

EVALUATION OF BREEDING METHODS IN TRITICALE

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Donald Frank Salmon

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"EVALUATION OF BREEDING METHODS IN TRITICALE"

by

DONALD FRANK SALMON

A dissertation submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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DOCTOR OF PHILOSOPHY

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ABSTRACT

Salmon, Donald Frank. Ph.D.
The University of Manitoba, May, 1977

EVALUATION OF BREEDING METHODS IN TRITICALE

MAJOR PROFESSOR: E.N. Larter

During the summers of 1972 and 1973, a total of eight hexaploid triticale (X Triticosecale Wittmack) populations were evaluated for their yielding potential based on the F_1 and F_3 generations. In each year, one low yielding, two intermediate and one high yielding F_1 population was retained for F_3 evaluation in an early generation yield trial during 1973 and 1974. Comparison of F_1 and F_3 yield rank and the number of high yielding F_3 families produced by each population indicated that evaluation of crosses on the basis of F_1 single plant yield was ineffective for the selection of crosses with a high yield potential in subsequent generations.

In 1973 and 1974, the same eight populations were visually evaluated for yield by experienced (plant breeders), novice (graduate students) and inexperienced (summer students) selectors. Results of chi-square analyses indicated that superior lines constituted a higher proportion of the selected lines than would have been expected if selection was random. These analyses also revealed that experienced and novice selectors selected a higher number of the top ten lines in each population relative to a random sample. Comparison of selection response and efficiency in 1973 and 1974 indicated that the experienced selectors were superior in their relative selective ability compared to the less experienced selectors. In

addition, the mean yield of the top twenty lines selected within populations did not in general deviate significantly from the best twenty lines selected by the yield trial.

The ten highest yielding, ten lowest yielding and a random sample of ten lines were retained from each of the four populations in the F_3 early generation yield trial (1974). In addition, ten headrows containing superior segregates were retained within each population grown in a headrow nursery concurrent with the F_3 early generation yield trial. Bults produced from each selection group in each population were grown in replicated yield trials at Glenlea and Carman, Manitoba and at the CIANO Research Station, Cd. Obregon, Mexico. Combined analysis of this material at each of the three locations indicated that no difference existed between bults produced from lines selected for high yield in the F_3 yield nursery and visually in the headrow nursery. Combined effects of both bults were superior to the random bults at all locations. Combined analysis of the two Manitoba locations indicated that bults produced from the headrow selections had a significantly higher number of spikelets per spike than all other selection bults. Selection of the lowest yielding ten lines in each population in the F_3 early generation yield trial resulted in a significant reduction in tiller number, relative to the random sample.

All lines exceeding the nearest check plot by 25 percent were retained from the four F_3 populations in 1973. All families were represented in a space-planted nursery at the CIANO Research Station, Cd. Obregon, Mexico during the winter of 1973-74 and in space-planted nursery at Winnipeg during the summer of 1974. All families

and lines within families in each population which were light insensitive at CIANO were retained. An equal proportion of families and lines were selected for yield on the basis of visual criteria and at random in Winnipeg. Bults produced within each population from each of the insensitive, random and visual selection groups were grown in a replicated yield trial at Glenlea and Carman, Manitoba (1975) and at CIANO (winter of 1975-76). Individual and combined analysis of the two Manitoba locations indicated that the insensitive bults had a significantly lower yield and test weight than the random bults. No significant differences occurred between bults for yield at CIANO. However, the insensitive bults had a significantly higher 200-kernel weight but a lower number of spikelets per spike than either the random or visual bults in the combined analysis at CIANO.

FOREWORD

This thesis has been written in manuscript format. It consists of a literature review, four manuscripts which were prepared as recommended by the Journal of Crop Science, a general discussion and a summary. Manuscript I, " F_1 Evaluation of Yield Potential in Hexaploid Triticale" will be submitted as a short note. Manuscript II, "Visual Selection as a Basis for Yield Prediction in Hexaploid Triticale"; Manuscript III, "A Comparison of Early Generation (F_3) and Pedigree Selection in Hexaploid Triticale"; and Manuscript IV, "The Effect of Selection Under Diverse Environmental Conditions on Yield and Yield Related Components in Hexaploid Triticale"; will be submitted to the Journal of Crop Science for publication.

INTRODUCTION

INTRODUCTION

According to a review by Lorenz (1974) early studies on triticales (X Triticosecale Wittmack) were limited by the occurrence of sterility in the F_1 . As a consequence, many early researchers doubted that commercially viable triticales could be produced. He pointed out that this remained a severe restriction on progress in triticales breeding until the discovery, in the 1930's, of a technique for chromosome doubling.

Qualset et al. (1969) concluded that one of the most serious problems with early triticales grown in southern latitudes was that they were light sensitive. A major step towards solving this problem and developing triticales on a large scale was the development of a cooperative program between the University of Manitoba and CIMMYT (International Center for the Improvement of Wheat and Maize) in 1964. This also facilitated the incorporation of genes for short stature from Mexican sources.

In general, triticales breeding programs have been based on techniques developed for other cereal crops. To the present time, triticales at the University of Manitoba are subjected to F_3 early generation yield selection (Shebeski, 1967). F_2 space-planted nurseries at the CIANO Research Station, Cd. Obregon (northwestern Mexico) during the winter months serve the purpose of rapid generation advance and the production of seed for the F_3 early generation yield trial.

The use of F_2 space-planted nurseries at CIANO requires that crosses

be light insensitive or contain light insensitive segregates. In addition, only a few crosses may be grown. Consequently, F_1 's must be discarded on the basis of visual evaluation and F_1 plant yield.

In comparison to other cereals, triticale has had a very short evolutionary period. At the present time, most of the primary and secondary triticales still show meiotic instability. Gustafson and Zillinsky (1973) and subsequent researchers have noted the occurrence of wheat-rye chromosome substitution. Gustafson and Qualset (1974) suggested that extreme selection in the F_1 and subsequent early generations could result in the loss of highly desirable genotypes. With these factors in mind, the present series of experiments were conducted to investigate: 1) the reliability of F_1 yield as a means of identifying crosses which produce high yielding segregates in an F_3 early generation yield trial; 2) the influence of experience on the ability of selectors to visually identify superior plots in an F_3 early generation yield trial; 3) visual selection (pedigree) and F_3 early generation yield selection as methods for the advancement of generations in triticale; and 4) the influence of selection for light insensitive genotypes on the yielding ability of triticales grown under long photoperiod conditions.

LITERATURE REVIEW

LITERATURE REVIEW

Parental Selection

As in most of the cereal species, a major problem in a triticales breeding program is the selection of parental material. For parental selection to be most effective, it must result in the establishment of cultivars which when crossed will produce the largest possible number of desirable segregates.

Smith (1966) suggested that parents should favorably express desirable characteristics and be of sufficiently diverse origin to result in desirable transgressive segregation. Bhatt (1973) working with wheat, found that breeding methods based on ecological diversity resulted in the higher degree of transgressive segregation necessary for yield improvement.

