15	13	17	14
Mean of top 20 F_4 selections in F_6 (as percentage of population mean)				
(a) per se	102.8	101.3	105.2	103.9
(b) % control	102.7	101.0	106.5	101.8
F_6 Population Parameters				
Error Variance				
(a) per se	.476	.657	.639	.513
(b) % control	.494	.620	.507	.514
Heritability				
(a) per se	68.68	50.79	53.05	65.31
(b) % control	67.13	54.81	66.02	65.29

for heritabilities of cross A at Winnipeg and of cross B at Swift Current. Adjusting for adjacent control plot protein increased the heritability estimate of cross B protein at Winnipeg (Glenlea) from 53.05 to 66.02%.

The greatest improvement in reliability of selection, for grain protein by adjusting on the basis of adjacent controls, was actually obtained for the cross B nursery at Winnipeg (Glenlea) in 1971 (Table 2.7). This corroborates the finding of very heterogeneous soil conditions deduced from Fig. 2.1 (c). While Table 2.7 shows no overwhelming evidence to favour adjustments on the basis of adjacent control in the case of the other nurseries, the appropriate graphs shown in Fig. 2.1 indicate the very definite presence of soil heterogeneity in those fields. Adjusting by using adjacent control plot protein contents would tend to reduce these effects of soil heterogeneity.

3. Selecting for wide yield adaptability

In order to assess the relationship between F_4 yield at one location or the "Mean over locations" and F_6 yield at Winnipeg, Swift Current and the "Mean over locations," rank correlations for yield were obtained (Table 3.1). This table indicates essentially no correlation between F_4 Winnipeg yield and F_6 yield at all three site variables. Swift Current F_4 yields were significantly (p=.01) correlated to F_6 yields at Swift Current and those for the "Mean over locations." Lower, but also significant (p=.05 or .01) correlations were obtained for "Mean over locations" F_4 yields and F_6 yields at Swift Current and as "Mean over locations."

Using the number of lines common for the top 10% (20) lines for yield in F_4 and F_6 as criterion of constancy of yield performance over generations, Table 3.2 is presented. At this selection intensity, in Cross A, the greatest agreement was found between F_4 Swift Current and F_6 Swift Current as well as F_4 "Mean over locations" and F_6 Swift Current; both of which had 5 of the top 20 lines in common. In cross B, F_4 Winnipeg and F_6 Winnipeg had 5 lines in common, as did F_4 Swift Current and F_6 Swift Current.

In selecting for wide adaptability, lines need to be selected which perform well at several locations. To test whether at either of the locations it was possible to identify average high yielding lines or families, Table 3.3 is presented. From this table it can be

TABLE 3.1

SPEARMAN'S RANK CORRELATION COEFFICIENTS FOR F_4 AND F_6 YIELD OVER LOCATIONS

Location of F_4	Location of F_6					
	Cross A (N = 193)			Cross B (N = 215)		
	Winnipeg	Swift Current	Mean over locations	Winnipeg	Swift Current	Mean over locations
Winnipeg	.02	-.05	.00	-.01	-.07	-.02
Swift Current	.10	.31**	.24**	.11	.40**	.31**
Mean over locations	.11	.15*	.16*	.06	.23**	.20**

* Significant at 5% level
** Significant at 1% level

TABLE 3.2

NUMBER OF LINES COMMON TO TOP YIELDING 10% (20) OF F_4 AND F_6

Location of F_4	Location of F_6					
	Cross A			Cross B		
	Winnipeg	Swift Current	Mean over locations	Winnipeg	Swift Current	Mean over locations
Winnipeg	3	3	4	5	2	4
Swift Current	3	5	4	2	5	4
Mean over locations	3	5	4	2	2	2

seen that on the average, for both crosses, in F_4 and F_6 more of the top yielding lines and families as "Mean over locations" were in the top 10% at Winnipeg than at Swift Current. The lines and families involved in the numbers of Tables 3.2 and 3.3 can be found in Appendix V. One family of cross A, number 42, was in the top ten percent (six) for yield in F_4 and F_6 at both locations as well as on a "Mean over locations" basis. Table 3.4 presents the yield performance of this family.

TABLE 3.4

MEAN YIELDS OF LINES IN FAMILY 42, CROSS A

(as percentage of population mean)

	Winnipeg	Swift Current	Mean over locations
F_4	150.3	115.9	133.1
F_6	114.3	112.4	113.4

Such a family is very desirable in breeding for yield: high year to year yield at such diverse sites as Winnipeg and Swift Current.

Table 3.5 presents the top two yielding lines and families in F_6 and indicates which ones were identified in the top 10% in F_4 and where. Clearly more of the top F_6 lines were selected in F_4 at Winnipeg than at Swift Current.

Table 3.6 summarizes the results of selecting for yield in F_4 at different intensities and testing the selected lines and families in

TABLE 3.3

NUMBER OF TOP YIELDING 10% F_4 AND F_6

LINES (20) AND FAMILIES (6) IN COMMON TO LOCATIONS

		Winnipeg F_4	Winnipeg F_6	Swift Current F_4	Swift Current F_6	Mean over Locations F_4	Mean over Locations F_6
Winnipeg				Cross B			
	lines			1	2	12	13
	families			1	1	5	2
		Cross A					
Swift Current							
	lines	2	6			4	9
	families	1	2			1	3
Mean over locations	lines	12	14	8	9		
	families	4	4	3	3		

TABLE 3.5

HIGHEST YIELDING F_6 LINES AND F_2 FAMILIES IN F_6

Yield Rank	Cross A Winnipeg	Cross A Swift Current	Cross A Mean over locations	Cross B Winnipeg	Cross B Swift Current	Cross B Mean over locations
			Top 2 F_6 lines			
1.	225	141[ac]	103	75	78[a]	76[ac]
2.	100	181	141[ac]	240[b]	231[b]	133[ac]
			Top 2 F_2 families in F_6			
1.	30	79	30	92	6	92
2.	80	58	42[abc]	82	51	82

a Selected by top 10% F_4's at Winnipeg

b Selected by top 10% F_4's at Swift Current

c Selected by top 10% F_4's as Mean over locations

TABLE 3.6

YIELD SELECTIONS IN F_4 AT EACH LOCATION TESTED IN F_6

Location of F_4 Yield Selections		Mean yields in F_6 (percentage of population mean)									
		Cross A					Cross B				
				Winnipeg	Swift Current	Mean over+ locations			Winnipeg	Swift Current	Mean over+ locations
Top 10% F_4 lines (20) and families (6)											
Winnipeg	Lines			100.5	101.1	100.8			105.1	103.3	104.2
	Families			98.9	100.4	98.5			102.4	106.6	104.5
Swift Current	Lines			100.3	105.2	102.7			103.5	106.9	105.2
	Families			105.5	105.4	105.4			101.8	105.7	103.7
Mean over locations+	Lines			100.1	101.3	102.9			101.7	107.3	106.0
	Families			101.0	101.7	101.3			103.7	106.7	105.2
Top 1% (2) F_4 lines											
			Lines					Lines			
Winnipeg			142,144	112.6	111.7	112.2		133,132	100.0	109.6	104.0
Swift Current			95,133	109.4	116.0	112.7		238,228	113.6	99.0	106.3
Mean over locations+			143,142	112.6	109.8	111.7		196,133	117.0	102.6	109.8
Top 1 F_4 line											
			Line					Line			
Winnipeg			142	107.4	119.6	113.5		133	102.9	106.5	104.7
Swift Current			95	105.7	114.7	110.2		238	105.3	109.5	107.4
Mean over locations+			143	117.9	100.1	109.0		196	102.9	106.5	114.9
Top 1 F_4 family											
		Family	Lines				Family	Lines			
Winnipeg		42	141,142 143,144	114.3	112.4	113.4	45	132,133 134,135	102.6	109.6	106.1
Swift Current		28	93, 94 95	111.7	113.3	112.5	90	236,237 238,239	104.1	104.8	104.5
Mean over locations+		42	141,142 143,144	114.3	112.4	113.4	62	187,188	98.3	102.6	100.5

+ Mean over locations = (Winnipeg data as percentage of their population mean + Swift Current data as percentage of their population mean)/2 the F_6. The main question to be answered by this table is: which F_4 site variable gave the highest F_6 yields as "Mean over locations?" At the lower intensities there was either not much difference between site variables in selecting for wide adaptability as measured by the "Mean over locations," or Swift Current F_4 selections tended to result in higher F_4 yields. However, when selecting the top F_6 line or family, the highest F_6 yield as "Mean over locations" was obtained by selecting at Winnipeg or on the basis of "Mean over locations."

Tables 3.3, 3.5, and 3.6 thus tend to indicate that for identifying lines or families of wide adaptability, Winnipeg was more reliable than Swift Current. Table 3.7 presents the coefficients of variation (C.V.) for yield at these two sites:

TABLE 3.7

YIELD VARIABILITY EXPRESSED IN COEFFICIENTS OF VARIATION

	Cross A		Cross B	
	F_4	F_6	F_4	F_6
Winnipeg	19.45	15.47	23.58	23.77
Swift Current	13.53	12.28	19.47	17.56

In each of the two years and for both crosses, Winnipeg had a greater C.V. -- thus greater variability for yield -- than Swift Current did. The high correlations obtained for Swift Current yields (Table 3.1) are in fact an indication of the lower variability expressed at that site. With intense selections for high yield, smaller differences expressed between lines and families at Swift Current enhance the likelihood of missing top yielders due to even small mechanical errors introduced in the plot technique. The wider variability expressed at Winnipeg would be as a result of more favourable growing conditions. High yielding lines or families could respond to these favourable growing conditions: resulting in yields substantially above that of the population mean. Thus, the yield differences being greater, the extreme top lines or families would not likely be missed with intense selections at Winnipeg, inspite of some degree of mechanical errors. Real yield differences could therefore be more readily selected for in the F_4 at Winnipeg than at Swift Current, resulting in high yielding lines and families at both locations in the F_6.

4. Visual selection for yield

In order to assess the effectiveness of visual selection for yield, in the F_4 and F_6 nurseries at Winnipeg and Swift Current, each selector was asked to choose the lines which in his opinion were the highest yielding lines. The average number of lines each selector chose from the actual top 10% (20) lines was recorded. The mean ratio of this number of lines included by each selector from the top 20 yielding lines to the number expected at random was calculated. The number of lines expected at random was calculated in the following manner:

> Number of lines expected at random = (No. of top yielding lines/total no. of lines) x No. of lines visually selected

For example: if a selector chose 22 lines, the number of lines expected at random in the top 20 yielding lines would be: (20/193) x 22 = 2.9.

In the F_4, visual selections for yield were carried out by two selectors at each of the two locations. Each selector, using his own criteria for visually assessing yield, selected as many lines as he felt were necessary to include the best yielding lines. The results of these visual selections for yield are summarized in Table 4.1. Selector 1 identified five times as many of the top 20 yielders as would be expected at random in cross A at Winnipeg, and 2.9 times the random expectation in cross B. On the average, the two selectors at

TABLE 4.1

VISUAL SELECTION FOR YIELD : F_4

	Cross A						Cross B					
	Winnipeg			Swift Current			Winnipeg			Swift Current		
	Selector 1	Selector 2	Mean+	Selector 2	Selector 3	Mean+	Selector 1	Selector 2	Mean+	Selector 2	Selector 3	Mean+
Lines selected	10	34	22.0	48	40	44.0	15	20	17.5	30	13	21.5
Lines in top 20 for yield												
selected	5	5	5.0	9	3	6.3	4	5	4.6	6	3	5.1
random	1.0	3.5	2.3	5.0	4.1	4.6	1.6	2.1	1.8	2.8	1.2	2.2
selected/random	5.0	1.4	2.2	1.8	0.7	1.4	2.9	2.6	2.6	2.1	2.5	2.3
Mean yield of the selected lines in % of population mean	128	105	110	106	102	104	125	117	120	102	104	102

+ Weighted mean using all lines included by both selectors each location were able to visually identify more than twice as many of the top 20 yielders as would be expected at random. At Winnipeg the visual selections averaged 110 and 120% of the population mean for crosses A and B respectively. At Swift Current the corresponding values were 104 and 102%. These differences to some extent reflect the different criteria that may have been employed by the different selectors in their visual selections. One selector, of two, was common to both locations. However, more importantly than selector differences, these differences between Winnipeg and Swift Current are a reflection of the differences in the variability for yield (Table 3.7). The greater variability at Winnipeg made it easier to visually identify lines with outstanding yield. With the lower variability at Swift Current, the yielding ability of lines tended to appear more uniform: hence high yielding lines could less readily be visually identified.

In the F_6, selectors with a great diversity of experience in breeding and selecting were asked to make visual selections for yield. These people were considered in three groups: experienced selectors, comprising people actively working in plant breeding; semi-experienced selectors, comprising graduate students in cereal breeding and/or students with farm backgrounds; and naive selectors, comprising people not associated with breeding or farming. Excepting selectors 7 and 11, different selectors were involved at the two locations. At Winnipeg each selector chose from 22 to 25 lines visually. At Swift Current several selectors made first, second, and third choices. For the sake of more uniform comparisons, only first choices are presented in Table 4.2, which summarizes the results of the F_6 visual selections. Excepting cross B at Winnipeg (Glenlea) in which case only one selector represented each group of selectors, the means of ratios of visually selected to randomly expected lines from the top 20 yielding lines and the yield means of visually selected lines show a very clear trend: experienced selectors with the highest means; semi-experienced selectors with intermediate means; and naive selectors with the lowest means.

It should be pointed out that most selectors in undertaking this exercise spent much less time selecting than should be reasonably expected of a breeder in his own programme, and generally observed the lines only once, just prior to harvest. Nevertheless, experienced and semi-experienced selectors were able to make very definite yield improvements beyond what would be expected from random selection. The fact that nine selectors (experienced and semi-experienced), in their visual yield selections, completely missed 3 of the top 20 yielding lines in each replicate of cross A at Winnipeg would suggest that in order to minimize the risk of discarding high yielding lines, the intensity of visual selections should be decreased.

