THE EFFECTIVENESS OF SELECTION FOR YIELD AND BREADMAKING QUALITY IN *TRITICUM AESTIVUM* L. IN THE F3 GENERATION

A Thesis

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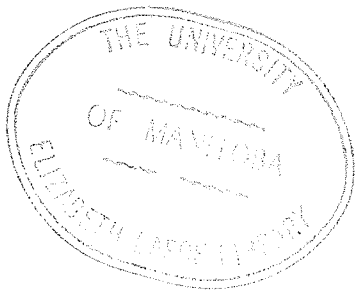
of the Requirements for the Degree

Doctor of Philosophy



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by

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ABSTRACT

A system of early generation selection for yield and breadmaking quality of Triticum aestivum L. was investigated in which initial selection was conducted between unreplicated F3 lines. This study differed from previous work by its radical approach to the design of F3 nurseries. The objectives of the study were a) to obtain some information about the amount and distribution of variability, due to environment, for yield and quality parameters in wheat breeding nurseries, as measured by frequent systematic controls; b) to examine the interrelationships of yield, wheat protein content and breadmaking quality in the variety Manitou in different years; and c) to examine the yield and quality performance in later generations of various selections made in F3 for various yield and breadmaking quality parameters.

In three different selection nurseries it was shown that the yields of control plots nine feet apart were highly significantly correlated. The correlation between yields decreased rapidly with increasing distance between plot centers. A similar analysis was conducted for fourteen breadmaking quality parameters for one nursery in which the variety Manitou was used as the control. Correlations calculated for control plots at specified distances apart indicated that, for all important breadmaking quality parameters, contiguous plots were significantly more similar than those further apart. Areas of high and low yield potential and high and low quality potential could be identified in wheat nurseries by using yield and quality data from controls at frequent intervals. This information should be used by plant breeders when assessing unreplicated breeding lines from a given area of the nursery.

A highly significant positive correlation was obtained between grain yield and wheat protein content in each of two years for the variety Manitou. The breadmaking quality of the Manitou controls was significantly different in the two years. In both years most of the quality parameters were significantly and positively correlated with wheat protein content. The actual quantitative relationship between each of the various parameters and wheat protein content was consistent from year to year only for flour protein content, flour ash, flour color and remix loaf volume. It was recommended that in each year a series of Manitou wheat samples with as wide a range as possible for wheat protein content should be analysed for breadmaking quality. Quality data from single breeding lines could then be compared to the data for Manitou samples of equivalent protein content.

Evaluation of the effect of selection in three different F3 populations was achieved for two yield parameters ("Plot grams yield" and "Percent of adjacent control yield") and for fourteen quality parameters by examining the performance of F3 selections in the F4 and F5 generations. The only characters for which the mean performance of F5 populations could be predicted from the F3 were wheat protein content and Farinograph characteristics (excluding mixing tolerance index), and in one year out of three for "Plot grams yield" and "Percent of adjacent control yield". The good relationship between F3 and F5 for the two yield variables was obtained in the only year of the three in which the maximum range of the yields in the F3 population was sampled. Selection within the upper region of the spectrum in F3 for either of the yield variables alone was ineffective in the other two years, but in all three years the "best yielding" F5 populations were derived from F3 plots which were in the higher area of the F3 population for both yield

variables. In each of the three years significant differences existed between F5 population means for the two yield variables, and also for the majority of the quality parameters. Selection between F5 populations should be very effective for those variables.

Evidence was obtained which indicated that the use of the variable "Percent of adjacent control yield" was effective in removing some of the effects of variability in yield caused by the influence of environment.

The format for this thesis is outlined below,and has been approved by the Council of the Faculty of Graduate Studies and Research of the University of Manitoba.

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INTRODUCTION

Canada has been an important world producer of hard red spring wheats for many years and the very desirable high breadmaking quality of these wheats has resulted in the establishment of a substantial export trade in grain and flour. There is considerable concern in many areas that the world requirement for this export commodity will fall as the result of major changes in breadmaking technology in importing countries, coupled with the development of higher quality wheats in those countries, and that this will result in diminishing demands for Canadian wheats. Any agricultural development which will assist in the reduction of production costs of wheat will help in keeping the commodity competitive on the world market. In this respect the breeding of higher yielding wheats which do not sacrifice the traditional Canadian standards of quality is a research project which demands considerable effort.

From the time that the first Western Canadian wheat crop was grown in the Selkirk area in 1812 a large number of different varieties has been developed and grown in Western Canada. The first variety produced from a program of crossing in Canada was developed by Dr. W. Saunders and resulted in the release of Marquis in 1907. The myriad of varieties released since then include such varieties as Selkirk, Pembina, Manitou, Rescue, Chinook, Saunders and Neepawa. Most of these varieties have two general features in common. Firstly, in the pedigree of these varieties it is noticeable that they all have a substantial amount of germplasm which relates back to the variety Marquis, or to the variety Thatcher which is itself a Marquis derivative [19]. Secondly, most of the varieties have been released to cope with a specific

problem of wheat production as it arose. Thus Selkirk was released to combat the stem rust epidemic caused by race 15B from 1950 onwards. Rescue and Chinook were developed specifically to overcome the susceptibility to sawfly attack in certain areas of Alberta and Saskatchewan. There is no doubt that this approach to breeding for specific phenotypic requirements, termed by Donald [33] breeding for "defect elimination", has been extremely successful in maintaining the growing of wheat in Canada as a profitable venture. Nevertheless, an examination of the historical records reveals that present day yields on the farm may not be very much greater than they were some eighty years ago. Macoun [87] in 1882 collected data from some 56 "respectable and intelligent" farmers and indicated that the average wheat yield in the Canadian North West was of the order of twenty-six bushels to the acre. Gray [46] also reported that the average wheat yield of twenty-six bushels to the acre reported in 1915 for the Palliser Triangle area of the Canadian prairies was a record which was unbeaten for forty years. In comparison with this is the reported average wheat yield of 20.5 bushels per acre in the Prairie provinces for the period 1961 to 1965, with a record average yield of 27.9 bushels per acre in 1966 [26]. In 1959 Hamilton [50] indicated that in spite of considerable plant breeding effort over a period of twenty years, a variety with greater yield potential than Thatcher had not been produced.

There are two possible major reasons for the limited advances in yield potential which have been made with Canadian varieties. The first possibility is that the limit for yield potential under Prairie conditions has been reached and that no further useful genetic variability for yield exists which could be incorporated into new varieties. Few Canadian wheat breeders support this viewpoint, although many of the Canadian wheat

programs have made extensive use of backrossing to Marquis type genetic backgrounds in order to ensure the quality standard of their lines, thus voluntarily limiting the potential genetic variability. The second possibility is that the conventional methods used in the production of new varieties are insufficiently sensitive to detect the real differences in yield potential of superior cultures which are actually present in the breeding program, and which are never identified. Hurd [64] working in Saskatchewan illustrated that the genetic variability for yield is not limiting and supported the view that it is the methods of selection which need re-examination. A critical appraisal of the range of selection methods presently used and a consideration of the relationship of these methods to the genetical processes for quantitative characters which are occurring in segregating populations would surely reveal that some selection methods were more efficient than others in obtaining the same objectives. Identification of the superior methods is a necessary objective for efficient plant breeding.

There are many methods of selection which are used throughout the world and experimental comparisons of these methods are beyond the physical research capacity which most plant breeding units possess. Because of the large amount of material which has to be carried for several generations, most investigations into plant breeding methodology are restricted either to examination of just one method, or at most to a comparison of two methods used simultaneously on the same genetic material. Shebeski [108] conducted a survey of wheat breeders throughout the world to find out the methods which are being used in the improvement of wheat varieties and found that despite similar objectives the methods used were extremely diverse. However, all of the breeders were concerned with attempts to isolate the superior

progenies or plants in their program and the common problem was obviously one of identification. The majority of the breeders were using the pedigree method, or modifications of it, though MacKey J. (personal comm.) indicated that many European breeders were using the bulk method up to the F4 generation, followed by pedigree selection.

In programs designed to select for quantitative characters such as yield, Shebeski considered that many of the methods used were based more on tradition than on a knowledge of the genetics of quantitative characters. He made specific criticisms of many of the systems of handling segregating populations and, on the basis of a particular model for quantitative inheritance, outlined a modified pedigree method for breadwheats, involving early generation selection. This method was designed to eliminate many of the defects of existing pedigree systems. The method relied primarily on a rigorous initial selection for measured yielding ability and breadmaking quality on the F3 line basis, the use of large populations at all stages of selection, coupled with the use of winter nurseries in Mexico, and on a new approach to the arrangement of field trials containing large numbers of entries. It was suggested that the F3 performance would provide a very good basis for prediction of both yield and quality in subsequent generations provided a) large F3 plots were used, containing up to 750 plants each, b) plots were separated from one another sufficiently to eliminate interplot competition and c) an adequate number of control plots was used in the nursery as an aid in allowing for fluctuating environmental effects throughout the field.

This study was initiated in 1965 in order to examine the effectiveness of the method suggested by Shebeski. The main areas of interest were

the relationship of the F3 to subsequent generations for yield and quality, and measurement of the amount and distribution of variability for the yield and quality of systematic controls in the breeding nurseries. Interrelationships of the quality parameters in the control variety Manitou were also obtained for two years. Consequences of the findings from each of these areas of research were discussed in relation to practical plant breeding procedures.

LITERATURE REVIEW

1. Variability in yield due to environmental effects in selection nurseries, and the use of control plots

The largest problem facing the plant breeder attempting to select superior lines for yield or other criteria from a breeding nursery is the limit of his ability to distinguish between the relative amounts of environmental and genetic effect on the phenotype. If environmental effects were very small or constant throughout the nursery, selection for genetically superior lines at any stage of the breeding program would be simple. This state is never obtained under field conditions and more commonly environment X genotype interactions occur which further complicate the ability to select the genetically superior lines on a rational basis. The plant breeder is therefore compelled to use experimental designs which will permit him to measure the environmental effects in the selection nursery and to allow for them when making selection decisions. The various approaches of experimental design which allow this to be done have been described by Cochran and Cox [30] and do not require reiteration. LeClerg [79] made an extensive review of the effects of soil heterogeneity on field experiments and illustrated the development of the principles of experimentation, starting from the use of uniformity trials in the early part of the 20th century.

An exact measurement of the amount of variability in yield due to environment can be obtained from uniformity trials, where a complete nursery is planted to a constant variety and the entire area is harvested in separate but equal sized plots. These plots are weighed separately, thus allowing an examination of both the amount and distribution of

variability for yield in the nursery. The majority of the variability is usually attributed to the effect of soil heterogeneity. Many such uniformity trials have been conducted since 1900 and the details and uses of the data from many of these were catologued by Cochran [29] in 1937, for many different crops and years. Several consistent findings emerged from this review and were confirmed by more recent results from uniformity trials by Elliott et al [34] using spring wheat, and by Garber et al [45] with oats and winter wheat. Firstly, the amount of variability for yield was large, even in fields which had been visually assessed as being uniform. Secondly, the variability was not distributed at random, but plots closer together tended to give more similar yields than those further apart. Correlations between yields of adjacent plots in uniformity trials of cereal crops, as reviewed by LeClerg [79] were usually high. "Student" [120] in 1923 had already highlighted some of these findings when he stated that in a field "... yield varies from point to point with an irregular regularity; there is consequently correlation between one plot and its neighbours and generally there is a tendency for one end of a field to yield more than the other". He attributed this effect mainly to soil heterogeneity.

Prior to the development of procedures of experimental design by Fisher [38] utilising replication and statistical analysis to measure the variance component due to environment, plant breeders tended to use field nurseries in which entries were unreplicated [79]. Direct comparisons of yield between lines in different parts of the nursery were thus confounded with the effect of environmental differences between the various sites. Cereal breeders in the United States were aware of these limitations and investigated the use of systematic control plots of single

varieties grown at regular intervals throughout the nursery. Wiancko [130] described and recommended the use of controls as every third plot in fertilizer experiments and described the various ways in which yield information from the controls could be used to correct the values of the treatment plots for effects of natural variation in the test. Salmon [107] outlined some of the problems relating to the use of check plots but recommended their use if circumstances did not permit replication. Pritchard [102] suggested that the greatest benefit from using controls would be obtained if the control and line under test were as close together as possible, provided interplot competition was avoided. Other methods of using control information, including the use of moving averages, have been adequately reviewed by LeClerg [79]. Interest in the methods of experimental design which use controls appeared to diminish rapidly after 1933, following the revised Report on Standardization of Field Experiments presented by the American Society of Agronomy [4]. This report recommended the use of replication as the "most effective means for reducing the effects of soil heterogeneity and other random errors", and suggested that this technique removed the necessity for including frequent check plots for the purpose of weighting yields. Yates [133] in 1936 described the "pseudofactorial design" suitable for testing large numbers of varieties and pointed out that information from systematic controls could be used in the analysis. Yields of entries would be corrected for position in the nursery, using any desirable function of the control data, and then the data would be analysed in the same way as in a normal Analysis of Variance. More recently Baker et al [12] recommended that if control plots are used in experiments with unreplicated treatments then the yield data from these controls should be used as a

covariate. He questioned the use of frequent controls for measuring the effects of heterogeneity in breeding nurseries, mainly on the basis that the extra precision which might be obtained in selection of superior lines would not compensate for the extra amount of labour involved in handling the controls. Richey [105] indicated in 1926 that the moving average method with controls was relatively successful in increasing the precision of field experiments, but he also expressed doubt whether the increase in precision was worth the extra effort involved.

A plant breeding method for self-pollinated crops suggested by Shebeski [110] in 1967 required the necessity of yield testing as many as 1000 unreplicated F3 lines in a test simultaneously. Acceptable and convenient experimental designs which would be suitable for using in this situation do not appear to be available. In the absence of such designs Shebeski therefore recommended the use of the control method, with controls every third plot throughout the nursery and F3 lines in the intervening two plots. Every F3 line was therefore grown next to a control and the yield of each line could be expressed both as the "Actual Grams Yield" and in relation to the yield of the adjacent control, as a percentage. The percentage method is just one of many covariate methods which could be used [133] and was chosen as being the most convenient. Haggag [49] used the adjacent control sytem in this way and found that the "percent control" measure was effective in removing environmental effects, particularly those due to location. Shebeski recommended the use of rodrow plots consisting of three rows each, with rows separated by six inches within plots and with two feet between rows in adjacent plots. The wide spacing between plots was chosen in an attempt to minimize the effects of interplot competition. Jensen and Federer [69] illustrated

that with winter wheat the competitive effects between plots separated by only one foot were quite severe and affected yields significantly. With rows separated by two feet this effect did not appear to be significant. However, the wide interplot spacing used by Shebeski may have introduced a separate source of variability in the form of genotype X alley effect interaction [4]. Brown and Weibel [24] described significant interaction of this type for yield in two out of four replicated winter wheat and spring oat tests, using two foot spacing between plots. A highly significant alley effect resulting in higher yields of the outer rows of four row plots was obtained in all four tests, and the difference in yield of inner and outer plot rows was attributed to differences in tillering capacity. Since all three rows are harvested in the three row plot suggested by Shebeski this effect of genotype X row spacing may be of considerable importance in determining the total plot yield. Selection of the highest yielding F3 plots in that case would tend to result in selection of lines which respond to conditions of wide row spacing, rather than to the conditions of relatively narrow spacing found in the solid stands in the farmer's fields. Further investigation of the use of various kinds of nursery plot would be very desirable, but is beyond the scope of this thesis which is restricted to an investigation of the three row plot method.

2. Variability in breadmaking quality of wheat due to environmental effects within selection nurseries

Shebeski [110] suggested that selection for breadmaking quality in wheat crosses could start on the single plot determination basis in the F3 generation. In a system of this kind decisions on whether to select or discard individual F3 lines are based on unreplicated observations

of quality. It is therefore very important to have some idea of the amount of variability for quality which could be expected from recommended commercial varieties grown under the same conditions, and to see whether the quality of particular F3 lines falls within this range. A review of the literature reveals that very little work has been carried out in this area of research. Studies equivalent to uniformity trials do not appear to have been attempted for the quality characteristics of any cereal crops. However, McKercher [91] reported in 1964 on the basis of six years work that differences of up to 7% in wheat protein content were found between different sampling topographical positions within single fields of summer-fallowed wheat crops in Saskatchewan. This within field variation was attributed to changes in soil profile and associated microclimate. In their review "Breeding Wheat for Quality" Hehn and Barmore [59] point out that successful breeding for quality would be aided by a knowledge of the environmental sensitivity of each of the quality factors under consideration. In the system of frequent controls of the same variety advocated by Shebeski, quality analysis of all of the controls in the nursery would provide a measure of both the amount and distribution of variability throughout the nursery for each of the parameters used in assessing quality. Data of this nature would apply only on a single year, single control and single nursery basis but if obtained over several years would provide a source for a better understanding of the effect of environment on wheat quality.

3. The relationship of wheat protein content to the yield of wheat

There have been many reports of a significant negative relationship between the protein content and grain yield within wheat varieties. Neatby

and McCalla [98] indicated that the negative relationship was stronger for wheats grown in areas of soil nitrogen deficiency. Haunold et al [56] confirmed this finding for four winter wheat varieties grown both in the greenhouse and in the field over a period of three years. Sosulski et al [115] varied the moisture, temperature and nitrogen level under conditions of controlled environment, using Thatcher wheat, and were able to demonstrate an inverse relationship between grain yield and grain protein content at constant levels of nitrogen. Hutcheon and Paul [65] demonstrated that for Thatcher wheat under growth chamber conditions the protein content of the grain could be controlled effectively by adjusting the nitrogen supply and soil moisture stress. In the lower protein range (11-16%) the protein and yields could be increased concurrently, while above the 16% protein level increases in protein content could only be obtained by keeping a growth factor such as moisture below optimum for maximum yields. Hill [62] compared the protein contents of hard red spring wheat grown in the Canadian Prairies under four different agronomic practices, over a four year period. He indicated that conditions of high moisture generally gave higher yields and lower protein content, while conditions of low moisture gave lower yields and higher protein content. The protein content was influenced by agronomic practice, moisture distribution, temperature, fertilizer application and weed infestation. Bingham [16] drew attention to the general inverse relationship between yield and wheat protein content which was found in English spring wheats and winter wheats. Shebeski [109] reported significant positive relationships between yield and protein of parents and F1's in a diallel cross of hard red spring wheats. Clark [28] also has reported some positive associations between yield and protein content.

Haunold et al [56] concluded that internal protein-fixing thresholds may exist in wheat varieties. The threshold represented the maximum grain protein level attainable regardless of the yield level of the variety, and operated only in the absence of soil nitrogen limitations. Considerations of the effect of soil moisture on soil nitrogen availability were not discussed by Haunold.

Schlehuber and Tucker [113] summarized much of the experimental data concerning the effect of cultural practices on wheat protein and yield. This summary revealed four main general principles, as follows: Firstly, with constant soil nitrogen the total grain nitrogen tends to stay constant as the yield increases. Secondly, given limited soil nitrogen the nitrogen content of the grain increases as the soil nitrogen is increased. Thirdly, any method of increasing yield (short of nitrogen addition) tends to decrease the nitrogen content of the grain. Fourthly, agronomic practices such as addition of nitrogen fertilizer at heading time can be used to increase the nitrogen content of the grain. Use of this latter practice in England was reported by Bingham [16] and was very effective in raising grain protein content.

As well as reports concerning environmental effects on protein/yield relationships within wheat varieties there have been many reports of studies of the protein/yield relationships of plants and lines within segregating populations obtained by crossing. Many of these studies suffer from the limitation that the effects of environment on the protein-yield relationships could not be separated from the genetic effects on this relationship. However, Baker et al [11] studied random lines in F7 and F8 from a single wheat cross of CT434 x Prelude and found large and highly significant negative phenotypic and genotypic correlation between yield

and protein on the plot basis. Schlehuber et al [111] reported no significant correlation between the grain protein and the yield of 112 F4 lines in a hard red winter wheat cross, and suggested that this was partly due to the fact that the parents were not widely different in protein content.

The performance of the segregates of a cross for both yield and protein on a population basis depends largely on the genotypic composition of the two parents and on the linkage relationships between the two characters in each of the parents. As a result the correlation between yield and protein in the population tends to reflect the correlation which is found in the parents. Crosses of the type "High yield, low protein" X "Low yield, high protein" where both characters are controlled by a multigenic system will therefore generally give rise to populations in which a negative relationship between yield and protein is obtained. This kind of cross is often used in genetic studies of yield and protein in wheat.

It would, therefore, appear that generalizations about relationships between yield and protein content cannot be correctly made unless the specific conditions of the test under consideration are known. Because of the large interactions between soil moisture, content and availability of soil nitrogen, variety and environmental conditions in different years, a wide range of correlation values between yield and protein is to be expected from different studies.

4. The relationship of wheat protein content to the breadmaking quality of wheat

The profound effect of protein content on breadmaking quality has

been established for some time. In a review article concerning breeding for wheat quality Hehn and Barmore [59] list the correlations between wheat protein and a wide range of other important breadmaking quality factors for twelve different studies carried out between 1928 and 1964. With one exception the significant correlations were all positive, but protein content alone did not account for all the quality differences.

McCalla [88] investigated the relation of loaf volume, using a malt phosphate bromate formula, to wheat protein for four Canadian hard red spring varieties. Data was obtained over several years for the varieties Red Bobs, Marquis, Reward and Garnet from Coop tests, fertilizer experiments, field sampling surveys and from replicated yield trials throughout Alberta. The main conclusion was that loaf volume was highly correlated with wheat protein in all varieties but that the regression of loaf volume on protein varied enormously between varieties. The slope of the regression was considered to be an important varietal characteristic, as well as the average protein content of the variety. Finney and Barmore [36] confirmed these findings for both hard winter and spring wheats and suggested a method by which the regression values could be used to separate the effects of protein quantity and quality on loaf volume. Varieties with steeper regression slopes of loaf volume on wheat protein content were considered to have higher protein quality. Support for this conclusion is now widespread (Thompson and Whitehouse [122], Schlehuber et al [112], Mesdag [95], Barmore and Bequette [13], Sunderman et al [121]). Analysis of loaf volume for samples with a wide range of total protein is an effective means of assessing the protein quality of a particular genotype.