The results of studies conducted on maize by Green (1948), Lonnquist (1953, 1968), Lonnquist and Lindsay (1964), also by Busch et al. (1974) with wheat, indicated that progenies with the highest absolute yields came from crosses of low x high yielding parents. They found, however, that the greatest number of high yielding lines stemmed from high x high combinations. In contrast, Johnson and Hayes (1940) found little difference in the number of superior maize inbreds produced by either high x high or low x high yielding crosses.

Consequently, although methods based on ecological diversity in theory give the greatest chance of obtaining crosses with segregates above the yield levels of the parents, no concrete conclusions can be

made in terms of which parental combinations give the best results when considering yield improvement.

Cross Selection in the F_1

Due to the variability in results on selection of parental material, many studies have been conducted on the evaluation of F_1 hybrids. As a consequence of these studies, the importance of environmental interactions and heterosis has been emphasized.

Evaluation of F_1 hybrids, on the basis of yield performance, has been hampered by their expression of "hybrid vigor" or heterosis. Cress (1966) proposed that intralocus interaction could result in negative heterosis in wheat, removing the validity of F_1 yield tests. Rosenquist (1931) working with wheat, observed that the degree of heterotic expression was greatly influenced by interplant competition. More recently, Knight (1973) reported that the expression of dominance and over-dominance was affected by environmental conditions.

Lupton (1961) concluded that F_1 yields were not indicative of yielding ability in wheat, although crosses with a high F_1 yield produced a higher frequency of desirable segregates. Busch et al. (1976) on the other hand, obtained high correlations between the F_1 and F_2 , and F_2 and F_3 yields. Briggs and Knowles (1967) summarized the inadequacies of conducting F_1 yield trials as follows: 1) seed quantities are frequently too small for replicated testing; 2) the yield of widely spaced F_1 plants are not correlated with the yields of more closely spaced plants; and 3) F_1 heterosis is a major obstacle for predicting yield potential in subsequent generations.

Early Generation Yield Selection

Based on Mendelian genetics, the highest degree of variability available in any population of segregating individuals occurs in the F_2 generation. Under this hypothesis, the greatest probability of gaining desirable segregates occurs in the F_2 . Studies conducted by Bell (1963) with barley, Allard (1967) and Mackey (1966) with wheat, have revealed that selection for single plant yield in the F_2 generation was not effective. McGinnis and Shebeski (1968) found no correlation between F_2 plant yield and yielding ability in the F_3 progenies but indicated that selected lines were higher yielding than those obtained from a random sample.

Based on the principle that the most efficient means of evaluating an individual is on the basis of its progeny performance, a number of studies have been conducted on the yielding ability of F_2 -derived lines. Heyne and Smith (1967) hypothesized that F_3 lines retain the unique ability to represent individual F_2 plants and the degree of genetic variability in the F_2 generation of wheat. As a consequence, they recommended the careful evaluation of F_3 lines in a yield nursery involving systematically placed check plots. The use of F_3 yield trials has also been recommended in barley by Fiuzat and Atkins (1953) and McKenzie and Lambert (1961), who found that early generation selection of high yielding lines would be most easily accomplished in crosses with a high degree of yield diversity.

Whitehouse (1953), although recommending the testing of F_2 progenies for wheat yield improvement, has indicated that this method physically limits the number of lines which may be evaluated in the F_3 . Even with this limitation, studies conducted by Kalinenko (1964), Briggs and

Shebeski (1971), DePauw (1970) and Mundel (1972) have indicated that yield improvement can be accomplished by the use of F_3 yield selection. Similar results have been obtained by Hurd (1967) where superior lines were retained from large trials involving F_2 -derived F_4 lines. Hurd further proposed that F_2 progeny testing could be even more successful if selection was conducted on the basis of F_3 line yield.

Recent results obtained by Cooper (1976) supported the use of early generation selection as a tool for yield improvement in soybeans. In this case, three different crosses were evaluated over a period of two years. Results indicated that yield testing of F_2 -derived lines in the F_3 and F_4 generations identified the best crosses and superior lines within each cross.

Visual Selection for Yield Improvement

Whitehouse (1953) stated that early generation yield trials limit the number of progeny which can be evaluated. The use of visual criteria for selection is not as severely affected by this problem. Consequently, a number of studies have been conducted on the efficiency of visual selection for yield.

In general, visual evaluation of early generation space-planted nurseries has not resulted in a significant yield improvement in subsequent generations. McGinnis and Shebeski (1968) found that selection of single F_2 plants, on the basis of yield, increased population mean yields but selection of plants with a high level of vigor was more effective. Knott (1972) found that visual selection improved the yield of eight wheat populations but recommended the use of F_3 yield trials. The results of an earlier study by Atkins (1953)

indicated that yield improvement could be obtained by visual evaluation of single plants. However, this method was only efficient in identifying lines which would be low yielding in subsequent generations.

Poor results have also been found when visual selection was conducted on a line basis. Studies conducted in soybeans by Boyce et al. (1947) and in wheat by Krull et al. (1966) showed that visual selection was as efficient as plot yield for improving yield. More recent studies in wheat conducted by Briggs and Shebeski (1970), Townley-Smith et al. (1973) and Mundel (1972) using F_3 early generation yield trials, concluded that little yield advancement could be obtained by visual selection. Briggs and Shebeski (1970) recommended that wherever necessary, visual selection should be conducted at a low intensity to ensure retention of the highest yielding lines in the nursery.

Stuthman and Steidl (1976) studied visual selection for yield in four diverse oat populations and showed a positive yield response in three of four populations. Deviations in one population prompted the suggestion that extreme elimination of large portions of populations, on the basis of visual criteria, should be considered with caution.

Studies conducted in soybeans by Kwon and Torrie (1964) and Hanson et al. (1962) indicated that visual selectors were only able to identify lines in the extremes of a yield distribution. Selectors were most efficient in selection of the lowest yielding lines. Kwon and Torrie (1964) found that visual selection was only 50 percent as efficient in selecting high yielding lines as selection based on plot yield.

On the basis of studies on visual evaluation of single spaced plants or lines, it can be concluded that: 1) visually selected lines are higher yielding than a random sample; 2) visual selection is most effective in eliminating low yielding lines; and 3) visual selection is greatly affected by the variability in the populations observed.

A Comparison of Early Generation and Pedigree Selection for Yield

Recently, Seitzer (1974) observed no significant difference in mean yield or variability between wheat lines selected by the pedigree method and the hill plot and F_3 contiguous method of early generation selection. He concluded, however, that early generation selection using check plots was most beneficial when dealing with crosses of low yield potential.

Leudders et al. (1973) testing early generation, bulk and pedigree selection methods in soybeans, found no difference between methods in terms of yield in the F_2 and F_7 . They found, however, that the bulk and early generation methods retained a greater number of high yielding lines than did the pedigree selection method.