In both crosses, yield means were higher at Winnipeg than at Swift Current (Table 4.2). Aside from the differences in power of visual selection among the different selectors, this difference can once again be partly accounted for by the greater variability expressed, hence the greater coefficient of variation for yield at Winnipeg than at Swift

TABLE 4.2

VISUAL SELECTION FOR YIELD : F_6

	Experienced Selectors							Semi-experienced Selectors					Naive Selectors				
	1	2	3	4	5	6	Mean+	7	8	9	10	Mean+	11	12	13	14	Mean+
Cross A, Winnipeg																	
Lines selected per rep. (average)	24.5	24.5	24.0	25.0	25.0	25.0	24.7	25.0	23.0	25.0	-	24.3	24.0	25.0++	25.0++	25.0++	24.6
Lines in top 20 for yield (average)																	
Selected	5.5	4.0	7.0	6.0	6.5	8.5	6.3	5.0	5.0	4.5	-	4.8	3.0	2.0	4.0	0.0	2.4
random	2.5	2.5	2.5	2.6	2.6	2.6	2.6	2.6	2.4	2.6	-	2.5	2.5	2.6	2.6	2.6	2.5
selected/random	2.2	1.6	2.8	2.3	2.5	3.3	2.4	1.9	2.1	1.7	-	1.9	1.2	0.8	1.5	0.0	1.0
Mean yield of all selected lines (% of population mean)	112	112	112	113	115	117	114	113	107	110	-	110	106	105	105	101	104
Cross A, Swift Current																	
Lines selected per rep. (average)	17.0	-	15.5	-	38.0++	-	20.6	20.5	6.0++	7.0++	11.0++	13.0	19.0++	-	-	-	19.0
Lines in top 20 for yield (average)																	
Selected	3.0	-	6.0	-	9.0	-	7.1	3.5	0.0	2.0	1.0	2.6	2.0	-	-	-	2.0
random	1.8	-	1.6	-	3.9	-	2.1	2.1	0.6	0.7	1.1	1.3	2.0	-	-	-	2.0
selected/random	1.7	-	3.8	-	2.3	-	3.4	1.6	0.0	2.9	0.9	2.0	1.0	-	-	-	1.0
Mean yield of all selected lines (% of population mean)	104	-	113	-	106	-	108	104	100	111	99	104	101	-	-	-	101
Cross B, Winnipeg																	
Lines selected per rep. (average)	-	-	-	-	22.0	-	22.0	18.0	-	-	-	18.0	20.5	-	-	-	20.5
Lines in top 20 for yield (average)																	
Selected	-	-	-	-	6.5	-	6.5	11.0	-	-	-	11.0	2.5	-	-	-	2.5
random	-	-	-	-	2.3	-	2.3	1.9	-	-	-	1.9	2.1	-	-	-	2.1
selected/random	-	-	-	-	2.8	-	2.8	5.9	-	-	-	5.9	1.2	-	-	-	1.2
Mean yield of all selected lines (% of population mean)	-	-	-	-	119	-	119	138	-	-	-	138	112	-	-	-	112
Cross B, Swift Current																	
Lines selected per rep. (average)	20.0	-	16.0	-	49.0++	-	24.2	22.0	7.0++	16.0++	12.0++	15.8	18.0++	-	-	-	18.0
Lines in top 20 for yield (average)																	
Selected	4.0	-	4.5	-	6.0	-	4.9	2.0	2.0	3.0	1.0	2.1	2.0	-	-	-	2.0
random	2.0	-	1.7	-	5.1	-	2.5	2.3	0.7	1.7	1.2	1.6	1.9	-	-	-	1.9
selected/random	2.0	-	2.6	-	1.2	-	2.0	0.9	2.9	1.8	0.8	1.3	1.1	-	-	-	1.1
Mean yield of all selected lines (% of population mean)	106	-	112	-	105	-	108	106	112	106	98	106	104	-	-	-	104

+ Weighted mean calculated by using lines included in both replicates

++ Selectors selecting in only one replicate

Current (Table 3.7).

In order to more adequately compare visual selections to yield selections, selected lines need to be tested in a later generation. Table 4.3 presents the F_6 yield means (as percentages of the respective population means) of lines visually selected in F_4, as well as the F_6 yields of the top 20 F_4 yielding lines. These results are for the same selectors, and hence lines visually selected, for which the F_4 data are summarized in Table 4.1. At Winnipeg, the F_6 mean yield of F_4 visually selected lines of both selectors in cross A exceeded the mean yield of F_4 yield selected lines (Table 4.3). In cross B at Winnipeg, both selectors' selections averaged below the F_4 yield selections. This was also the case for cross A at Swift Current. In cross B at Swift Current, lines chosen visually by one of the selectors averaged above the F_4 yield selections. As an average over both locations, actual F_4 yield selections were 1.8% above visual selections. Thus, on the average, in the material tested, visual selection in one generation was not very effective in increasing yield in a following generation. However, actual yield selection of the top 10% F_4 lines was only slightly more effective in raising the F_6 yield above the population mean.

TABLE 4.3

VISUAL SELECTIONS FOR YIELD IN F_4 : TESTED IN F_6

	Mean yield of F4 selected lines in F6 as percentage of population mean						
	Winnipeg			Swift Current			
	Cross A	Cross B	Location Mean	Cross A	Cross B	Location Mean	Mean over Crosses and Locations
Selector 1	107.5	104.7	106.1	-	-	-	
Selector 2	102.6	102.8	102.7	102.7	102.4	102.6	
Selector 3	-	-	-	98.9	107.3	103.1	
Mean of lines visually selected	103.7	103.6	103.7	101.0	103.9	101.9	102.6
Mean of top 20 yielding F_4 lines	100.5	105.1	102.8	105.2	106.9	106.1	104.4

5. Plot yield per se and as percentage of adjacent control plot

(a). Control plot correlations

Rapid decreases in correlation of yields of control plots at increasing distances apart led Shebeski (1967) and Briggs and Shebeski (1968) to conclude that frequent controls are essential for efficient selection for yield in hybrid nurseries. Such sequential autocorrelations were obtained for controls of the F_4 and F_6 hybrid nurseries of both crosses A and B and for both locations, Winnipeg and Swift Current (Fig. 5.1). Sums of values obtained over all ranges in the field were used to calculate individual correlation coefficients. In 1970 the F_4 bulks were the controls; in 1971 the variety Neepawa.

At Winnipeg in 1970, for the F_4 bulk control of cross A, yield correlations were rather uniform up to 41.2 m between control plots beyond which distance a substantial drop occurred (Fig. 5.1 (a)). This would indicate a rather uniform gradient of local environmental differences (e.g. soil fertility and moisture) in that field over a considerable distance. The F_4 bulk of cross B at Winnipeg in 1970 (Fig. 5.1 (a)) and Neepawa controls at both Winnipeg locations in 1971 (Fig. 5.1 (b)) showed a rapid decrease in yield correlations of plots of decreasing contiguity. At control plots between 25 and 35 m apart the correlation coefficients approached or passed below zero. This is the same general trend observed by Shebeski (1967) and Briggs and Shebeski (1968): emphasizing the utility

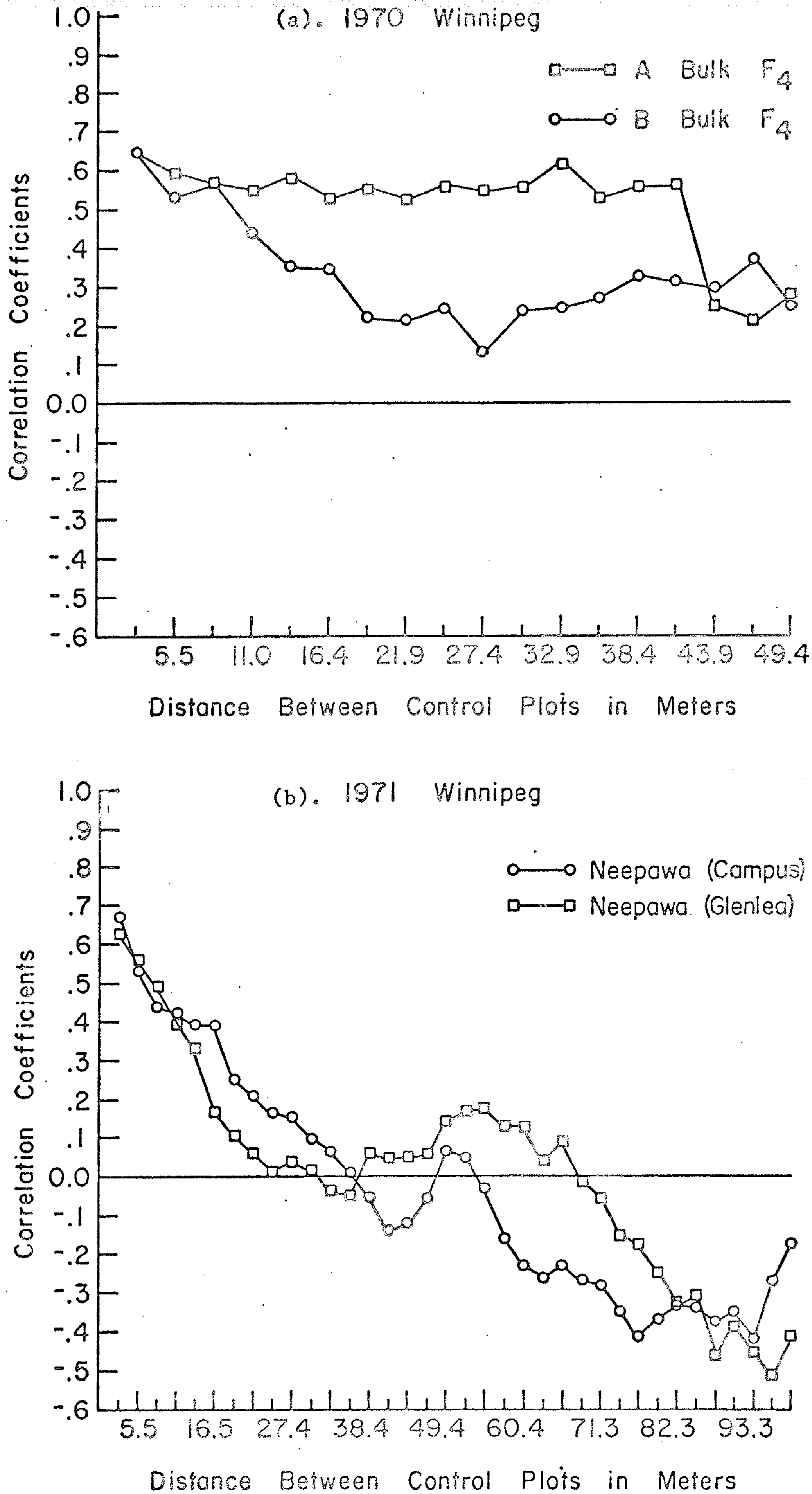
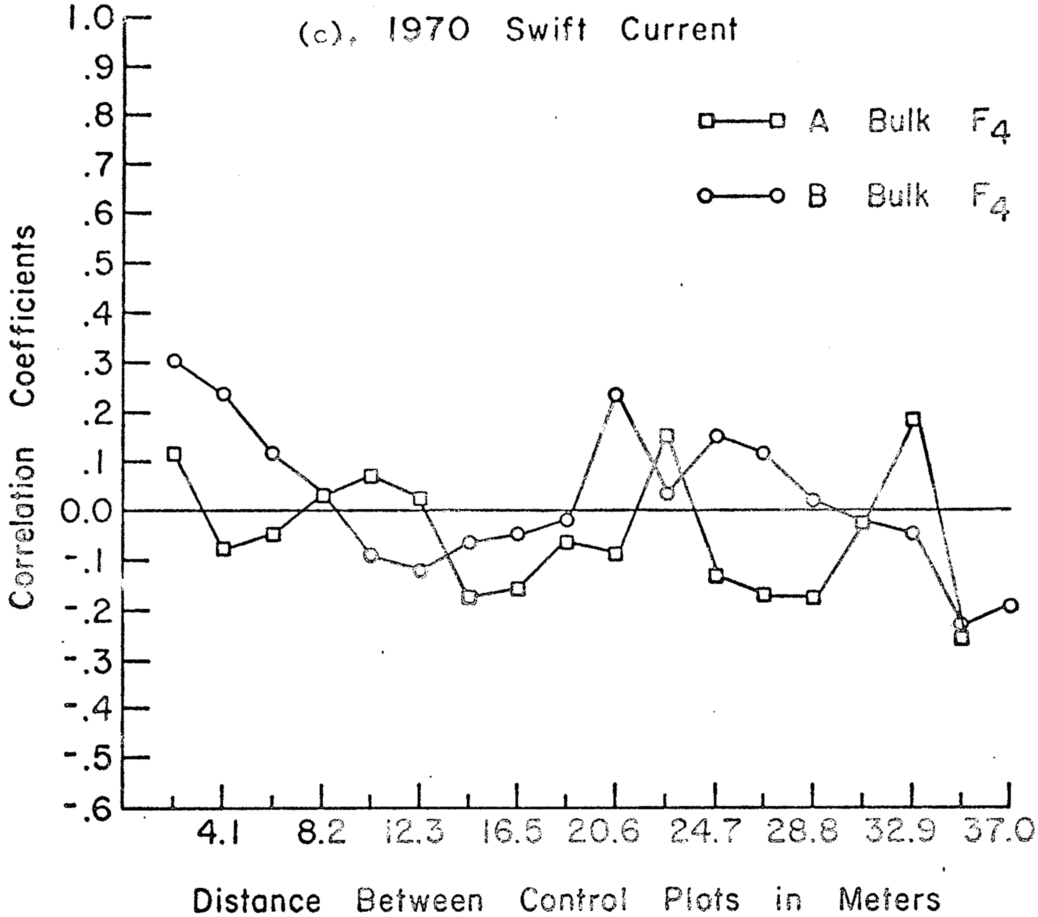


Fig. 5.1. Correlation between yields of control plots of decreasing contiguity



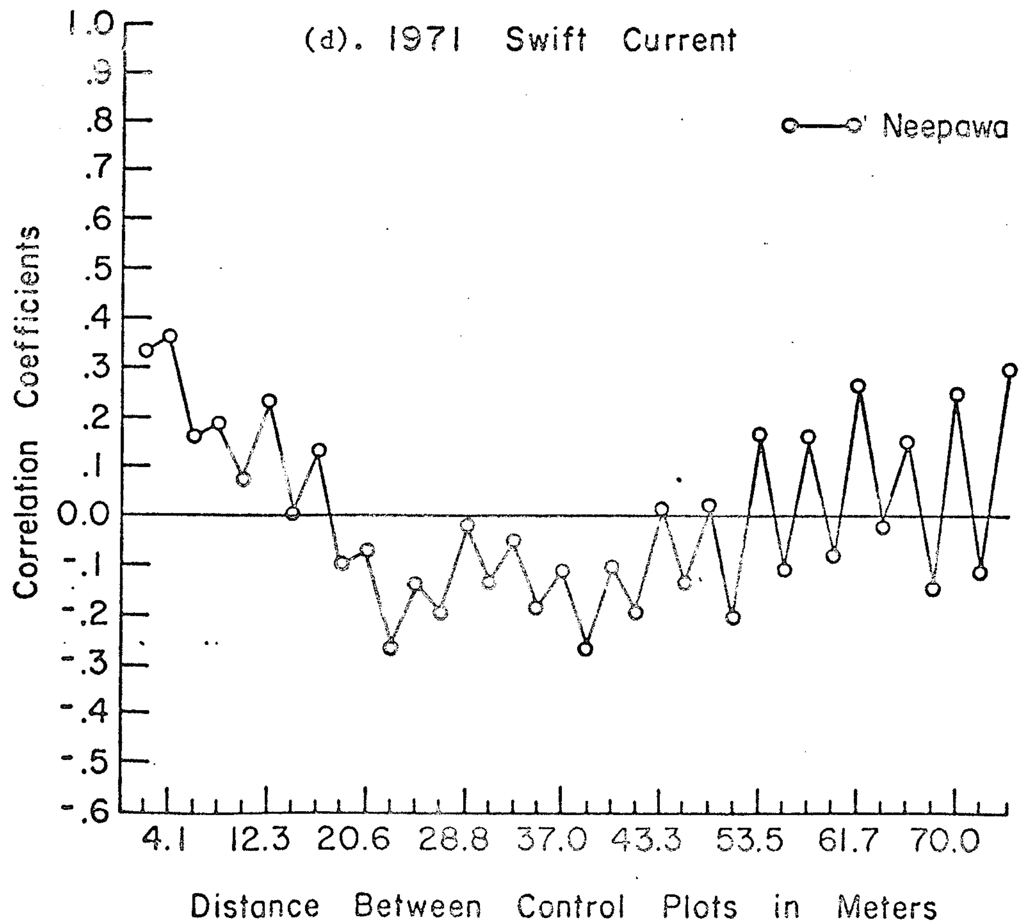


Fig. 5.1 (continued). Correlation between yields of control plots of decreasing contiguity