Wheat breeders use many tests in assessing the overall breadmaking

quality of a flour. Many of these tests have been developed as being good predictors of the loaf volume to be expected from a baking test, and require only small amounts of flour compared to the bake test (e.g., Sedimentation test, Pelshenke). Other tests were specifically designed to test the rheological properties of the dough made from the flour (e.g., Mixograph, Brabender Farinograph). A knowledge of the effect of total protein on the results from these tests is important, and has been reviewed by Hehn and Barmore [59]. Significant positive correlations between protein content and Zeleny sedimentation value have been frequently reported (Lebsock et al [78], Mesdag [95], Miller et al [96], Sunderman et al [121]). Barmore and Bequette [13] indicated that the regressions of loaf volume and sedimentation value on protein content could both be used for distinguishing between wheats in the hard red winter, common white and white club classes. Mesdag [95] indicated that the sedimentation value was a product of both the total protein content and the protein quality, and recommended that a measure of protein quality could be obtained from the specific sedimentation value, which is the value per unit protein content. Baker et al [11] examined the relationship between wheat protein and sedimentation value in derived F7 and F8 lines from a Low content, strong protein X High content, weak protein cross. No correlation was found between these two characters, and this unusual result was attributed to being a property of the cross.

A positive relationship of protein content with Brabender farinograph characteristics has been commonly reported (Sunderman et al [121], McNeal et al [93], Pratt [101]). Bingham [16] indicated that protein quality could be conveniently estimated relatively independently of protein content by use of the Simon Extensometer. Many plant breeders

have made use of the Mixograph [27]. Mixograph values have demonstrated a mainly linear response to increased protein content (Lebsock et al [78], Miller et al [96]). In a review of the factors affecting flour quality for breadmaking Pratt [101] indicated that protein content was the most important factor affecting the water absorption of a flour. Thompson and Whitehouse [122] found that all of the quality characteristics they studied, including absorption, mechanical dough properties and flour nitrogen content, exhibited complex genotype x environment interactions. These results highlighted the necessity of testing breeding materials for quality, and for examining relationships between different quality parameters, under a wide range of environments.

Because so many of the measures used in assessing breadmaking quality are dependent on total wheat protein, positive relationships between the various tests are to be expected, and are frequently reported (Baker [11], Schlehuber et al [111], McNeal et al [93], Hehn and Barmore [59]). No definite interpretations of these various interrelationships have yet been forthcoming, other than the general indication that variability in quality parameters that cannot be accounted for by protein quantity is due to protein quality, or other undetermined characteristics of the flour. Pomeranz [100] made an extensive review of work conducted to investigate the chemical causes of differences in breadmaking potentiality of wheat flours. In his summary he indicated a need to improve the methods used in assessing protein quality for breadmaking purposes, if wheat improvement is to progress satisfactorily. In 1968 Wrigley and Moss [132] reported on a factor analysis, conducted in 1963 by Jardine et al [68], of thirty-two wheat quality tests. They indicated that not more than four characteristics governed the test responses and these

were "Strength", Hardness", "Stability", and "Stiffness". Two-thirds of the variation in the test data was accounted for by the factor "Strength" which was largely associated with protein content, and was more under environmental than genetic control. "Hardness" reflected mainly the milling characteristics and appeared to be heritable. It could be measured by many tests, each uncomplicated by other factors. Mixing "Stability" and stretching "Stiffness" were two factors affecting the rheological characteristics of the dough and were considered to be two aspects of the quality of the protein. A logical extension of the interpretation by Wrigley and Moss might be to ensure that screening tests for quality in breadwheat breeding programs should include at least one test specifically suited to measuring the effect of each of the quality "factors". Use of several quality tests for which the majority of variation is all accounted for by a single factor would represent a poor allocation of program resources. Whatever the exact biochemical nature of the "factors" might prove to be, it is obvious that measurement of total wheat protein will continue to be one of the more important tests which needs to be conducted in assessing the breadmaking quality of wheat samples.

5. The inheritance of yield in wheat

Haggag [49] reviewed studies on the inheritance of grain yield in wheat and divided them into those which were concerned with yield as a quantitative character controlled polygenically and those in which the measurable yield components contributing to the final yield had been investigated independently. The majority of yield component analysis indicated that the yield components exhibited a range from nonsignificant

to high heritability, according to the method used in the determination, and that they had a variable influence on final yield. Thus Rosenquist [106] indicated that the number of fertile tillers per plant was closely related to plant yield and was inherited as a partially dominant character. Sprague [116] reported a negative relation of both grains per spike and kernel weight, with grain yield per unit area in wheat. Shebeski [109] found that all the yield components which he studied in hybrid wheat were significantly correlated with yield, but that none were transmitted from parent to hybrid in a consistent manner. Fonseca and Patterson [40] reported that the three components of yield which they measured in winter wheat were all significantly correlated with grain weight. Whilst the positive relationship of many individual yield components with final plant yield has been established it is also clear that significant negative correlations between yield components also exist (Fonseca et al [40], Johnson et al [70]). Selection for higher expression of single yield components does not therefore always tend to result in higher plant yields, because of negative associated response of other yield components, and it has not been a successful selection method.

Attempts to measure the heritability of yield have not been particularly extensive in spring wheats, but have led to the general conclusion that the heritability is low (Stuber et al [119], Davis et al [32]). Whitehouse [129] examined both the yield components and final yields in four English grown wheats and concluded that particular components of yield are of limited use in a breeding program and that breeding should be aimed at accumulating the largest number of favourable genes, thus treating yield as an additively controlled genetic system. Using a

diallel cross of six winter wheat varieties Lupton [81] found that high yielding capacity was inherited as a dominant character in drilled trials, but in an indeterminable manner in space-planted trials, illustrating that the heritability for yield can be influenced by the manner in which the study is conducted.

Rasmusson and Glass [104] described a method which they used in two populations of barley for estimating the heritability of seven different traits, including yield on a plot basis, according to six different methods of assessment. The six methods represented various combinations of number of replicates, number of locations and number of years. They found that extended testing due to increase in any of these three resulted in a corresponding increase in the heritability for yield, and also for the other six traits. They were able to use this information to determine which method of testing would be most efficient for a limited allocation of resources. Baker et al [11] used the same method for analyzing fifty random lines in F7 and F8 generations from a hard red spring wheat cross grown in replicated rodrow plots in Alberta. They examined the heritability of yield and six quality traits according to six hypothetical methods of testing, involving combinations of up to three replicates, two years and two locations. The heritability for yield measured in the F7 and F8 generation ranged from 0.47 (with a one replicate, one location, one year test) to 0.82 (with a three replicate, two location, two year test). Baker made the point that from the point of view of practical plant improvement heritability is not the only important parameter but that the expected gain from selection is also partly proportional to the amount of available phenotypic variability. He also stressed that estimates of heritability obtained in near homozygous

lines (F7 and F8) are most realistic with respect to improvement of self-pollinated species because the genetic variance in that generation consists mostly of additive and additive epistatic components. Estimates of heritability made in early generations are either subject to the effects of nonadditive gene action (broad sense heritability) or require that these effects be estimated (narrow sense heritability). Shebeski [110] suggested that improvements in the methods of testing in early generations might lead to more favourable estimates of heritability for yield in those generations.

6. The inheritance of breadmaking quality in wheat

Breakmaking quality is a complex physical character, and attempts to obtain information about its mode of inheritance have therefore generally been limited to studies of the inheritance of those components which contribute to overall quality (e.g., Inheritance of protein content; inheritance of milling characteristics of the grain; inheritance of rheological properties of the dough as measured by various instruments). It is well known that these various components contributing to the final breadmaking quality of a flour are not independent of one another, and that studies of the inheritance of single components are likely to be influenced by variability due to other components. Despite this fact, Wrigley and Moss [132] after reviewing the major effects of the D genome, and chromosome 1D in particular, on overall wheat quality indicated that a full understanding of the meaning of quality and its inheritance would only come from full analysis of the components of quality. Reports on the heritability of various numbers of these components are frequent in the literature, but both plant breeders and biochemists are a long way

from a full understanding of the chemistry and inheritance of breadmaking quality. Lofgren et al [80] has pointed out that the polyploid nature of wheat and the strong influence of environment on quality traits are both complicating factors which limit the ability to determine how many genes are involved in controlling particular quality traits.

The most important single component contributing to breadmaking quality appears to be the protein content of the wheat. Aamodt and Torrie [1] reported in 1935 that, for several crosses in spring wheat, protein content was inherited in a polymeric manner and that the mode of inheritance was readily influenced by environment. Kuspira and Unrau [76] showed that for a series of whole chromosome substitution lines in which the variety Chinese spring was the recipient and the variety Thatcher the donor, at least five Thatcher chromosomes were involved in affecting the wheat protein content. They concluded that inheritance of wheat protein was polymeric, and that the effects of individual genes though small were not always equal. Stuber et al [119] confirmed these findings with results obtained from a low protein x high protein cross. Protein content was under polygenic control and heritabilities from 0.68 to 0.83 were found. Haunold et al [55] also reported multigenic control and heritability as high as 0.65 for grain protein content of wheat, using parents differing widely in protein content. Baker et al [11] reported heritabilities for grain nitrogen content of spring wheat in F7 and F8 ranging from 0.47 to 0.82 according to the method of testing used, but did not make estimates of the number of genes involved. One instance of inheritance of high protein content due to a one gene difference has been reported by Davis et al [32] for the Brazilian varieties Frondosa and Fronteira. In these wheat varieties a single gene difference accounts

for a 2 to 3% increase in wheat protein. With this one exception, most recent studies indicate that protein content is controlled polygenically, but with a fairly high heritability (Ausemus et al [8], Lofgren et al [80], Kaul and Sosulski [73], Lebsock et al [78]). Thompson and Whitehouse [122] conducted diallel crosses between a wide range of European biscuit and bread wheats grown in four locations and showed that flour nitrogen content was inherited in a different manner in different locations. Epistatic gene action and epistasis X environment interaction were significant in their study, and it was suggested that tests for protein content should therefore be conducted at several locations.

Everson and Seeborg [35] estimated the heritability of milling quality in a spring wheat cross to be 35-50%, using the variance partitioning method, but were not able to estimate the number of genes involved. Welsh et al [128] using substitution methods showed that chromosomes 3D, 4D and 5D in the variety Hope contributed to flour yield, whilst for the variety Timstein chromosomes 3B, 6B, 5D and 7D all affected flour yield. Bingham [15] investigated the grain milling characteristics of progenies derived from single F2 wheat grains classified according to endosperm structure. He concluded that the milling type of an individual grain on a heterozygous plant was determined by the genotype of the endosperm rather than by the parent, and suggested that other quality components might be similarly determined. Hehn and Barmore [59] also suggested that for certain aspects of wheat quality the effect of the maternal tissue on the endosperm might determine the desirable direction of a cross. McNeal et al [94] investigated this proposition, using reciprocal crosses between four spring wheat varieties with very diverse milling and baking characteristics. They were unable to find any major

differences between reciprocal crosses assessed in the F2 generation, either for wheat protein content, milling yield, sedimentation value or farinograph characteristics.

Values of heritability reported for the quality parameter sedimentation value have usually been high, depending on the material used. Baker [11] tested lines from a single wheat cross in F7 and F8 and reported heritabilities from 0.71 to 0.90, using the variance component method. Schlehuber et al [111] reported a heritability of 0.66 for sedimentation value in a hard red winter wheat cross, whilst Lebsock et al [78] reported heritabilities from 56 to 60% in a spring wheat cross. Kaul and Sosulski [73] obtained heritability values ranging from 80% to 92%, depending on the method of calculation, in a Selkirk x Gabo wheat cross. They suggested that only two genes were responsible for determination of sedimentation value in that cross. Because of the relatively high heritability of sedimentation value and also because of its close relationship to other important parameters of breadmaking quality this character has been used extensively by plant breeders for rapid screening of large populations for identifying lines with potential high quality.

Using series of monosomic substitution lines with three hard red spring varieties and the variety Chinese Spring, Welsh et al [128] were unable to find chromosomes which produced consistent effects in different varieties for farinograph characteristics, baking absorption or loaf volume. They were able to show, however, that for different substitution series the number of chromosomes significantly affecting baking absorption ranged from one to seven, and that one to ten chromosomes affected loaf volume. One to three chromosomes affected farinograph stability and four to five chromosomes affected valorimeter score. The actual chromosomes

affecting quality parameters were not always in common in different substitution series. Heyne and Finney [60] reported that for a series of crosses between hard red winter wheats heritability in F6 was high for most of the important breadmaking parameters including milling yield, baking tests and rheological tests. No estimates of gene number or mode of inheritance were made. Baker et al [11] recently reported heritabilities for farinograph characteristics in a hard red spring wheat cross. Heritability for dough development time ranged from 0.38 to 0.59, and for mixing tolerance index ranged from 0.48 to 0.75. These heritabilities were not considered to be very high, but genetic advance by selection would have been effective because of the large phenotypic variance which was available. Schlehuber et al [111] reported heritabilites in a hard red winter wheat cross in the F4 generation of 0.78 for bake mixing time, 0.53 for loaf volume and 0.69 for mixogram mixing time. These heritabilities were considered to be high but no estimates of gene frequency or mode of gene action were made. Thompson and Whitehouse [122] were able to determine the modes of gene action and interaction with environment for six parameters of breadmaking quality in a diallel cross between six European wheats representing a wide range in quality. Their results indicated the presence of complex genotype X environment interactions for most quality parameters. Additive gene action was found for the characters Extensibility, Maximum Stress and Maximum Resistance (all three being rheological tests of the dough measured with a Simon extensometer), for % bran after milling and for flour water absorption. Epistatic gene action was found for the "Area under the Curve" of the Simon extensometer but this character showed less interaction with environment than other measures of dough properties. These results stressed the need to

test breeding material for quality in a wide range of environments.

Investigation into the inheritance of the breadmaking quality of wheat appears to be progressing by three different general methods. The first of these is the gene number determination method involving conventional genetic analysis of parents, F1 and backcross generations, as used by Kaul and Sosulski [73]. The second method is the use of the partitioning of variance into its genetic and environmental components, so that estimates of heritability in the broad and/or narrow sense can be made, as used by Baker [11]. This approach can be used in any generation in which replication is possible, but estimates of gene numbers are not always obtainable from this method. The third method involves the determination of quality parameters in the early generations of a cross and then comparison of the performance with these selections for those quality parameters in later generations. This approach uses the regression of later generations on earlier generations as an approximation to heritability, as used by Lofgren et al [80]. All three methods have provided information of use to the plant breeder, but the genetics of breadmaking quality and of its components are still relatively unknown.

7. General considerations of breeding methods and selection in self-pollinated crops

The division of plant breeding programs into two main types, namely those based on "defect elimination" and those based on "selection for yield" has been widely recognized (Frankel [42], Joshi and Dhawan [71], Whitehouse [129], Bingham [17], Donald [33]). Donald suggested that a third type of program is available by breeding for crop ideotypes, which are plants with model characteristics known to influence photosynthesis,

growth and yield. This method involves the positive approach of "character incorporation" of phenotypic features which are known to or considered to contribute to higher yields under specific agronomic conditions.

As early as 1935 Vavilov [125] listed 46 clear objectives required in new wheat varieties, most of which involved "character incorporation". Selection for particular phenotypic attributes in an attempt to increase yields has been used in many breeding programs. Thus Lupton [82] advocated the use of physiological characters concerned with translocation and assimilation rates as criteria for selection for yield in wheat. MacKey [86] also recommended the physiological approach to selection for yield. This could be achieved by selecting for high intensity of plant components which exert their maximum effect on grain yield during the peak of the plant's Net Assimilation Rate curve. Burrows [25] has used the relative growth rate of 14-21 day seedlings as a criterion of selection for yielding ability in oats and has been successful in isolating higher yielding lines by this method. Stoskopf [117] recommended that selection for upright leaf habit in winter wheats would increase yield potential. In Mexico, selection of short strawed, high tillering types which respond to conditions of high fertilizer and irrigation resulted in isolation of superior high yielding varieties.

Such methods of "character incorporation" are important and are undoubtedly very effective, but suffer from several limitations in relation to longterm breeding plans. Firstly, the effect of a particular character on final yield is often difficult to exactly determine, due to variability in other factors, and there is probably a finite limit to the number of such characters which can be identified and usefully incorporated into a

variety. Secondly, selection for high intensity of certain characters may often be associated with negative responses of other characters which affect yield (Stoskopf and Reinbergs [118]). Thirdly, the breeder is limited to working only with those traits which have been demonstrated to affect yield under specified agronomic conditions and would theoretically be limited to a "perfect variety" in which all those traits have been accumulated. Fourthly, the screening method used in testing for one particular character often limits the ability to identify useful variabiliyt in the population due to other factors. Methods which are based on "selection for yield", using proven yielding ability as the main selection criterion, are not prone to these restrictions and yet do not themselves restrict the ability to incorporate desirable characters.

An approach which is of interest to plant breeders is that of transgressive breeding, in which new intensities of given characters may be created, beyond that exhibited by the parents (Heyne and Smith [61]). Smith [114] indicated that transgressive segregation can occur for both complex and simply inherited characters, and was more likely to be found in crosses involving parents which were genetically distantly related. Haggag [49] indicated that in a spring wheat cross of Pembina X Manitou one backcross to the higher parent (Manitou) increased the proability of obtaining transgressive segregation for yield. Investigations of methods which can be used in self-pollinated crops for obtaining and identifying the best genotypes from single crosses, especially those demonstrating transgressive segregation, are of great importance to plant breeders. The methods most suitable for simply inherited characters have been well documented in many plant breeding texts (Allard [2], Hayes, Immer and Smith [58], Briggs and Knowles [19]), and are generally well

suited to "character incorporation" programs. A great diversity of methods has, however, been recommended for use in programs in which improvements in polygenically controlled characters, such as yield, is desired.

Harrington [53] described the pedigree and mass methods of handling segregating generations from a cross. Raeber and Weber [103] were unable to demonstrate any significant difference in the effectiveness of the mass or pedigree system of selection for yield in four soybean crosses. Torrie [123] was also unable to demonstrate that one system was superior to the other in soybeans. Frey [44] showed that the mass selection system was very effective in a program of selection for seed width in oats. Copp [31] stated that the bulk (mass) method of breeding wheat was abandoned in New Zealand because of its relative nonproductivity of new varieties compared to the pedigree system. Lupton and Whitehouse [84] indicated how the mass and pedigree systems are the two extremes by which segregating materials can be handled, and pointed out that success has been obtained by both methods. They did, however, comment on the danger of loss of valuable lines in the random sampling of early generation material by the mass method and recommended the use of a pedigree trial method of selection, rather than mass selection, for increasing yields in cereals. For any hybrid population the choice of mass or pedigree system is not one method to the exclusion of the other. Breeders have devised schemes which utilise the advantages of each (Briggs and Knowles [19]). In 1937 Harrington [52], for example, suggested the use of the mass pedigree system which combined the genetic advantages of the pedigree method with the ease of operation of the bulk method. It is nevertheless clear that, at least in wheat, those programs which have made the most dramatic progress in variety production have predominantly been primarily pedigree

systems (CIMMYT in Mexico, Vogel in Washington, MacKey in Sweden).

Hanson suggested in 1959 [51] that in self-pollinated crops after a cross had been made several generations of random intermating between progeny of the cross from F2 onwards would theoretically aid in the breakup of undesirable linkage blocks, thus increasing the frequency of desirable recombinants, including transgressive segregants. Miller and Rawlings [97] supported this viewpoint with data obtained with cotton. Baker [10] undertook a Monte Carlo simulation study to establish how many random intercrosses would be necessary per generation in self-pollinated crops in order to make the effects of intermating sufficiently worthwhile. He concluded that in F2 intermating among as few as 30 pairs of F2 plants would serve to realize the expected results of random mating, but suggested that the method would be most useful in conjunction with a recurrent selection scheme. Such methods of random intermating, the use of complex crosses suggested by Harrington [53] and the system of progressive improvement recommended by Palmer [99] are all directed towards increasing the within cross frequency of favourable genotypes (Andrus [5]). This phase of the breeding program is quite distinct from the phase of identification and isolation of these favourable genotypes.

A consideration of the genetical basis of selection for polygenically controlled characters is necessary if rational plant breeding procedures are to be recommended. The main problem which exists is that for self-pollinated crops, such as wheat, the breeder is most interested in the quantitative performance of particular lines in advanced generations when a high percentage of homozygosity has been attained (e.g., F8 generation and later). In these generations the important mode of gene action is of the fixable additive and additive epistatic type. However, in the F2

generations and onwards in which selection has to be conducted the relatively heterozygous nature of the population may result in a considerable degree of nonadditive gene action which will affect the degree of expression of the character. Van der Kley [124] suggested that because of such gene interaction the phenotypic value of heterozygous plants was not a reliable guide to the value of lines which could be derived from them. He also indicated that plants that might segregate valuable gene combinations after selfing could be lost if plants, that were dominant or intermediate for some detrimental genes, were eliminated from heterozygous populations by phenotypic selection.

Van der Kley discussed the theoretical efficiency of various selection systems on polygenic characters and based this discussion on an analysis of the effect of inbreeding on gene frequencies. He gave formulae for calculating the frequencies of different homozygous and heterozygous types in perfect Mendelian populations from F2 to F∞, for crosses differing by any number of genes, in the absence of selection and with 100% self-fertilization. This description of the effect of inbreeding on gene frequencies in Mendelian populations has been made by other authors (Allard [2], Briggs and Knowles [19]). Van der Kley illustrated that for crosses in which the parents differ by as few as 20 desirable genes the frequency of the best homozygous genotype in F2 is extremely low and, therefore, that even in very large F2 populations the chance of isolating the genotypically best plant in F2 is remote. The chance of isolating this type from an unselected Mendelian population at the end of segregation was higher, but still remote. Shebeski [110] carried out similar calculations to assess the frequency of plants which would contain all desirable genes, in either heterozygous or homozygous condition, in F2 and subsequent generations for a cross involving 25 gene differences. His

table showed that plants of this type would be present with a frequency of 0.075% in F2, 0.000056% in F4 and 0.0000064% in F6. Delay in generations obviously reduced the probability of the presence of the best genotypes, for a population of a given size.

These theoretical frequencies of Van der Kley and Shebeski are based on models of additive gene action in which the populations segregate in a strictly Mendelian manner, uninfluenced by any kind of selection. Several authors have indicated that when segregating populations are grown in bulk for succeeding generations, as in the bulk method, homozygosity is not reached at the theoretical rate and heterozygosity may be very high even in the F6 generation (Jain and Jain [67], Palmer [99]). Jain et al attributed this to a differential survival of heterozygous plants under conditions of competition and natural selection within the populations. Donald [33] also supported this view, and stressed how in the mass selection system this might lead to loss of the most desirable genotypes.

Selection for quantitative characters controlled by an undetermined but large number of genes can be justified to some extent in either early or late generations, but disadvantages exist for both systems. Selection in later generations between relatively homozygous lines allows definitive comparisons of cultures in which the additive genetic variability is already fixed and in which nonadditive genetic effects are not a major component. Identification of the superior lines in the advanced generations is therefore straightforward. Brim [23] suggested a modified pedigree method of selection in soybeans in which one seed per plant is used to propagate the F2 generation through to homozygosity, followed by comparison of plant progenies on the line basis. The method requires very little effort compared to a strict pedigree method and allows

effective comparison between lines in which the genotypic variability is fixed. This system, however, minimizes the probability that the best genotype possessing the largest number of favourable genes which was available from the cross will be present in later generations, even if it was present in the F2. This genotype will probably have been lost due to the random effects of Mendelian segregation in small populations, and due to possible detrimental effects of natural selection during the segregating generations [67].