Similar results were obtained by Boerma and Cooper (1975). In that study, no difference in mean yield was observed for lines selected by either single seed descent, early generation selection or pedigree selection. They found, however, that lines selected by means of single seed descent and pedigree selection were generally earlier in maturity than lines selected by means of early generation evaluation.

An earlier study by Raeber and Weber (1953) indicated that a compromise should be made between early generation and pedigree selection. They recommended that where possible, lines should be

tested for yielding ability in a replicated F_3 nursery and superior plants selected simultaneously from a space-planted nursery.

Yield Components and Harvest Index

Yield components have been important factors in methods involving early generation yield and pedigree selection. Yap and Harvey (1972) suggested that yield components are considered to be controlled primarily by additive gene action. The presence of negative correlations and compensation between components have been major problems in yield prediction. The presence of negative relationships has been observed in barley (Rasmusson and Cannell, 1970; Stoskoff and Reinbergs, 1966), field beans (Duarte and Adams, 1972), soybeans (Pandey and Torrie, 1973), triticale (Gebremariam, 1974) and in wheat (Fonseca and Patterson, 1968; Knott and Talukdar, 1971; Reddi *et al.*, 1969).

Yield component compensation has been explained on the basis of two possible models. Rasmusson and Cannell (1970) explained the phenomenon as being due to linkage between genes which promote an optimal balance among components. Adams and Grafius (1971) observed that this model does not allow a sufficiently high degree of flexibility expressed by components in response to available resources. They explained compensation as a balance among sequential components achieved primarily through an oscillatory response to a limited quantity of resources. Thus in seed crops, a compromise occurs for the utilization of available resources.

According to Adams and Grafius (1971), basic differences in these two models require different approaches in terms of selection techniques.

In the case of the linkage model, selection must be practised to break unfavorable linkages and to identify superior recombinations. As for the oscillatory model, the breeder must promote desirable recombinations, increase the flow of environmental resources through a period of need by the components and raise, by means of selection, the genetic ceilings that influence the capacity of a component to respond when resources are available.

Studies conducted with wheat on factors related to yield have shown a wide range of variability in results. Studying F_2 populations, Lee and Kaltsikes (1973) and Utz et al. (1973) have indicated a correlation between yield and plant height. The importance of tillering for yield prediction in wheat has been stressed by Fonseca and Patterson (1968), McGinnis and Shebeski (1968), Hsu and Walton (1970), Das (1972), Mundel (1972), Walton (1972) and Dunder (1974). Other factors shown to have a significant effect on wheat yield are: 1) kernel weight (Fonseca and Patterson, 1968; Das, 1972; Walton, 1972; Dunder 1974; Ketata et al., 1976); and 2) kernels per spike (Fonseca and Patterson, 1968; Walton, 1972; Dunder, 1974). Ketata et al. (1976) indicated that problems could occur in selection for yield improvement using yield related factors. Results of an inheritance study showed that plant height, tiller number, kernels per spikelet and grain yield per se are influenced by epistatic genetic effects. Kernels per spikelet, kernels per spike and kernel weight were governed mainly by additive gene effects.

Yield component studies conducted in barley and oats tend to indicate similar variability in results. Sampson (1971) found, on the basis of inheritance studies conducted on yield and related factors in

the F_1 , F_2 and F_3 generations, that yield component gene action in oats was mainly additive. In this study, yield per panicle was estimated as being a good criterion for yield selection. Stoskopf and Reinbergs (1966) have found that seed per head (barley) and panicle (oats) were important factors relating to yield. They stated, however, that the poor relationship of yield and tillering, and the negative correlation of tillers and kernels per spike could in some cases result in yield reduction if selection was carried out for tiller number. Rasmusson and Cannell (1970) studying barley, have shown that selection of spikes per plant and kernel weight are effective in increasing yield, however, selection on the basis of kernels per spike could in some cases reduce yield. As a consequence, they concluded that although some yield improvement will occur with selection for yield on the basis of yield components, the fact that both genetic and environmental factors affect phenotypic correlations reduces their reliability as indicators of yield. They concluded that selection on the basis of components should not be employed as a general procedure in a practical breeding program.

As in many other aspects of study, very little data have been compiled on the influence of yield components in triticales. Sethi and Singh (1972) found a strong positive correlation between tillering capacity and yield. Gebremariam (1974) on the other hand, found a negative correlation between tillering and yield. Kernels per spike has been shown to be an important yield-related factor by Gustafson (1972), Barnett et al. (1973), Gebremariam (1974) and Chen (1974). In addition, Gustafson, Gebremariam and Chen have indicated positive correlations between yield and kernels per spikelet. Gebremariam has

also suggested that days to maturity and plant height are important yield factors in the triticale cultivars 'Rosner' and 'Armadillo'. By regression analysis, he found that plant height accounted for 65.1 percent of the residual sum of squares for plot yield.

A study conducted by Zillinsky and Borlaug (1971) emphasized the effect of environment on the expression of certain yield components in triticale. They observed that selection for light insensitive triticale lines resulted in a yield reduction due to the fact that light insensitive lines produced a considerably lower number of tillers than light sensitive types.

Donald (1968) summarized the problems which may be involved in the prediction of yield on the basis of yield components as follows: 1) the proportion of additive variance relative to environmental and error variance; and 2) differences occur in the competitive environment between spaced plantings and actual crop conditions. Earlier, Donald (1962) proposed harvest index as a means of yield evaluation rather than yield components.

Studies conducted by Syme (1972), Nass (1973) and Fischer and Aquilar (1975) have shown highly significant correlations between harvest index and grain yield. More recently, Fischer and Kertesz (1976) studying a number of yield related factors and harvest index, concluded that harvest index was a valuable criteria for estimating plot yield on the basis of single, spaced plants.

The Influence of Photoperiod and Its Interactions With Environment on the Development of Wheat and Triticale

With the beginning of the "Green Revolution" an increased demand

for widely adapted light insensitive cereal varieties occurred. One of the major sources of light insensitive wheat and triticale lines has been the CIMMYT (International Maize and Wheat Improvement Center) organization in Mexico. Krull et al. (1968) indicated that environmental problems caused by light sensitivity have been overcome in the CIMMYT breeding program.

Selection of light insensitive lines, in addition to incurring adaptive advantage, is an important means of increasing seed stocks in the lower latitudes, and by growing winter nurseries the time required from hybridization to the testing of advanced generations is reduced. Quick (1971) has estimated that in durum wheat, one bushel could be multiplied to four million bushels by the use of winter nurseries in Arizona and California. Kilpatrick et al. (1972) have stated that incorporation of light insensitivity would also allow a more adequate means of measuring disease resistance under short-day conditions. At the present time, the University of Manitoba utilizes winter nurseries in northwestern Mexico.