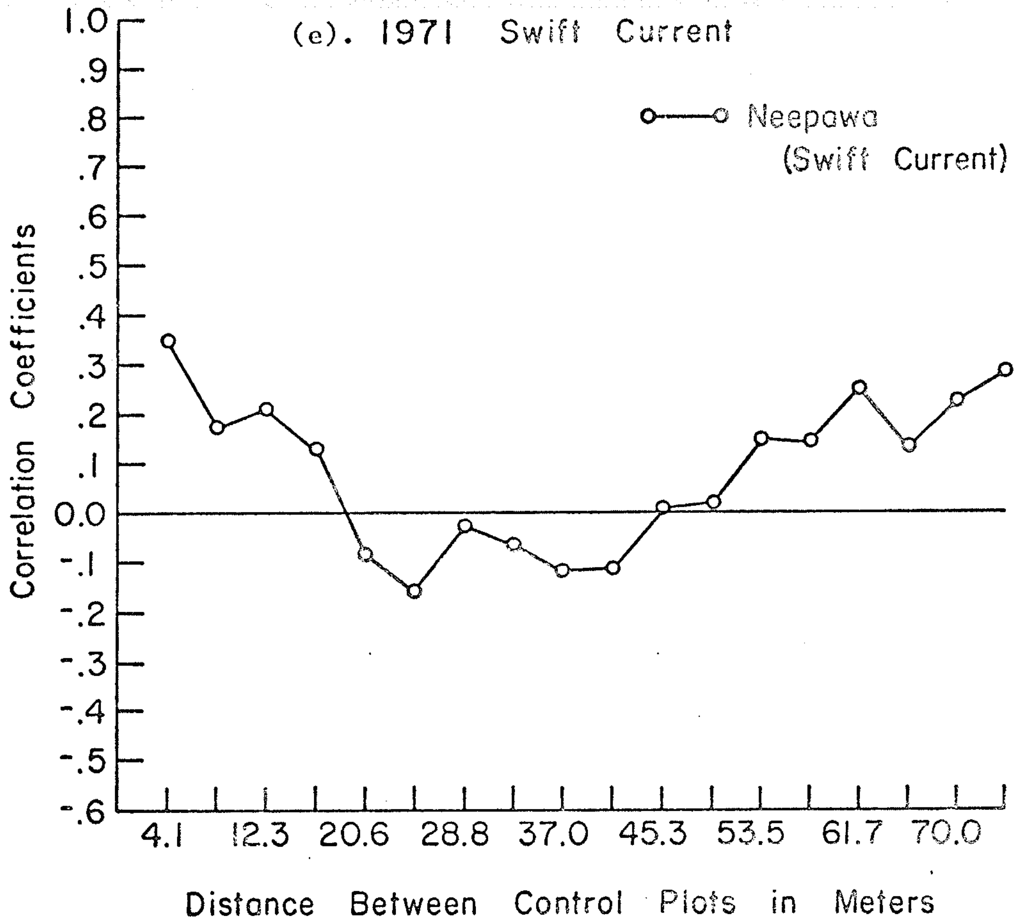


Fig. 5.1 (continued). Correlation between yields of control plots of decreasing contiguity

of yields of frequent control plots for adjusting test line yields.

Corresponding data for both years at Swift Current are presented in Fig. 5.1 (c) and 5.1 (d). Because in 1971 the F_6 of both crosses was planted in one field and the control variety was constant (Neepawa), controls of the whole field were analyzed together (Fig. 5.1 (d)). These Swift Current data show a generally much lower initial correlation of control plot yields than the Winnipeg data did (Fig. 5.1 (a) and 5.1 (b)). However, an initial drop in correlations can nevertheless be observed for these Swift Current data: indicating that control plots the smallest distance apart tended to yield the most alike. The fluctuations of correlation coefficients about zero observed at the Swift Current site could possibly be the result of rather uniform soil conditions. However, the protein correlations (particularly for 1971) of control plots of decreasing contiguity, having shown very pronounced decreases (Fig. 2.1 (d)), tend to counter this possibility. The closer spacing between plots at Swift Current (45.7 cm) contrasted to that at Winnipeg (61 cm) may in large measure account for the differences in correlations observed. Jensen and Federer (1964) concluded that spacings closer than two feet (61 cm) between wheat plots could result in competition among plots. The material in the two crosses used in this study segregated considerably for height. Since all lines were randomized throughout the yield nurseries (thus tall and short lines tending to be randomly distributed in the fields), any potential competitive effects between test lines' genotypes and the controls would be at random. Thus random fluctuations near zero of correlations of control plots of decreasing contiguity could reasonably be expected under the closer spacings at Swift Current (Fig. 5.1 (d)). In view of the above considerations and the curves presented in Fig. 5.1 (a) and (b), the 61 cm distance between plots, used at Winnipeg, was sufficient to minimize interplot competition.

The results shown in Fig. 5.1 (d) of alternating higher and lower correlations are indicative of a systematic error introduced which is associated with the direction of field operations. Every second plot in a range, hence every second control plot along a range, was worked in the opposite direction from the previous one. Thus every odd correlation coefficient is obtained from such comparisons; while every even correlation coefficient is obtained from control plots worked in the same direction. Consequently, Fig. 5.1 (e) was drawn, giving only all comparisons of control plots worked in the same direction.

Strong winds at harvest time, parallel to the rows, were thought to have been associated with the systematic yield error introduced in the 1971 Swift Current fields. To test the effect on yield of the direction of combine harvesting, a two level nested ANOVA was performed on the control plots. Direction of harvesting and field ranges were the two levels used. The mean yields and C.V.'s for the two directions of harvesting are presented in Table 5.1

TABLE 5.1

COMPARING DIRECTION OF HARVEST OF NEEPAWA CONTROLS AT SWIFT CURRENT, 1971

	Mean Plot Yield (gm)	Coefficient of Variation (%)
One Direction	497.6	10.2
Other Direction	459.8	13.4

The yields differed significantly ($p = .01$). Thus one can deduce that under the conditions of the trial, contiguous plots, harvested in opposite directions, would not have yielded alike had they been planted to the same variety. Under these conditions, adjusting a test line's yield on the basis of yield of an adjacent control plot would be unreliable because the difference in yield of the control plot would be due to the soil heterogeneity effect confounded by the effect of direction of harvest. In other words, with adjacent plot sites thus tending to yield differently due to the systematic direction-of-harvest error introduced, the benefits of increased accuracy of yield assessments sought by the use of frequent control plots are largely obviated.

The above results concerning the Swift Current site emphasize the necessity of minimizing all possible types of agronomic, mechanical, and other human errors for obtaining meaningful results by the use of frequent controls.

(b). Agreement between "yield per se" and "yield as percentage of adjacent control plot."

The degree of agreement between the methods used to express yield can be measured by the simple correlation coefficient. Correlation coefficients between "yield per se" and "yield as percentage of adjacent control plot" for the eight yield tests, are shown in Table 5.2. All correlations were highly significant. This is in agreement with the F_5 results of Briggs (1969). However, F_6 correlations for both crosses at Winnipeg while significant were not high: cross A at 0.57 and cross B at 0.44. Thus the coefficients of determination were only 0.33 and 0.19 respectively. These are the two tests with the most pronounced decrease in correlation of control plots at increasing distances (Fig. 5.1 (b)).

To ascertain the degree of agreement between two methods of selection, Haggag (1967) counted the number of lines common to both. By this method the number in the top 10% lines (20) and families (6) which were in common to both methods of selecting, "yield per se" and "yield as percentage of adjacent control plot" were ascertained for both the F_4 and the F_6 (Table 5.2). Only in the F_4 of cross B at Swift Current were more than half (12) of the lines common to the top 20 yielders by each method of expression. In five of the eight comparisons 3 or more of the 6 families were common to the methods of expression.

TABLE 5.2

TESTS FOR AGREEMENT BETWEEN "YIELD PER SE" AND "YIELD AS PERCENTAGE OF ADJACENT CONTROL PLOT"

Comparison between methods	Cross A				Cross B			
	Winnipeg		Swift Current		Winnipeg		Swift Current	
	F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6
Correlation coefficients	.77**	.57**	.82**	.76**	.76**	.44**	.85**	.73**
No. of lines in common to top 20	9	7	9	7	8	6	12	8
No. of families in common to top 6	2	2	4	4	4	1	4	3

** Significant at 1% level

TABLE 5.3

POPULATION PARAMETERS IN F_6 FOR COMPARING "YIELD PER SE" AND "YIELD AS PERCENTAGE OF ADJACENT CONTROL PLOT"

	Cross A		Cross B	
	Winnipeg	Swift Current	Winnipeg	Swift Current
Error variance				
(i) per se	.675	.576	.925	.665
(ii) % control	.719	.687	.741	.670
(iii) % control, alternate ones omitted	.744	.643	.760	.631
$(EMS_{unadj}/EEMS)^{+}$ x 100	139.6	100.3	215.4	132.5
Heritability				
(i) per se	49.10	59.61	14.03	50.22
(ii) % control	43.83	47.60	41.14	49.59

+ See text for explanation

Table 5.2 gives a general indication of greater agreement between methods of expressing yield at Swift Current than at Winnipeg. To a large extent this difference could be accounted for by any potential competitive effects associated with the narrower spacings between Swift Current plots. Thus a vigorous, high yielding test line would tend to compete favourably with an adjacent control and cause the latter to yield less than its potential for that site: with a resulting increased "yield as percentage of adjacent control plot" for the test line. The reverse could be true for a weak, low yielding, test line, compared to the control. With this potential spacing-bias removed, less agreement between the two methods of expressing yield would be expected, as was found at Winnipeg.

(c). Reliability of methods

(i) Population parameters

Having established a deviation from perfect correspondence, between "yield per se" and "yield as percentage of adjacent control plot", in classification of lines and families, it is necessary to establish which method is more reliable.

A reduction in error variance is frequently used as an indication of more reliable results. Since F_6 data were replicated twice, these were analyzed by ANOVA. Data were converted to standard units so that error variances could be compared directly (Table 5.3). The high error variance (0.925) obtained for "yield per se" for cross B at Winnipeg (Glenlea) is indicative of the unreliability of straight yield data at this site. "Yield as percentage of adjacent control plot" had still a high, but nevertheless significantly (p = .10) lower error variance associated with it. All other error variance differences between methods were non-significant.

Because of the systematic error introduced at Swift Current in 1971 by the direction of harvesting, expressing yield as percentage of adjacent control plots resulted in adjusting on the basis of a plot worked in the opposite direction. To partially remove this possible source of bias, every second control plot was ignored: test plots were thus adjacent or one plot removed from controls. Thus using the nearest control plot yield for adjustment, half the plots were adjusted on the basis of control plots worked in the same direction. The error variances from the resulting ANOVA's are also presented in Table 5.3. The use of "percentage of control, alternate ones omitted" resulted in increased error variances over adjacent control plot adjustments for both Winnipeg locations. This could be expected on the basis of the decreasing correlations of control plots at increasing distances (Fig. 5.1 (b)). At Swift Current, in both crosses, "percentage of control, alternate ones omitted" had lower error variances than "percentage of adjacent control." On the basis of the near zero fluctuations of control plots at increasing distances apart (Fig. 5.1 (e)), it could be expected that the error variances for both the methods mentioned would be the same. However, a reduction in error variance can only reasonably be explained by partial removal of the bias associated with plots worked in opposite directions.

An ANOCOVA, using the yield of adjacent control plots as covariates, was performed. To test the effectiveness of covariance for controlling error, the method outlined by Steel and Torrie (1960, p. 317) for comparing the variance of treatment means before and after adjustment for the independent variable, control plot yield, was used. The error variance is adjusted to allow for sampling error in the regression coefficient used in adjusting.

Thus: $$EEMS = s^2_{y,x} (1 + T_{xx} / (t-1)E_{xx})$$

where EEMS is the effective error variance after adjustment for control plot yield, $S^2_{y,x}$ is the adjusted error variance, T_{xx} is the treatment sum of squares of the covariates (control plot yields), E_{xx} is the error sum of squares for the covariates, "t" is the number of treatments (test lines). The relative precision of use of covariance is given by:

$$(EMS_{unadj.} / EEMS) \times 100$$

where $EMS_{unadj.}$ is the unadjusted error mean square. These values are presented in Table 5.3. For cross B at Winnipeg (Glenlea), the results indicate that 100 replicates with covariance are as effective as 215 without; or: for two replicates used with covariance, 4.3 or rather five would be required without the use of control plots as covariates. Only cross A at Swift Current showed no apparent improvement by adjusting for covariance. This cross was most affected by the systematic error introduced by harvesting adjacent plots in opposite directions. Heavier winds at the time of harvest of cross A (29-32 kmph) at Swift Current than for cross B (16-19 kmph) can at least partially account for the difference for these adjacent fields between 100.3% for cross A to 132.5% for cross B (Table 5.3).

Heritability percentages based on the F_6 variance components were calculated from the standard unit ANOVA's for "yield per se" and "yield as percentage of adjacent control plot" (Table 5.3). The greatest difference in heritability percentage was obtained for cross B at Winnipeg (Glenlea). The value 41.14% obtained for "yield as percentage of adjacent control plot" was close to three times as high as the 14.03% obtained for yield per se. This result emphasizes the particular need of frequent controls for such exceedingly heterogeneous fields. The lower heritability of cross A at Swift Current for yield as percentage of adjacent control plot" in contrast to that for "yield per se" is associated with the higher error variance of the former method (Table 5.3) at this site, for which an explanation has been given above.