Selection in the early generations, on the other hand, permits comparisons between plants or lines at a stage when the total genetic variability from the cross is at a maximum, and the frequency of the most favourable genotypes is at its greatest (Shebeski [110]). Identification of the superior genotypes in the earliest generations would permit a more efficient allocation of plant breeding resources (Lupton and Whitehouse [84]). The disadvantage of early selection is that of possible misclassification of cultures due to the effects of nonfixable genetic variation, and this is reflected by the heritability of the character as measured in the early generations. Heyne and Smith [61] suggested that the primary guide to choosing characters suited to "early testing" should be heritability. If heritability was high in early generations, testing should start as early as possible. They concluded that because reported heritabilities for yield were low, selection for yield should be delayed until a large degree of homozygosity had been achieved. In their plant breeding texts Allard [2], and Briggs and Knowles [19] also recommend this approach. Since the measure of heritability is affected by the method of testing, and because plant breeders use such a wide variety of testing methods in early generations, variable results have been obtained with

early generation selection for yield.

8. F2 progeny tests and the use of early generation selection in self-pollinated crops

As long as 100 years ago Louis de Vilmorin [58] established the plant breeding principle that "the way to evaluate an individual is to test its progeny". In their introduction to a paper on the reliability of plant selection for yield in F2 McGinnis and Shebeski [89] indicated that there was a general view among present day breeders that selection for yield in F2 on the single plant basis was ineffective (Bell [14]). Allard [2], MacKey [85]). They concluded from their own study of a hard red spring wheat cross that selection of particular F2 plants for yield was ineffective in isolating the superior yielding genotypes, but that selection of vigorous, well tillered F2 plants was effective in raising the general yield capacity of the population. Atkins [6], working with barley, reported that visual selection of single spaced F3 plants for agronomic superiority was not effective in isolating superior yielding genotypes. However, Krull et al [75] in Columbia indicated that visual selection of wheat lines on the basis of agronomic characters was effective in isolating superior yielding genotypes. In two soybean populations Kwon and Torrie [77] concluded that some progress could be made by visual selection of higher yielding types on a line basis, but that this was not so effective as selection by the criterion of measured plot yield. The two approaches of visual selection of single plants and visual selection for yield potential between plant progenies are both widely used in plant breeding programs, though the evidence supporting either method is conflicting.

In a pedigree trial method described by Bell [14] F2 single plants

of barley are assessed by the performance of their F3 bulk progenies. A large proportion of the F3 progenies is discarded and single plant selection is practised on those retained. Heyne and Smith [61] drew attention to the uniqueness of F3 lines and how each represents an F2 plant and the limitations of the F2 genotype. They recommended that careful evaluation of and rigorous selection between F3 lines would be of considerable value. Hamilton [50] suggested that selection for yield and breadmaking quality in Canadian hard red spring wheat programs could profitably start in early generations, with selection between F3 lines. Lupton et al [84] described the use of cubic lattice yield trials of F2 plant progenies in wheat. Their results indicated that these F3 yield tests led to retention of useful lines which would probably have been discarded if "eye judgement" had been used as the selection criterion. Fiuzat and Atkins [39] and McKenzie and Lambert [90] each worked with barley and recommended that the yield of F3 lines was a reliable criterion for selecting cultures which would be high yielding in later generations. McKenzie and Lambert also concluded that the method would be more effective for crosses in which the total genetic variability for yield was large.

Raeber and Weber [103] compared the effectiveness of the bulk and pedigree method of breeding soybeans and concluded that the greatest genetic advance in yield could be made by testing F2 progenies in replicated yield trials in F3. Also working with soybeans Green and Pinnell [47] recommended the use of F3 family performance for assessing F2 plants, for field emergence and germination of the seed. Whitehouse [129] also recommended such F2 progeny trials for improving yield in wheat, but criticised the method for the physical limitation on the number of F3 lines which could be handled in this manner. In Norway, Bjaanes [18]

obtained evidence in wheat supporting the use of yield trials of F2 families, for isolating superior genotypes from segregating populations. Recommendation for selection in F3 on a line basis for yield and grain quality of wheat was also made by Kalinenko [72] in Russia. He stressed the need to select before the random processes of inbreeding decreased the probability of retaining the superior genotypes. In work conducted in Saskatchewan, Hurd [63] described how selection of the superior lines in a yield test of a large number of F2-derived F4 lines from a single cross resulted in isolation of a large number of superior yielding lines. He suggested that selection between F3 lines should be even more successful.

Not all workers who have used early generation progeny tests for selection of quantitative traits have reported favourable results. Frey [43] indicated that in two barley crosses the performance of F2 derived lines was not a reliable selection criterion for either yield or grain test weight. He suggested that evaluation for yield should not start until F4 or F5. Fowler and Heyne [41] with winter wheat, Atkins and Murphy [7] with oats, and Weiss et al [127] with soybeans have all questioned the predictive value of tests in the F2 and F3.

Reports on the effectiveness of progeny testing in early generations for breadmaking quality of wheat have, in general, indicated that this method is successful. The CIMMYT wheat program in Mexico [27] using the Pelshenke test on individual plants in F2, F3 and F4 and the alveograph and mixograph tests on F3 and F4 lines has achieved the objective of raising the breadmaking quality of Mexican wheats. Heyne and Finney [60] concluded that the F2 progeny test was useful in classifying F3 lines as to their potential baking quality in later generations. The mixograph was particularly effective for screening F3 lines for

potential quality, in their study. Lebsock et al [78] also recommended the use of mixogram and sedimentation value in the F3 for screening out lines with desirable breadmaking quality. McNeal et al [93] showed that in a Lemhi X Thatcher wheat cross selection for farinograph characteristics between lines in both the F3 and F4 generations was effective in improving those characters, compared to no selection. Selection was more effective in the F3 than in the F4. Baldridge (MS Thesis, Montana) showed that selection of F2 derived wheat lines for favourable doughball test values in any generation from F3 to F5 resulted in lines with superior farinograph stability and/or loaf volume.

Shebeski [110] suggested a method in which large numbers of F2 plants are evaluated by the performance of their respective F3 lines in both yield and baking quality trials. F3 plots are larger than those that have been reported previously, with some 750 plants in a triple rodrow plot. Rigorous selection between F3 lines is conducted for both yield and quality. Sufficient seed (> 800 grams) is harvested in bulk from individual F3 lines to enable fullscale milling and baking tests, farinograph, sedimentation and other tests to be conducted at the F3 level. The effectiveness of this method could be determined by examining the performance of selections for yield and quality in later generations, as homozygosity was attained.

9. Methods used by present day wheat breeders for managing early generation material from wheat crosses

The recommended procedures of breeding and selection in self-pollinated crops by conventional methods such as the mass, pedigree, mass-pedigree, and backcross methods have been very adequately reviewed

in several texts (Harrington [53], Allard [2], Briggs and Knowles [19], Hayes, Immer and Smith [58]). A review of the methods actually being used in current wheat breeding programs has not been available in recent years. In an attempt to obtain some information on this subject, Shebeski in 1966 circulated a questionnaire, entitled "Pedigree method for breeding spring wheat" [108], to a worldwide cross-section of wheat breeders. The main objective of this questionnaire (Appendix 1) was to determine sizes of populations, methods of growing plants and plant progenies, and methods of selection up to and including the F3 generation. Some of the important results from this survey of wheat breeders in Canada, USA, UAR, New Zealand, Australia, Yugoslavia, Germany, Netherlands, Israel, Hungary, Norway, Mexico and Sweden are reviewed in this section.

Whilst many of the breeders surveyed were using the pedigree system up to and including the F3 generation, several European breeders indicated a preference for modified bulk methods in early generations. Thus Rajki in Hungary was using an "improved bulk method" in which single plants were visually selected for superior agronomic type until the F3 generation, followed by replicated yield tests in the F4. An average sized F2 population of 48,000 plants per year was represented in his system by an average of 1,200 F4 lines per year. In Norway, Strand used a method in which many crosses were grown in bulk trials in F1 and F2, and crosses were discarded on the basis of their yield performance in these tests. Selection was practised in F2 and F3 within the best crosses and yield trials were conducted for 3 to 4 years on the bulks derived from selected plants. Reselection was practised on the basis of yield in the F5 to F7 generations. A method similar to this was described in the literature by Lupton [84]. The questionnaire response by Strand was the only one which indicated the

use of yield tests of any sort prior to the F4 generation. MacKey in Sweden indicated that in his own wheat program, and in those of many European breeders, mass selection was conducted until the F4 generation, followed by pedigree selection thereafter. This method was also used by Zeven in the Netherlands.

Kaufmann in Alberta indicated that the single seed descent method attributable to Brim [23] could be used in breeding for yield in wheat. From the F2 generation onwards, each plant would be propagated by 1 seed per plant until homozygosity was reached. At this time 300 to 400 lines could be yield tested. Kaufmann indicated that the method had been relatively successful in oats.

With the exception of the five methods just described the remaining breeders who were canvassed described pedigree breeding systems which were very similar in their general approach towards handling material in early generations. Thus the number of crosses made per year was in the order of 40 to 50, with a maximum number of 1,000 crosses per year made in the Mexican program of Borlaug, F2 plants were in all cases grown spaced out, and the number of F2 plants per cross was usually quite large, ranging from 400 to 10,000. Selection between F2 plants was rigorous in all programs and was confined to those agronomic and morphological characters which were simply inherited (e.g., Resistance to diseases, straw strength, height, awnedness, etc.). Borlaug in Mexico was the only breeder who indicated the use of tests for quality on F2 plants, using Pelshenke values and protein tests as a preliminary screening for high breadmaking quality potential. In Kansas, Heyne indicated that the F2 progeny test method was used in the wheat program.

In nearly all programs, selected F2 plants were continued into F3

as headrows. These were used primarily for observational purposes, were suitable for selection of agronomically superior plants within rows, and were not intended as a preliminary yield trial. The number of F3 lines per cross was very variable, ranging from 10 to 1,000, whilst the total number of F3 lines grown per year ranged from 600 to the 20,000 of Schmidt in Nebraska. The use of these F3 nurseries as observational rather than yield trials obviously had a considerable effect on the way in which individual F3 were seeded. Thus, few of the breeders used F3 plots which were solid seeded (drilled) at rates which would approximate agricultural conditions. Selection of single plants within such solid seeded stands would be very difficult. Some breeders, including Kate in the Netherlands and Heyne in Kansas, were using headhills for seeding the F3 generation. The number of plants within each F3 line was in all cases fairly small, ranging from 10 to 250. Because of this limitation, F3 plots were either single rowed, or multi-rowed with rows containing very few plants at a wide within-row spacing (e.g., as used by Mohammed in the UAR). Several breeders, including Heyne in Kansas and McNeal in Montana, used single row F3 plots in several locations.

The most common spacing between rows and between F3 plots was 1 foot. The frequency of the control plots in the F3 nurseries ranged from 1 in 3 (Mohammed, UAR) to 1 in 200 (Campbell, Canada) with a mean of about one control per 50 plots. The selection pressure in F3 was fairly high in all programs, with a maximum of 30% of the F3 lines retained in the program of Knott, in Saskatchewan. The number of plants selected within F3 lines was in all cases very small, ranging from 2 (Copp in New Zealand and Ephrat in Israel) to 40 (Schmalz in Germany). In nearly all programs the criterion for selection in F3 was mainly visual assessment

for desirable agronomic traits on the line basis, followed by visual selection of single plants within lines. In programs in New Zealand, Yugoslavia, Germany, Israel, Mexico and the USA preliminary screening and selection for potential breadmaking quality was also conducted in the F3 generation. Because of the relatively small quantities of seed available from single F3 plants, or from bulks of fairly small F3 plots, only quality tests requiring small amounts of seed were used in the F3 generation (e.g., protein content, sedimentation test, Pelshenke, mixograph).

Whilst concise summary of the results of the questionnaire circulated by Shebeski is difficult it was obvious that, of those breeders questioned, very few were engaged in methods which were specifically orientated towards selection for yield on a quantitative basis in the generations prior to F4. Emphasis in most programs was on the visual selection of single plants and/or lines until the later generations when yield testing was started (e.g., Borlaug's program in Mexico). In the F3 generation, the first generation in which yield testing of lines could be conducted, breeders were apparently not concerned in obtaining estimates of the yield potential of F3 lines. In most of the F3 nurseries little attempt was made to organize F3 seeding rates, plot shapes or control plot frequencies such that reliable yield estimates could be obtained in F3.

Shebeski [110] suggested that many of the methods which were used at that time were based somewhat on tradition, and were the relics of systems used when breeders were working primarily with simply inherited characters. He suggested that in programs which were designed to increase yield (considered as a quantitative character) a system of

handling early generations was required which was more closely related to the genetic expectations for quantitative characters segregating in the early generations of a cross. Shebeski recommended the use of large within cross populations at all stages from F2 to homozygosity. F2 populations were space planted in the winter in Mexico and selection practised between plants for agronomic characters. Individual selected F2 plants were harvested, each providing a large amount of seed. A first critical assessment of lines for yield and breadmaking quality was conducted in the F3 generation. As many as 1,000 F3 lines per cross were recommended, with each F3 line being grown in a large 3-rodrow plot. Seeding rates approximated those used agriculturally, and duplicate F3 nurseries were planted for lines which had sufficient seed. An improved design of F3 nursery plots and a nursery plan using frequent controls was suggested that would provide a better method of assessing yield at the F3 level. Selection at the F3 level was strictly between lines, on the basis of yield performance and baking quality of the F3 line, and less than 5% of the F3 lines would be retained. Each selected F3 was increased by a large number of random F4 spaced plants grown in Mexico during the winter. Reselection of single F4 plants for agronomic desirability was practised and each F3 was thus represented in the following year by 50 to 100 F5 lines grown in large plots, in the same way as the F3. The effectiveness of the method recommended by Shebeski in 1967 had not been investigated in detail at that time, and further results from the use of the system were clearly desirable.

SECTION 2

Results of research, in publication form

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

Appendix 2

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

Appendix 3

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

Appendix 4

(The candidate wishes to indicate that, whilst all of the experimental materials used in this project were obtained from the thesis program, the investigations described in Part I of this paper were not part of that program.)

Early generation selection for yield and breadmaking quality of Triticum aestivum L. K. G. Briggs.

ABSTRACT

A three year study was conducted to examine the effectiveness of selection on the unreplicated line basis in F3, for yielding ability and for breadmaking quality. Evaluation of the effect of selection in three different F3 populations was achieved for two yield parameters and fourteen quality parameters by examining the performance of the selections in the following year in replicated F4 bulk yield trials, and as populations of F5 lines. Breadmaking quality was assessed by fourteen tests including bushel weight, 1000 kernel weight, wheat protein percentage, milling and flour characteristics, sedimentation value, two bread-baking tests and Brabender farinograph characteristics. The only quality parameters for which the mean performance of the F5 populations could be consistently predicted from the F3 were wheat protein percentage and farinograph characteristics, excluding farinograph mixing tolerance index. For the other quality characters significant differences were found between the F5 populations but these did not relate to the performance in F3. A predictable positive relationship between the yield of F3 plots and the mean yield of F5 populations was found in only one of the three years. In the other two years the relationship between F3 and F5 yields ranged from nonsignificant to high, negative and significant. The results obtained in the latter two years were possibly related to the fact that only a relatively narrow high yielding range of the total F3 yield spectrum was sampled in each of those years. In each of the three years

the highest yielding F5 populations were derived from F3 lines which were high yielding on a plot basis and also very high yielding relative to the yield of their adjacent control in the F3 nursery. The highest yielding F5 populations were not obtained from the lower yielding F3 lines.

Evidence was obtained, from F5 nurseries grown in three different years, that a yield testing method using yield data from contiguous control plots gave very similar results to a conventional experimental design in which data from control plots was not used. Data from one year of testing also illustrated that the environmental effects on the yields of F5 lines, due to location, could be minimised by the use of yield data from contiguous controls.

INTRODUCTION

Increasing attention has been paid by plant breeders during recent years to the various methods which are being used in the breeding of improved varieties in the selfpollinated crops. This re-examination of methodology and the quest for more efficient breeding systems has been mainly orientated towards improvements in quantitatively determined genetic characters. Two factors of overriding importance in breeding hard red spring wheats for the Canadian prairies are grain yield and breadmaking quality. Donald [14] has indicated that all breeding programs can be divided into two groups, the first group consisting of programs aimed at "defect elimination" and the second group where the basic procedure is "selection for yield". Examples of objectives in "defect elimination" are breeding for specifically defined characters such as drought and disease resistance, and lodging resistance. By contrast the objectives of "selection for yield" are to identify superior genotypes which give reliably high yield at the producer level regardless of any preconcieved notions of what the specific physiological, morphological or developmental features of those individuals ought to be. Selection in a program of the latter type depends mainly on the proven yield performance of lines grown in the field under conditions similar to those found agriculturally. It is into this second group, defined by Donald, that a pedigree breeding method suggested in 1967 by Shebeski [26] falls.

Shebeski commented on the genetically quantitative nature of yield and suggested that "any gene that is involved in the development of the plant must be considered a yield gene". In their review of the genetics

of wheat Ausemus et al [3] supported the viewpoint that all the chromosomes of wheat have some influence on yield. It was on this basis that Shebeski developed a genetic model illustrating the expected frequencies of desirable genotypes in later generations for crosses between parents differing by up to fifty unlinked genes for yield. The development from this model of an optimal plant breeding program using early generation testing for yield required the assumption that the important mode of gene action for this character is additive and/or additive epistatic. This assumption is frequently made in modelling studies of this kind, as for example by Baker [4] and Van der Kley [27].

Research by many workers has indicated that the inheritance of overall breadmaking quality is quite complex. Some workers have been able to isolate simple genetic systems controlling specific facets of quality, for example the 2% advantage in protein for the S. American varieties Frondosa and Fronteira reviewed by Villegas [28] and considered to be due to only a single gene difference. However, the majority of results indicate that quality is polygenically controlled. This was particularly indicated by the work of Welsh et al [30] using substitution methods with three different varieties of wheat. The number of chromosomes significantly affecting quality in their study ranged from one to sixteen for the three varieties and the chromosomes involved were not always in common. Their conclusion was that there was little uniformity of the location of genetic factors affecting flour quality in different wheat varieties. On the basis of this kind of information there is therefore considerable justification for treating breadmaking quality as a polygenically controlled system in the same way as for yield. The revised method of pedigree

breeding suggested by Shebeski uses this approach and is directed specifically towards an initial selection for the two quantitative characters yield and quality in the F3 generation.

Many studies have been made to investigate the worth of selection in earlier generations, when it is known that nonfixable heterozygosity and complex gene action may be very significant in contributing a large amount to the total phenotype. MacKey has indicated the possible hazards of this method [22], and the problem of identifying in a highly heterozygous population individuals which will have the greatest potential in their homozygous condition in later generations. As Bell [7] very clearly pointed out, any attempt to use early generation selection methods depends on the assumption "that there is sound genetic basis for concluding that the performance of homozygous segregates in later generations can be estimated by the yield of early generation selections". In breeding for high yield in early generations most workers have found that genotype by environment interactions on spaced single plants from the F2 generation onwards have been too large to allow effective selection on the single plant basis (Bell [7], Allard [1], Briggs and Knowles [10]). Because of this factor the most effective early generation tests are likely to be those which use the performance of single plant progenies as the criterion for identifying the most worthwhile portion of the population. In the pedigree trial method described by Bell [7] F2 single plants of barley are assessed by the performance of their F3 bulk progenies, where each progeny consists of from 40 to 45 plants. A large proportion of the F3 progenies is discarded and single plant selection is practised on those retained. Lupton et al [21] have described this method in wheat, using

replicated cubic lattice trials of F2 plant progenies. Their results indicated that the use of such early generation yield tests in F3 resulted in the isolation of useful cultures which would probably have been discarded if "eye judgement" alone had been used as the criterion of selection. Fiuzat and Atkins [15] working with barley recommended that, because of the relatively low heritability of yield, selection for yield should be based upon progeny tests rather than upon individual plant values, both in F3 and in later generations. McKenzie and Lambert [23] determined that, for one out of two barley crosses they examined, the relationship between the F3 yield performance on a line basis and the progeny in F6 was very good. Their main conclusion was that crosses between varieties differing very little in yield genes would likely not be suited to early generation testing, but that this method would be very effective for crosses involving a wider genetic base. Results obtained in soybeans by Raeber and Weber [25] comparing the effectiveness of the bulk and pedigree methods of breeding also indicated that the greatest genetic advance for yield could be made by testing F2 derived lines in replicated trials in the F3. Whitehouse [31] has recommended the use of F2 progeny trials for assessing yielding ability directly, followed by plant selection of superior agronomic types within the high yielding progenies. His only criticism of the method has been that only relatively few progenies can be examined in this manner, the amount of work involved severely limiting the size of population which can be handled. In Norway, Bjaanes [8] made a critical review of wheat breeding methods and obtained evidence for supporting the use of yield trials of F2 progenies, for isolating superior yielding genotypes from segregating populations. Not all workers have

agreed with these conclusions in favour of F2 progeny tests. Fowler and Heyne [16] with wheat, Atkins and Murphy [2] with oats and Weiss et al [29] with soybeans have all questioned the predictive value of tests in the F2 and F3.

Considerable research effort has been directed towards evaluating the utility of early generation selection for complex quality characteristics, such as breadmaking quality in wheat and malting quality in barley. The main problem in this area has been one of devising reliable microtests which can be used with the relatively small quantities of seed which are usually available in the early generations of a pedigree breeding program. Large numbers of such tests are now available and are being used extensively in wheat breeding programs throughout the world. The CIMMYT program in Mexico [13] using the Pelshenke test on individual plants in F2, F3, and F4 and the alveograph and mixograph tests on F3 and F4 lines has achieved the objective of raising the breadmaking quality of Mexican wheats. Heyne and Finney [19] used the F2 progeny test to study the quality characteristics of hard red winter wheats and related them to performance in later generations. They concluded that the mixograph (requiring some 200 grams of seed) was more reliable than the wheat meal fermentation time for classifying F3 lines as to their potential baking quality in later generations. They recommended the screening of F3 lines for quality using the mixograph test but indicated that the final analysis could only be made with full milling and baking trials. Lebsock et al [20] also recommended the use of mixograph and sedimentation value in the F3 for screening out lines with desirable quality. A study by McNeal et al [24] indicated that for farinograph characteristics selection in the F3 and F4 generations in

a Lemhi x Thatcher wheat cross was effective in improving those characteristics, compared to no selection. Selection was more effective in the F3 than in the F4 generation. In their review "Breeding wheat for quality" Hehn and Barmore [18] describe results obtained by Baldridge (M.Sc. Thesis, Montana). He showed that selection of F2 derived wheat lines for favourable doughball test values in any generation from F3 to F5 resulted in lines with superior farinograph stability and/or loaf volume. Further unpublished data from that study indicated that the greatest number of good quality selections made in the F5 originated from superior F2-derived lines.