Selection of light insensitive lines has been facilitated by the simple inheritance of photoperiod response. Pinthus (1963) found that the wheat varieties 'Yuma' (sensitive) and 'Zenati/Bontielle' (insensitive) differed by two linked loci. Similarly, studies conducted by Pugsley (1965, 1966) indicated that day-length response was controlled by one or two gene system. Borlaug (1965) found that day-length insensitivity in the hexaploid variety 'Sonora 64' was inherited as a simple dominant. He also indicated that light insensitivity was inherited as a dominant but was transmitted with lower

penetrance in tetraploid wheats than in hexaploid types. In a more recent study Lebsock et al. (1973) found that light insensitivity was simply inherited in three crosses of spring wheat. Studies conducted in common wheats have shown that a large portion of environmental variability may be attributed to complex interactions between vernalization (genes for winter habit), temperature during the early stages of development and photoperiod response. Evidence of such interactions has been reported by Syme (1968), Pugsley (1970), Halse and Weir (1970) and Levy and Peterson (1972). These researchers found that vernalization of spring wheats insensitive to photoperiod resulted in reduced tiller number per plant and spikelet number per spike. In addition, Heiner (1971) has indicated that many of the common wheats may contain genes which are responsive to low temperatures. Consequently, when combined with light insensitivity, rapid development results in reduced tiller production, shorter straw and earlier maturity than temperature responsive but light insensitive genotypes. Alternatively, Hurd-Karrer (1933) and Syme (1968) have shown a similar effect if light insensitive lines are grown under a long-day environment with high temperatures during early seedling development.

Similar studies, conducted on the effect of short day-length on the development of cereal crops, have indicated that increased developmental periods in photoperiod sensitive lines have a significant influence on many of the yield components. Rawson (1971), studying this effect on both wheat and triticale lines, found an increased number of spikelets per spike in both species under short-day conditions. The most extreme effect was found in triticale which continued to

respond after the wheat genotypes had reached an apparent maximum number of spikelets per spike. In addition under extreme conditions, the triticales produced a larger number of infertile terminal florets. Zillinsky and Borlaug (1971) also noted that a short photoperiod had a drastic effect on the number of tillers produced by light sensitive genotypes. They found that light sensitive segregates required at least two weeks longer to reach maturity but produced twice as many tillers as light insensitive genotypes.

Lebsock et al. (1973) conducted a study on the yielding ability of near-isogenic light sensitive and insensitive wheat lines to determine if selection for light insensitivity had an adverse effect on the yield potential of lines grown in yield trials throughout the northern United States. Results showed that sensitive and insensitive F_3 bulks and near-isogenic F_6 lines differed little in terms of yield when compared over all locations. Analyses of individual locations showed that insensitive F_6 lines yielded as high or higher than sensitive lines at two of three locations but were 40 percent lower yielding than sensitive lines at the third location. They concluded that high atmospheric temperatures and long-day conditions resulted in the lower yield at one location and that selection for light insensitivity was not adversely affecting the development of lines with a high yield potential for higher latitudes.

Reliability of Check Plots in Removing Environmental Variation

The quantity of seed available in early generations has been a major limiting factor in conducting early generation yield trials. One prominent solution to this problem has been the use of check varieties

to account for environmental variation in place of replication.

Shebeski (1967) formulated a system of early generation yield testing based on systematically placed check plots. With this method, the yield of superior plots are identified by yield in grams and plot yield expressed as a percentage of the nearest check plot.

In general, however, the reliability of analyses based on check plots has been questioned. As early as 1914, Salmon stated that although check plots detected variation due to soil heterogeneity, they should not be used in place of adequate replication. Pritchard (1916) on the other hand, indicated that check plots were adequate when used to compensate for variability due to soil heterogeneity. Yates (1936) and Baker and McKenzie (1967) have questioned the value of check plots, on the basis of theoretical considerations, unless an analysis of covariance was used in place of an analysis of variance. Milton and Finkner (1967) have found that analysis of covariance involving check varieties in alfalfa increased the efficiency of tests from 38 percent to 528 percent.

The Implications of Competition in Plant Breeding

Many of the methods of early generation selection used for yield determination involved the evaluation of entire segregating populations or single plant progenies on the basis of their bulk yield. Previous studies have indicated that evaluation of F_1 hybrids is substantially influenced by environmental factors. Consequently, wide variation occurs in type and degree of heterotic expression. In many cases this is due primarily to interplant competition. This type of interaction could be of paramount importance in the evaluation of segregating

populations based on bulk yields.

Donald (1958) studied the effect of competition for light and nutrients on the productivity of *Lolium* and *Phalaris* species. The resulting data indicated the superior competitive ability of the *Lolium* species for these factors. *Phalaris* species on the other hand, under competition showed a definite reduction in ability to assimilate both light and nutrients for the production of photosynthate.

Henson and Hanson (1962) studied the effect of competition on the productivity of soybean mixtures. It was found that blending of varieties did not result in superior yields but within the mixtures certain varieties yielded more at the expense of others. As a result, they concluded that genetic analyses of plant variability for yield may be extremely misleading when either plant competition or differential response to space is not taken into consideration.

Studies based on the effects of competition in cereals frequently show dramatic changes in yields relative to pure stands. Allard and Adams (1969) studied this problem in both wheat and barley. Results indicated that lines which perform well in mixtures generally are inferior in pure stands. Neutral competitors were little affected by competition but strong competitors which were poor in a pure stand were superior in mixtures. High yielding lines of poor competitive ability were found to suffer severe reduction in productivity in mixtures. Similar results were obtained in Russia by Konovalova (1974) with Russian wheat varieties.

To determine if results from competition studies involving pure varieties were indicative of the effect of competition on segregating

progenies, Khalifa and Qualset (1974, 1975) conducted two studies on this subject. The first experiment involved the evaluation of bulks consisting of an equal mixture of a short statured, high yielding wheat variety and a low yielding, standard height variety. It was found that bulk yields were superior to pure line stands and the contribution of the lower yielding variety was increased at the expense of the semi-dwarf as exemplified by a reduction in spikes per plant and seed per spike. The second study involving bulk evaluation of a cross between the same two varieties, indicated a severe reduction in semi-dwarf segregates and a trend towards tallness in advanced generations. It was concluded that: 1) bulk performance is not necessarily a measure of agricultural merit; and 2) the use of bulks in crosses from which desirable semi-dwarfs are to be selected is not a recommended practice due to a reduced chance of retaining those segregates as a result of adverse competition.

These results may be partially substantiated by results from early generation trials which show an increase in plant height in wheat. This could be a definite problem in existing triticales breeding programs in which one of the major objectives has been the incorporation of short stature. The existing relationship of infertility and short stature, in combination with competitive effects, could further reduce the probability of obtaining a wide range of desirable segregates.

Meiotic Instability in Triticales

One of the most important considerations in any triticales breeding program is the lack of meiotic stability in many lines, particularly in early generations. Meiotic instability results in a high frequency of

aneuploidy which in turn results in poor plant vigor with an accompanying reduction in yield (Merker, 1974). As a consequence, meiotic instability is an important factor in the production of high yielding triticales lines.