The error variances and heritability estimates apply only to the specific climatic and field conditions of the F_6 generation. These values would be of use in assessing the performance of subsequent generations. For example, the increased heritability and reduced error variance from adjusting cross B, Winnipeg (Glenlea) to "yield as percentage of adjacent control plot" would be more reliable predictors of future generation yields than the corresponding estimates from the unadjusted yields (Table 5.3).

In endeavoring to ascertain which method is the best predictor of future generation actual yield, rank correlations were obtained between F_4 and F_6 yields, for lines and families, for "yield per se" and "yield as percentage of adjacent control plot" (Table 5.4 (i)). The Winnipeg data for both crosses show a general tendency for increased yield rank correlations, of the correlations of unadjusted yields, when the yields of the selecting generation are adjusted as "yield as percentage of adjacent control plot." The Swift Current data tend towards higher rank correlations for unadjusted yields: but these results are subject to the biases of competitive effects due to narrower spacings.

(ii) Yield selections

The population parameters presented in the above sub-section are descriptions of whole populations: with average values. The high yielding lines or families do not necessarily correspond perfectly to these averages.

In order to ascertain whether "yield per se," "yield as percentage of adjacent control plot," or a combination of both used for F_4 lines and families would most readily identify the best F_6 lines or families, different intensities of selection were applied in the F_4. An indication of the predictiveness of the methods of selection is the number of the top 10% of lines (20) and families (6) which exceed the F_6 actual yield population mean (Table 5.4 (ii)). For cross A at Winnipeg , "yield as percentage of

TABLE 5.4

COMPARISON OF USE OF "YIELD PER SE" AND "YIELD AS PERCENTAGE OF ADJACENT CONTROL PLOT" IN F_4 AS METHODS FOR IDENTIFYING SUPERIOR F_6 LINES AND FAMILIES

Method of expressing F_4 yield	Cross A				Cross B			
	Winnipeg		Swift Current		Winnipeg		Swift Current	
	Lines	Families	Lines	Families	Lines	Families	Lines	Families
(i) Rank correlation of F_4 to F_6 actual yield								
Per se	.02	-.05	.31**	.42**	-.01	.01	.40**	.48**
% control	.15*	.11	.27**	.32**	.02	.20**	.36**	.45**
(ii) Number of lines and families from top 10% F_4's above F_6 actual yield mean								
Per se	11	2	15	4	10	3	11	5
% control	15	4	14	6	11	3	11	5
Per se and % control	12	2	15	5	13	3	11	4
(iii) Mean F_6 yield (as % of population mean) of top 10% F_4's								
Per se	100.5	98.9	105.2	105.4	105.1	102.4	106.9	105.7
% control	107.4	104.6	104.9	110.3	105.3	100.7	105.3	104.4
Per se and % control	103.1	99.8	105.9	107.3	106.2	99.7	105.9	102.2
(iv) Mean F_6 yield (as % of population mean) of top F_4 family								
	Value	Family Number	Value	Family Number	Value	Family Number	Value	Family Number
Per se	114.3	42	114.7	28	102.6	45	104.8	90
% control	114.3	42	114.7	28	94.0	34	103.8	44
Per se and % control	114.3	42	114.7	28	102.6	45	104.8	90
(v) Mean F_6 yield (as % population mean) of top 2 F_4 lines								
	Value	Line Number	Value	Line Number	Value	Line Number	Value	Line Number
Per se	112.6	142,144	116.0	95,133	100.0	133,132	99.0	238,228
% control	112.8	72,103	101.5	226,230	111.2	101, 63	104.7	238,269
Per se and % control	112.6	143,142	105.3	230, 95	115.1	63,133	115.5	238,353
(vi) Mean F_6 yield (as % of population mean) of top F_4 line								
	Value	Line Number	Value	Line Number	Value	Line Number	Value	Line Number
Per se	107.4	142	114.7	95	102.9	133	109.5	238
% control	104.2	72	107.2	226	95.2	101	109.5	238
Per se and % control	117.9	143	95.8	230	127.3	63	109.5	238

* Rank correlations significant at 5% level
** Rank correlations significant at 1% level

Note: Cross A total lines = 193, total families = 63; Cross B total lines = 215, total families = 64 adjacent control plot," and the combination of both methods for cross B, had the largest number of F_4 selected lines above the F_6 mean. For the two crosses at the Winnipeg locations, these two methods mentioned were thus better predictors of future generation yield than the other. Control plots were required in both cases. Thus, these results emphasize the use of adjacent control plots for these fields at Winnipeg. In cross A at Swift Current all six F_4 families selected by "yield as percentage of adjacent control plot" had F_6 yields above the mean.

The actual mean yield in F_6 of the F_4 selected top lines and families gives a quantitative measure of yield improvement over the mean. These data, expressed as percentage of the mean of all lines in a trial, are also presented in Table 5.4.

Selecting in F_4 the top 10% of lines and families resulted in increases of 3% or more above the other methods in the F_6 only for "yield as percentage of adjacent control plot" for: cross A Winnipeg lines and families; and cross A Swift Current, families (Table 5.4 (iii)). All other comparisons at this selection intensity varied by less than 3%.

By increasing the selection intensity to the top family (Table 5.4 (iv)), or one percent (i.e. two lines) in F_4 (Table 5.4 (v)) or by selecting only the single top yielding F_4 line (Table 5.4 (vi)) in each case, greater yield increases would be expected in the F_6 to the extent that the F_4 phenotype for yield measures the genotype. Thus, whichever of the two methods, or the combination of both, gives the greatest consistent yield increases, is the best estimator of the genotype. The largest consistent F_6 yield increase was obtained in cross B at Winnipeg by using the combination of both methods for selecting top lines in the F_4. In this case yield was increased by 15.1 and 27.3% over the F_6 mean by selecting the top two and top one F_4 lines respectively. Thus, under the rather non uniform conditions prevailing in that Winnipeg (Glenlea) field, a line needed to perform well in the F_4 for "yield per se" as well as for "yield as percentage of adjacent control plot" in order to maximize its chances of performing well in the F_6. While the top two F_4 lines at Winnipeg of cross A, selected by the different methods, showed no real differences in their F_6 yield, the top F_4 line selected by the combination of both methods had the highest F_6 yield. At Swift Current for cross A, "yield per se" F_4 selections resulted in the greatest F_6 yields at both of these intense selections. At each location for cross A, all three methods of F_4 selection identified the same family as top: with over 14% yield increases over the respective F_6 population means. In cross B at Swift Current, all three methods selected the same top F_4 line; while the highest F_6 yielding other line, of the top two in F_4, was selected by combining the two other methods in F_4.

In order to ascertain whether or not lines selected in common by both methods, "yield per se" and "yield as percentage of adjacent control plot," as being in the top 20 for F_4 yield, as opposed to the top 20 lines on the average of the two methods, mean yields in F_4 and F_6 are presented in Table 5.5. In both crosses and at both locations, these lines

TABLE 5.5

COMPARISON OF YIELDS OF F_4 SELECTIONS BY DIFFERENT METHODS

Method of selecting top F_4 lines		Cross A				Cross B			
		Winnipeg		Swift Current		Winnipeg		Swift Current	
		F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6
(a) Top 20	per se	133.8	100.5	122.4	105.2	136.9	105.1	133.9	106.1
(b)	% control	121.3	107.4	115.4	104.9	123.8	105.3	127.5	105.3
(c) Common to (a) and (b)		136.6	109.1	124.6	106.5	143.3	106.2	135.2	105.7
(d) Not common to (a) and (b)	per se	131.5	93.6	120.5	104.1	132.6	104.4	132.0	108.5
(e)	% control	108.8	105.9	107.9	102.0	110.8	104.7	116.0	104.7

which were in common (number of lines involved are shown in Table 5.2) had higher F_4 mean yields than the whole 20 selected for yield "per se". This indicates clearly that the power of selection for yield has been improved upon by selecting only lines in common to the top selections of each of the two methods. Furthermore, in three of the four comparisons, the F_6 yields of the lines in common to the two methods were higher than yields of selections of top 20 F_4's by either of the methods; in the fourth (cross B at Swift Current), mean yields in F_6 were virtually identical. Selected lines of cross A at Winnipeg common to both methods exceeded the F_6 yields of "yield per se" F_4 selections by 8.6%. These results indicate that selecting lines which are high for "yield per se" and for "yield as percentage of adjacent control plot" is a more reliable method for identifying lines with high yield potential in future generations than the use of either of the methods alone.

The top F_4 line for each, cross A and cross B, at Winnipeg (Table 5.4 (vi)) selected on the basis of the combinations of "yield per se" and "yield as percentage of adjacent control plot" had a better F_6 yield performance than either the average of the best two F_4 lines (Table 5.4 (vi)), the top F_4 family (Table 5.4 (iv)) or the top 10% F_4 lines and families (Table 5.4 (iii)).

These results would indicate that by this combination of methods ("yield per se" and "yield as percentage of adjacent control plot"), a breeder could narrow down his first yield-testing generation (in this case, F_4; otherwise the F_3) to a very few lines and select extensively within these. The lack of agreement of the Swift Current data with the above consideration is not so much an argument against the method as an indication of how a method may readily appear unworkable or of little value, when in fact confounding factors have been introduced.

6. Selected agronomic characters

(a). Potential for selection progress and reliability

A high coefficient of variation (C.V.) among lines gives an indication of the potential for progress when selecting within a particular character, provided the genetic variance is largely additive. Table 6.1 presents the means and coefficients of variation of F_4 and F_6 for Winnipeg and Swift Current of yield, protein, kernel weight, test weight, height and days to maturity. The two agronomic characters with the highest coefficients of variation are height and kernel weight. In the F_4, the selecting generation, for both crosses at Winnipeg, the C.V. for kernel weight was higher than that for height. In the F_4, for both crosses at Swift Current, the C.V. for height was considerably higher than that for kernel weight. In consideration of selection for desired levels of a certain character a high potential for such progress is essential. The two characters, kernel weight and height, exhibiting the greatest potential for selection progress, will therefore be emphasized in this section.

Indications as to the reliability of values associated with the selected agronomic characters (comprising the genotypes concerned, the effect and interaction with the environment, and the effects associated with measurement errors) were obtained from the error variances (Table 6.2) and variance-component heritabilities (Table 6.3) based on ANOVA's of the

TABLE 6.1

MEANS AND COEFFICIENTS OF VARIATION OF YIELD, PROTEIN, AND SELECTED AGRONOMIC CHARACTERS

		Cross A				Cross B			
		F_4		F_6		F_4		F_6	
Characters	Location	Mean	Coefficient of variation	Mean	Coefficient of variation	Mean	Coefficient of variation	Mean	Coefficient of variation
Yield (kg/ha)	Winnipeg	2022.98	19.45	3491.98	15.47	2042.89	23.58	1634.47	23.77
	Swift Current	2369.81	13.53	2245.30	12.28	2011.02	19.47	2019.72	17.56
Protein (%, 13.5% m.b.)	Winnipeg	14.04	7.48	13.99	6.22	14.30	9.23	12.94	10.43
	Swift Current	14.89	5.51	16.46	4.07	15.33	6.13	16.19	4.45
Kernel weight (g/1000)	Winnipeg	30.78	11.86	34.40	7.30	35.32	10.90	34.37	7.56
	Swift Current	30.95	8.37	26.54	7.54	34.23	6.46	30.28	8.72
Test weight (kg/hl)	Winnipeg	82.32	2.93	85.28	1.61	82.79	2.31	82.42	2.54
	Swift Current	81.97	7.60	78.23	2.52	82.21	1.80	79.18	2.36
Height (cm)	Winnipeg	87.87	11.79	95.62	9.78	87.50	9.53	75.90	11.44
	Swift Current	84.58	11.98	83.84	7.68	92.77	18.13	85.52	6.52
Days to Maturity	Winnipeg	90.12	3.18	97.62	2.82	89.33	2.35	95.90	3.28
	Swift Current	88.36	2.46	92.92	1.99	88.41	2.15	92.61	2.22

TABLE 6.2

ERROR VARIANCES OF SELECTED AGRONOMIC CHARACTERS (IN STANDARD UNITS) IN F_6, PER SE AND AS PERCENTAGE OF ADJACENT CONTROL PLOT

Character	Method of Expression	Cross A		Cross B	
		Winnipeg	Swift Current	Winnipeg	Swift Current
Kernel weight	per se	.375	.278	.437	.471
	% of control	.395	.320	.558	.480
Test weight	per se	.562	.439	.648	.514
	% of control	.502	.473	.634	.583
Height	per se	.217	.285	.319	.250
	% of control	.206	.388	.281	.191
Days to maturity	per se	.688	.559	.582	.534
	% of control	.568	.587	.390	.525

TABLE 6.3

HERITABILITY PERCENTAGES OF SELECTED AGRONOMIC CHARACTERS (IN STANDARD UNITS) IN F_6, PER SE AND AS PERCENTAGE OF ADJACENT CONTROL PLOT

Character	Method of Expression	Cross A		Cross B	
		Winnipeg	Swift Current	Winnipeg	Swift Current
Kernel weight	per se	76.92	83.85	72.04	69.20
	% of control	75.36	80.94	61.30	68.40
Test weight	per se	60.89	71.86	52.04	65.39
	% of control	67.47	69.15	52.83	59.00
Height	per se	87.82	83.38	81.02	85.71
	% of control	88.51	75.89	83.64	89.42
Days to maturity	per se	47.48	61.15	58.96	63.52
	% of control	59.83	57.06	75.43	63.24

data in standard units. These parameters could only be estimated for the 1971 data, the F_6, because the 1970 (F_4) lines were not replicated. Error variances and heritabilities were obtained for unadjusted data as well as for data adjusted as percentage of adjacent control plot. Kernel weight and height had by and large the lowest error variances (Table 6.2) and the highest heritabilities (Table 6.3). For both these agronomic characters adjustments on the basis of adjacent control plots added little if anything to the reliability of their unadjusted values.

To be of use in selection, a character must be transmitted in a predictable manner from year to year. Table 6.4 presents the F_4 to F_6 rank correlations for the four selected agronomic characters. All correlations were highly significant (p = .01). Height ranks were most consistent from F_4 to F_6, with the exception of the data for cross B at Swift Current. This significant negative rank correlation could possibly be the result of a strong interaction with the environments obtaining in 1970 and 1971. However, by comparison to the other height rank correlations, this seems an unlikely explanation. More probably some very definite human error was introduced in the measurement or recording of height.