In the method of pedigree breeding for wheat suggested by Shebeski [26] large numbers of F2 plants are evaluated by the performance of their respective F3 lines in yield and baking quality trials. The F3 plots are large, consisting of some 750 plants per F3 line, and the F3 serves as the first generation in which selection for yield and quality takes place. Sufficient seed is obtained from an F3 plot harvested in bulk to allow the use of very extensive quality tests. With F3 plot yields of the order of 1000 grams or more considerably more seed is available than has been in other breeding programs, which were therefore restricted to the use of microtests for quality in the F3. As a result, fullscale milling and baking tests as well as farinograph, sedimentation and other tests can be used in F3, the complete quality analysis requiring 800 grams of seed.

It was considered by Shebeski that at least part of the reason for the reported low heritability for yield in earlier generations was due to the manner in which the earlier generations had been grown. For example, limitations in the amount of seed available from spaced F2 plants in

conventional programs automatically limited the size of F2 progeny plots, and these were often grown as single rows adjacent to one another. Under these circumstances, instances of interplot competition and genotype interaction with methods of seeding and environment would all tend to reduce relationships between the F3 yields and the yields of later generations grown in conventional plots of the four rodrow solid stand type. In an effort to minimise interplot competition and to overcome the sampling effects and larger error of small plots Shebeski adopted a three rodrow plot for the F3 yield test, with plots separated by 2 feet, a seeding rate equivalent to commercial rates, and 6 inches between the rows within a plot. As a further aid in testing the yielding ability of the F3 lines, control plots of a single recommended variety were planted as every third plot throughout the nursery. Thus each F3 line was grown adjacent to a constant control variety, the latter serving as a measure of the heterogeneity for yield and quality potential throughout the nursery (Briggs and Shebeski [11], Briggs, Bushuk and Shebeski [9]). Baker [5,6] has been opposed to this approach of using extensive controls, mainly on the basis that the amount of advantage gained by using controls does not compensate for the extra amount of work involved. Certainly the use of extensive controls should not be considered as a system superior to proper replication, but the latter is not always possible in F3 due to insufficiency of seed.

In the light of the rather conflicting evidence concerning all phases of early generation selection it was considered of interest to initiate a study to evaluate as far as possible the breeding system suggested by Shebeski in 1967. The purpose of this three year study was

threefold: Firstly, to examine how effective the selection of F3 lines classified as superior for yielding ability would be in terms of performance in later generations (F4 and F5); Secondly, to simultaneously do the same study for breadmaking quality, wherever possible; Thirdly, to make some attempt to gauge how reliable the extensive control system is in aiding early generation selection, for both yield and quality.

MATERIALS AND METHODS

Yield data on a single plot basis in the F3 generation were obtained for different F3 populations grown at the University of Manitoba in three different years, 1965, 1966, and 1967. Effectiveness of selection for yield at the F3 level in any one year was assessed by the performance of F3 derived selections in the following year, both in a replicated bulk F4 test and by the mean yield of a population of F5 lines randomly derived from the F3 selection. The effectiveness of selection for breadmaking quality in F3, in the two years 1965 and 1966, was assessed by both bulk F4 tests and F5 populations, grown in 1966 and 1967 respectively. A similar study was made for total wheat protein using the F3 population grown in 1967 and assessing the derived F5 populations in 1968. The F3 populations were different in each year and the methods of growing them varied somewhat from year to year.

With the exception of the 1965 F3 nursery and the 1966 bulk F4 trial, all plots seeded for yield determinations were three rowed, with 6 inches between rows within a plot and 2 feet between plots, making an effective plot width of 3 feet. The seeding rate was constant at 250 seeds per row drilled over 18-1/2 feet, and plots were trimmed to 16-1/2 feet before harvest. In the 1965 F3 nursery and in the 1966 F4 bulk trial similar seeding methods were used except that 2 row plots were used similar to the 3 row plots but with the center row absent. The F3 nurseries in all three years were organised in ranges in such a manner that every third plot within a range was a control plot (Pembina in 1965, Manitou in 1966 and an F3 bulk control in 1967) seeded in the same way as the F3 lines. Thus each line was growing adjacent to a constant control variety. All nurseries

were harvested in their entirety. For grain yield determination entire plots were harvested at maturity, the samples dried on racks in an air-drying room, threshed in a Vogel thresher and weighed.

Extensive use was made of winter nurseries grown at the CIMMYT research station, Ciudad Obregon, Mexico during the program and in each year these nurseries provided the material for the F3 and F5 Winnipeg summer nurseries. The use of space planted F2 and F4 generations in Mexico during the winter allows at least two advantages peculiar to this method of handling early generations in pedigree breeding. Firstly, winter increases permit an accelerated breeding program with two growing seasons per year and the production of excellent seed samples from Mexico. Secondly, and more importantly, sufficient seed is produced on the single F2 and F4 plants under conditions of high fertility and wide spacing to enable large three rowed yield plots to be grown in F3 and F5. The largest number of seeds produced on a single plant in any of the Mexico nurseries was 4000 and plants with over 1500 seeds were common. As a result of this fact duplicate F5 nurseries containing those F5 lines with sufficient seed were sown at the Glenlea Research Station in each of the three years. Unfortunately none of these Glenlea nurseries were harvested, due to inclement harvesting conditions. However, in 1968 the Glenlea duplicates for the best nine F5 lines for yield in the University of Manitoba nursery were harvested, with their adjacent Manitou controls. The yield performance of these nine lines in the two locations was compared.

In all nurseries grown, either in Mexico or Winnipeg, complete notes were kept on the agronomic features of all entries. Extensive analysis of the yields and quality of the control plots in the F3 and F5

nurseries was undertaken and has been previously reported (Briggs et al [11], Bushuk et al [12]). This information, describing the areas in the nursery of potentially high and low yield and of potentially high and low wheat quality, was used to help in assessing the true yield and breadmaking quality potential of an individual line growing in a particular part of the nursery.

1. Method of selection in the F3 generation

All materials used in this program were derived from one of two wheat projects. In 1965 and 1966 the F3 arose from the University of Manitoba hybrid wheat project, and in 1967 the F3 were obtained from a study concerning the ability to select for yield on the single plant basis. The diversity of origin of the various F3 populations was not considered to have any limiting effect on the ability to study the effectiveness of selection among F3 lines.

The 1965 F3 nursery consisted of 180 F3 plots from fourteen different crosses. After yield determinations were completed thirty lines were selected, representing the wide range of yielding ability of the F3 on the single plot basis. For each selection yielding capacity was assessed by both the actual grams yield of the plot and by the yield of the plot as a percentage of the yield of the adjacent control. Seed from each of the selected F3 lines was tested for overall breadmaking quality, using fourteen tests of quality as described previously by Briggs et al [9]. These tests included determination of wheat protein, bushel weight, 1000 kernel weight, milling characteristics, sedimentation value, farinograph characteristics and two baking tests, and required 800 grams of seed. Reselection was practised on the basis of the quality results, so that 11 F3 selections were finally retained which represented as wide a range of quality as

possible and also a wide range in yielding ability.

Selection in the 1966 and 1967 F3 nurseries was conducted in a similar manner but with one main difference. Because of the very encouraging results obtained from the first cycle of selection in F3, in which the complete spectrum of F3 yielding ability was represented by the selections, it was considered of interest to determine how effective selection within the upper range of the spectrum of F3 yielding ability might be. Thus, in both 1966 and 1967 selections for yielding ability were chosen mainly from the upper regions of the F3 nursery yield distributions. In both years selection was practised in order to retain as wide a range of quality characters as possible, within the initial selections for yield. In 1966 22 F3 selections were retained from a nursery of 1092 F3 lines, and in 1967 14 F3 selections were retained from a nursery of 335 F3 lines.

2. Method of assessment in F4 and F5

In each year, individual F3 selections were increased in the winter in Mexico as spaced plants, with approximately 600 randomly derived F4 plants per selected F3. Up to 100 F4 plants per F3-derived population were visually selected for desirable agronomic characters (e.g., leaf and stem rust resistance, lodging resistance) and for their ability to produce at least 800 seeds, sufficient to seed an adequate F5 yield plot. Each selected F3 was then represented in the following summer by a number (population) of F5 lines grown in an F5 nursery yield trial. F5 nurseries were grown in the same way as the F3 nurseries described earlier, with Manitou controls adjacent to each F5 line. The arrangement of a typical F3 or F5 nursery is shown in Fig. 1. F3-derived F5 populations were grown in blocks in the 1966 F5 nursery and in a completely randomised

Figure 1: View of typical F_3 nursery, showing three row plots with controls (marked with white stakes) every third plot.

design in the 1967 and 1968 F5 nurseries. Entire nurseries, including Manitou controls, were harvested and the yield of individual F5 lines expressed both in "Grams per Plot" and "% of Adjacent Control". In each year analyses of variance were conducted for these two variables to determine whether significant differences existed between the mean yields of the F5 populations.

Quality determinations were also made in 1966 and 1967 for as many lines as possible within each F5 population, and analyses of variances conducted to test for significant differences between F5 populations for each of up to 14 quality variables. In 1968 this analysis was only conducted on one quality parameter, that of wheat protein. The pedigrees of selected F3 lines, and the number of determinations made for yield and quality per F3-derived F5 population are shown in Table I, for each of the three years.

In two of the years bulk F4 tests, sown with reserve seed from the F3 selections, were grown in the same field as the F5 nursery containing the related F5 populations. The F4 bulk tests were of the randomised block design, with 4 replicates in 1966 and 6 replicates in 1967. Analyses of variance were conducted to test for significant differences in yield of the F4 bulks. Single determinations of quality were made on the F4 bulks, using 14 tests of breadmaking quality.

In each year, and for each of the yield and quality variables in turn, the regressions were calculated of 1) the F5 population means on the related F3 values, 2) the bulk F4 means on the related F3 values and 3) the F5 population means on the related F4 values. In 1968, when no F4 bulk test was grown, only the first of these three regressions was

TABLE I

Pedigrees of selected F3 lines, and number of F5 lines per selection used in determinations of yield and quality, for three years.

Pedigree of F3 selection[1]		Number of F5 lines per F5 population used for determination of: Yield	Quality
1965 F3	TZPP/Pembina- 19	1966 F5 53	20
	TZPP/Pembina- 21	57	18
	Son 64/Pembina-180	60	19
	Son 64/Pembina-184	55	12
	Son 64/Pembina-313	48	21
	Son 64/Pembina--315	48	19
	Son 64/TZPP -237	98	9
	Son 64/TZPP -238	100	3
	CT244/TZPP - 66	39	12
	CT244/TZPP - 81	35	20
	TZPP/CT244 -102	68	19

Pedigree of F3 selection		Number of F5 lines per F5 population used for determination of: Yield	Quality
1966 F3	UM530/CB179-4112B	1967 F5 50	9
	" " -4218B	50	6
	" " -5017A	50	-
	" " -5414B	50	-
	" " -4611A	50	-
	" " -4419A	50	-
	UM530/CB100- 203B	50	4
	" " - 343A	50	4
	" " - 463A	50	9
	" " - 604B	50	16
	" " - 405A	50	2
	" " - 147A	50	-
	" " - 250B	50	-
	" " - 415A	50	-
	" " - 133A	50	-
	" " - 132A	50	-
	" " - 116A	50	-
	" " - 253B	50	-
	" " - 240A	50	-
	" " - 513A	50	-
	" " - 637B	50	-
	" " - 510A	50	-

TABLE I (cont'd.)

Pedigree of F3 selection[1]		Number of F5 lines per F5 population used for determination of:	
		Yield	Quality
1967 F3 (LR64A/Son 63)	Justin-110X	1968 F5	20	20
"	" -125Y		21	21
"	" -131X		19	19
"	" -156Y		20	20
"	" -168Y		23	23
"	" -170Y		16	16
"	" -176Y		19	19
"	" -178X		34	34
"	" -180Y		29	29
"	" -205Y		15	15
"	" -215Y		14	14
"	" -220X		40	40
"	" -232X		23	23
"	" -247X		21	21

[1]Abbreviations are used for some parental varieties. Description of these varieties is given in Appendix 5.

calculated. In all cases where a regression value was determined, a value for the Spearman rank correlation coefficient was also calculated.

In order to test the worth of using extensive control plots in the F5 nursery, the correlation was calculated between the mean yields of the F5 populations on a "Grams per Plot" basis and on a "% of Adjacent Control" basis, for each of the years.

RESULTS

In each of the three years the mean yield of the F3 lines was significantly higher than the mean yield of the controls in the nursery (Table II). Table II also shows how in each of the three years the mean of the selected F3 lines was higher than the mean of the F3 nursery lines from which they were selected, for both "Plot grams yield" and "% of adjacent control yield". The widest representation of the yielding ability of the F3 nurseries was by the F3 selections chosen in 1965, which ranged from the maximum F3 line yield of 1622 grams down to the lowest yielding F3 on which a complete quality analysis could be conducted (819 grams). In 1966, and 1967 especially, F3 selections were chosen mainly from the high end of the F3 nursery yield spectrum.

In all three years, Analysis of Variance between the F3-derived F5 populations indicated that significant differences ($P \leq 0.05$) existed between the means of F5 populations for yield, measured both by "Plot grams yield" and by "% of adjacent control" (Table III). Significant differences ($P \leq 0.05$) also occurred between the mean yields of selections in the 1966 F4 bulk test, but no significant differences were found between the mean yields of selections in the 1967 F4 bulk test. The latter test was characterised by highly significant differences between replications, and a high coefficient of variation (CV = 26%). The yield performance of F3 selections made in 1965, 1966, and 1967, and the performance of their related F4 bulks and F5 populations are shown in Table III, for both yield variables.

In all three years, Analysis of Variance between F3-derived populations indicated that significant differences existed between the means

TABLE II

Yield statistics of F3 lines and controls, and unpaired t test for differences between mean yields of lines and controls, for three F3 selection nurseries. The range and mean of the selected F3 lines is also indicated.

	Mean	SE	N	Min	Max	t	DF
1965							
F3 lines, plot grams yield	1096.5	14.5	180	367	1622	6.17**	280
Pembina controls, grams yield	965.7	11.9	102	545	1237		
F3 selections, grams yield	1295.0		11	819	1622		
F3 lines, % of control yield	115.0		180	37	247		
F3 selections, % of control yield	139.7		11	80	247		
1966							
F3 lines, plot grams yield	1156.8	6.0	1092	422	1848	11.62**	1711
Manitou controls, grams yield	1058.0	4.0	621	575	1427		
F3 selections, grams yield	1421.7		22	956	1848		
F3 lines, % of control yield	110.0		1092	57	167		
F3 selections, % of control yield	132.6		22	78	167		
1967							
F3 lines, plot grams yield	1446.6	12.3	335	813	2068	4.31**	519
F3 bulk control, grams yield	1362.6	13.9	186	896	1888		
F3 selections, grams yield	1800.6		14	1615	2068		
F3 lines, % of control yield	107.0		335	65	171		
F3 selections, % of control yield	128.6		14	119	148		

** Significant at the 99% confidence level.

TABLE III

F3 values, F4 bulk means and F5 population means of selections made in F3 in each of three years, for two yield variables. Anova tests of significance are also included for the F4 and F5 data.

Plot yield in grams

1965 F3 Selection	F3 Value	1966 F4 Mean	1/	1966 F5 Mean	SE	2/
238	1622	1308	a	1055.7	21.1	c
66	1548	1144	ab	890.5	26.2	d
102	1509	1047	bc	1139.9	23.7	b
237	1496	1292	a	1221.1	19.3	a
81	1359	917	cd	866.3	35.9	de
180	1355	1295	a	925.3	26.3	d
19	1350	1125	b	935.4	27.7	d
313	1136	1167	ab	890.6	22.4	d
21	1108	817	d	793.6	22.3	ef
184	942	909	cd	592.0	24.4	g
315	819	1120	b	726.9	19.9	f
Highest Pembina control in F3 nursery = 1237						

Yield, % of adjacent control (Pembina)

1965 F3 Selection	F3 Value	1966 F4 Mean	1966 F5 Mean	SE	2/
81	246	80.5	104.3	4.34	b
238	193	114.5	104.1	1.93	b
66	164	100.4	118.4	4.98	a
237	150	113.3	115.8	2.58	a
102	141	91.8	114.2	2.05	a
19	129	98.8	89.1	2.37	cd
313	122	102.4	92.4	2.66	c
180	118	113.7	100.6	2.83	b
21	106	71.7	83.8	2.08	de
315	88	98.3	80.1	2.36	e
184	80	79.8	68.4	3.07	f

1/ Duncan's new multiple range test ($P < 0.05$). Treatments with the same letter are not significantly different from one another, at the 95% confidence level.

2/ LSD multiple range test ($P \leq 0.05$). Treatments with the same letter are not significantly different from one another, at the 95% confidence level.

TABLE III (cont'd.)

Plot yield in grams

1966 F3 Selection	F3 Value	1967 F4 Mean	1/	1967 F5 Mean	SE	1/
4611A	1848	1430	a	999.3	44.1	fgh
415A	1650	1458	a	1202.5	42.3	bcd
133A	1637	1355	a	1231.7	53.4	bc
203B	1627	1810	a	1423.0	55.8	a
132A	1617	1624	a	1194.9	53.2	bcde
4112B	1539	1614	a	1046.3	42.5	efgh
147A	1534	1507	a	938.1	47.1	gh
250B	1534	1299	a	911.4	50.5	gh
5017A	1523	1369	a	751.1	35.4	i
253A	1477	1140	a	1213.9	45.9	bc
604B	1474	1279	a	1323.0	51.8	ab
463A	1454	1270	a	1128.6	50.1	cdef
510A	1438	-		1222.0	52.5	bc
116A	1415	1485	a	1341.9	51.0	ab
405A	1306	-		1275.9	52.8	bc
4419A	1297	1567	a	1052.4	40.4	efg
4218B	1294	1265	a	942.8	44.7	gh
240A	1284	1729	a	1235.3	54.6	bc
343A	1269	1071	a	1145.2	39.4	cdef
5414B	1078	1572	a	897.5	45.4	h
637B	1027	1154	a	1015.1	40.9	fgh
513A	956	1073	a	1060.2	40.9	defg
Highest Manitou control in F3 nursery =	1427					

Yield, % of adjacent control (Manitou)

1966 F3 Selection	F3 Value	1967 F4 Mean	1967 F5 Mean	SE	1/
5414B	167	117.1	97.3	1.69	fgh
5017A	153	102.0	89.7	2.09	i
116A	152	110.7	115.6	1.86	b
253A	149	85.0	97.4	1.74	efgh
343A	149	79.8	100.0	1.86	efg
240A	147	128.8	116.2	1.97	b
250B	143	96.9	102.9	2.94	de
4611A	143	106.6	106.8	1.79	cd
510A	141	-	111.4	2.52	bc
4218B	140	94.3	97.6	2.32	efgh
133A	138	101.0	106.7	1.55	cd
4419A	136	116.8	100.6	1.90	def
463A	136	94.6	102.7	1.68	def
4112B	132	120.3	112.9	2.06	b
203B	130	134.9	125.3	2.20	a
132A	127	121.1	106.4	1.79	cd
147A	124	112.3	97.9	1.93	efgh
604B	121	95.3	116.9	2.19	b
415A	116	108.7	101.7	1.67	def
405A	105	-	115.0	2.21	b
637B	90	86.0	93.3	1.66	hi
513A	78	86.0	93.9	2.41	ghi

1/ Duncan's new multiple range test ($P < 0.05$). Treatments with the same letter are not significantly different from one another, at the 95% confidence level.

2/ LSD multiple range test ($P < 0.05$). Treatments with the same letter are not significantly different from one another, at the 95% confidence level.

TABLE III (cont'd.)

Plot yield in grams

1967 F3 Selections	F3 Value	1968 F5 Mean	SE	2/
180Y	2068	1350.5	45.7	ab
176Y	2000	1109.4	46.9	e
125Y	1967	1145.4	62.8	de
178X	1938	1209.1	36.1	cde
215Y	1891	1309.1	102.3	abcd
220X	1825	1119.9	42.3	e
110X	1794	1274.3	61.7	bcd
205Y	1764	1208.9	58.4	cde
168Y	1744	1325.7	42.5	abc
170Y	1694	1318.9	58.7	abc
156Y	1646	1358.7	27.5	ab
131X	1645	1393.3	65.1	ab
247X	1618	1427.3	50.3	a
232X	1615	1273.8	43.7	bcd
Highest F3 bulk control in F3 nursery =	1888			

Yield, % of adjacent control (F3 bulk)

1967 F3 Selections	F3 Value	1968 F5 Mean	SE	2/
247X	148	111.9	3.18	ab
232X	137	104.6	4.66	bcd
215Y	136	106.8	8.02	abcd
131X	133	113.2	4.49	ab
110X	131	105.0	4.16	bcd
178X	130	102.7	3.13	bcde
180Y	127	116.3	4.04	a
156Y	127	112.5	2.72	ab
125Y	127	94.5	5.28	de
205Y	123	104.4	5.60	bcde
168Y	122	112.9	3.08	ab
170Y	121	108.3	3.67	abc
220X	120	93.3	3.08	e
176Y	119	95.8	4.46	cde

1/ Duncan's new multiple range test ($P < 0.05$). Treatments with the same letter are not significantly different from one another, at the 95% confidence level.

2/ LSD multiple range test ($P < 0.05$). Treatments with the same letter are not significantly different from one another, at the 95% confidence level.

of F5 populations for all quality parameters which were measured, with three exceptions (Table IV). For the F5 populations derived from the 1966 F3 no significant differences existed ($P \leq 0.05$) for 1000 kernel weight, blend load volume or for farinograph mixing tolerance index. Lack of significant differences for these three variables was not related to the range available in the F3 selections, which was in all cases quite wide (Table IV). For all quality parameters in which the means of F5 populations were significantly different, the range for the F5 population means was of the same order as the range represented by the F3 selections (Table IV). Only for the variable sedimentation value did this range in F5 exceed the range represented by the F3 selections, in both 1966 and 1967.