According to Hsam and Larter (1973) attributes which have been used for the assessment of meiotic instability are frequencies of univalents, open bivalents, arm pairs, lagging and excluded chromosomes at telophase I, micronuclei per quartet and pollen viability. Kaltsikes (1974) has stated that three possible factors contribute to the occurrence of univalents: 1) allocycly and precocious chromosome separation; 2) inbreeding depression, deleterious genes, genome ratio and ploidy barriers; and 3) cytoplasmic effects. Although these possibilities have been thoroughly studied, no concrete conclusions have been obtained in regard to meiotic anomalies in triticales. Presence of a hybrid system in triticales, rather than one controlled by either wheat or rye genomes, has been suggested by Bennett and Kaltsikes (1973). The fact that this type of system is responsive to selection in terms of meiotic stability has been determined by Hsam and Larter (1973).

As reported by Merker (1974), many of the early studies on triticales were conducted on the premise that meiotic instability had a direct effect on the fertility of triticales lines. Riley and Chapman (1957), Riley and Bell (1959), Muntzing (1966), Muntzing et al. (1963), Tsuchiya (1972), Hsam and Larter (1973, 1974), Merker (1973) and Gustafson and Qualset (1975) have indicated little direct influence of meiotic instability on fertility in either hexaploid or octoploid triticales. Tsuchiya (1972) qualified his conclusions on the basis that

meiotic instability and fertility may become associated when meiotic instability is extreme.

Recent studies have shown that many triticales differ in the number of rye chromosomes present. In addition, changes in chromosome structure have been observed. Gustafson and Zillinsky (1973), Gustafson and Qualset (1974, 1975), Darvey and Gustafson (1975), Merker (1975), Gustafson and Bennett (1976), Gustafson and Zillinsky (1976) and Qualset et al. (1976) have indicated the substitution of wheat for rye chromosomes in hexaploid triticales. In addition, Darvey and Gustafson (1975), Gustafson and Bennett (1976) and Gustafson and Zillinsky (1976) found that changes occur in the quantity of heterochromatin present in the rye chromosomes. Gustafson and Zillinsky (1976) and Merker (1976) noted that changes can occur in heterochromatin content without damage to the euchromatin or plant development. Gustafson and Qualset (1975) have suggested that crosses between triticales differing in R chromosome substitutions should be considered analogous to interspecific crosses in which both homologous and nonhomologous relationships exist, resulting in reduced fertility in the F_1 and later generations.

Qualset et al. (1976) have summarized the possible reasons for the common occurrence of infertility in triticales hybrids and the consequences in developing a triticales breeding program. These causes are: 1) intercrosses of substitutional triticales are expected to show sterility if the parents entering the cross do not have the same A, B, D or R chromosomes; 2) translocations in rye chromosomes are known and sterility would be expected in hybrids if the triticales differed for

chromosomal translocations; and 3) triticales, differing for incompatibility genes because of the two locus system of incompatibility in rye, may show sterility when hybridized.

Due to the resulting sterility in crosses between an ever increasing number of substitutional triticales, Qualset et al. (1976) recommended that hybrids and populations should not be discarded wholly on the basis of poor fertility. In subsequent generations, some of these crosses produce highly fertile segregates due to selection for fertility in the F_2 to F_4 . Gustafson and Qualset (1974) have further indicated that fertility in many triticales hybrids may be due to genetic similarity. Consequently, these lines would show a limited potential for improvement.

MANUSCRIPTS

MANUSCRIPT I

F₁ EVALUATION OF YIELD POTENTIAL
IN HEXAPLOID TRITICALE

F_1 EVALUATION OF YIELD POTENTIAL IN HEXAPLOID TRITICALEAbstract

During the summers of 1972 and 1973, a total of eight hexaploid triticale (X Triticosecale Wittmack) F_1 populations were evaluated on the basis of yield. In each year, one low yielding, two intermediate and one high yielding F_1 population was retained for evaluation in an F_3 yield trial. Comparison of F_1 and F_3 yield rank and the number of high yielding F_3 families produced by each population indicated that evaluation of crosses on the basis of F_1 single plant yield was ineffective for the selection of crosses with a high yield potential in subsequent generations.

Introduction

A major problem in conducting a breeding program in triticale (X Triticosecale Wittmack) or any other cereal crop, is the selection of either desirable parents or the identification of superior progenies. Smith (1966) suggested that parents should; 1) present favorable expression of desirable characteristics; and 2) be of sufficiently diverse origin to give desirable transgressive segregation. Similarly, Bhatt (1973) working with wheat, found that breeding methods based on ecological diversity resulted in the high degree of transgressive segregation necessary for yield improvement. Green (1948), Lonnquist (1953, 1968), Lonnquist and Lindsay (1964) working with maize, and Busch et al. (1974) working with wheat, found that crosses with the highest yielding lines came from crosses of high x high yielding parents. Johnson and Hayes (1940) working with maize on the other hand, found no difference between high x high or high x low yielding parental crosses.

Evaluation of F_1 hybrids on the basis of yield performance is confounded by the degree of "hybrid vigor" or heterotic expression. Rosenquist (1931) found that the degree of heterotic expression was greatly influenced by interplant competition in wheat. Cress (1966) indicated that intralocus interaction could result in negative heterosis thereby removing the validity of F_1 yield testing. More recently, Knight (1973) concluded that hybrids in wheat varied greatly in their response to environment as shown by differences in expression of dominance and over-dominance.

Lupton (1961) concluded that F_1 yields were not indicative of yielding ability in wheat although crosses with a high F_1 yield produced a higher frequency of desirable segregates. Busch et al.

(1976) on the other hand, found high correlations between the F_1 and F_2 generations and between the F_2 and F_3 generations. Briggs and Knowles (1967) summarized the inadequacies of conducting F_1 yield trials as follows: 1) seed quantities are frequently too small for replicated testing; 2) the yield of widely spaced F_1 plants are not correlated with the yields of more closely spaced plants; and 3) F_1 heterosis is a major obstacle for predicting yield potential for subsequent generations.

A basic problem in triticales breeding program is the relatively small number of documented cultivars available for cross evaluation as compared to many other cereal species. As a consequence, a large number of crosses must be produced and evaluated if rapid improvement is to be expected. Because the number of F_1 hybrids which can be evaluated is limited by space available, a large portion of the F_1 hybrids at the University of Manitoba are advanced on the basis of agronomic characteristics and single plant yield. This study was initiated to determine the validity of this method of F_1 selection by comparing the F_1 and F_3 generations on the basis of yield.

Materials and Methods

During the summers of 1972 and 1973, F_1 triticales were grown in 3-row plots, 3.0 meters long with a row spacing of 0.15 m. Individual hybrids were evaluated on the basis of agronomic characteristics. The yielding ability of individual hybrids was expressed as plot yield divided by the number of plants in each plot. In both years, one low yielding, two intermediate and one high yielding F_1 hybrid was retained for subsequent F_3 evaluation. Selected crosses were designated as A through D and 1 through 4 in the two years,

respectively. Parentages of the crosses are shown in Table 1.