(b). Relationship to yield

High positive correlation to yield would be essential for effective use of another character to select for high yield. Tables 6.5 (a) and 6.5 (b) present the half-matrices of simple correlations among yield, protein, and the four selected agronomic characters for the F_4 and F_6. This table

TABLE 6.4

RANK CORRELATIONS OF F_4 TO F_6 OF

SELECTED AGRONOMIC CHARACTERS

Character	Cross A		Cross B	
	Winnipeg	Swift Current	Winnipeg	Swift Current
Kernel weight	.543	.489	.524	.195
Test weight	.481	.400	.422	.348
Height	.794	.773	.728	-.358
Days to maturity	.389	.500	.524	.195

NB. All correlations are highly significant (p=.01)

TABLE 6.5 (a)

SIMPLE CORRELATION COEFFICIENTS AMONG YIELD, PROTEIN AND SELECTED AGRONOMIC CHARACTERS: CROSS A

Character	Location	Protein		Kernel weight		Test weight		Height		Days to Maturity	
		F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6
Yield	Winnipeg	.01	.24**	.36**	.17**	.57**	.04	.14*	-.14**	.04	.42**
	Swift Current	-.42**	-.20**	-.05	.06	.00	-.04	-.27**	-.34**	.14*	.10*
Protein	Winnipeg			.28**	.15**	.02	-.12*	.30**	.12*	.35**	.32**
	Swift Current			.32**	-.11*	.17*	-.14**	.36**	.23**	.06	.17**
Kernel weight	Winnipeg					.59**	.29**	.23**	.11	.06	-.06
	Swift Current					.11	.46**	.09	-.03	.29**	-.08
Test weight	Winnipeg							.30**	.29**	-.10	-.44**
	Swift Current							.17*	.12*	.09	-.21**
Height	Winnipeg									.10	-.26**
	Swift Current									.05	.03

F_4 sample size = 193

F_6 sample size = 386

* Significant at 5% level
** Significant at 1% level

TABLE 6.5 (b)

SIMPLE CORRELATION COEFFICIENTS AMONG YIELD, PROTEIN AND SELECTED AGRONOMIC CHARACTERS: CROSS B

Character	Location	Protein		Kernel weight		Test weight		Height		Days to Maturity	
		F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6
Yield	Winnipeg	.13	.31**	.30**	.13**	.47**	.02	.12	.45**	.02	.17**
	Swift Current	-.27**	-.11*	.07	-.08	.20*	.00	.08	-.01	.16*	.26**
Protein	Winnipeg			.08	.13**	-.17*	-.18**	.09	.12*	.14*	.28**
	Swift Current			.10	-.19**	-.14*	-.19**	-.04	.16**	.18**	.27**
Kernel weight	Winnipeg					.50**	-.05	.34**	.18**	.07	-.10*
	Swift Current					.07	.31**	-.07	-.05	.28**	-.15**
Test weight	Winnipeg							.23**	-.07	-.23**	-.14**
	Swift Current							.35**	-.10*	.01	-.15**
Height	Winnipeg									-.11	.17**
	Swift Current									-.15	.17**

F_4 sample size = 215

F_6 sample size = 430

* Significant at 5% level

** Significant at 1% level

is partly presented to show the range of relationships among characters used in this study. Height showed significant negative correlations to yield in both generations for cross A at Swift Current and in cross A in the F_6 at Winnipeg (Table 6.5 (a)). At the latter site for cross A, height was positively correlated ($p = .05$) to yield in the F_4. Kernel weight of cross A (Table 6.5 (a)) had significant ($p = .01$) positive correlations to yield of both generations tested at Winnipeg but non-significant correlations at Swift Current. Kernel weight of cross B (Table 6.5 (b)) showed the same pattern as that for cross A. Height of cross B (Table 6.5 (b)) was positively ($p = .01$) correlated to yield in the F_6 at Winnipeg and non-significantly for the remaining three comparisons. The diverse results obtained from generation to generation and location to location, aside from reflecting differential errors in measurements, also emphasize the effect of environment on the relationship between such characters as are being discussed. Therefore, such agronomic characters are not generally very precise indicators of future generation yields.

Because of the diversity of genotypes present in the nurseries, it would be reasonable to assume that individual lines have different associations of the selected agronomic characters to yield than would be expected from the simple correlation coefficients, which represent average values over the germ plasm pool. In order to ascertain if selecting the top lines or bottom lines for each of the four agronomic characters would result in selecting any of the top yielding lines, Table 6.6 was set up.

The random expectation would be two of the top yielding lines (10%). Selecting for high or low kernel weight in cross A and B did not result in any positive selection for high yield. As a matter of fact, in cross B at Swift Current, the lowest 20 lines for kernel weight included 4 of the top yielding lines. In spite of a negative correlation ($p = .01$) of F_6 height to yield in cross A at Winnipeg (Table 6.5 (a)) high and low height selections included the same number (3) of high yielding lines. In cross A at Swift Current, also with a significant negative ($p = .01$) correlation of height to yield (Table 6.5 (a)), the shortest 20 lines included 4 of the top 20 yielders. Four of the highest yielding lines were included in the tallest 20 lines in cross B at Winnipeg (Table 6.6): with a significant ($p = .01$) positive correlation between height and yield (Table 6.5 (b)). At Swift Current, for cross B, selections based on height were not correlated with yield (Table 6.5 (b)) and this was further indicated by an equal number of lines from tall and short selections in the top 20 high yielding lines (Table 6.6).

For characters to be of predictive value for yield, high rank correlations between the character in the selecting generation and yield in the testing generation must exist. Table 6.7 presents rank correlations of the selected four agronomic characters in the F_4 to the yield of corresponding lines in the F_6. While several of the positive correlations were significant ($p = .05$), none were high. Highly significant ($p = .01$) negative correlations were obtained for F_4 height to F_6 yield for cross A at both locations. Thus, in cross A, the shortest lines in F_4 tended to have the highest F_6 yields. But even these correlations were not

TABLE 6.6

NUMBER OF LINES IN TOP 20 AND BOTTOM 20
FOR SELECTED AGRONOMIC CHARACTERS INCLUDED IN THE
TOP 20 FOR YIELD IN THE F_6 GENERATION

	Cross A				Cross B			
	Winnipeg		Swift Current		Winnipeg		Swift Current	
Character	High	Low	High	Low	High	Low	High	Low
Kernel weight	2	1	1	1	0	2	1	4
Test weight	4	0	2	0	0	3	0	5
Height	3	3	1	4	4	0	2	2
Days to maturity	4	1	2	1	5	0	4	0

TABLE 6.7

RANK CORRELATIONS OF F_4 OF SELECTED AGRONOMIC
CHARACTERS TO F_6 YIELD

	Cross A		Cross B	
Character	Winnipeg	Swift Current	Winnipeg	Swift Current
Kernel weight	.008	.062	.103	.017
Test weight	.018	.055	.027	.164*
Height	-.257**	-.349**	.151*	.115
Days to maturity	-.008	.145*	.152*	.068

* Significant at 5% level
** Significant at 1% level

very high.

To ascertain the association of characters to yield in the highest yielding F_2 families, a profile is presented in Tables 6.8 (a) and 6.8 (b) of the top yielding 10% (six) F_2 families for their yield, protein, kernel weight, test weight, height, and days to maturity. The families chosen averaged the highest yields over the F_4 and F_6 generations at both locations (Winnipeg and Swift Current). Means of the selected characters for the families and the relation to the population means for each character are presented in Table 6.9. As this table illustrates, test weight and days to maturity of the top yielding families were very close to the population mean. This result emphasizes the low C.V.'s observed for these two characters (Table 6.1) and hence the low possibility for progress from selection. In cross A, kernel weight of the top yielding families averaged well below the population mean at both locations (Table 6.9). This contrasts with the significant ($p = .01$) positive correlations between kernel weight and yield obtained at Winnipeg (Table 6.5 (a)). Height of the top yielding families of cross A averaged also well below the population mean (Table 6.9); for this character largely corroborating the predominantly negative correlations of height to yield (Table 6.5 (a)). In cross B, kernel weight of top yielding families tended to exceed mean kernel weight at Winnipeg but be equal to it at Swift Current; while height at both locations was above the mean (Table 6.9).

TABLE 6.8 (a)

PROFILE OF TOP YIELDING 10% (6) F_2 FAMILIES FOR YIELD, PROTEIN, AND SELECTED AGRONOMIC CHARACTERS IN F_4 AND F_6 AT WINNIPEG AND SWIFT CURRENT: CROSS A

Rank	Family Number	Test line numbers	Location	Yield (kg/ha)		Protein (%@13.5%m.b.)		Kernel weight (gm/1000Kernels)		Test weight (kg/hl)		Height (cm)		Days to maturity	
				F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_4	F_4	F_6
1	42	141,142,	Winnipeg	3056.25	3991.75	12.63	13.28	33.80	35.00	86.03	85.93	76.25	80.63	92.00	101.00
		143,144	Swift Current	2747.25	2524.50	13.65	16.31	27.90	26.94	79.16	78.03	68.75	74.25	86.50	93.38
2	28	93, 94,	Winnipeg	1856.33	3901.67	12.17	13.25	25.80	33.75	79.88	85.77	71.67	81.33	87.00	96.17
		95	Swift Current	3016.33	2543.50	13.63	15.22	31.33	28.33	83.62	80.18	67.33	76.00	88.67	91.33
3	45	151	Winnipeg	2235.00	3571.50	14.40	13.15	32.00	35.25	82.55	85.13	97.00	102.50	92.00	100.50
			Swift Current	2836.00	2600.50	14.50	15.60	32.80	27.75	83.19	78.68	91.00	86.50	91.00	92.50
4	82	231,232,	Winnipeg	2154.00	3907.00	12.97	13.55	30.73	34.50	84.27	85.77	76.00	87.00	91.33	100.50
		233	Swift Current	2355.33	2272.17	13.73	15.77	26.87	25.58	81.04	77.82	71.33	79.83	87.67	93.00
5	80	225,226	Winnipeg	1563.50	4098.75	12.50	13.23	26.15	32.13	77.58	84.80	94.50	113.50	91.50	97.50
			Swift Current	2674.50	2345.25	13.15	15.68	27.20	22.50	79.32	75.45	99.50	90.00	88.00	93.75
6	30	100,101,	Winnipeg	1825.00	4121.00	12.90	13.43	25.37	33.25	82.46	84.91	65.00	80.50	87.67	97.17
		103	Swift Current	2133.33	2466.67	14.27	15.20	25.33	24.58	80.40	77.39	63.33	73.17	87.00	91.00

TABLE 6.8 (b)

PROFILE OF TOP YIELDING 10% (6) F_2 FAMILIES FOR YIELD, PROTEIN, AND SELECTED AGRONOMIC CHARACTERS IN F_4 AND F_6 AT WINNIPEG AND SWIFT CURRENT: CROSS B

Rank	Family Number	Test line numbers	Location	Yield (kg/ha)		Protein (%@13.5%m.b.)		Kernel weight (gm/1000Kernels)		Test weight (kg/hl)		Height (cm)		Days to maturity	
				F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6
1	45	132,133	Winnipeg	2975.75	1676.38	13.95	12.66	35.70	33.50	84.54	83.03	97.50	83.63	89.00	95.63
		134,135	Swift Current	2091.50	2214.50	15.15	16.10	31.90	28.50	82.39	79.81	103.25	90.63	87.00	92.50
2	61	181,182	Winnipeg	2555.00	1735.15	14.88	12.16	38.60	34.75	84.61	83.03	92.00	74.50	88.75	93.25
		183,184	Swift Current	2368.75	2162.88	15.20	16.14	34.88	33.19	85.13	80.61	113.75	84.13	86.75	91.50
3	66	195,196	Winnipeg	2660.25	1877.75	16.20	13.66	37.15	34.38	82.29	81.42	94.50	79.00	90.00	96.25
		197,198	Swift Current	2140.50	1995.75	15.53	16.15	34.35	30.50	80.94	77.23	94.50	86.38	87.50	91.00
4	84	224,225,	Winnipeg	2593.67	1695.67	13.83	12.27	40.57	36.25	84.78	82.33	99.00	81.83	89.67	94.50
		227	Swift Current	2116.33	2235.83	15.30	16.10	37.07	31.08	82.55	79.75	87.00	89.17	87.00	93.50
5	82	220,221,	Winnipeg	1889.67	2015.50	13.43	12.37	38.00	35.33	83.92	83.19	91.67	83.67	89.33	96.33
		223	Swift Current	2279.00	2288.33	15.57	16.63	34.43	29.67	82.98	78.68	82.67	89.33	88.33	94.67
6	92	240,241,	Winnipeg	1740.75	2105.50	12.30	12.29	38.35	35.75	83.51	80.94	91.25	80.00	90.00	97.38
		242,243	Swift Current	2286.50	2162.75	14.80	17.10	33.45	28.00	80.94	76.26	92.00	87.13	88.25	95.63

TABLE 6.9

PROFILE OF MEANS OF TOP YIELDING 10% (6) F_2 FAMILIES FOR YIELD, PROTEIN, AND SELECTED AGRONOMIC CHARACTERS

		Cross A						Cross B					
Family Means	Method of expression	Yield (kg/ha)	Protein (%,13.5%m.b.)	Kernel weight (g/100)	Test weight (Kg/hl)	Height (cm)	Days to maturity (days)	Yield (kg/ha)	Protein (%,13.5%m.b.)	Kernel weight (g/100)	Test weight (kg/hl)	Height (cm)	Days to maturity (days)
Winnipeg	Per se	3023.48	13.13	31.48	83.76	85.49	94.53	2126.76	13.34	36.53	83.14	87.38	92.51
	% of population mean	109.65	93.62	96.59	99.95	93.18	100.70	115.67	97.91	104.82	100.64	106.95	99.88
Swift Current	Per se	2542.95	14.73	27.26	79.53	78.42	90.32	2191.06	15.82	32.26	80.61	91.66	90.30
	% of population mean	110.20	93.93	94.82	99.28	93.12	99.65	108.72	100.35	99.98	99.88	102.82	99.77
F_4	Per se	2364.14	13.38	28.78	81.63	78.47	89.20	2303.98	14.68	36.21	83.22	94.93	88.47
	% of population mean	107.64	92.44	93.21	99.36	91.00	99.95	113.67	99.06	104.10	100.87	105.31	99.55
F_6	Per se	3195.36	14.48	29.97	81.66	85.44	95.65	2013.84	14.47	32.86	80.53	84.12	94.35
	% or population mean	111.39	95.05	98.34	99.88	95.22	100.40	110.22	99.31	101.64	99.66	104.22	100.09
Grand Mean	Per se	2783.22	13.93	29.37	81.65	81.96	92.43	2158.91	14.58	34.40	81.88	89.52	91.41
	% of population mean	109.90	93.80	95.76	99.63	93.15	100.18	112.03	99.25	102.49	100.26	104.79	99.82

The results presented in this section would tend to indicate that without having prior knowledge of the material, using either height or kernel weight as adjuncts in selection would tend to result in opposite effects on yield in the two crosses studied. Therefore, in spite of the highest heritabilities and C.V.'s exhibited by these characters, height and/or kernel weight did not exhibit a good predictive value as aids in yield selection.