Intergeneration regressions and rank correlations were not calculated between the 1967 F4 and 1966 F3, nor between the 1967 F5 and 1967 F4, because no significant yield differences were found in the F4 generation. Intergeneration relationships calculated using the data from the 1966 F4 bulk test indicated that the F4 selection means were not significantly related ($P \leq 0.05$) to the 1965 F3 values for either "Plot grams yield" or for "% control yield", nor were they significantly related to the 1966 F5 population means for the variable "% control yield". The Spearman rank correlation of the 1966 F5 population means with the 1966 F4 means for "Plot grams yield" was significant ($r = 0.64$, $P \leq 0.05$), but the regression coefficient was nonsignificant.

Significant regressions and rank correlations between the means of the F5 populations and their F3 selection values were found for both "Plot grams yield" and "% of control yield" in the first year of selection

TABLE IV

Range in value of F3 selections, range in value of related F5 population means, and results of Analysis of variance between F3-derived F5 populations, for 2 yield variables and 14 quality variables.

	1965 F3 population				1966 F3 population				1967 F3 population			
	Range in F3 (1965)		Range of F5 means (1966)		Range in F3 (1966)		Range of F5 means (1967)		Range in F3 (1967)		Range of F5 means (1968)	
	Min	Max	Min	Max 1/	Min	Max	Min	Max 1/	Min	Max	Min	Max 1/
Plot grams yield	819	1622	592	1221 *	956	1848	752	1423 *2	1615	2068	1109	1427 *
% of control yield	80	247	68	118 *	78	167	90	125 *2	119	148	93	116 *
Bushel weight, lbs.					62	64	64	66 *				
1000 kernel weight, grams	22.1	33.7	31.0	36.7 *	37.6	49.6	42.2	47.8 NS				
Wheat protein, %	11.7	15.2	13.4	16.7 *	13.7	16.1	12.6	15.6 *	14.2	16.0	14.2	16.1 *
Flour yield, %	72.5	78.1	70.4	73.9 *	72.8	75.2	72.6	74.6 *				
Flour protein, %	10.8	14.7	12.7	16.1 *	12.8	15.4	11.7	15.1 *				
Flour ash, %	0.40	0.57	0.43	0.52 *	0.46	0.54	0.46	0.48 *				
Flour color, units	1.2	2.8	1.4	2.6 *	1.9	2.8	0.8	1.7 *				
Baking absorption, %	51.6	62.2	53.8	63.1 *	57.2	60.7	57.1	62.0 *				
Sedimentation value	69.4	71.6	68.7	73.4 *	62.7	72.8	61.9	72.2 *				
Remix loaf volume, ccs.	790	1135	785	1178 *	535	1045	521	979 *				
Blend loaf volume, ccs.	680	800	722	858 *	815	915	700	787 NS				
Farinograph absorption, %	54.6	66.2	57.8	66.5 *	61.2	64.7	61.4	66.3 *				
Farinograph development time, mins.	2.5	8.5	6.0	9.8 *	2.6	8.0	3.0	7.7 *				
Farinograph M.T.I., mins.	25	55	18	40 *	20	35	23	45 NS				

1/ Analysis of variance of means of F5 populations, using Multiple Range LSD Test.
* Significant differences exist between means ($P < 0.05$)
NS No significant differences exist between means ($P \leq 0.05$)
2/ As for 1/ except that Duncan's New Multiple Range Test replaces the Multiple Range LSD Test.

in F3 (Table V). Rank correlations were high for both yield variables, and indicated that the relative yield performance of an F3 line was a good indicator of the likely performance of an F5 population derived from it. No significant relationship was found between the yield performance of 1966 F3 selections and their related 1967 F5 populations, for either "Plot grams yield" or "% of control". The relationship for "% of control" between the 1967 F3 and the 1968 F5 was nonsignificant (by both rank correlation and regression), but a significant negative regression of the 1968 F5 populations on the 1967 F3 selections was found for "Plot grams yield".

The intergeneration relationships between the F3, F4 and F5 generations for those quality data which were obtained during the three year study are given in Table VI. In the first year in which F3 selections were made, significant rank correlations and regressions between F4 and F3, between F5 and F4 and between F5 and F3 were obtained for wheat protein percent, flour protein percent, baking absorption percent, blend loaf volume, farinograph absorption and farinograph development time. Significant rank correlation and regression was also obtained between the 1966 F4 means and the 1966 F5 population means for flour ash percent, remix loaf volume and farinograph stability. All other intergeneration comparisons for these three variables were insignificant.

For some of the intergeneration comparisons in Table VI, and in Table V, differences between the significance of the Spearman rank correlation and that of the simple regression coefficient are apparent (e.g., 1965 F3 vs 1966 F5 for flour yield; 1966 F3 vs 1967 F5 for baking absorption). These differences are probably attributable to the sampling effect of the low number of comparisons used in the tests in each year.

TABLE V

Intergeneration relationships between F3 values and related F5 population means, for two yield variables, as measured by Spearman rank correlation and simple regression.

	Plot grams yield		Yield, % of control	
	Rank r	b value	Rank r	b value
1965 F3 to 1966 F5	0.71 *	0.56 **	0.83 **	0.22 *
1966 F3 to 1967 F5	0.11 NS	NS	-0.09 NS	NS
1967 F3 to 1968 F5	-0.53 NS	-0.36 *	0.31 NS	NS

NS Not significant at the 95% confidence level.
* Significant at the 95% confidence level.
** Significant at the 99% confidence level.

TABLE VI

Intergeneration relationships between F3, F4 and F5 means for up to 14 quality variables, in three different years, as measured by Spearman rank correlation and simple regression.

	1965 F3						1966 F3		1967 F3	
	F3 to F4		F4 to F5		F3 to F5		F3 to F5		F3 to F5	
	Rank r	b value	Rank r	b value	Rank r	b value	Rank r	b value	Rank r	b value
Bushel weight, lbs.							0.69 NS	NS		
1000 kernel weight	0.15 NS	NS	0.35 NS	NS	0.69 *	NS	0.32 NS	NS		
Wheat protein, %	0.73 **	0.41 **	0.91 **	1.29 **	0.88 **	0.66 **	0.39 NS	NS	0.91 **	0.65 **
Flour yield, %	0.23 NS	NS	0.03 NS	NS	0.67 *	NS	0.15 NS	NS		
Flour protein, %	0.67 *	0.35 *	0.67 *	1.11 **	0.77 **	0.62 **	0.07 NS	NS		
Flour ash, %	0.25 NS	NS	0.79 **	0.60 *	0.38 NS	NS	-0.20 NS	NS		
Flour color, units	0.62 *	0.51 *	0.48 NS	NS	0.05 NS	NS	0.71 NS	0.77 *		
Baking absorption, %	0.99 **	0.81 **	0.97 **	1.01 **	0.98 **	0.84 **	0.69 NS	1.02 *		
Sedimentation value	0.85 **	0.70 **	0.67 *	1.34 *	0.47 NS	NS	0.82 *	NS		
Remix loaf vol. ccs.	0.33 NS	NS	0.82 **	0.48 **	0.57 NS	NS	0.57 NS	NS		
Blend loaf vol. ccs.	0.74 **	1.06 **	0.73 **	0.65 **	0.85 **	0.84 *	-0.64 NS	NS		
Farinograph absorp., %	0.99 **	0.77 **	0.97 **	0.99 **	0.98 **	0.79 **	0.83 *	1.17 **		
Farinograph dev. time	0.75 **	NS	0.84 **	0.41 *	0.71 *	0.70 *	0.86 *	0.76 *		
Farinograph M.T.I.	0.04 NS	NS	0.48 NS	0.54 **	0.21 NS	NS	0.68 NS	NS		

NS Not significant at the 95% confidence level.
* Significant at the 95% confidence level.
** Significant at the 99% confidence level.

The 1967 F5 population means were significantly related to the performance of the 1966 F3 selections only for flour color, baking absorption, farinograph absorption and farinograph development time. Large and highly significant relationships between the F3 value and the F5 population mean were obtained for the quality character wheat protein % in the first and third year of the study, but no significant relationship was obtained in the second year.

Comparison by paired t test of nine F5 lines grown at two locations in 1968 showed that the University of Manitoba location was significantly higher yielding ($P \leq 0.01$) on a "Grams per plot" basis than the Glenlea Research Station location (Table VII). This apparent difference in yielding ability of the F5 lines at the two locations was removed when the same paired t test was made using the yield variable "% of adjacent control".

In each of the three years a highly significant correlation ($P \leq 0.01$) was obtained between the means of F5 populations classified on a "Plot yield in grams" basis and on a "% of adjacent control" basis (Table VIII).

TABLE VII

Yield data from two locations, for the best nine F5 lines grown at the University of Manitoba in 1968.

1968 F5 line code #	University of Manitoba: Plot grams Yield	University of Manitoba: % of adjacent Manitou control	Glenlea Research Station: Plot grams Yield	Glenlea Research Station: % of adjacent Manitou control
113	1808	140.8	857	120.5
359	1675	134.0	523	87.0
287	1648	133.4	801	128.2
226	1812	124.8	777	168.9
58	1775	122.4	867	122.1
67	1717	121.8	962	139.0
53	1810	120.5	933	122.4
251	1740	119.0	698	92.8
310	1631	110.9	904	106.2
Mean	1735.1	125.3	813.6	120.8

Paired t test of location means (8 df):

1. Plot grams yield, t = 13.13 Significant at the 99% confidence level.
2. % of adjacent Manitou control, t = 0.52 Not significant at the 95% confidence level.

TABLE VIII

Correlation between the means of F5 populations classified on a "Plot yield in grams" basis and on a "% of adjacent control" basis, for 3 years.

1966 F5 r = 0.82 (** N = 11)
1967 F5 r = 0.78 (** N = 22)
1968 F5 r = 0.94 (** N = 14)

** Significant at the 99% confidence level.

DISCUSSION

This study of relationships between different generations for yield and breadmaking quality characteristics was limited by certain restrictions of the experimental designs which were used. For example, the use of related generations grown in different years results in a confounding of intergeneration comparisons with interyear comparisons and the possible occurrence of generation x year interactions. In the earlier phases of the study (1965 F3 and 1966 F4) two row plots were used, whilst three row plots were used later in the study. Because of these differences possible interactions between method of seeding, year differences and genotype may also have occured. Estimates of these effects were not obtainable from this study and thus the reported intergeneration relationships are subject to possible bias from these sources of variability.

Estimates of heritability in the strict sense were not obtained from this study due to the absence of replication of lines in both the F3 and F5 generations, and the consequent inability to separate sources of variability due to environment and genotype in those generations. Rank correlations and simple regressions were used instead, as a means of measuring actual relationships between generations.

The climatic conditions in the three years of this study were as diverse as are obtained in Manitoba, with 1966 being a year of average rainfall and temperature, 1967 being a year of near drought conditions and 1968 being an extremely wet and cool year. These large differences in climate are the very conditions under which the plant breeder has to operate, and the final selections from his program should be those which

perform well or above average under each of these conditions. The results from this study are therefore considered to be quite relevant to the actuality of plant breeding programs.

1. Selection for yield in F3

The selection of individual F3 lines for yielding ability on both a "Plot grams yield" basis and on a "% of adjacent control" basis was effective, as assessed by performance of related F5 families, only in one of the three years of study (1965). That year was the one in which the widest possible range of yield in the F3 nursery was represented by the selections. F3 yield performance was so effective in predicting yielding performance of related F5 populations in the first year of study that selections in the subsequent two years of study were restricted mainly to the upper portion of the F3 spectrum of yield. Classification for yield within the upper portion of the F3 yields was not effective in either 1966 or 1967 for either of "Plot grams yield" or "% of control yield", and a negative relationship was actually obtained between the 1967 F3 and 1968 F5 for "Plot grams yield". The results from these two years do not support the recommendation of selection for either of "Plot grams yield" or "% of control yield" alone in the F3 generation, when selection is between F3 lines representing only the highest yielding portion of the F3 population. Further studies are needed in which F3 lines representing the middle, lower and upper portions of the yield distribution of the F3 population are assessed by their performance in the F5 generation. Studies of this kind are at present being conducted at the University of Manitoba.

Despite the discouraging rank correlations and regressions between

F3 and F5 obtained in two years out of three, it was apparent that the highest yielding populations in each year were obtained from F3 lines which were relatively high for both "Plot grams yield" and "% of control yield" (Table IX). In all three years the two F5 populations classified as being the "best" yielders (on the basis of both "Plot grams yield" and "% of control") were derived from F3 lines which were high for "% of control". In two years out of three the best two F5 populations were derived from F3 lines which yielded nearly as high or higher (in grams per plot) than the highest yielding control in the nursery. Though the supporting evidence is not strong, one might suggest that in F3 yield nurseries selection only of F3 lines which are higher yielding in "Plot grams yield" than the highest yielding control (best variety) in the F3 nursery, and which are also high for "% of control", would be a worthwhile procedure. Misclassification of some F3 lines as to their yield potential would undoubtedly occur under this system, but the F3 lines with the greatest yield potential would probably be retained.

2. Selection for breadmaking quality in F3

Breadmaking quality is a function of the total amount of protein in the flour, and the quality of the protein (Bushuk et al [12]). In studies concerning the breadmaking quality of segregating lines in early generations from crosses between parents differing in overall breadmaking quality one may expect differences in both protein quantity and quality to be present. In this program, tests of breadmaking quality have included both actual baking tests, estimates of total protein in both wheat and flour, and measures of the mixing characteristics of the dough using the

TABLE IX

Classification of "best" two and "worst" two F5 populations for overall yielding performance, and relationship to F3 performance, for 3 years.

		F3 Value		F5 Mean		
1. 1965 F3		Grams	% Control	N	Grams	% Control
Best two in F5	237	1496	150	98	1221.1	115.8
	102	1509	141	68	1139.9	114.2
Worst two in F5	21	1108	106	57	793.6	83.8
	315	819	88	48	726.9	80.1
Mean of F3 nursery		1097	115			
Max. Pembina control		1237				

		F3 Value		F5 Mean		
2. 1966 F3		Grams	% Control	N	Grams	% Control
Best two in F5	203B	1627	130	50	1423.0	125.3
	116A	1415	152	50	1341.9	115.6
Worst two in F5	5414B	1078	167	50	897.5	97.3
	5017A	1523	153	50	751.1	89.7
Mean of F3 nursery		1157	110			
Max. Manitou control		1427				

		F3 Value		F5 Mean		
3. 1967 F3		Grams	% Control	N	Grams	% Control
Best two in F5	247X	1618	148	21	1427.3	111.9
	131X	1645	133	19	1393.3	113.2
Worst two in F5	220X	1825	120	40	1119.9	93.3
	176Y	2000	119	19	1109.4	95.8
Mean of F3 nursery		1447	107			
Max. F3 bulk control		1888				

N Number of determinations used to obtain the F5 mean.

Brabender Farinograph. It is realised that the results from these tests are to a certain extent interrelated simply because each of the tests measures a property of the flour which is related to total protein content. However, for the purposes of this study, the various quality parameters were treated as independent variables, in the same way as was done by McNeal et al [24].

The predictable value of selecting for quality in F3 varied from year to year. In two years out of three, wheat protein determinations in F3 very satisfactorily predicted the performance for wheat protein in the F5. In one of these years the F5 performance for blend loaf volume was also predictable in the F3. Baking absorption, farinograph absorption and farinograph development time could also be satisfactorily classified in F3 for their later performance in F5, in the two years in which they were studied. This was possible despite the fact that in one of these two years selection for wheat protein in the F3 proved to be unreliable. There was no relationship between the F3 and F5 for farinograph mixing tolerance index in either of the years in which it was studied. In all studies carried out this variable was characterised by an extremely high coefficient of variation, both in studies of F5 populations and in the study of the quality of Manitou controls (Bushuk et al [12]). The continued use of farinograph mixing tolerance index as a selection criterion in early generations is questionable. Summary of the three years results supports the use of wheat protein content and farinograph characteristics (excluding mixing tolerance index) as selection criteria in the F3 generation.

In the one year in which the relationship of the F3 to the F5 for wheat protein was nonsignificant (1966 F3) nine of the other quality

variables also demonstrated a nonsignificant relationship between the performance in the F3 and in the F5 generations. It is possible that some of these nonsignificant relationships were the result of some dependence of the quality variables on total protein content, as has been frequently reported in the literature.

3. The use of control plots

The objectives of using control plots adjacent to every line in an F3 nursery have been described in detail previously (Briggs and Shebeski [11]). No extensive evidence has been available comparing the actual efficiency in evaluation of breeding lines by methods using controls and methods which do not use controls. Methods of field experimentation and statistical analysis are now legitimately established, and alternative methods must be compared to those currently used as standard. In the absence of replication of individual lines in the F3 generation, in the selection method of Shebeski, this comparison could not be made in that generation. The use of the completely randomised design for the F3 derived F5 populations grown in each of the three years, and the use of adjacent controls throughout these nurseries, allowed proper comparison of the control vs no control methods of assessing F5 populations. The use of the variable "Plot grams yield" in the analysis of variance of the F5 populations uses the method of dividing the total amount of variation into that due to variability between populations, and that due to variability within F5 populations (the error variance). The error variance in this case is attributable mainly to environmental effects, including effects of soil heterogeneity. Use of the variable "% of control yield"

should theoretically remove some of the variability due to environment, and nursery location in particular, before the Analysis of Variance is conducted. The main assumption is that by expressing the yield of a given F5 plot as a % of the yield of the adjacent control the effects of location in a nursery with heterogeneous soil will be minimised. If the yields of contiguous plots planted to the same variety are very closely related (Briggs and Shebeski [11]) then the difference in yield of an F3 line and an adjacent control, expressed as a percentage, ought to more closely reflect a genetic difference in yield potential than an environmental difference.

A high correlation was obtained in each of the three years between the means of F5 populations classified for yielding ability by "Plot grams yield" and the means of F5 populations classified by "% of control yield". Thus the method of using yield information from controls appeared to classify the F5 populations for yielding ability in a very similar manner to that obtained by the use of the conventional variable "Plot grams yield". There would, therefore, appear to be little apparent justification in investing a great deal of effort in an extensive use of control plots in an F5 nursery of the type used in this study, if the results obtained from the use of controls are essentially the same as those obtained from conventional experimental methods without controls. However, controls are necessary in the F5 nursery if the program calls for reselection of superior lines within F5 populations, which are still likely to be genetically heterogeneous. In the absence of replication of individual F5 lines the use of information from adjacent control plots at least provides some basis for allowing for environmental effects on yield.

The results obtained in 1968 from the nine best yielding F5 lines at the University of Manitoba, which were also harvested at a second location, indicated that the grain productivity level as measured by "Plot grams yield" was significantly different at the two locations. The effect of this location difference was removed when yields were expressed as "% of adjacent control", providing some indirect evidence that environmental influences can be minimised from the use of controls, as previously demonstrated by Haggag [17].

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SECTION 3

Discussion of entire research program.

DISCUSSION

Extensive discussion of the results from the four year study of early generation selection for yield and breadmaking quality of Triticum aestivum L. was presented in each of the four papers comprising the third section of this thesis. The main conclusions from those papers are presented in this section, together with further discussion and suggestions for continued research.

In three different selection nurseries it was shown that the yields of control plots of the variety Manitou nine feet apart in a wheat breeding nursery were highly significantly correlated. The correlation between yields decreased rapidly with increasing distance between plot centers. A similar analysis was conducted for fourteen breadmaking qaulity parameters for one nursery in which the variety Manitou was used as the control. Correlations calculated for control plots at specified distances apart indicated that, for all important breadmaking quality parameters, contiguous plots were significantly more similar than those further apart. Areas of high and low yield potential and high and low quality potential could be identified in wheat nurseries by using yield and quality data from controls at frequent intervals. This information should be used by the plant breeder when assessing unreplicated breeding lines from a given area of the nursery.

Further investigation of the system of using adjacent control plots, as a means of controlling variability in yield due to environmental effects, would be desirable. This could be achieved by growing large multilocation replicated tests of a series of wheat varieties which are known to represent a very wide range in yield capacity. These tests would contain control plots of a fixed variety adjacent to every entry, and a comparison of the performance of varieties for the variables "Plot grams yield" and "Percent

of adjacent control yield" could be made. An analysis of covariance for the varieties, in which the yield of the adjacent control is used as the covariate, would give some indication of the amount of variability due to environment which could be accounted for by yield data from the control plots, as described by Baker [9]. Such a study could also be accomplished for breadmaking quality, and would provide useful information if the varieties used represented a wide range in quality.

A highly significant positive correlation was obtained between grain yield and wheat protein content in each of two years for the variety Manitou. The breadmaking quality of the Manitou controls was significantly different in the two years. In both years most of the quality parameters were significantly and positively correlated with wheat protein content. The actual quantitative relationship between each of the various parameters and wheat protein content was consistent from year to year only for flour protein content, flour ash, flour color and remix loaf volume. It was recommended that in each year a series of Manitou wheat samples with as wide a range as possible for wheat protein content should be analysed for breadmaking quality. Quality data from single breeding lines could then be compared to the data for Manitou samples of equivalent protein content from the same nursery. The wheat protein content of an individual breeding line could also be compared with the wheat protein content of the adjacent control. The latter value would provide an estimate of the wheat protein content "potential" of that part of the selection nursery, and the wheat protein content of the line would have to be of a similar order in order for the line to be retained in a breeding program in which high breadmaking quality was a major objective.

The fourth part of this project constituted a study of the effectiveness

of selection for certain yield and breadmaking quality parameters of Triticum aestivum L. on the unreplicated F3 line basis. The only characters for which the mean performance of F5 populations could be predicted from the F3 line performance were wheat protein content and Farinograph characteristics (excluding mixing tolerance index), and in one year out of three for "Plot grams yield" and "Percent of adjacent control yield." The good relationship between F3 and F5 for the two yield variables was obtained in the only year of the three in which the maximum range of yields in the F3 population was sampled. Selection within the upper region of the spectrum in F3 for either of the yield variables alone was ineffective in the other two years, but in all three years the "best yielding" F5 populations were derived from F3 plots which were in the higher area of the F3 population for both yield variables.

Results from intergeneration comparisons for yield involving F4 bulk tests indicated that in this study the latter test was not particularly useful from a plant breeding point of view. Significant yield differences between the F4 bulks were obtained in only one of the two years in which the F4 bulk test was grown, even though significant yield differences existed between related F5 populations in both of these years. The relationship between the mean F4 bulk yield and the mean F5 population yield was significant in only one year of the two. Since the F4 bulk test and the test of related F5 populations are grown in the same year, and because the data from the F5 generation is likely to be more useful to the breeder due to an increased amount of homozygosity of the F5 over the F4 generation, the continued use of the F4 bulk test is of rather questionable value in the system of selection suggested by Shebeski [110].