F_2 space-planted nurseries were grown at the CIANO Research Station, Cd. Obregon in northwestern Mexico during the winters of 1972-73 and 1973-74. Each population was represented by approximately 2,000 F_2 plants. In each year only those plants producing sufficient seed for a 3-row plot, 5.6 meters long were retained for F_3 evaluation in Manitoba. In populations A through D, 381, 207, 50 and 34 plants, respectively, were retained for F_3 evaluation in 1973. Similarly, 98, 99, 100 and 98 lines were evaluated in populations 1 through 4, respectively in 1974.

F_2 -derived F_3 families were grown in an early generation yield trial consisting of 3-row plots, 5.6 meters long, with a row spacing of 0.15 meters. Individual plots were separated by 0.60 meters. Plots were seeded at a rate of 250 seeds per row with every seventh plot in the nursery seeded to the check cultivar 'Rosner'.

Initially each F_3 plot was evaluated for yield as a percentage of the nearest check plot. Populations were subsequently tested for deviations from a normal distribution. Where deviations from normality occurred, populations were evaluated by transforming the data to plot yield minus check yield, or log plot minus log check yield. In each year the populations were compared by one-way analysis of variance with Duncan's multiple range test.

Results and Discussion

In both 1973 and 1974 evaluation of population mean yields, expressed as a percentage of the check, resulted in distributions which deviated significantly from normal. Evaluation of populations A through

Table 1. Pedigrees of triticale populations evaluated on the basis of F_1 single plant yields in 1972 and 1973.

Year	Pop'n.	Pedigree
1972	A	[(Susan-V4) O.C. Line] [(UM70-S.F.S.) (Hari-Arm ²)]
	B	(8A95 x Rosner) (Hari-Arm ²)
	C	(4B909-2D53) (Badger-Arm)
	D	(Tcl-M x R) (Badger)
1973	1	83/Koala-3
	2	(Maya II-Arm ²)/6TA204
	3	(6TA204-Bronco-90) (Beaver-Arm)
	4	Koala-3/6TA518

D was subsequently based on the difference in yield between the plot and the nearest check. Because both percent and deviation from the check resulted in non-normal distributions, populations 1 through 4 were evaluated on the basis of the transformation $\log \text{plot} - \log \text{check}$.

The present study indicated no distinct relationship between the F_1 yield ranking and yield in the F_3 generation. Although the highest yielding F_1 's had the best yielding lines in the F_3 yield trial in both years (Table 2), F_1 hybrids with the lowest yield produced F_3 populations with the highest mean yield in 1973 and 1974. Alternatively, the highest yielding F_1 's were the second poorest crosses in terms of F_3 mean yield in both years. In 1973, no significant differences occurred between the two lowest yielding and the two highest yielding F_3 populations ($P = 0.05$). In 1973, no significant difference occurred between the two lowest or between the two intermediate yielding F_3 populations. The highest yielding F_3 (originating from a low yielding F_1) was significantly higher yielding ($P = 0.05$) than all other populations in 1974.

The present results correspond with previous information on the reliability of F_1 evaluation as a tool for the identification of superior crosses. However, other problems peculiar to triticales may further hamper the use of F_1 selection for the identification of desirable crosses. Merker (1973) and Qualset *et al.* (1976) have noted that an increase in meiotic instability and reduced fertility are common occurrences in the production of triticales hybrids.

Merker (1974) reported that many of the early studies in triticales

Table 2. Comparison of single F_1 plant yields and mean F_3 population yields.

F ₁				F ₃									
Year	Pop'n.	Number of plants	Yield/plant (g)	Year	N	Yield (% check)	Yield (plot minus check) (g)	Yield (log)	Highest yield %	Lowest yield %	Total lines $\geq$ check	Lines in top 25	Lines in top 10
1972	A	18	90.7	1973	381	78.08	-194.30a [†]	-	212.0	33.1	75	6	3
	B	12	33.3		207	96.82	- 35.59b	-	176.0	30.8	84	13	6
	C	14	26.8		50	82.08	-218.38a	-	138.0	26.4	13	0	0
	D	13	9.6		34	99.64	- 25.00b	-	157.0	48.4	17	6	1
1973	1	13	27.5	1974	98	70.08	-	-0.422ab	148.9	41.1	8	4	2
	2	14	26.4		99	66.10	-	-0.516a	185.5	34.0	15	9	5
	3	21	16.0		100	72.36	-	-0.359b	125.5	25.3	11	3	0
	4	18	7.2		98	90.91	-	-0.122c	145.5	47.7	28	11	3

[†] Duncan's multiple range test at $P=0.05$; values followed by same letter are not significantly different.

assumed that meiotic instability was directly responsible for reduced fertility in many triticales lines. Riley and Chapman (1957), Riley and Bell (1959), Muntzing et al. (1963), Muntzing (1966), Tsuchya (1972), Hsam and Larter (1973, 1974), Merker (1973, 1974) and Gustafson and Qualset (1975) have shown that no direct relationship occurs between meiotic instability and fertility in either the hexaploid or octoploid triticales. Tsuchya (1972) proposed, however, that the two phenomena may become related under extreme conditions of meiotic instability. As indicated by Merker (1974), meiotic instability frequently results in the production of aneuploid plants which have poor vigor and fertility which results in reduced yield potential.

Recent studies have shown that many triticales differ in the number of rye chromosomes present. In addition, changes in chromosome structure have been observed. Gustafson and Zillinsky (1973), Gustafson and Qualset (1974, 1975), Darvey and Gustafson (1975), Merker (1975), Gustafson and Bennett (1976), Gustafson and Zillinsky (1976) and Qualset et al. (1976) have verified the occurrence of substitutions of wheat for rye chromosomes in hexaploid triticales. In addition, Darvey and Gustafson (1975), Gustafson and Bennett (1976) and Gustafson and Zillinsky (1976) have found that changes occur in the heterochromatin content of rye chromosomes. Gustafson and Zillinsky (1976) and Merker (1976) have concluded, on the basis of measurement, that changes in heterochromatin content can occur without apparent damage to the euchromatin and plant development.

Due to increased meiotic instability and lower fertility, Gustafson and Qualset (1975) have suggested that crosses between triticales

differing in R chromosome substitutions should be considered analogous to interspecific crosses where homologous and nonhomologous relationships exist. Qualset et al. (1976) indicated that a number of factors causing the common occurrence of infertility in triticales hybrids may be summarized as: 1) intercrosses of substitutional triticales will show sterility if the parents differ in terms of A, B, D or R chromosome content; 2) translocations in rye chromosomes may cause sterility if the parents differ for rye chromosome translocations; and 3) crosses of triticales differing for rye incompatibility genes may cause hybrid sterility. Gustafson and Qualset (1974) concluded that triticales hybrids should not be discarded on the basis of infertility because with selection some crosses may produce desirable, highly fertile segregates in future generations. These workers also suggested that fertility in F_1 hybrids may be due to genetic similarity in the parents. Consequently, response to selection in subsequent generations would not be expected.