7. Relation of quality parameters to loaf volume

The great concern for protein in wheat breeding in Western Canada has been due to the well established dependence of bread loaf volume on protein content, rather than on the quantity of protein produced per unit area. Table 7.1 shows highly significant positive correlations, for both crosses tested, of kernel protein and of flour protein to the remix loaf volume.

Quality parameters, in order to be of predictive value for loaf volume, in early generation screening must be related to loaf volume and also be constant from year to year.

Table 7.1 presents simple correlation coefficients for all combinations of the tested quality parameters in both crosses. Flour yield and mixing tolerance index (MTI) showed nonsignificant to significant negative correlations to loaf volume in opposite crosses. Baker and Campbell (1971) found flour yield to be the least repeatable of numerous quality tests. Briggs (1969) found that F_5 MTI could not be predicted from the F_3 value. Dough development time was significantly correlated to loaf volume in both crosses. This is in agreement with the findings of Orth _et al_. (1972) on 26 cultivars at Saskatoon in 1969. Farinograph absorption showed nonsignificant correlations to loaf volume. The sedimentation value was significantly ($p=0.01$) correlated to loaf volume in cross A; but nonsignificantly in cross B.

TABLE 7.1

SIMPLE CORRELATION COEFFICIENTS AMONG QUALITY PARAMETERS OVER TWO YEARS AND LOCATIONS

	Cross A (N = 65)							Cross B (N = 79)						
Character	Kernel protein	Flour yield	Flour protein	Sedimentation value	Farinograph absorption	Farinograph development time	Mixing tolerance index	Kernel protein	Flour yield	Flour protein	Sedimentation value	Farinograph absorption	Farinograph development time	Mixing tolerance index
Loaf volume (remix)	.31**	-.25*	.62**	.34**	-.08	.25*	-.22	.57**	-.19	.68**	-.12	.14	.30**	-.56**
Kernel protein		-.17	.71**	-.13	.29*	-.07	-.03		-.38**	-.81**	-.11	.61**	.32**	.27*
Flour yield			-.27*	-.14	.39**	-.28*	.32			-.43**	.19	-.35**	.18	-.36**
Flour protein				.18	.21	.31**	-.27*				-.05	.62**	.30**	.15
Sedimentation value					.00	.61**	-.45					.14	.30**	-.56**
Farinograph absorption						.00	.09						.24*	.19
Farinograph development time							-.56**							-.30**

Loaf volume, farinograph absorption, farinograph dough development time and sedimentation value were chosen for a small selection study. The simple correlations for these characters from F_4 to F_6 are presented in Table 7.2. The three parameters, aside from loaf volume, were all significantly (p=0.01) correlated from F_4 to F_6 in Winnipeg. Only farinograph absorption showed a significant correlation (p=0.01) of the F_4 Winnipeg performance to the F_6 performance at Swift Current. Sedimentation value was the only one of these parameters which had a highly significant correlation for the F_6 Winnipeg to the F_6 Swift Current performance.

Table 7.3 presents the values for "high" and "low" F_4 selection for the chosen quality parameters in the F_4 at Winnipeg and in the F_6 at both Winnipeg and Swift Current. Though the differences between the "high" group and the "low" group were decreased in the F_6, the group means maintained their relative positions of "high" and "low" as in the F_4, for loaf volume, farinograph absorption, and sedimentation value at both locations, as well as development time at Winnipeg. At Swift Current, in the F_6 the mean development times were reversed: the F_4 "high" group averaged lower than the F_4 "low" group. This can only reasonably be explained by a misnumbering in the F_6 of the upper "low" line. Loaf volume values and sedimentation values were individually most consistent, with the greatest relative differences between the "high" and "low" groups.

TABLE 7.2

SIMPLE CORRELATIONS OVER GENERATIONS AND LOCATIONS FOR SELECTED QUALITY PARAMETERS

Character	F_4 Winnipeg to F_6 Winnipeg		F_4 Winnipeg to F_6 Swift Current		F_6 Winnipeg to F_6 Swift Current	
	r	N	r	N	r	N
Loaf volume	.28	22	.49	9	.28	15
Farinograph absorption	.45**	37	.60**	25	.30	31
Farinograph development time	.46**	37	-.12	25	.23	31
Sedimentation value	.70**	37	.28	25	.64**	31

** Significant at 1% level

TABLE 7.3

PERFORMANCE IN F_6 OF LINES SELECTED FOR HIGH AND LOW VALUES IN F_4 FOR LOAF VOLUME, ABSORPTION, DEVELOPMENT TIME, AND SEDIMENTATION VALUE

Character	F_4 selection group		F_4 Winnipeg	F_6 Winnipeg	F_6 Swift Current
Remix loaf volume (cc)	High		1210	850	1065
			1250	875	1125
			1125	865	1095
		Mean	1195.0	863.3	1095.0
	Low		850	550	-
			820	915	945
			715	825	1010
			850	-	910
		Mean	808.8	763.3	955.5
Farinograph absorption (%)	High		72.6	71.0	66.4
			67.4	65.3	66.9
			68.5	64.9	65.7
		Mean	69.5	67.1	66.3
	Low		60.1	63.7	65.4
			59.4	63.5	61.3
			60.6	60.8	65.5
		Mean	60.0	62.7	64.1
Farinograph development time (minutes)	High		9.0	8.5	6.0
			9.5	4.0	8.5
			8.5	9.0	6.0
		Mean	9.0	7.2	6.8
	Low		2.5	10.0	9.5
			2.5	2.5	8.0
			3.5	4.0	4.5
		Mean	2.8	5.5	7.3
Zeleny sedimentation value (ml)	High		69.0	-	71.0
			69.0	62.0	66.0
			74.0	70.0	71.0
		Mean	70.7	66.0	69.3
	Low		51.0	54.0	67.0
			54.0	55.0	50.0
			46.0	49.0	53.0
		Mean	50.3	52.7	56.7

Although farinograph absorption was significantly correlated (p=0.01) from F_4 to F_6 (Table 7.2) and the selection of "high" and "low" was somewhat effective (more so for the F_6 at Winnipeg than at Swift Current) (Table 7.3), both crosses showed nonsignificant correlations to loaf volume (Table 7.1). Farinograph absorption was significantly correlated to kernel protein (Table 7.1). However, this association alone is inadequate for absorption being a reliable screening parameter for breadmaking quality for the lines tested in this study

Development time, while showing a significant (p=0.01) F_4 to F_6 correlation at Winnipeg (Table 7.2) and positive correlations to loaf volume (Table 7.2) was the least predictive of the chosen parameters in terms of "high" and "low" selections (Table 7.3). Even on the exclusion of the one line put in question above, the selection results are not very definitive. This is corroborated by the high genotype-year interaction and low heritability for development time found by Baker _et al._ (1968). However Briggs (1969), in his Ph.D. thesis, found that F_5 dough development time could be predicted from the F_3 performance.

The more stable reaction of sedimentation value as judged by the highest F_4 to F_6 Winnipeg correlations and highly significant F_6 Winnipeg to Swift Current correlations (Table 7.2), as well as "high" and "low" selections (Table 7.3), is in agreement with the high heritability found for this parameter by Baker _et al._ (1968) and Orth _et al._ (1972). However, while a highly significant positive correlation ($p=0.01$) was obtained for cross A (Table 7.1), as was also found for the 1969 Uniform Quality Nursery in Saskatchewan by Orth et al. (1972), cross B had a nonsignificant correlation, as did Manitou in one year of two in a study by Bushuk et al. (1969). Furthermore, both crosses showed nonsignificant negative correlations of sedimentation value to kernel protein (Table 7.1). This finding is of particular importance, as pointed out by Bushuk et al. (1969), in that the sedimentation test is used by some cereal technologists as the main criterion of bread-making quality. It thus appears that the particular year, locations and/or genotypes involved greatly affect the nature of this correlation of sedimentation value to loaf volume.

On the basis of this study and previous literature, one must conclude that none of the three parameters of farinograph absorption, farinograph development time, and Zeleny sedimentation value are ideal characters to use by themselves in screening early generation material for high loaf volume.

GENERAL DISCUSSION AND CONCLUSIONS

Although in this study the F_4 generation was the first yield nursery instead of the F_3 as suggested for the pedigree programme by Shebeski (1967), it is felt the results should be in no way different from initial selections being made in the F_3 and evaluations made in the F_5 generation.

Bulked seed samples were used as F_6 plots, instead of lines derived from single plant or head selections in the F_4 and/or F_5. The use of F_6 bulks enabled the author to more adequately sample the genetic variability present in the material tested and thus aided in decisions as to how to reduce a breeding population to manageable proportions without unduly diminishing the chances of success.

In a study as the present one, there is a definite conflict between the need for size, for large numbers being handled for meaningful results, on the one hand and the ability to obtain accurate results on the other. Often large numbers of disinterested helpers with little understanding of the need for accuracy are required. One example of possibly mislabeled samples for a quality analysis has been indicated. Other such possible errors were no doubt introduced without having become as strikingly apparent.

The fact that speed of handling the material must not take precendence over care, if much progress is sought in a breeding programme, has been amply illustrated by the 1971 data from combine harvested plots at Swift

Current. With harvesting all plots into the wind, the significant direction-of-harvest yield difference could have been avoided. This would of course require more time because the combine would have to travel idly with the wind across the plot ranges, when strong winds prevent accurate harvesting with the wind.

The data in this study demonstrated how planting plans and handling of the material could lead to quite erroneous conclusions about the methods being evaluated. The confounding factor of interplot competition, from too narrow between-plot spacings at Swift Current could result in apparently random fluctuations of control plot yields in spite of the fact that protein content of the same control plots indicated definite gradients of soil nutrient availability.

Results of this study indicated that above average tillering (20 or more tillers) of F_2 plants was a useful selection criterion in breeding for high yield. Well-tillered F_2 plants were generally associated with higher yielding progeny lines than were poorly-tillered F_2 plants. Furthermore, higher F_2 tillering results in more F_2 seeds being produced, thus increasing the probability that the preferred, highest yielding, genotypes will be present and thus available for selection in later generations.

The data permit one to suggest that selecting for high protein in the F_2 was generally successful in increasing future generation protein content; and that in breeding for high yield, protein quantity need not necessarily be sacrificed. Relatively high heritability for protein and significant intergeneration rank correlations were indicators of potential progress from selections for protein. In selecting for high yielding lines, generally only slightly lower than mean protein levels, for the particular population, were observed; with some lines high in yield actually having protein levels above the population mean. Thus the possibility of breeding primarily for high yield but maintaining protein levels at that of standard varieties (e.g. Neepawa) grown in adjacent control plots, is indicated.

In order to breed for lines of wide adaptability for yield, data from this study permit the suggestion of using the mean yields of at least two locations (Winnipeg and Swift Current) in identifying a few exceptionally good lines of wide adaptability (as indicated by subsequent generation yields). Swift Current selections were somewhat less likely than Winnipeg selections in identifying lines of high yield performance over these two locations. All results dealing with the average performance over the two locations were subject to the direction-of-harvest error and interplot competition effect due to narrower spacings at Swift Current. Therefore the difference between the two locations can be more readily explained on the basis of the somewhat greater variability expressed among lines at Winnipeg. Thus, as Johnson (1967) recommended, selection for genetic gain could be more readily evaluated under conditions permitting full expression of relevant genes, under low environmental stress: at Winnipeg. By the use of winter nurseries in southern latitudes (e.g. Mexico), single plants can readily produce enough seeds for plots at two sites. Many plants will have seed adequate for more plots. Thus, a larger number of yield nurseries could possibly be planted for screening intensely in one year for wide adaptability of yield of early generation lines.

Though visual selection was not very effective in raising yields of selected lines above the population mean in a subsequent generation, it can serve as a useful tool in reducing material to be harvested and processed, providing the expressed variability among lines is great enough to be able to identify high yielders. More lines in more crosses could be handled in a breeding programme. Actual yield tests were only very slightly more effective in identifying lines with high yield potential. With the greater variability among lines found at Winnipeg, in contrast to Swift Current, at the former site high yielding lines could be more readily identified visually. In order to minimize missing some of the top yielding lines, the intensity of visual selections should be reduced from the 10% mainly employed in the present study. A similar suggestion had been made by Briggs and Shebeski (1970).

Some selectors were consistently more capable of visually assessing plot yield than others. It might thus be worthwhile in a future study to try to ascertain the yield-enhancing agronomic features pertaining to the selected lines by the most successful selectors, in order to enable other breeders in improving their power of visual discrimination.

The results presented in this study indicate the value of selecting for yield on the basis of a combination of actual plot yield and on the relation to the yield of an adjacent control plot. At Winnipeg, without the two confounding factors previously mentioned as being present at Swift

Current, top yielding lines in the F_4 on the basis of both criteria mentioned above gave substantial yield improvements in the F_6. These yield levels were considerably greater than those attained with the same selection intensities by either method alone. At lower selection intensities the differences decreased considerably. But even when selecting the top 10% of the lines, those lines included by both methods of selecting have greater yield improvements than either of the methods alone did in the case of one cross (cross A) at Winnipeg. This is in general agreement with the findings of Briggs (1969) of the highest F_5 lines coming from F_3's which were relatively high for both plot yield and percentage of control. The few very high lines are the lines of most value to the breeder which should thus be fully exploited. Remnant F_2 seed could be used to more fully test the range of potentially useful genotypes from F_2's with proven high yielding progeny lines.

Neither tillering in plot rows, nor kernel weight, test weight, height, nor days to maturity were found to be reliable selection criteria for yield of subsequent generations. No consistent correlations, over crosses and locations, were obtained between the expression of any of the above characters in the F_4 and yield in the F_6.

Aside from protein content, none of the quality parameters tested most fully (farinograph absorption, farinograph development time, and sedimentation value) were found to be reliable aids for selecting for good breadmaking quality, as measured by high loaf volume. In this conclusion, it must be borne in mind that the selection test was very small in numbers of lines included. Both kernel and flour protein showed highly significant positive correlations to loaf volume in both crosses. Farinograph development time was also significantly correlated to loaf volume in both crosses. However, lines selected for high and low values of this characteristic in the F_4 did not consistently maintain their relative positions in the F_6 at either Winnipeg or Swift Current. The two other characteristics, farinograph absorption and sedimentation value had inconsistent correlations, over the two crosses, to loaf volume.

REFERENCES CITED

Adams, M. W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, Phaseolus vulgaris. Crop Sci. 7:505-510.