In each of the three years significant differences were found between

the means of the F5 populations for each of the yield and breadmaking quality parameters, with only minor exceptions. For those characters which show significant differences between populations in F5, and in which a good relationship is demonstrated between the performance of selections in the F3 and F5 generations, selection in the F3 generation can be recommended. Selection between F5 populations on the basis of significant differences would appear to be a useful procedure for making genetic progress, as each F5 population traces back to a different F2 plant. Quantitative differences between the F5 populations should therefore imply real genetic differences between the populations.

Though this was not one of the main objectives of the thesis estimates of broad sense heritabilities were calculated in F5 for each of the yield and breadmaking quality parameters, in each of the three years. The method of calculation and results are given in APPENDIX 6. The heritability values give some indication of the likely effectiveness of selection between F5 populations, the effectiveness being greater for characters with higher heritability values.

In the system of growing F3 lines which has been used in this study, each F3 plot yield or quality determination represents the mean yield or mean quality performance of a mixture of genotypically different plants grown in the same plot. The number of plants in each F3 plot limits the range of genotypes which will be retained from each F2 progeny, as does the size of the F4 population of spaced plants and the size of each F5 population per F3 line. However, whatever the size of population used in each generation the mean of the population is an estimate of the mean genotype in that generation. The mean of an F5 population as used in this study represents

the mean of a series of genotypically different F5 lines all of which are derived from the same F3 line. Thus the variability which exists within the F5 populations is due to 1) genetic variability between F5 lines, 2) environmentally induced variability both within and between F5 lines, and 3) variability due to interaction of F5 genotypes with environment. It is suggested that useful estimates of the relative amounts of variation due to these three different sources within F5 populations could be obtained by the use of replicated F5 lines in the F5 nurseries. A similar system could also be used in the F3 generation. Use of replication would, of course, concurrently reduce the number of different F3 and F5 lines which could be handled in the program but would allow proper estimates of heritability in both the F3 and F5 generations to be made.

As an extension of this approach, it is suggested that some of the following methods could usefully be adopted for further investigation of the system of selection in the F3 generation for quantitative characters, that was suggested by Shebeski in 1967.

1. The F3 nursery should be of a design where each F3 line is represented by two replicates in the same nursery. In the three year study reported above, approximately two-thirds to three-quarters of the harvested F2 plants would have had sufficient seed for this to be done. Statistical comparisons between genotypically different F3 lines could thus be made, heritability estimates could be calculated in the F3 generation, and the use of replication might somewhat reduce the requirement for frequent control plots in the nursery. Replication of F3 lines would also allow a measure of the experimental error involved in the use of yield information from adjacent control plots.

2. The sampling of F3 populations to determine which F3 lines will be

studied in subsequent generations should be conducted in a statistically defined manner. The use of completely random sampling or stratified sampling of an F3 population would be useful for ensuring that the range of variability for the particular character in the F3 population is fully represented by the selections. In the initial stages of investigation emphasis should be placed more on the selection of a large number of F3 lines, each to be represented by relatively few F5 lines, rather than on selection of few F3 lines each to be represented by a large number of F5 lines. Depending on the results obtained from studying the effect of selection in the F3 generation on the broad basis, subsequent investigations could be restricted to the use of fewer F3 selections from each F3 population. These selections would represent only the phenotypically more desirable portion of the spectrum available in the F3 population. Determination of the relative amounts of genetic variability available within each of the F3 lines could then be achieved by growing and analysing large numbers of F5 lines derived from each selected F3 line.

3. The F5 nurseries should be of a design where each F5 line is represented by two replicates. Estimates of the amount of genotypic variability within and between F5 populations could thus be obtained and reliable estimates of heritability calculated. Replication of F5 lines might also reduce the requirements for frequent control plots, as previously mentioned for the F3 nurseries.

4. An agronomic study of the performance of wheat varieties which represent a wide range of known yielding ability should be conducted, in order to determine the extent to which the methods of small plot seeding influence the final yield of wheat varieties in small plot trials. Such experiments should investigate the relative merits of two, three and four

row plots at various combinations of seeding rate and row spacings, and should relate the results from the small plot trials to the performance of the varieties grown in large scale field trials. Results from such a study might indicate whether the three row plot type as used in this study was the best for small plot nurseries, or whether some other plot type would be more reliable.

SECTION 4

Bibliography
Appendices

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APPENDIX 1

QUESTIONNAIRE RE PEDIGREE METHOD FOR BREEDING SPRING WHEAT

	Question	Answer	Comments
F1	1. Number of crosses made per year.		
F2	1. How many F2 plants per cross are grown?		
	2. How many F2 plants for all crosses are grown?		
	3. What is the seeding rate used, spaced or otherwise?		
	4. What are the criteria for selection on the single plant basis?		
F3	1. How many F3 lines per cross are grown?		
	2. How many F3 lines for all crosses are grown?		
	3. How many plants in an F3 line?		
	4. What spacing is used between plants?		
	5. What spacing is used between rows?		
	6. What length row is used in an F3 plot?		
	7. How many rows in an F3 plot?		
	8. Frequency of control or check plots.		
	9. What % of F3 lines are selected for F4?		

Question	Answer	Comments
F3 (Cont'd.)		
10. How many plants are selected per line for F4?		
11. What is the basis for selection on the plant and line level?		
What are the main breeding problems in your area (e.g. drought, disease resistance, etc.)?		

APPENDIX 2

IMPLICATIONS CONCERNING THE FREQUENCY OF CONTROL PLOTS IN WHEAT BREEDING NURSERIES[1]

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ABSTRACT

Control plots of *Triticum aestivum* var. Manitou were grown adjacent to every plot of breeding material in three hard red spring wheat nurseries at the University of Manitoba. Simple correlations between yields were high ($r = .88, .87$ and $.63$) and significant (P .01) for control plots at 2.7-m (9-ft) centers but decreased rapidly to nonsignificance with increasing distance between plot centers. The data indicate that for the particular type of plot used, the yield of a control plot provides a good measure of the soil fertility in terms of the yielding ability of an adjacent plot.

INTRODUCTION

There is recent widespread concern among wheat breeders about the need to improve the methods of handling hybrid populations to obtain maximum improvement when selecting for quantitatively inherited characters, such as quality and yield. Hamilton (4) suggested in 1959 that the methods used in breeding programs be examined with a view to determining whether it was the genetic material itself or the methods by which it was being handled that was limiting progress. The response to a questionnaire circulated by the authors to a worldwide cross-section of wheat breeders indicates that the methods used vary markedly relative to such features as the number of crosses made, the size of F_2 populations, the number of lines grown in F_3 and the number of plants per line, the frequency of controls, the number of F_3 lines retained for further selection and the number of plants selected per line. For example, the frequency of control plots as reported by the breeders ranged from 1 in 200 plots to one every third plot, with an average of about one control per 50 plots.

In the pedigree-wheat selection nurseries now in use at the University of Manitoba, a plot of the control variety *Triticum aestivum* var. Manitou is grown adjacent to every plot of breeding material (3, 9). The yield of each experimental plot (or line) is expressed in terms of the yield of its adjacent control, and this criterion is used directly as a selection index. The main assumption for the approach is that the yield of the control plot provides a good measure of the fertility of the adjacent plot on which the experimental line is grown. Any difference in yield between the control and the experimental line therefore will be due more to the genetic difference than to a difference in soil fertility. Confirmation of this assumption requires that the correlation between the yields of adjacent plots be very high.

Recent literature on this subject in cereals appears to be lacking. Student (10) indicated that the greater the contiguity of two plots in a field, the more alike they would be expected to be in yield. Other workers including Harris (5), McLelland (7), Pritchard (8) and Yates (12), have supported this view but only a few have attempted to show the degree of correspondence of contiguous plots. Garber *et al.* (1), using plots of oats and wheat 19.6 m (61 ft) long by 4.3 m (14 ft) wide in uniformity trials, demonstrated simple correla-

[1]Contribution No. 133 of the Department of Plant Science.

tions between contiguous plots of 0.668 for oats and 0.553 for wheat. Wiebe (11), in an extensive uniformity trial with 1,500 wheat nursery plots, each 4.6 m (15 ft) long and spaced 0.3 m (1 ft) apart in twelve ranges, showed that the correlation between the yield of the rows in the nursery decreased almost linearly as the distance between the rows increased. The correlation between adjacent rows 0.3 m (1 ft) apart was 0.82 and decreased to a nonsignificant value of 0.18 with rows 17.1 m (56 ft) apart. Hayes (6) and Griffee (2) working with wheat also illustrated a decrease in correlation for yields of plots of decreasing contiguity.

The objective of this study was to examine the correlation for yield between control plots of decreasing contiguity, with a view to assessing an adequate frequency of controls in a breeding nursery.

MATERIALS AND METHODS

The results to be reported here were obtained from three separate spring wheat-breeding nurseries, one grown in 1966 and the other two in 1967. Each of these three fields was on the same soil type, which is described as Riverdale clay.

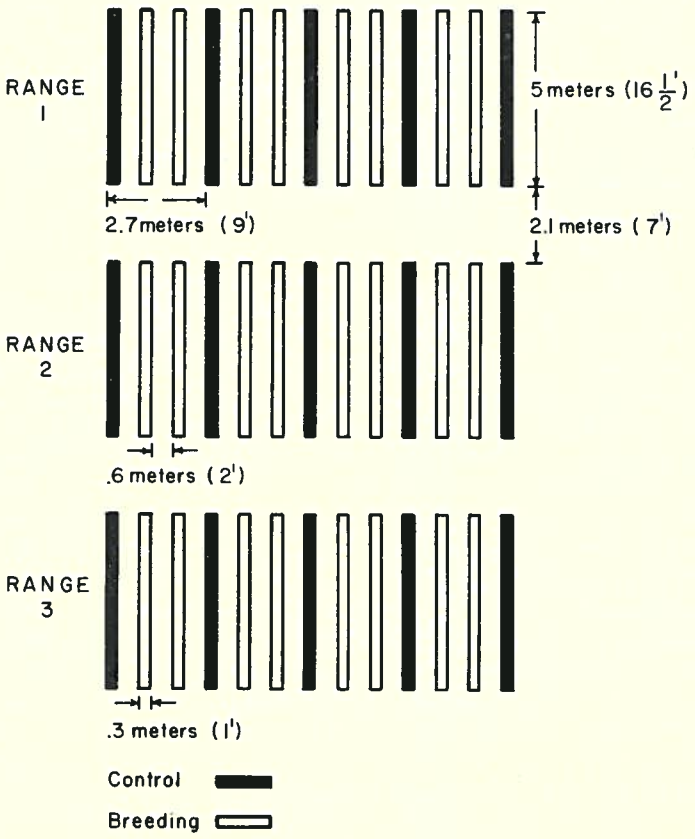

FIG. 1. Diagrammatic arrangement of a portion of the nursery at harvest time. Only three of the six ranges are illustrated.

Field 1 in 1966 and field 3 in 1967 had been fallowed prior to planting, whereas the wheat on field 2 in 1967 was grown on corn stubble. The climatic conditions in the 2 years were quite dissimilar.

Each experimental-plot area was arranged in the manner shown in Fig. 1. Every third plot constituted a control (Manitou), the two intervening plots being the experimental hybrid under investigation. All plots in a field were seeded on the same day at a rate of 250 seeds per row by means of a disc power seeder. The plots consisted of three rows and were 5.6 m (18½ ft) long with a 15-cm (6-in.) spacing between rows. Plots were spaced 0.6 m (2 ft) apart in order to minimize interplot competition. For yield assessment, the plots at harvest time were trimmed to 5.0 m (16½ ft), all three rows were harvested by hand and the threshed samples were dried and cleaned before weighing. This report deals with the yields of the control plots in three separate nurseries containing 56 control plots per range (field 1, 1966), 34 control plots per range (field 2, 1967), and 59 control plots per range (field 3, 1967).

Simple correlation coefficients for the yield of control plots at increasing multiples of 2.7 m (9 ft) apart along the range were calculated in such a way that the maximum number of observations was included in the calculation of each coefficient. For example, the value at the 2.7-m (9-ft) center was calculated by using the sum of the observations over all six ranges of all the possible pairs of control plots 2.7 m (9 ft) apart within a range. This was repeated for the 5.5-m (18-ft) center, the 8.2-m (27-ft) center and for each additional spacing to obtain the 18 correlation coefficients. In 1966, two correlation coefficients corresponding to a 0.9-m (3-ft) and 1.8-m (6-ft) spacing were also available from a different part of the same nursery, but both were based on a very limited number of observations.

RESULTS

The correlation between the yield of control plots located 2.7 m (9 ft) apart was 0.63 in 1966 and 0.88 for field 2 and 0.87 for field 3 in 1967. The correlation coefficients decreased rapidly as the distance between plots increased, until at a distance of 19.2 m (63 ft) the correlation in two of the nurseries (field 1, 1966 and field 2, 1967) was no longer significant at the 95% confidence level (Fig. 2). In field 3, 1967, this correlation was nonsignificant when controls were 35.7 m (117 ft) apart. The correlations between the yield of control plots 0.9 m (3 ft) and 1.8 m (6 ft) apart obtained in 1966 were very high, although the former was nonsignificant at the 95% level.

DISCUSSION

One of the common problems in the past has been the difficulty of comparing soil-heterogeneity measurements reported by different authors. Lack of a clear picture of the exact pattern of the soil fluctuations which cause the heterogeneity is due to the use of plots of varying size and shape. Since heterogeneity is measured biologically (by plot yield), the size and shape of the plot is critical in the detection of soil fluctuations. Thus certain plot sizes will detect soil fluctuations in small areas which larger plot sizes, each encompassing several of these small areas, may be unable to detect.

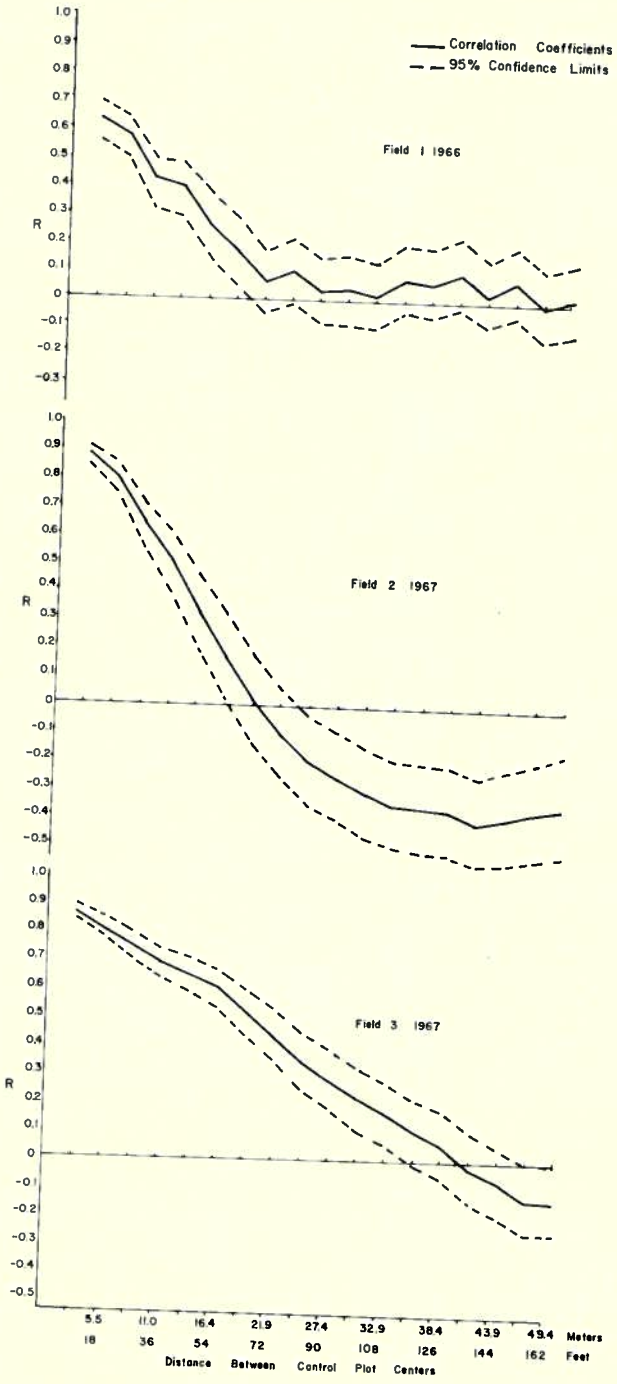

FIG. 2. Correlation between yields of control plots of decreasing contiguity.

The results in this study agree closely with those of Wiebe (11) even though he used a different plot type. In both studies, a high correlation was obtained for yields of adjacent plots which rapidly decreased as the distance between the correlated plots increased. The distance at which the correlation became nonsignificant was 17.1 m (56 ft) in Wiebe's material and 19.2 m (63 ft) in two out of three fields in this study, a correspondence which probably is not coincidental.

From this study only limited information was available concerning the correlation between control plots 0.9 m (3 ft) apart, which is the distance between an experimental plot and its control, although a correlation coefficient of 0.75 was obtained on the basis of only six observations in another part of the nursery. However, extrapolation of the correlation curve to the 0.9-m (3-ft) center between plots would suggest that the correlation between plots this far apart is quite high, giving some evidence that a control-plot yield provides a good measure of the yielding ability of the site of an adjacent plot.

The results of our questionnaire indicate that in their nurseries the majority of wheat breeders use controls which are separated by about 50 plots, which is at least 15.2 m (50 ft) or more. Our data and those of previous workers indicate that the correlation between plots separated by this distance is effectively zero, so that at this frequency any benefit from using controls will be lost. The rapid decrease in correlation of yields as distance between control plots increases, obtained in this study and in earlier reports, confirms our belief that frequent controls are essential for efficient selection for yield in hybrid nurseries. The paucity of controls used in most wheat-breeding programs is one of the limiting factors for efficiency of selection.

ACKNOWLEDGEMENT

The financial assistance provided by the University of Manitoba and by the National Research Council of Canada is gratefully acknowledged.

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APPENDIX 3

VARIATION IN BREADMAKING QUALITY OF SYSTEMATIC CONTROLS IN A WHEAT BREEDING NURSERY AND ITS RELATIONSHIP TO PLANT BREEDING PROCEDURES[1]

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ABSTRACT

In a spring wheat breeding nursery at the University of Manitoba in 1967, the wheat protein content of systematic control plots of *Triticum aestivum* cv. Manitou varied from 10.3% to 16.5% (at 13.5% moisture basis). The correlation between grain yield and protein content of these plots was 0.88 and significant at the 99% confidence level. Correlations calculated for control plots at specified distances apart indicate that for all breadmaking quality test characteristics except bushel weight and flour yield, contiguous plots are significantly more similar in quality than those further apart. The correlation between control plots 2.7 m (9 ft) apart is 0.84 ($P = 0.05$) for wheat protein percent and of similar order for those quality characteristics which are dependent on total protein. Areas of high and low quality "potential" can be identified in a wheat nursery by using quality data from controls at frequent intervals, and this information should be used by the breeder when assessing the single quality test of a breeding line from a given area of the nursery.

INTRODUCTION

In pedigree wheat breeding programs which involve early generation selection, it is necessary to use as large a base population as can be handled by the breeder if maximum progress is to be made. It is also necessary to use methods which make possible the identification and selection of the best genotypes within this population. In the University of Manitoba selection program, as many as 1000 F_3 lines per cross are assessed for yield by direct comparison with adjacent controls. At the F_3 level, replication is difficult if the plot size is to be meaningful. In this generation an adequate control system permits a reasonably good yield assessment because of the high correlation which is expected between the yields of contiguous plots (4).

There have been many reports on uniformity trials with wheat showing that variability exists for grain yield due to the effect of soil heterogeneity, but no similar data exist concerning the effect of soil heterogeneity on wheat breadmaking quality. It is of considerable importance to the plant breeder to know how soil variability in the breeding nursery might affect the performance of a segregating line assessed in a breadmaking quality test. To be worthy of selection, a line must perform at least as well in the test as a control variety grown under the same soil conditions. With this objective in mind, full-scale quality tests were run on a series of systematic control plots of *Triticum aestivum* cv. Manitou at the University of Manitoba. The purpose of this test was to determine the extent of variation in protein and other breadmaking quality characteristics in the cultivar Manitou which can exist in a single 1-ha (2½-acre) nursery, and to examine the relationship between yield and protein in this cultivar.

MATERIALS AND METHODS

The results described were obtained from material harvested from a spring wheat breeding nursery (field 3, 1967) at the University of Manitoba on pre-

[1]Contribution No. 156 of the Department of Plant Science, University of Manitoba, Winnipeg, Manitoba.

viously fallowed land classified as Riverdale clay. Moisture conditions for the field were considered to be average for the area but the general fertility of the field, determined both by visual observation and by soil tests, was low. Considerable variation in soil fertility was apparent and several small areas of severe nitrogen deficiency could be identified visually. The arrangement and management of the systematic control plots of Manitou wheat in this particular nursery have been described (3, 4). The nursery consisted of six parallel ranges where every third plot in each range was a control (Manitou) and the two intervening plots were breeding material under investigation. All plots in the nursery were seeded on the same day at a rate of 250 seeds per row, using a disc power seeder. The plots consisted of three rows and were 5.6 m (18½ ft) long with a 15-cm (6-in.) spacing between rows. Plots were spaced 0.6 m (2 ft) apart in order to minimize interplot competition. After trimming to 5 m (16½ ft), the plots were harvested as a bulk of all three rows and the samples were threshed, dried and cleaned before weighing for yield assessment. After yield data were obtained, wheat protein content (N × 5.7) was determined by the Kjeldahl method for every control plot in the nursery, and the correlation between yield and protein content for all controls was calculated.

For three ranges of the nursery, comprising 22 control plots per range, the breadmaking quality of Manitou controls was assessed by a large number of standard tests. The following is a key to the quality parameters and the methods by which they were determined. (Prefixes are included for ease of reference to Table 1 and to the Figures.)

(1) Weight per liter in kilograms (Bushel weight in lb)
(2) 1000-kernel weight in grams
(3) Wheat protein, percent [13.5% moisture basis (m.b.), using the Kjeldahl method, N × 5.7]
(4) Flour yield, percent [AACC method 26-20, ref. (1)]
(5) Flour protein, percent (14.0% m.b., using the Kjeldahl method, N × 5.7)
(6) Flour ash, percent (14.0% m.b.)
(7) Flour color, units [Kent-Jones and Martin (8)]
(8) Baking absorption, percent [Irvine and McMullan (7)]
(9) Zeleny sedimentation value (AACC method 56-60)
(10) Remix loaf volume in cc (As for character 8)
(11) Blend loaf volume in cc (As for remix loaf volume but using a flour containing 50% of the test flour and 50% of soft white Ontario wheat flour of 8.5% protein)
(12) Farinogram absorption, percent (AACC method 54-21)
(13) Farinogram development time in minutes (AACC method 54-21)
(14) Farinogram mixing tolerance index in Brabender units (AACC method 54-21).