Observation of the pedigrees presented in Table 1 suggest that the parents involved in the crosses may have differed in terms of rye chromosomes which were present. Gustafson and Zillinsky (1973) found that the CIMMYT cultivar 'Armadillo' was lacking the rye chromosome 2R. More recently, Merker (1975) found that the Armadillo derivatives, Beaver, Maya II-Arm "S" and Bronco-90 also contained rye chromosome substitutions. Gustafson (personal communication) has indicated that Koala-3 may possibly contain wheat-rye substitutions. The remaining parents are expected to have contained a full complement of rye chromosomes.

Evaluation of eight genetically diverse populations suggests that F_1 single plant selection should not be utilized as a criterion for yield prediction in a triticales breeding program. A major reason for this conclusion is the inadequacies of F_1 yield selection explained by Briggs and Knowles (1967). In addition, the loss of desirable crosses, as noted by Gustafson and Qualset (1974), may be serious if the parents differ for wheat-rye substitutions.

MANUSCRIPT II

VISUAL SELECTION AS A BASIS FOR YIELD
PREDICTION IN HEXAPLOID TRITICALE

VISUAL SELECTION AS A BASIS FOR YIELD PREDICTION IN
HEXAPLOID TRITICALE

Abstract

During the summers of 1973 and 1974, a total of eight F_3 hexaploid triticale (X Triticosecale Wittmack) populations were each visually evaluated by a group of selectors working independently. Each group was comprised of experienced (plant breeders), novice (graduate students) and inexperienced (summer students) selectors. In both years, all selectors were requested to visually select lines which they predicted would equal or out yield the nearest check plot. The results of chi-square analyses indicated that, in general, selectors were superior to random sampling in six of the eight populations. In 1974, the selectors were also requested to identify the twenty highest yielding lines in each population. Chi-square analyses indicated that all of the experienced selectors and most of the novices selected a high number of the top ten lines in each population relative to a random sample. Comparison of response to selection and selector efficiencies in 1973 and 1974 indicated that the experienced evaluators were superior in their selective ability compared to the inexperienced selectors. In addition, the mean yield of the top twenty lines selected within each of the populations by experienced selectors did not, in general, deviate significantly from the best yielding twenty lines identified by the yield trial. Consequently, it appears that visual selection on a line basis may be a means of yield selection in triticale, providing the intensity of selection is not restrictively high.

Introduction

Kwon and Torrie (1964) and Hanson et al. (1962) found visual selection in soybeans to be 50 percent as efficient as selection based on plot yield but effective in raising the mean yield above that of the population. Both studies showed that the selectors could determine population yield extremes, with the best results being obtained in the identification of the low yielding lines.

In barley, McKenzie and Lambert (1961) were unable to find a consistent relationship between visually selected lines and their yields in the F_3 and F_6 generations. On the other hand, Krull et al. (1966) found a close association between the visual ranking of wheat lines on the basis of desirable agronomic characteristics and their yield. Briggs and Shebeski (1970), using fourteen selectors, found that visual selection for yield in wheat was superior to random sampling but that the ability to visually select the absolute highest yielding lines was limited. As a result, they suggested that the intensity of selection be reduced so as to ensure that the highest yielding lines are retained. More recently, Mundel (1972) using numerous selectors in wheat, found that the yields of visually selected lines were slightly lower than those selected on the basis of plot yield.

Townley-Smith et al. (1973) also working with wheat, conducted a test to determine the effect of selector experience on the ability to advance a population mean yield by visual selection. Selecting in an

early generation yield test, they found no difference between experienced and inexperienced selectors in their ability to differentiate yield potential of plant families on a visual basis.

More recently, Stuthman and Steidl (1976) studied visual selection for yield in four diverse oat populations. They found that visual selection resulted in a positive yield response in three of the four populations studied. The negative results obtained from one population provided evidence that extreme reduction of populations, on the basis of visual criteria, should be considered with caution.

In triticales (X Triticosecale Wittmack), populations show a wide range of variability for morphological characteristics (fertility, spike length, tillering, etc.). Consequently, there may be higher potential for success with visual selection in triticales than within many other cereal species. The primary objectives of this study were twofold: 1) to determine if visual selection would be purely random within a population of F_3 lines or if advances in yield could be made; and 2) to determine if a differential ability to select visually for yield occurred between experienced and inexperienced selectors.

Method

F_3 yield trials were grown at the University of Manitoba during the summers of 1973 and 1974 using four different genetically diverse populations each year (See Table 1, p.34 of thesis). Populations grown in 1973 and 1974 were designated as A through D and 1 through 4, respectively. In 1973, 381, 207, 50 and 34 families were grown in populations A through D, respectively; whereas in 1974, 98, 99, 100 and 98 families were grown in populations 1 through 4, respectively.

Each family was represented by a 3-row plot, 5.6 meters long with a row spacing of 0.15 meters. Individual plots were separated by 0.60 meters. The seeding rate was 750 seeds per plot. Every seventh plot in the nursery was sown to the check cultivar 'Rosner'.

Ten selectors in 1973 and eleven selectors in 1974 were chosen to visually select within each of the populations. They were instructed to score those lines which they estimated were equal to or higher yielding than the nearest check plot. Selectors in 1973 consisted of three plant breeders (experienced), four graduate students (novice), one Postdoctoral Fellow (novice) and two summer students (inexperienced). In 1974, the selectors comprised three plant breeders, five graduate students and three summer students. If a selector was involved both years, his identification number was maintained so that his performance could be followed for the two-year period.

Each population in 1973 and 1974 was tested for deviations from normality when yield was expressed as a percentage of the nearest check. Where significant deviations occurred due to skewness, tests for normality were conducted on plot yield minus check yield, or the transformation $\log \text{plot yield} - \log \text{check yield}$. Regardless of the method used to express yield, the ability of selectors to select lines equal to or greater than the nearest check versus purely random sampling, was tested using a contingency chi-square for independence.

The efficiency of the individual selectors was determined by the formula $R = i\sigma_p h^2$ (Falconer, 1960) where R equals the response to selection, σ_p is the standard deviation of the populations, i the intensity of selection in terms of deviations from the mean (i values

were estimated from Fig. 11.3, page 193, Falconer, 1960) and $\underline{h}^2$ (heritability) the efficiency of the selector. Overall mean response and efficiency comparisons were based on a one-way analysis of variance utilizing Duncan's multiple range test ($P=0.05$).

In 1974, the selectors were also requested to select the twenty top yielding lines in each of the four populations. The results of individual selectors were compared with random sampling by means of a contingency chi-square for independence. The mean responses and efficiencies of selectors were compared by means of one-way analysis of variance to determine if differences occurred between selectors while selecting at equal intensities of selection.