________, and J. E. Grafius. 1971. Yield component compensation -- alternative interpretations. Crop Sci. 11:33-35.

Alber, Karl-Dieter. 1969. Merkmalskorrelationen bei Winter-weizen und ihre Bedeutung für die Selektion von F_2 - Einzelpflanzen. Ph.D. Thesis, Landwirtschaftliche Hochschule, Hohenheim.

Allard, R. W. 1960. Principles of plant breeding, Wiley and Sons, Inc., New York.

________, and J. Adams. 1969. The role of intergenotypic interactions on plant breeding. Proc. of 12th Internat. Congress of Genetics 3:349-370.

________, and A. D. Bradshaw. 1964. Implications of genotype-environmental interactions in applied plant breeding. Crop Sci. 4:503-508.

American Society of Agronomy, Minutes of the Annual Meeting. 1921. Report of Committee on Standardization of Field Experiments. J. Amer. Soc. Agron. 13:358-374.

________. 1933. Report of Committee on Standardization of Field Experiments. J. Amer. Soc. Agron. 25:803-828.

Bains, K. S., K. S. Gill, and K. L. Sehgal. 1972. Epistatic bias in additive and dominance variation and genetic associations between two quality traits in bread wheat. Can. J. Genet. Cytol. 14:49-55.

Baker, R. J. 1968. Effectiveness of control plots. Cereal News 13:26-27.

________. 1971. Effects of stem rust and leaf rust of wheat on genotype-environment interaction for yield. Can. J. Plant Sci. 51:457-461.

________, V. M. Bendelow, and M. L. Kaufmann. 1968. Inheritance of and interrelationships among yield and several quality traits in common wheat. Crop Sci. 8:725-728.

________, and A. B. Campbell. 1971. Evaluation of screening tests for quality of bread wheat. Can. J. Plant Sci. 51:449-455.

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

________, K. H. Tipples, and A. B. Campbell. 1971. Heritabilities of and correlations among quality traits in wheat. Can. J. Plant Sci. 51:441-448.

Bell, G. D. H. and E. J. Kirby. 1966. "Utilization of growth responses in breeding new varieties of cereals." p. 308-319 in The growth of cereals and grasses. ed. F. L. Milthorpe and J. D. Ivins, Butterworths, London.

Bhatt, G. M. 1972. Inheritance of heading date, plant height, and kernel weight in two spring wheat crosses. Crop Sci. 12: 95-98.

Bingham, J. 1968. Zur genetischen und pflanzenzüchterischen Betrachtung der Weizenqualität. Getreide und Mehl 18 (8):61-66.

Boyce, S. W., L. G. L. Copp, and O. H. Frankel. 1947. The effectiveness of selection for yield in wheat. Heredity 1:223-233.

Brandenburger, H. 1970. Einwirkung der Umwelt auf Backqualität bei Weizen und deren Beeinflussbarkeit. Getreide und Mehl 9 (10): 78-80.

Briggs, F. N. and P. F. Knowles. 1967. Introduction to plant breeding. Reinhold Publ. Co., New York.

Briggs, K. G. 1969. The effectiveness of selection for yield and breadmaking quality in *Triticum aestivum* L. in the F_3 generation. Ph.D. Thesis, University of Manitoba.

________, W. Bushuk, and L. H. Shebeski. 1969. Variation in breadmaking quality of systematic controls in a wheat breeding nursery and its relationship to plant breeding procedures. Can. J. Plant Sci. 49:21-28.

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

________, and L. H. Shebeski. 1970. Visual selection for yielding ability of F_3 lines in a hard red spring wheat breeding program. Crop Sci. 10:400-402.

Brown, C. M., R. O. Weibel, and R. D. Seif. 1966. Heterosis and combining ability in common winter wheat. Crop Sci. 6:382-383.

Bushuk, W., K. G. Briggs, and L. H. Shebeski. 1969. Protein quantity and quality as factors in the evaluation of bread wheats. Can. J. Plant Sci. 49:113-122.

Chapman, S. R. and F. H. McNeal. 1970. Gene effects for grain protein in five spring wheat crosses. Crop Sci. 10:45-46.

________, and __________. 1971. Gene action for yield components and plant height in a spring wheat cross. Crop Sci. 11:384-386.

DePauw, R. M. 1970. An evaluation of early generation selection procedures in Triticum aestivum L. M.Sc. Thesis, University of Manitoba.

Dickerson, G. E. 1963. "Biological interpretation of the genetic parameters of populations." p. 95-107. in Statistical Genetics and Plant Breeding. NAS-NRC, Publ. 982.

Donald, C. M. 1968. The breeding of crop ideotypes. Euphytica 17: 385-403.

Dudley, J. W. and R. H. Moll. 1969. Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Sci. 9:257-262.

Environment Canada. 1970-1971. Monthly Record, Meteorological Observations in Canada. Downsview, Ont.

Falconer, D. S. 1960. Introduction to quantitative genetics. Ronald Press Co., New York.

Finlay, K. W. and G. N. Wilkinson. 1963. The analysis of adaptation in a plant breeding programme. Australian J. Agr. Res. 14: 742-754.

Fonseca, Santiago and Fred L. Patterson. 1968. Yield component heritabilities and interrelationships in winter wheat (Triticum aestivum L.). Crop Sci. 8:614-617.

Frankel, O. H. 1947. The theory of plant breeding for yield. Heredity 1:109-120.

Frey, K. J. 1954. The use of F_3 lines in predicting the performance of F selections in two barley crosses. Agron. J. 46:541-544.

________. 1968. Expected genetic advances from three simulated selection schemes. Crop Sci. 8:235-238.

________, and T. Horner. 1955. Comparison of actual and predicted gains in barley selection experiments. Agron. J. 47:186-188.

________, and ________. 1957. Heritability in standard units. Agron. J. 49:59-62.

Gamble, E. E. 1962. Gene effects in corn (Zea mays L.) III. Relative stability of the gene effects in different environments. Can. J. Plant Sci. 42:628-634.

Grafius, J. E. 1956. Components of yield in oats: a geometrical interpretation. Agron. J. 48:419-423.

________. 1965. A geometry of plant breeding. Michigan State University, Research Bul. 7.

________. 1972. Competition for environmental resources by component characters. Crop Sci. 12:364-367.

Grant, M. N. and Hugh McKenzie. 1970. Heterosis in F_1 hybrids between spring and winter wheats. Can. J. Plant Sci. 50:137-140.

Haggag, M. E. A. 1967. Analysis of yield in two high yielding wheat varieties. M.Sc. Thesis. University of Manitoba.

Hamilton, D. G. 1959. Improving Canada's wheats. Agr. Inst. Review 14 (6).

Hänsel, H. 1969. Die verwendung von Intercross-Generationen in der Weizenzüchtung (Zuchtmethode:"Kreuzungsverband"). Z. Pflanzenzücht. 62:24-46.

Hanson, W. D. 1963. "Heritability." p. 125-139. in Statistical genetics and plant breeding. NAS-NRC, Publ. 982.

Harrington, J. B., W. W. Worzella, L. P. Reitz, and E. R. Ausemus. 1946. A summary of genetic studies in hexaploid and tetraploid wheats. J. Amer. Soc. Agron. 38:1082-1099.

Haufe, W. 1969. Planung, Verrechnung und Auswertung von Feldversuchen fur die Zuckerrübenzüchtung mit Hilfe von elektronischen Datenverarbeitungsanlagen. Zucker, (January):40-46.

Hayes, H. K. and R. J. Garber, 1927. Breeding crop plants. McGraw Hill Book Co., New York.

Hazel, L. N. 1943. The genetic basis for constructing selection indexes. Genetics 28:476-490.

Heyne, E. G. and Karl F. Finney. 1965. F_2 progeny test for studying agronomic and quality characteristics in hard winter wheats. Crop Sci. 5:129-132.

Hsu, P. and P. D. Walton. 1971. Relationship between yield and its components and structures above the flag leaf node in spring wheat. Crop Sci. 11:190-193.

Hurd, E. A. 1969. A method of breeding for yield of wheat in semi-arid climates. Euphytica 18:217-226.

________. 1971. "Can we breed for drought resistance?" in Drought injury and resistance in crops. Special Publ. No. 2, CSSA, Madison, Wisc.

Jensen, N. F. and W. T. Federer. 1964. Adjacent row cometition in wheat. Crop Sci. 4:641-645.

Johnson, G. R. 1967. Effectiveness of index selection relative to selection on yield alone at several levels of soil phosphorus. Crop Sci. 7:257-259.

Johnson, H. B., H. F. Robinson, and R. E. Comstock. 1955. Estimates of genetic and environmental variability in soybeans. Agron. J. 47:314-318.

Johnson, V. A., J. W. Schmidt, and W. Mekasha. 1966. Comparison of yield components and agronomic characteristics of four wheat varieties differing in plant height. Agron. J. 58:438-441.

________, S. L. Shafer, and J. W. Schmidt. 1968. Regression analysis of general adaptation in hard red winter wheat (Triticum aestivum L.). Crop Sci. 8:187-191.

Knott, D. R. and B. Talukdar. 1971. Increasing seed weight in wheat and its effect on yield, yield components, and quality. Crop Sci. 11:280-283.

Kronstad, W. E. and W. H. Foote. 1964. General and specific combining ability estimates in winter wheat (Triticum aestivum Vill., Hist.). Crop Sci. 4:616-619.

Kuspira, J. and J. Unrau. 1957. Genetic analysis of certain characters of common wheat using whole chromosome substitution lines. Can. J. Plant Sci. 37:300-326.

Lashin, M. and K. Schrimpf. 1962. Analyse der Ertragsstruktur von Winterweizensorten mit besonderer Berücksichtigung der ertragsbestimmenden Faktoren. Z. Acker- u. Pflanzenbau 114: 253-280.

Lebsock, K. L. and Arnoldo Amaya. 1969. Variation and covariation of agronomic traits in durum wheat. Crop Sci. 9:372-375.

Leng, E. R. 1963. Component analysis in inheritance studies of grain yield in maize. Crop Sci. 3:187-190.

Love, H. H. 1927. A programme for selecting and testing small grains in successive generations following hybridization. J. Amer. Soc. Agron. 19:705-712.

Lupton, F. G. H. 1970. The physiology of cereal yield. FAO Information Bulletin, Near East Wheat and Barley Improvement and Production Project 7 (2):1-6.

McGinnis, R. C. and L. H. Shebeski. 1968. The reliability of single plant selection for yield in F_2. p. 410-415. Proc. 3rd Int. Wheat Genet. Symp., Canberra.

Mac Key, J. 1966. The wheat plant as a model in adaptation to high productivity under different environments. Contemp. Agriculture 11-12:37-48.

McNeal, F. H., M. A. Berg, R. K. Bequette, C. A. Watson, and E. J. Koch. 1964. Early generation selection for flour absorption and dough mixing properties in a Lemhi x Thatcher wheat cross. Crop Sci. 4:105-108.

_______, M. A. Berg, C. A. Watson, and E. J. Koch. 1969. Selection for baking quality in early generations of a Lemhi x Thatcher wheat cross. Crop Sci. 9:501-503.

Matzinger, D. F. 1963. "Experimental estimates of genetic parameters and their applications in self-fertilizing plants." p. 253-276. in <u>Statistical Genetics and Plant Breeding</u>. NRC-NAS, Publ. 982.

Melton, B. and M. D. Finkner. 1967. Relative efficiency of experimental designs with systematic control plots for alfalfa yield tests. Crop Sci. 7:305-307.

Moll, R. H., K. Kojima, and H. F. Robinson. 1962. Components of yield and overdominance in corn. Crop Sci. 2:78-79.

Morley, F. H. W. 1961. Discussion: "Statistics and plant selection." P. 218-222. in Statistical Genetics and Plant Breeding. NAS-NRC, Publ. 982.

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

Orth, R. A., R. J. Baker, and W. Bushuk. 1972. Statistical evaluation of techniques for predicting baking quality of wheat cultivars. Can. J. Plant Sci. 52:139-146.

Palmer, R. P. 1952. Population and selection studies in a Triticum cross. Heredity 6:171-185.

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

Petr, F. C. and K. J. Frey. 1966. Genotypic correlations, dominance, and heritability of quantitative characters in oats. Crop Sci. 6:259-262.

Plarre, W. 1971. Die Züchtung leistungsfähiger Getreidesorten als Beitrag zur Sicherung der Welternährung. Supplement 2, Z. Pflanzenzücht.

Platzer, H. 1971. Genetisch-züchterische Untersuchungen zur Kornqualität des Weizens. Z. Pflanzenzücht. 66:55-66.

Pollmer, W. G. 1957. Untersuchungen zur Ertragsbildung bei Sommerweizen. Z. Pflanzenzücht. 37:231-262.

_______. 1961. Ertragsstrukturen von Winter- und Sommerweizen. Z. Acker- u. Pflanzenbau 113:361-370.

Rasmusson, D. C. 1968. Yield and stability of yield in barley populations. Crop Sci. 8:600-602.

_______, and R. Q. Cannell. 1970. Selection for grain yield and components of yield in barley. Crop sci. 10:51-54.

Reddi, M. V., E. G. Heyne, and G. H. L. Liang. 1969. Heritability and interrelationships of shortness and other agronomic characters in F_3 and F_4 generations of two wheat crosses (Triticum aestivum L. em Thell.). Crop Sci. 9:222-225.

Robinson, H. F., R. E. Comstock, and P. H. Harvey. 1951. Genotypic and phenotypic correlations in corn and their implications in selection. Agron. J. 43:282-287.

Robinson, P. 1963. "Heritability: a second look." p. 609-614. in Statistical Genetics and Plant Breeding. NAS-NRC, Publ. 982.

Rod, Jan and Franz Weiling. 1971. Untersuchungen zur Analyse der Ertragsstruktur bei Sommergerste mit besonderer Berücksichtigung der Stabilität von Einzelmerkmalen. Z. Pflanzenzücht. 66:93-129.

Roy, R. K., R. N. Sinha, and R. Prasad. 1969. Relationship of the plant characters attributing to the yield of dwarf wheat varieties. Indian J. Agron. 14:233-235.

Salmon, Cecil. 1914. Check plats -- a source of error in varietal tests. J. Amer. Soc. Agron. 6:128-131.

Schrimpf, K. 1960. Die Bedeutung bestimmter entwicklungsphysiologischer Beobachtungen für die Züchtung auf Ertrag. Z. Pflanzenzücht. 43:390-403.

Seed Scoop. 1972. (May). Canadian Seed Growers' Association, Ottawa. 19 (4):5.

Shebeski, L. H. 1966. Quality and yield studies in hybrid wheat (*Triticum aestivum* L.). Can. J. Genet. Cytol. 8:375-386.

________. 1967. "Wheat and breeding." p. 249-272. in Proc. Can. Centennial Wheat Symp. ed. K. F. Nielson, Modern Press, Saskatoon.