For each of the quality characters in turn, simple correlation coefficients between the values of control plots at increasing multiples of 2.7 m (9 ft) apart along the range were calculated in such a way that the maximum number of observations was included in the calculation of each coefficient. For example, the value at the 2.7-m (9-ft) center was calculated by using the sum of the

observations over all six ranges of all the possible pairs of control plots 2.7 m (9 ft) apart within a range. This was repeated for the 5.5-m (18-ft) center, the 8.2-m (27-ft) center and for each additional spacing to obtain a series of values for each quality character. Each correlation coefficient represents the degree of similarity in expression of the character for control plots a specified distance apart. The coefficients were plotted against the distance separating the controls which had been correlated, to produce the curves as illustrated and which are hereafter referred to as contiguity curves. The values for a contiguity curve were also calculated for the character wheat protein percent, using data from the whole of the nursery (six ranges each containing 59 control plots).

RESULTS

Material in the complete area of the nursery had a wheat protein percent ranging from 10.3% to 16.5% with a mean of 12.8%, and plot yields ranging from 425 g to 1,788 g, with a mean of 1,144 g. These values are equivalent to a range in yield of from 855 lb/acre (959 kg/ha) to 3,600 lb/acre (4,036 kg/ha), with a mean of 2,303 lb/acre (2,582 kg/ha).

For the complete set of 354 Manitou controls in the nursery, a positive correlation between grain yield and wheat protein content of 0.88 was obtained. This coefficient is significant at the 99% confidence level. The contiguity curve for wheat protein data was extremely similar to that reported earlier (4) for the yield data from this nursery. The correlation between control plots 2.7 m (9 ft) apart was 0.88, and decreased rapidly to nonsignificance when the correlated controls were 29.7 m (99 ft) apart (Fig. 1A).

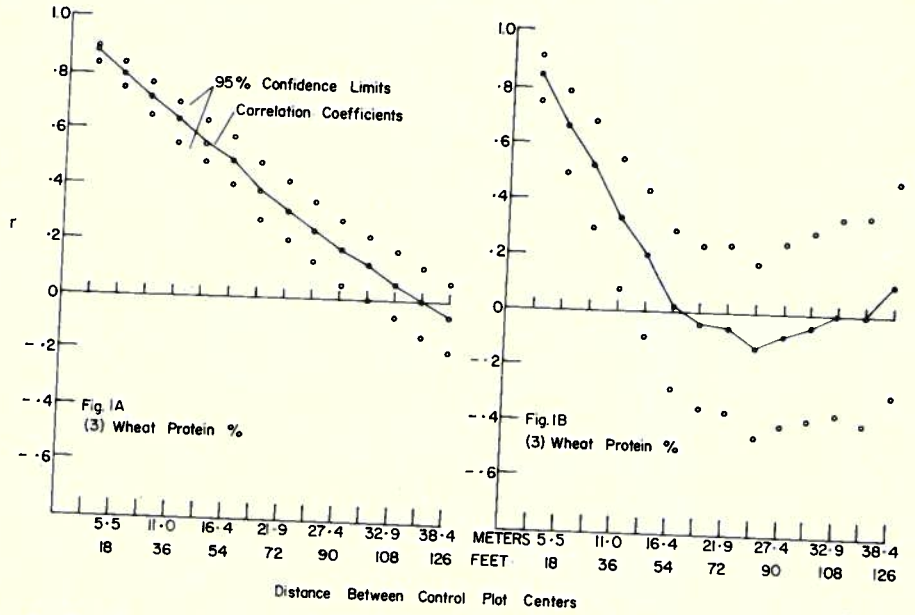

FIG. 1. Correlation between control plots of decreasing contiguity for wheat protein content of Manitou wheat: A, for complete field 3; B, for smaller area of field 3.

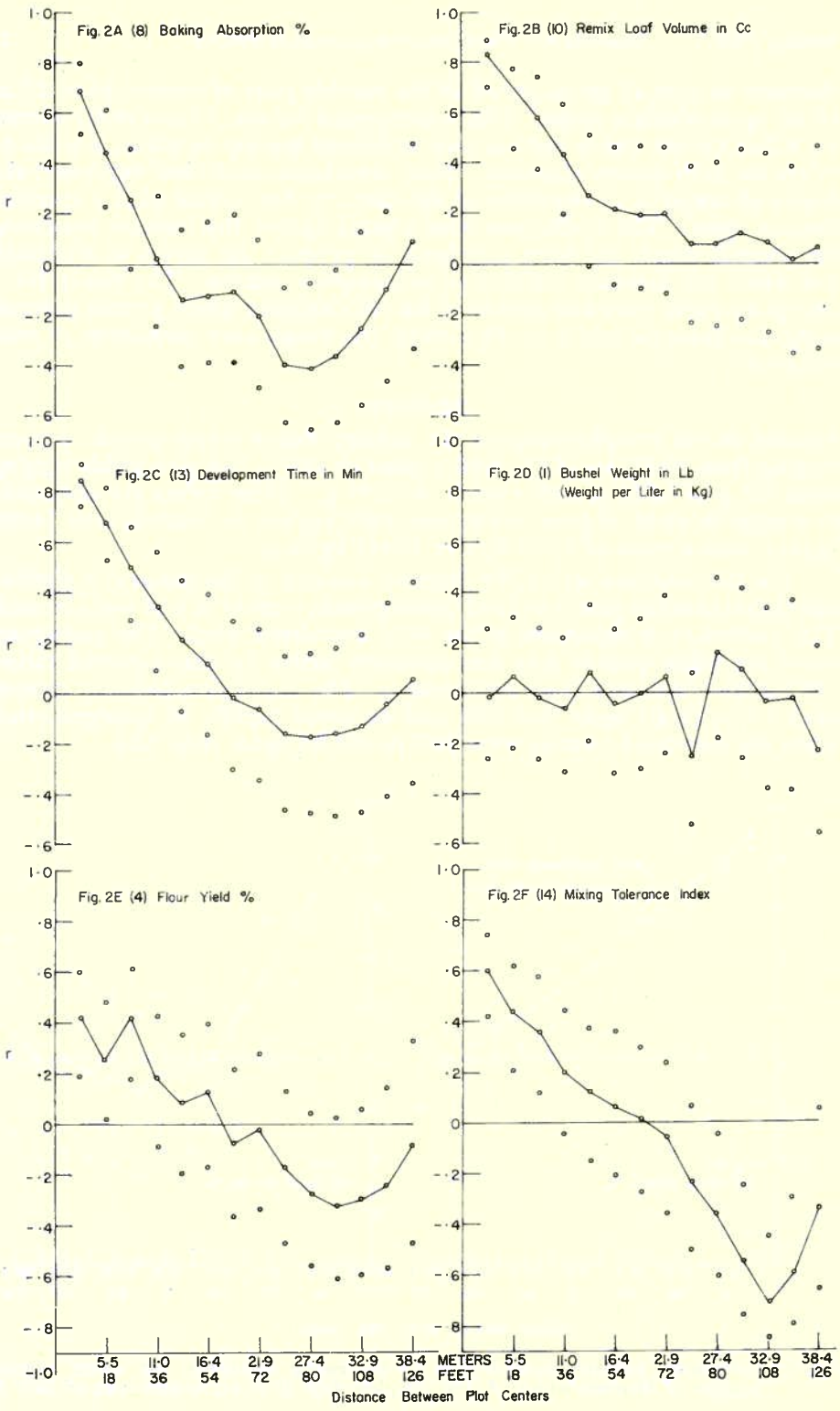

FIG. 2. Correlation between control plots of decreasing contiguity for six quality parameters of Manitou wheat, for the smaller area of field 3.

In the smaller area of field 3 (three ranges by 22 control plots long), the correlation between grain yield and wheat protein was 0.81 and significant at the 99% confidence level. The contiguity analysis for wheat protein percent gave a correlation of 0.84 ($P = 0.01$) for controls 2.7 m (9 ft) apart, decreasing rapidly to nonsignificance when correlated controls were 13.5 m (45 ft) apart, and remaining nonsignificant for controls further apart than 13.5 m (Fig. 1B). The majority of the other quality characteristics examined had contiguity curves which closely resembled that for wheat protein percent (Figs. 2A–2C). These included 1000-kernel weight, flour protein, flour ash, flour color, baking absorption, sedimentation value, remix loaf volume, blend loaf volume, farinogram absorption and farinogram development time. Three of the quality characteristics are distinguishable as having contiguity curves which differ markedly in form from that obtained for wheat protein content, namely bushel weight (Fig. 2D), flour yield (Fig. 2E), and mixing tolerance index (Fig. 2F). The correlation between controls 2.7 m (9 ft) apart, and the minimum distance by which two controls must be separated for the correlation between them to be nonsignificant at the 95% confidence level, are summarized in Table 1 (A, B) for each of the quality characters.

Table 1. Summary of contiguity analyses and correlations

	A	B	C
Quality character	Correlation between controls 9 ft apart	Distance in ft for nonsig. correlation between controls	Correlation with wheat protein ($N = 66$, $P < 0.01$)
1. Bushel weight, lb	NS	9	NS
2. 1000-kernel weight, g	0.75	63	0.83
3. Wheat protein, % (13.5% m.b.)	0.84	45	—
4. Flour yield, %	0.43	36	NS
5. Flour protein, % (14.0% m.b.)	0.85	45	0.84
6. Flour ash, % (14% m.b.)	0.64	81	−0.74
7. Flour color, units	0.64	27	0.52
8. Baking absorption, % (14% m.b.)	0.69	27	0.64
9. Zeleny sedimentation value	0.78	45	0.77
10. Remix loaf volume, cc	0.83	45	0.85
11. Blend loaf volume, cc	0.73	36	0.71
12. Farinogram absorption, %	0.70	36	0.67
13. Farinogram development time, min	0.84	45	0.85
14. Mixing tolerance index, Brabender units	0.61	36	NS
Wheat protein, % (complete field 3, $N = 354$)	0.88	99	—
Plot yield, g (complete field 3, $N = 354$)	0.87*	117*	0.88

*Reported previously by Briggs and Shebeski (4).

Columns A and B give the characteristics of contiguity curves for 14 quality characters and column C gives simple correlations between wheat protein and other quality parameters for the same data. The first 14 rows are for the portion of the nursery examined in detail, and the lowest two rows are the results obtained using data from the complete nursery.

The simple correlations of each of the quality characters in turn with wheat protein content were high and significant (Table 1, column C) with the exception of bushel weight, flour yield and mixing tolerance index which all had nonsignificant correlations. The correlation between flour ash and wheat protein was −0.74 and is highly significant ($P = 0.01$).

A more extensive analysis of the interrelationships of the various characters used in measuring breadmaking quality will be presented in a future report based on data from several years.

DISCUSSION

Negative correlations between wheat protein content and grain yields have been reported by a number of workers, as reviewed by Haunold *et al.* (6). Neatby and McCalla (9) have indicated that this negative correlation is greater for wheats grown in areas of soil nitrogen deficiency. However, Shebeski (11), Clark (5) and others have reported significant positive correlations. In this study a highly significant positive correlation of 0.88 between yield and protein content was obtained across a fairly wide protein range, in the cultivar Manitou, strongly suggesting that in areas of nitrogen deficiency both yield and protein level are adversely affected by lack of soil fertility. This was confirmed by the observation that the lowest yields and wheat protein contents were obtained from those areas of the field which on a visual basis appeared to be suffering from severe soil nitrogen deficiency. Because of the large interactions between soil moisture, content and availability of soil nitrogen, cultivar, and environmental conditions in different years, a wide range of correlation values between yield and protein content is possible, both positive and negative. Generalizations about expected relationships between these two variables cannot be made unless the specific conditions of the test under consideration are described in detail, as is made clear by Schlehuber and Tucker (10).

The extreme similarity of the contiguity curves for protein content and yield (4) for the complete field 3 is not surprising in the light of the high simple correlation between these two characters. The curve for protein content indicates that controls closer together are very much more alike for this character than those further apart. That the relationship diminishes to nonsignificance when controls are at 29.7 m (99 ft) in the case of the complete field 3, and 13.5 m (45 ft) in the case of the smaller area within field 3, is probably due to the fact that the latter only samples a portion of the pattern of variability which is present in the complete field.

Curves obtained for the smaller area of field 3 for the quality characters other than wheat protein nearly all follow a curve similar to that for wheat protein. This type of curve is characterized by a very high and positive correlation between adjacent controls 2.7 m (9 ft) apart, falling off rapidly to nonsignificant correlation when controls are at most, as in the case of flour ash percent, 24.3 m (81 ft) apart (Table 1, column B). Two notable exceptions to this shape of curve occur for the characters bushel weight (Fig. 2D) and flour yield (Fig. 2E). The curve for bushel weight lacks any significant correlations at all, indicating that the expression of this character varies at random throughout the field and that there is no predictable relationship between controls separated by a known distance. The character flour yield

has a significant but low correlation of 0.43 between adjacent Manitou controls. It can be seen from Table 1, column C that neither bushel weight nor flour ash is significantly correlated with protein content, whereas the majority of the other characters are highly significantly correlated with this quality parameter. This relationship between quality characters and total protein has been very adequately described by Barmore and Bequette (2). The similarity of many of the contiguity curves to that for wheat protein may largely be due to a simple dependence of the quality characters on total wheat protein alone. This interpretation may or may not be true, but at least one exception is obvious from these data. The character mixing tolerance index is not significantly correlated with wheat protein, and yet its contiguity curve (Fig. 2F) indicates the same effect as was obtained for wheat protein, with a significant correlation of 0.61 for adjacent controls. The significant negative correlations between controls greater than 27 m (90 ft) apart for mixing tolerance index are difficult to interpret.

It is obvious that the amount of variability for yield, wheat protein content and other quality measures which can occur even in one wheat nursery for a fixed cultivar, in this case Manitou, is very large. The extent by which this variability may be reduced by growing under high-fertility conditions is currently under study. Nevertheless, these results indicate that the variability of breadmaking quality parameters of systematic control plots is not distributed at random throughout the nursery, but that controls situated more closely together in the field are more similar in quality. Control plots separated by 2.7 m (9 ft) were more closely related for all quality characters except bushel weight. It logically follows that controls separated by only 0.9 m (3 ft) would be even more closely related. This indicates that the breeder should ideally compare quality results from a selection grown in the breeding nursery with the specific quality of the control plot which was grown nearest to it, and preferably adjacent. The results from the control plot provide a good measure of the quality "potential" of the area in which the selection was grown, for all the major quality characters, where quality "potential" is defined as the quality which would be expected from a recommended cultivar growing in that area. Any difference between the qualities of the selection and the control will have greater meaning in the sense that a large proportion of the environmental effect attributable to position in the nursery will have been taken into account. The use of any control for quality comparison other than the closest one in the nursery will only serve to minimize the advantages of using controls at all. The greatest advantage should be obtained when an experimental selection is compared for quality with a control plot which was grown alongside it in the nursery.

ACKNOWLEDGEMENTS

The financial assistance of the National Research Council of Canada and the Northwest Line Elevators Association is gratefully acknowledged.

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APPENDIX 4

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PROTEIN QUANTITY AND QUALITY AS FACTORS IN THE EVALUATION OF BREAD WHEATS[1]

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ABSTRACT

In evaluating new wheat varieties for breadmaking quality, it is necessary to separate the effects of protein quality and protein content. By the remix bread baking test, there is a particular protein quality that gives the optimum baking performance. Poor baking results are obtained for wheats that are weaker or stronger as judged by the farinograph test. High-quality varieties such as Manitou give poor baking results by standard baking tests if the protein content is too low. For bread wheats of different protein quality, the loaf volume is positively correlated with protein content. Wheats that have too little or too much of the peculiar protein quality necessary for optimum bread quality as assessed by the remix baking test can be improved by physical modification of the dough by means of variable mixing. This procedure can be used in some cases to place wheats on a constant quality base, whereby different wheat varieties can give similar bread quality for the same protein content. For a single variety (Manitou) grown in the same location during two years, most of the standard breadmaking quality parameters are significantly correlated with protein content.

INTRODUCTION

In the evaluation of new bread wheat varieties for their breadmaking potential, it is extremely important to separate two closely related factors, quantity and quality of the protein in the grain. Quality is that property of flour proteins which gives rise to different baking performance with flours of the same protein content. It is commonly accepted by cereal chemists that protein quality under normal growing conditions is almost entirely an inherited characteristic, whereas protein quantity depends primarily on soil and climatic conditions during the growing period (3). Furthermore, even the best-quality variety will give high-quality bread only if it contains a sufficient quantity of protein.

It became possible to re-examine the relationship of protein quality and quantity to breadmaking quality when, in 1967, one experimental field at the University of Manitoba produced samples of Manitou and a number of experimental lines ranging in protein content from about 9.5 to 15.5%. This apparently resulted from a wide variability in soil fertility. The relationship between yield, protein content, and a number of other breadmaking quality indicators for samples of Manitou (used as control in breeding studies) has been discussed in a previous paper (2).

The first part of this paper will deal with the question of protein quantity and quality. The effect of protein quantity on a number of breadmaking

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quality indicators for samples of standard variety Manitou grown in 1966 and 1967 will be discussed in the second part.

MATERIALS AND METHODS

Manitou and two experimental lines grown in 1967 were selected to demonstrate the effects of protein quality and quantity. For the second part of the study, results for samples of Manitou grown in 1966 were used. All wheats were milled to about 73% extraction on the experimental Buhler mill, under constant conditions, to give a straight grade flour of about 0.40% ash.

Mixing properties of the doughs from the various wheats were examined by the standard AACC farinograph procedure (1), using a 50-g mixer and enough water to center the curve on the 500 Brabender units (BU) line. This amount of water, in percent, is referred to as farinograph absorption. Dough development time, used as an indicator of mixing requirements, is the time in the farinograph at which the dough reaches maximum consistency. In cereal technology, wheats that have long dough-development times are considered to be strong.

Breadmaking quality was evaluated by the remix baking test (4). This test was originally developed to bring out the optimum baking quality of Canadian hard red spring wheats. Baking absorption of each flour was taken as the farinograph absorption less 4 percentage units. To test the interaction between remixing time and protein content, the standard procedure ($2\frac{1}{2}$ min remix) was modified to include a variable remixing time. The actual times used will be indicated below.

Other quality parameters that will be discussed in their interrelationships with protein content in the second part of the paper were determined by standard procedures. References to these have been given in the previous paper (2). All protein contents for wheat are reported on a 13.5% moisture basis. Flour protein contents are from 0.7 to 1.0% lower than that of the original wheat.

RESULTS AND DISCUSSION

Part I. Effect of Protein Quality and Quantity on Breadmaking Quality

Figure 1 shows farinograph curves, protein contents and loaf volumes for three wheats of different protein quality but of the same protein content, and three Manitou samples of different protein contents. The results in the center row are for the three wheats of different protein quality. FW-136 is judged weak, Manitou strong, and 11-463A very strong on the basis of the farinograph curves. The loaf volume by the remix baking procedure is highest for Manitou (945 cc), and decreases with decreasing or increasing strength as judged by the farinograph test. This relationship is shown more strikingly in Fig. 2, where loaf volumes are plotted against farinograph dough development time. These results show that evaluation of wheats on the basis of the farinograph curve only is of limited value. The line 11-463A, which appears much stronger than Manitou by this test, gave a considerably lower loaf volume. The weaker wheat, FW-136, is rated inferior to Manitou of the same protein content by both the farinograph and baking tests.

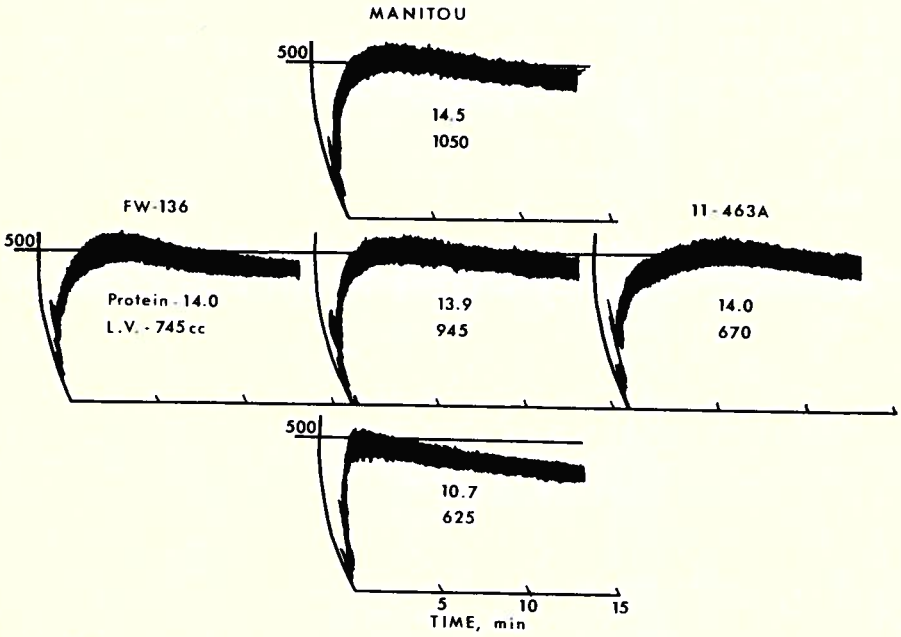

FIG. 1. Farinograph curves, protein contents and remix loaf volumes for three wheats of different protein quality but similar protein content and three samples of Manitou of different protein contents.

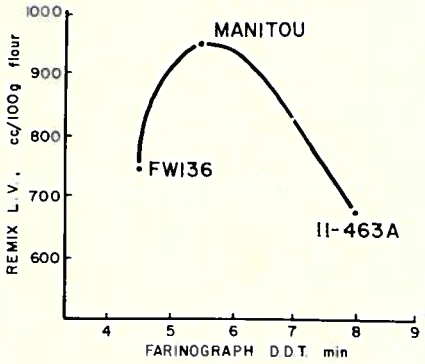

FIG. 2. Remix loaf volume plotted against farinograph dough development time for wheats of different quality.

The three sets of data in the center column of Fig. 1 show that for a single variety (Manitou), both the farinograph curves and loaf volumes depend strongly on the protein content. With most baking tests (3), the plot of loaf volume versus protein content is relatively linear over most of the practical range of flour protein content (9–16%). Figure 3 shows that this relationship is also true for the remix baking test on the basis of the two varieties examined. The figure in parentheses is the statistically calculated slope of the line, and theoretically is the loaf volume per unit protein content. This parameter is sometimes

used as the indicator of breadmaking quality by a specific baking test. It must be emphasized that this quality parameter is directly dependent on the baking test used. This relationship was not obtained for the weak wheat (FW-136) because material having a wide range of protein content was not available.

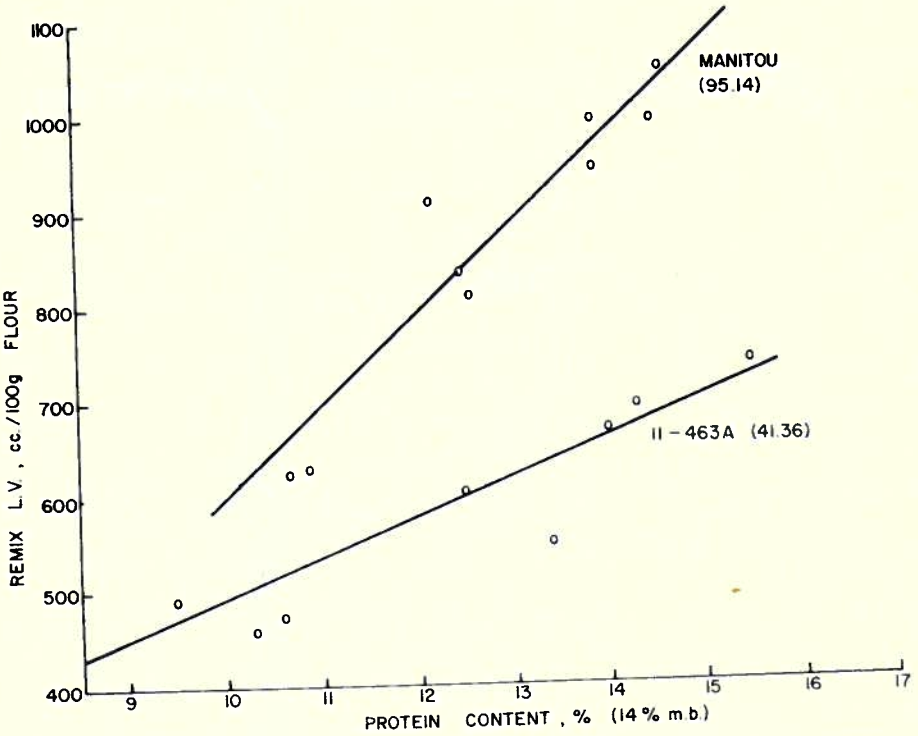

FIG. 3. Remix loaf volume plotted against protein content for two wheats of different mixing properties.

The farinograph test (Fig. 1) suggested that the strong wheat 11-463A does not perform as well as Manitou in the standard remix test because the normal 2½ min remix time was inadequate to develop the gluten properly. Accordingly, it was of interest to examine the effect of variable remix times on loaf volume from flour of different protein contents. With the available material, this study could be made for Manitou and line 11-463A only. Results for three protein levels, covering the complete range, are shown in Fig. 4. Each sample shows an optimum mixing time which increases with decreasing proteint contents. Furthermore, for approximately the same protein content, the strong wheat 11-463A requires much longer remixing time for optimum loaf volume. On the basis of these observations, the results in Fig. 3 obtained by a constant remix time of 2½ min do not show the true breadmaking potential of this wheat. In the case of Manitou, the loaf volumes for the low-protein samples are too low because of undermixing, and this tends to exaggerate the slope of the loaf volume vs. protein content line. On the other hand, the loaf

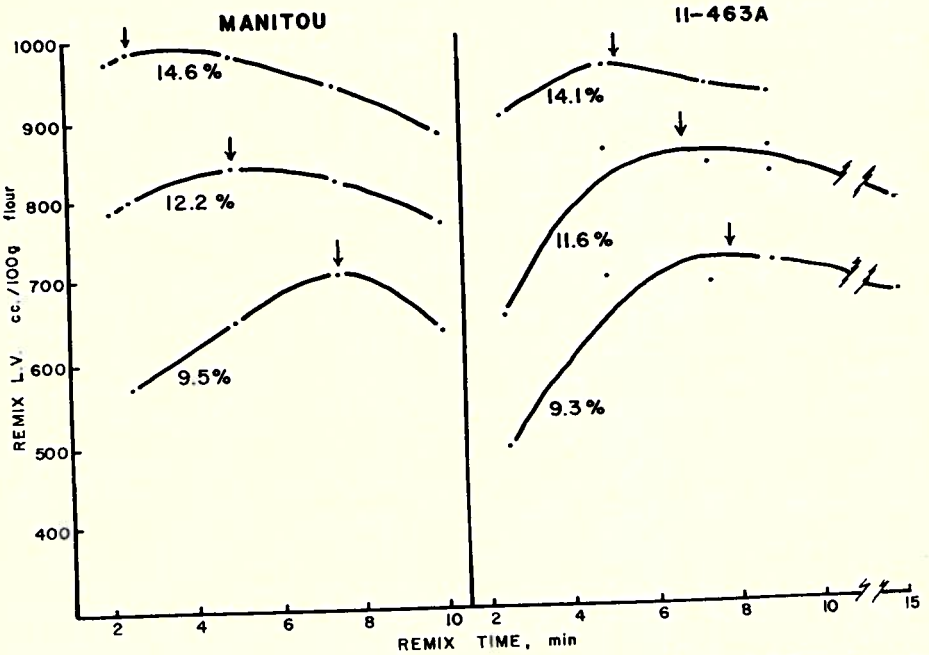

FIG. 4. Remix loaf volume plotted against remix time for two wheats of different protein contents.

volumes for 11-463A are too low for the entire protein range because of undermixing.

If the loaf volume at optimum remixing time from Fig. 4 is plotted against protein content, the results for both Manitou and 11-463A fall on the same curve (Fig. 5). The slope in this case (about 60) is considerably less than the value for Manitou at constant remix time (95.14), and slightly higher than the analogous value for 11-463A (41.36). Accordingly, it is seen that in order to evaluate the breadmaking potential of a new variety, it is not sufficient to test

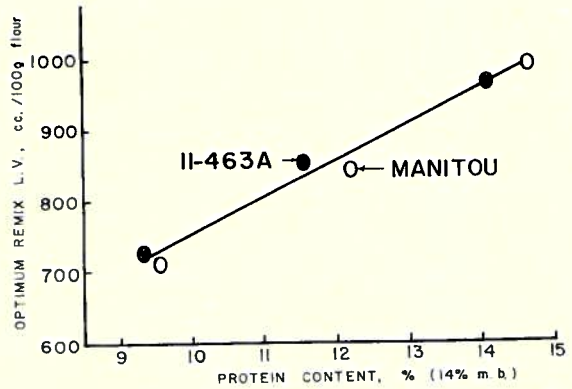

FIG. 5. Remix load volume at optimum remixing time plotted against flour protein content for two wheats of different mixing properties.

it by a single baking procedure. The procedure must be modified in order to express the optimum potential of the wheat variety. It was demonstrated here that by simply increasing the remix time for 11-463A from 2½ min to about 5 min (for 14% protein) its baking performance can be made to equal that of Manitou, whereas by the standard test (Fig. 1) it is judged considerably inferior to Manitou. The question of optimum mixing requirements is an extremely important factor commercially. In Canada, varieties having mixing properties similar to those for Manitou are preferred.

The weaker wheat (FW-136) could not be brought up to the level of loaf volume produced by a strong variety (such as Manitou) by decreasing the length of remixing in the remix baking test. However, some improvement in loaf volume was obtained by using the AACC malt phosphate-bromate test baking procedure (1). Because of the small amount of FW-136 wheat that was available, only one test for each baking procedure could be made. Further studies are obviously needed in this area.

Part II. Statistical Analysis of the Relationship Between Protein Content and Other Quality Parameters for the Variety Manitou for Two Years

Again, this investigation proved useful because the range of variability of protein content in 1967 was wide enough to make the results meaningful. The range for the 1966 samples was somewhat less (3.31% compared with 4.9% for 1967); however, it seemed worthwhile to compare the data for the two consecutive years for which this information was available.

Table 1 gives all the quality data for the Manitou samples of the two years that were analyzed statistically. The data in this table show a number of interesting features. Using the *t*-test, all quality parameters but farinograph mixing tolerance index (MTI) are significantly different for the two years. In general, data for 1967 are more variable than for 1966. Mean protein for 1966 was higher than for 1967, whereas the reverse is true for yield.

For each year, the regression of protein content against yield gave a highly significant positive relationship. The data within years indicate a positive correlation between yield and protein content, whilst comparison of means between years results in a negative relationship. It is therefore necessary to specify in detail the type of experiment and conditions under which the data relating protein content and yield have been obtained. Both year and location effects can affect the relationship in either direction.

Table 2 gives the simple correlation coefficients between the 14 quality parameters examined. The main purpose of this table is to record this information for a large number of samples of a single variety (Manitou) grown during two years in one location. It is felt that the information will be of value to plant breeders. The most important feature of these data is the significant correlation between protein content and the majority of other quality parameters. Nonsignificant correlations were obtained for flour yield for both years, sedimentation value for 1966, farinograph development time for 1966, and the farinograph MTI for 1966. The nonsignificant correlation between protein content and sedimentation value for 1966 is quite important, since some cereal technologists use the Sedimentation Test as the main criterion of bread-making quality. For 1966, the sedimentation value is inadequate as a predictor

for total protein, but for 1967 it is a very good predictor. This is probably because of low variability for protein content in 1966 (coefficient of variation = 4.31) and high variability in 1967 (coefficient of variation = 11.36). It is common knowledge that sedimentation value is a better predictor over a wide range of protein quantity and quality than over a narrow range.

Table 3 gives the simple regressions for the quality parameters against wheat protein content. The main purpose of this analysis was to determine if protein content can be used as a prediction parameter for more than one year. The slopes (b values) are not significantly different for the two years for four quality parameters: flour protein content; flour ash content; flour color; and remix loaf volume. Accordingly, for a single variety these four parameters can be reasonably accurately predicted from protein content over a period of at least two years. All other quality parameters which correlate significantly with protein content (Table 2) have to be considered on a yearly basis.

Table 1. Statistical analysis of the quality and yield data for Manitou wheat for two crop years

Quality parameter	Min.	Max.	Mean	Standard deviation	Coeff. of variation	T test signif. for year diffs.†
Bushel weight (lb)	60.0‡ 63.6	64.1 65.9	62.7 65.0	1.22 0.39	1.95 0.60	**
1000-kernel wt. (g)	23.0 28.6	42.0 36.0	31.2 33.1	2.80 1.84	8.96 5.57	**
Wheat protein (%, 13.5% m.b.)	13.4 11.0	16.7 15.9	15.4 13.0	0.66 1.48	4.31 11.36	**
Flour yield (%)	69.3 72.3	75.4 75.8	73.0 74.0	0.96 0.81	1.32 1.10	**
Flour protein (%, 14% m.b.)	12.8 10.2	15.9 15.2	14.5 12.2	0.65 1.40	4.49 11.52	**
Flour ash (%, 14% m.b.)	0.39 0.42	0.54 0.58	0.47 0.50	0.08 0.09	17.40 17.28	*
Flour color (K.J. units)	0.9 0.1	3.6 1.7	1.6 0.9	0.43 0.34	27.80 38.02	**
Baking absorption (%, 14% m.b.)	59.4 61.5	63.5 65.2	61.7 62.8	0.96 0.99	1.57 1.58	**
Sedimentation value (ml)	67.8 44.8	72.0 67.5	69.9 54.4	1.07 7.09	1.53 13.03	**
Remix loaf vol. (cc)	900 680	1215 1120	1026 853	77.69 112.34	7.58 13.17	**
Blend loaf vol. (cc)	695 635	930 785	792 686	60.64 29.18	7.59 4.25	**
Farinograph development time (min)	4.2 2.3	7.0 6.0	5.6 3.9	0.60 1.11	10.67 28.07	**
Farinograph MTI (BU)	20 20	50 40	36.4 37.2	5.67 6.06	15.60 16.27	NS
Plot yield (g)	645 598	1355 1699	1018 1229	149.54 281.42	14.69 22.91	**

†NS = not significant; * = significant at $P \leqslant 0.05$; ** = significant at $P \leqslant 0.01$.
‡Upper values for 1966 samples, $N = 62$; lower values for 1967, $N = 66$.

Table 2. Simple correlation coefficients between quality parameters and yield
(Upper values: data for 1966, $N = 62$; lower values: data for 1967, $N = 66$)

	1000-k. wt	Wheat protein	Flour yield	Flour protein	Flour ash	Flour color	Baking absorption	Sed. value	Remix loaf vol.	Blend loaf vol.	Dev. time	MTI	Plot yield
Bu. wt.	0.44** 0.40**	0.27* —	— —	— —	−0.62** −0.42**	— —	0.64** —	— —	0.32* —	0.69** —	−0.36** —	— —	0.49** 0.40**
1000-k. wt.		— 0.83**	— —	— 0.84	−0.51** −0.74**	— —	0.42** 0.64**	−0.34** 0.77**	— 0.85**	0.50** 0.71**	— 0.85**	— —	0.30* 0.83**
Wheat protein			— —	0.90** 0.98**	−0.37** −0.74**	0.33* 0.61**	0.56** 0.76**	— 0.92**	0.72** 0.96**	0.36** 0.86**	— 0.93**	0.27* —	0.46** 0.81**
Flour yield				— —	— —	— 0.32*	−0.29* —	−0.38** —	−0.36** —	— —	— —	— 0.37**	— —
Flour protein					−0.29** −0.72**	0.40** 0.68**	0.56** 0.79**	0.27** 0.93**	0.74** 0.97**	0.34** 0.89**	0.32* 0.96**	0.27* —	0.43** 0.80**
Flour ash						0.31* —	−0.55** −0.40**	— −0.61**	−0.41** −0.72**	−0.52** −0.63**	— −0.72**	— —	−0.41** −0.79**
Flour color							— 0.71**	— 0.64**	0.29* 0.58**	— 0.58**	— 0.65**	0.30* —	— 0.37**
Baking absorption								— 0.77**	0.59** 0.76**	0.70** 0.76**	— 0.79**	— —	0.51** 0.47**
Sed. value									— 0.89**	— 0.80**	0.28* 0.90**	— —	— 0.69**
Remix loaf vol.										0.42** 0.86**	— 0.93**	— —	0.27* 0.82**
Blend loaf vol.											— 0.86**	— —	0.33* 0.69**
Dev. time												— —	— 0.81**
MTI													—
Plot yield													—

Table 3. Simple regressions for various quality parameters (y) against wheat protein (x) for Manitou samples for 1966 ($N = 62$) and 1967 ($N = 66$)†

Quality parameter	Regression equation	Standard error of b value	Level of significance of regression	Significance level for difference between b values for 1966 and 1967
Bushel weight (lb)	$y = 54.92 + 0.51x$	0.23	*	**
	$y = 64.21 + 0.06x$	0.03	*	
1000-k. wt. (g)	$y = 13.86 + 0.05x$	0.03	NS	N/A‡
	$y = 19.58 + 1.04x$	0.09	**	
Flour yield (%)	$y = 74.95 - 0.13x$	0.19	NS	N/A
	$y = 74.74 - 0.06x$	0.07	NS	
Flour protein (%, 14% m.b.)	$y = 0.94 + 0.88x$	0.06	**	NS
	$y = 0.12 + 0.93x$	0.03	**	
Flour ash (%, 14% m.b.)	$y = 0.72 - 0.017x$	0.005	**	NS
	$y = 0.76 - 0.020x$	0.002	**	
Flour color (K.J. units)	$y = -1.76 + 0.22x$	0.08	**	*
	$y = -0.89 + 0.14x$	0.02	**	
Baking absorption (%, 14% m.b.)	$y = 48.51 + 0.82x$	0.15	**	N/A
	$y = 56.17 + 0.51x$	0.05	**	
Sedimentation value (ml)	$y = 66.10 + 0.25x$	0.21	NS	NS
	$y = -3.49 + 4.44x$	0.23	**	
Remix loaf volume (cc)	$y = -294.87 + 85.96x$	10.64	**	*
	$y = -98.89 + 73.08x$	2.71	**	
Blend loaf volume (cc)	$y = 284.84 + 33.02x$	11.09	**	N/A
	$y = 465.21 + 17.00x$	1.27	**	
Farinograph development time (min)	$y = 2.24 + 0.22x$	0.11	NS	N/A
	$y = -5.16 + 0.70x$	0.03	**	
Farinograph MTI (min)	$y = 0.07 + 2.36x$	1.08	*	
	$y = 48.72 - 0.88x$	0.50	NS	

†Upper data for 1966; lower data for 1967.
‡N/A = not applicable.

GENERAL DISCUSSION

Consideration of the breadmaking quality of three types of wheat, weak, strong and very strong, of various protein contents as described in Part I of this paper reveals four major features of consequence to quality-screening procedure. First, breadmaking quality as measured by the loaf volume obtained by the remix baking test is dependent on total protein content for each type of wheat. Secondly, within each wheat type there is an optimum remix requirement for each level of protein, above or below which remix loaf volumes will be diminished. As the protein content decreases the optimum remix time requirement increases for both strong and very strong wheats. Also, the remix requirements for obtaining optimum remix loaf volumes increases with the strength of the wheat as judged with the farinograph. Thirdly, the remix baking test used in current quality screening procedures in Canada is one which provides optimum development for wheats of a particular strength (such as Manitou), but underdevelops wheats of greater strength, (such as 11-463A) and probably overdevelops weaker wheats (such as FW-136). The development of doughs

from both weak and very strong flours in the standard remix test is not optimum for these flours, and hence reduced loaf volumes, compared with Manitou-type wheats of the same protein content, are obtained. Fourthly, when very strong wheats receive their optimum remix requirements they are able to produce remix loaf volumes of the same order as acceptable hard red spring wheats at the same protein content. Lack of material made it impossible to investigate the possibility of improving the loaf volume of the weak wheat by optimizing the mixing.

Data obtained for a single variety of wheat (Manitou) over two years indicate that breadmaking quality as measured by 12 of 13 different quality parameters can be significantly different in different crop years. Seven of the quality parameters were significantly correlated with total wheat protein during both years, and another four in one year out of two. This indicates very clearly the marked dependence of breadmaking quality on total wheat protein content for a pure variety, which presumably has constant protein quality. However, it was also shown that the quantitative relationship between the parameters and total wheat protein was inconsistent from year to year for eight of the 13 parameters. Only the parameters flour protein, flour ash, flour color, and remix loaf volume retained a constant relationship to total wheat protein over the two years.

In the light of this evidence, the following procedure is recommended. Each crop year a series of Manitou wheat samples with a wide range in protein content should be analyzed for breadmaking quality. This annual data would provide a reliable reference with which the breadmaking quality of Manitou samples of known protein content could be predicted, and with which the breadmaking quality of breeding lines of known protein content could be compared.

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Appendix 5

Origin of parents used in the various crosses used as sources for the F3 populations.

TZPP Tezanos Pintos Precoz, an Argentinian variety with both good yield and quality potential. A tall awned variety with average maturity, and resistance to leaf rust.

Pembina An awnless hard red spring wheat of medium height and maturity and with strong straw. Selected at the CDA, Winnipeg from a cross of Thatcher x (McMurachy-Exchange x Redman^3) it has good yield with medium test weight. Though acceptable for quality by Canadian standards, it is considered to have excessively strong dough characteristics.

Son 64 Sonora 64 is a short strawed, leaf rust susceptible Mexican variety. It has fair to poor quality, with a low absorption.

CT244 A promising line from Canada which was never released because of quality considerations. It is a derivative from the cross (Lee^2 x Kenya Farmer). It is tall, awned, resistant to stem rust and fairly lodging resistant.

UM530 A selection from the cross (Penbina^2 x Bage) derived at the University of Manitoba, It is awnless, fairly tall, with average maturity and good lodging resistance.

CB 179 A selection from the cross (Sonora 64 x Klein Patiso), it is an early, awned semidwarf.

CB 100 A selection from the cross (Sonora 64 (TZPP x Nainari 60)), it is a low quality, high yielding, early, awned semidwarf.

LR 64A Lerma Rojo 64A is a Mexican semidwarf wheat with wide adaptation and high yield potential.

Justin A hard red spring wheat developed at the N. Dakota Agricultural Experiment Station. It is an awnless, stiff-strawed late maturing variety, susceptible to leaf rust but resistant to stem rust. It has good yield and test weight. The quality is similar to that of Canadian varieties with the exception that the dough is considered to be too strong by Canadian standards. Justin is a selection from the cross (Conley x (Thatcher-Kenya Farmer x Mida-Lee)).

APPENDIX 6

Calculation of broad sense heritabilities from analysis of F3-derived F5 populations, for yield and breadmaking quality parameters of Triticum aestivum L.

1. Method of calculation

The random model was used in the completely randomised Analysis of Variance of F5 populations, as shown below. (Ref. Steele R. G. D. and Torrie J. H., 1960 Principles and Procedures of Statistics, Ch. 7, p. 116, McGraw-Hill Book Company, Inc., New York.)

Source of Variation	df.	Mean square is an estimate of:
F3-derived F5 populations	$t - 1$	$\sigma_E^2 + r\sigma_G^2$
Error	$\sum(r_i - 1) - t$	σ_E^2
Total	$\sum r_i - 1$	

t = Number of F3-derived populations.

r_i = Number of F5 lines (determinations) per F5 population.

σ_G^2 = Variance attributable to genetic differences between F5 populations.

σ_E^2 = Variance attributable to environmental differences within F5 populations.

For unequal replication of treatments, the coefficient corresponding to r for the average value of the treatment mean square is:

$$r_o = \left| \sum r_i - \frac{\sum r_i^2}{\sum r_i} \right| \frac{1}{t - 1}$$

Broad sense heritability was estimated as:

$$H = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_E^2}$$

APPENDIX 6 (cont'd.)

2. Calculated broad sense heritabilities, for three genetically different sets of F3-derived F5 populations grown in different years, for various yield and breadmaking quality parameters.

Yield and quality parameters	1966 F5	1967 F5	1968 F5
Plot yield, in grams	0.510	0.215	0.122
Percent of control yield	0.354	0.623	0.110
Bushel weight, lbs.		0.439	
1000 kernel weight, grams	0.346	0.133	
Wheat protein, % (13.5% m.b.)	0.625	0.269	0.345
Flour yield, %	0.482	0.297	
Flour protein, % (14.0% m.b.)	0.652	0.330	
Flour ash, % (14.0% m.b.)	0.237	0.187	
Flour color, units	0.305	0.258	
Baking absorption, % (14.0% m.b.)	0.775	0.326	
Zeleny sedimentation value	0.556	0.242	
Remix loaf volume, cc	0.543	0.700	
Blend loaf volume, cc	0.619	0.094	
Farinograph absorption, %	0.805	0.523	
Farinograph development time, min.	0.516	0.508	
Mixing tolerance index, Brabender units	0.236	0.036	

These estimates of heritability in the F5 generation are probably biased downwards due to the likely occurence of genetic variability within F5 populations,and the consequent confounding of some genetic variance with the error variance. The amount of this bias cannot be estimated in the absence of replication of individual F5 lines.