Singh, S. P., M. S. Shrivastava, and S. V. Valanker. 1970. Variability and correlation coefficients for grain yield and other quantitative characters in *Triticum durum* Desf. Indian J. Agric. Sci. 40:1042-1045.

Smith, E. L. and J. W. Lambert. 1968. Evaluation of early generation testing in spring barley. Crop Sci. 8:490-493.

Smith, H. F. 1936-1937. A discriminant function for plant selection. Annals of Eugenics 7:240-250.

________. 1938. An empirical law describing heterogeneity in the yields of agricultural crops. J. Agr. Sci. 28:1-23.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods. Iowa State Univ. Press, Ames.

Sprague, G. F. 1966. "Quantitative genetics." p. 315-354. in Plant breeding. ed. K. J. Frey, Iowa State University Press, Ames.

Stebbins, G. L. jr. 1950. Variation and evolution in plants. Columbia University Press, New York and London.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw Hill Book Co., Inc. New York.

Stoskopf, N. C. and E. Reinbergs. 1966. Breeding for yield in spring cereals. Can. J. Plant Sci. 46:513-519.

Sun, P. L. F., H. L. Shands, and R. A. Forsberg. 1972. Inheritance of kernel weight in six spring wheat crosses. Crop Sci. 12: 1-5.

Swamy Rao T. and J. V. Goud. 1971. Recent trends in rice breeding in Mysore State: IV. Correlations, coheritability and selection indices for yield components in three environments. Z. Pflanzenzücht. 65:121-128.

Thorne, G. N. 1966. "Physiological aspects of grain yield in cereals." p. 88-105. in The growth of cereals and grasses. ed. F.L. Milthorpe and J. D. Ivins, Butterworths, London.

Trujillo-Figueroa Rafael. 1968. Indirekte Frühselektion auf induzierte genetische Variabilität in Ertragsmerkmalen nach EMS-Behandlung von Weizen. Z. Pflanzenzücht. 60:327-348.

Virk, D. S. and S. C. Anand. 1970. Studies on correlations and their implications in selection in wheat (Triticum aestivum L.). Madras Agr. J. 57:713-717.

Walker, J. T. 1969. Selection and quantitative characters in field crops. Biol. Rev. 44:207-243.

Walton, P. D. 1970. The inheritance of morphological characters associated with yield in spring wheat. Proc. 16th Annual Meeting, Can. Soc. Agron. p. 7-11.

________. 1971. The genetics of yield in spring wheat (Triticum aestivum L.). Can. J. Genet. Cytol. 13:110-114.

Watson, D. J. 1952. The physiological basis of variation in yield. Adv. Agron. 4:101-145.

Whitehouse, R. N. H., J. B. Thompson, and M. A. M. Do Valle Ribeiro. 1958. Studies on the breeding of self-pollinated cereals. 2. The use of a diallel cross analysis in yield prediction. Euphytica 7:147-169.

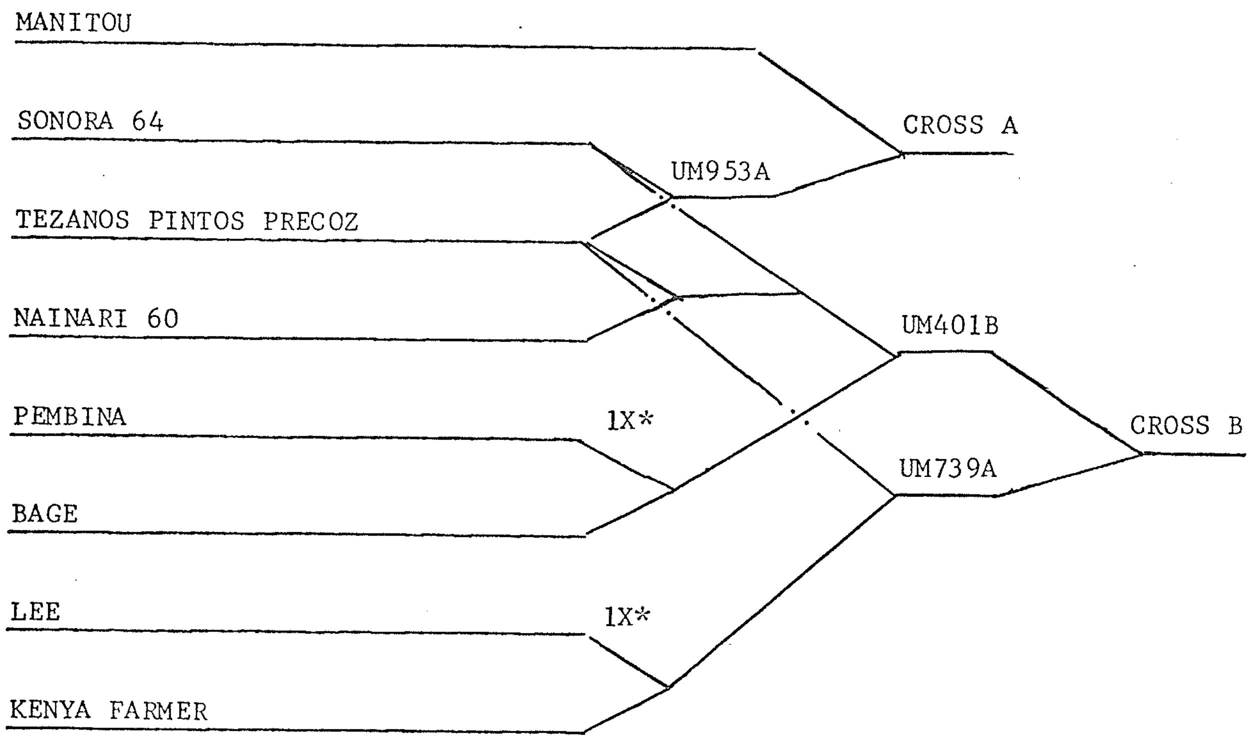
Yates, F. 1936. A new method of arranging variety trials involving a large number of varieties. J. Agr. Sci. 26:424-455.

APPENDIX I

Parents and varietal background of the two crosses

Cross A:	UM953A x Manitou
Manitou	A standard awnless, tall Canadian hard red spring wheat of good baking quality. Its parentage is: ((Thatcher^5 x Kenya Farmer) (Thatcher^6 x Frontana)) (Thatcher^5 x P.I. 170925).
UM953A	A hard red spring wheat selection at the University of Manitoba from the cross: Sonora 64 x Tezanos Pintos Precoz (TZPP). It is somewhat higher yielding than Manitou at Winnipeg; equal to Manitou at Swift Current. Seed weight is somewhat greater and height slightly shorter than Manitou. Breadmaking quality is somewhat inferior to that of Manitou.
Cross B:	UM401B x UM739A
UM401B	A hard red spring wheat selection at the University of Manitoba from the cross: (Pembina^2 x Bage) x (Sonora 64 x (TZPP-Nainari 60)). It is an awnless, semidwarf, strong dough wheat.
UM739A	A hard red spring wheat selection at the University of Manitoba from the cross: (Lee^2 x Kenya Farmer) x TZPP. It is an awned, tall, good quality wheat.

APPENDIX I. (con't)



* Number of backcrosses to top variety.

APPENDIX II.

Field and laboratory data obtained

Yield	Plot grain yield in grams converted to kg/ha for comparing results from different plot sizes.
Tillers	F_2 and F_3: effective tillers (with mature seed or nearly so at harvest time) of single plants.
	F_4: fertile heads in a uniform meter length of one row, near harvest time.
Height	In centimeters, average of three readings along the plot, from soil level to the tip of heads (excluding awns) of taller plants in a group.
Days to maturity	Days from seeding date to the day when the extreme top part of about 75% of the stems was completely yellow (i.e. no green traces evident).
Lodging	Scale from 1 = erect to 5 = severely lodged, near harvest time.
Leaf rust reaction ..	F_4: Scale from 1 = least affected to 9 = large area of flag leaves affected.
	F_6: Percentage of flag leaf area covered.
Stem rust reaction ..	F_4: Scale from 1 = resistant to 13 = fully susceptible, with values in between indicating medium resistance (MR) and medium susceptibility (MS) as well as the lines' segregation for reaction types.
	F_6: Percentage of plants affected.
Kernel weight	Weight in grams of 100 sound seeds manually counted, multiplied by 10 to give "thousand kernel weight."
Test weight	Weight of seeds per unit volume (kg/hl) as measured by use of a 0.529 liter (one pint) cylinder and a calibrated scale.

APPENDIX II. (con't)

Protein percentage ..	Seed protein as determined by oven drying and Kjeldahl analyzing one gram of ground seeds and converting to a 13.5% seed moisture basis.
	F_4 Winnipeg: triplicate samples averaged out.
	F_4 Swift Current: duplicate samples averaged out.
	F_6: single samples.

APPENDIX III

TEMPERATURE AND PRECIPITATION DATA

	1970				1971					
	Winnipeg		Swift Current		Winnipeg		Glenlea		Swift Current	
Month	Average Temp. °C	Total Precipit. mm	Average Temp. °C	Total Precipit. mm	Average Temp. °C	Total Precipit. mm	Average Temp. °C	Total Precipit. mm	Average Temp. °C	Total Precipit. mm
April	1.4	59.7	2.0	31.5	3.2	35.6	3.1	59.4	4.4	15.5
May	9.3	82.0	9.4	22.6	10.2	32.8	10.4	28.7	12.2	10.7
June	18.9	56.4	18.0	185.9	17.5	75.7	17.9	52.8	15.4	68.1
July	20.5	98.0	18.7	27.2	16.4	134.1	16.9	83.3	16.7	42.4
August	18.9	26.7	18.5	9.4	18.8	22.6	18.6	33.5	21.5	3.8

Winnipeg: Temperature taken at International Airport
Precipitation taken at University of Manitoba (Campus)

Glenlea: Data taken at University of Manitoba Glenlea Research Farm

Swift Current: Data taken at CDA Research Station, South Farm

Note: Winnipeg International Airport, Glenlea, and Swift Current readings obtained from: Environment Canada (1970-1971)

APPENDIX IV

TESTS FOR NORMALITY OF YIELD DATA

Generation	Cross	Number of lines	Location	Form of data	Yield per se		Yield as percentage of adjacent controls	
					Skewness	Kurtosis	Skewness	Kurtosis
F_4	A	193	Winnipeg	untransformed	-.052	3.83	-.329	3.14
				log transformed	-.713**	3.92*	-.577**	2.72
			Swift Current	untransformed	-.190	2.73	-.106	2.37*
				log transformed	-.388*	2.49*	-.335*	2.41*
	B	215	Winnipeg	untransformed	-.233	2.47*	.103	3.38
				log transformed	-.649**	2.62	-.396*	2.95
			Swift Current	untransformed	.023	2.72	.061	3.06
				log transformed	-.504**	3.35	-.223	2.72
F_6	A	193	Winnipeg	untransformed	-.561**	3.98**	.458**	5.39**
				log transformed	-.746**	3.95*	-.169	5.03**
			Swift Current	untransformed	.062	2.83	.121	2.93
				log transformed	-.238	2.42*	-.196	3.06
	B	215	Winnipeg	untransformed	.323*	2.75	.187	3.06
				log transformed	-.304*	2.80	-.247	3.21
			Swift Current	untransformed	.009	2.48*	.017	2.79
				log transformed	-.156	2.10**	-.434**	3.23

* Significant at 5% level
** Significant at 1% level

(See Snedecor and Cochran, 1967, p. 552)

APPENDIX V (a)

TOP YIELDING TEN PERCENT (20) LINES

Line Rank	Cross A				Cross B			
	Winnipeg		Swift Current		Winnipeg		Swift Current	
	F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6
(i) "Yield per se" basis								
1	142	225	95	141	133	75	238	78
2	144	100	133	181	132	240	228	231
3	143	103	230	13	196	208	239	63
4	139	232	143	221	78	241	209	206
5	173	144	94	222	63	197	110	159
6	137	86	93	42	76	22	53	15
7	188	143	226	142	134	115	123	158
8	141	18	26	76	224	147	124	214
9	187	146	49	147	181	196	223	113
10	152	33	184	133	135	85	70	18
11	138	94	74	86	195	156	231	17
12	140	135	194	18	147	179	236	171
13	157	228	60	103	79	220	112	53
14	177	76	151	219	188	53	184	182
15	129	141	29	151	43	11	230	180
16	166	24	145	178	140	63	229	236
17	126	209	195	95	11	221	215	66
18	170	233	187	94	197	194	19	229
19	176	93	222	186	124	213	24	230
20	72	4	178	188	87	170	240	190
(ii) "Yield as percentage of adjacent control plot" basis								
1	72	76	226	222	101	208	238	173
2	103	5	230	180	63	230	169	78
3	143	17	185	79	224	215	61	231
4	38	118	133	13	132	100	53	214
5	129	217	95	133	211	179	129	182
6	137	226	49	15	88	214	101	230
7	22	225	169	56	100	132	181	208
8	142	23	234	231	94	200	229	215
9	47	159	187	76	207	196	124	20
10	17	104	72	219	135	55	123	221
11	100	100	94	33	225	241	110	174
12	209	82	231	3	227	101	19	62
13	132	144	151	194	102	54	66	125
14	31	202	236	204	133	84	135	66
15	166	24	134	48	242	22	236	159
16	138	233	103	145	78	113	239	180
17	35	7	81	181	181	57	209	76
18	50	133	145	178	119	73	112	86
19	144	207	46	159	196	159	184	70
20	176	33	136	158	93	75	93	233

APPENDIX V (b)

TOP YIELDING TEN F_2 FAMILIES IN F_4 AND F_6

F_2 Family Rank	Cross A				Cross B			
	Winnipeg		Swift Current		Winnipeg		Swift Current	
	F_4	F_6	F_4	F_6	F_4	F_6	F_4	F_6
(i) "Yield per se" basis								
1	42	30	28	79	45	92	90	6
2	41	80	17	58	27	82	86	51
3	46	42	45	45	66	39	7	57
4	62	82	40	28	21	60	44	86
5	38	28	42	42	62	74	62	24
6	53	6	9	26	84	18	75	82
7	39	44	23	30	15	7	41	50
8	57	83	38	62	30	66	81	57
9	68	39	80	5	61	26	61	84
10	33	8	62	44	63	74	74	5
(ii) "Yield as percentage of adjacent control plot" basis								
1	42	80	28	79	34	34	44	57
2	13	23	45	58	84	69	90	75
3	41	2	40	5	32	73	34	86
4	6	35	13	45	45	92	62	24
5	39	45	62	28	21	32	86	6
6	74	6	42	80	27	19	61	59
7	17	70	80	16	61	44	32	82
8	7	82	83	40	35	75	45	81
9	11	20	38	30	15	59	41	51
10	30	8	7	26	48	45	7	27