Results

Using the check plots for yield estimation, selectors were generally able to visually select a significantly greater number of lines with yields equal to or greater than the nearest check plot relative to random sampling ($P < 0.05$ or $P < 0.01$) (Tables 3 and 4). However, in the two small populations (C and D) in 1973 only the group of experienced and novice selectors included individuals whose selections were superior to random sampling ($P < 0.05$).

Similar results were found in the 1974 tests when selectors' ability to select the top ten lines in each population, at a selection intensity of approximately 20 percent, was compared to random selection (Table 5). Differences again were found in the selecting ability between the more experienced and inexperienced selectors when limited to an equal intensity of selection. The results of the experienced selectors were superior to a random sample ($P < 0.05$ or $P < 0.01$) in populations 1

Table 3. Chi-square analysis of the proportion of lines selected as $\geq$ the nearest check (1973).

Selector	Pop'n. A		Pop'n. B		Pop'n. C		Pop'n. D	
	Selected $\geq$ check	χ^2	Selected $\geq$ check	χ^2	Selected $\geq$ check	χ^2	Selected $\geq$ check	χ^2
Plant Breeder								
1	35	66.438**	36	17.841**	4	0.526	2	0.011
2	23	51.878**	17	12.586**	4	5.590*	5	3.752
3	24	34.070**	12	10.758**	2	0.299	5	3.752
Novice								
5	36	21.775**	33	7.982**	9	6.584*	6	1.471
7	29	48.798**	22	12.520**	2	0.955	6	2.878
8	30	52.763**	21	2.747	2	0.955	2	0.938
9	32	73.811**	6	0.906	3	1.663	2	0.531
10	34	53.546**	22	14.062**	4	2.437	7	5.440*
Inexperienced								
4	43	43.590**	30	5.505*	5	0.178	9	3.219
6	36	25.030**	32	14.962**	5	1.629	4	0.202

* $P < 0.05$.

** $P < 0.01$.

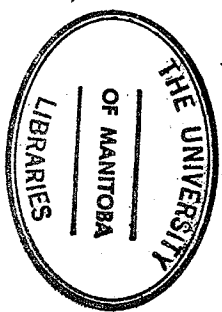


Table 4. Chi-square analysis of the proportion of lines selected as $\geq$ the nearest check (1974).

Selector	Pop.'n. #1		Pop'n. #2		Pop'n. #3		Pop'n. #4	
	Selected $\geq$ check	χ^2	Selected $\geq$ check	χ^2	Selected $\geq$ check	χ^2	Selected $\geq$ check	χ^2
Plant Breeder								
1	2	4.787*	2	2.923	7	33.095**	3	2.328
2	4	13.369**	7	16.168**	7	33.095**	13	23.123**
3	2	25.438**	14	25.540**	10	30.826**	22	26.083**
Novice								
5	5	17.723**	9	16.008**	7	15.320**	11	7.869**
7	4	10.698**	8	41.823**	5	9.782**	12	13.087**
8	5	8.439**	8	14.939**	11	25.215**	10	7.517**
11	3	1.420	4	1.613	8	12.291**	17	29.964**
14	5	6.889*	13	15.954**	10	16.787**	25	20.075**
Inexperienced								
4	10	6.646*	5	4.409*	7	12.085**	10	2.387
12	7	4.379*	14	11.031**	11	11.150**	20	6.049*
13	7	2.067	12	6.946*	11	6.790*	21	4.760*

* $P < 0.05$.

** $P < 0.01$.

Table 5. Chi-square analysis of the proportion of the top ten lines selected visually at an intensity of 20% (1974).

Selector	Pop'n. #1		Pop'n. #2		Pop'n. #3		Pop'n. #4	
	Selected top 10	X ²	Selected top 10	X ²	Selected top 10	X ²	Selected top 10	X ²
Plant Breeder								
1	5	4.146*	7	13.848**	8	21.007**	6	8.204**
2	8	20.433**	8	18.305**	8	21.007**	6	8.204**
3	7	13.627**	7	13.848**	7	14.063**	5	4.146*
Novice								
5	6	8.204**	7	13.848**	8	21.007**	5	4.146*
7	8	20.433**	7	13.848**	4	1.562	6	8.204**
8	6	8.203**	6	8.355**	7	14.063**	4	1.162
11	5	4.146*	9	28.972**	5	4.341*	4	1.162
14	6	8.202**	8	18.305**	7	14.063**	4	1.162
Inexperienced								
4	7	13.633**	6	8.355**	6	8.507**	2	0.105
12	4	1.162	4	1.511	2	0.173	4	1.162
13	4	1.162	4	1.511	7	14.063**	5	4.146*

* P < 0.05.

** P < 0.01.

through 4. Novice selectors working in populations 1 and 2 retained a higher number of superior families than a random sample, however, in populations 3 and 4, only six of the total of eleven selectors selected on a non-random basis ($P < 0.05$ or $P < 0.01$). In the inexperienced group, only one selector in populations 1, 2 and 4 and two selectors in population 3 retained a greater number of superior lines than would have been retained by random sampling ($P < 0.05$ or $P < 0.01$).

The mean response to selection by all groups of selectors was superior to a random sample at $P=0.05$ (Tables 6 and 7). In 1973 and 1974, the selector with the greatest mean response was experienced while the selector with the poorest response was inexperienced (Tables 6 and 7). In both years, the lowest ranked experienced and novice selectors were not superior to the inexperienced selectors. In 1974, the highest ranked inexperienced selector was not significantly different from the highest ranked experienced selector ($P=0.05$) when selecting lines estimated (visually) to be greater than or equal to the nearest check.

Similar results were found when selector responses were adjusted according to intensity of selection ($h^2 = R/i\sigma_p$) in 1973 and 1974 (Tables 8 and 9). In both years, selectors with the highest and lowest mean efficiencies were experienced and inexperienced, respectively. In 1973, the experienced selector with the lowest efficiency was not superior ($P=0.05$) to the inexperienced selectors, nor was the inexperienced selector with the highest efficiency significantly lower than the highest ranking experienced selector. In 1974, however, complete categorization of selector groups occurred. All three of the experienced

Table 6. Comparison of the response to selection when selecting lines estimated (visually) to be $\geq$ the yield of the nearest check plot (1973).

Selector	Rank	Experience	R pop'n. A ξ (g)	R pop'n. B (g)	R pop'n. C (g)	R pop'n. D (g)	Mean R
2	1	Plant breeder	285.890	189.938	366.980	286.200	282.252 a [†]
3	2	Plant breeder	194.717	231.378	292.713	268.400	246.801 ab
9	3	Novice	277.383	94.980	329.380	279.000	245.186 ab
10	4	Novice	215.009	167.223	239.380	247.000	217.153 abc
7	5	Novice	207.831	119.757	268.713	159.286	188.897 abcd
8	6	Novice	202.404	105.979	214.380	201.200	183.491 abcd
4	7	Inexperienced	136.229	118.753	208.309	165.417	157.177 bcde
1	8	Plant breeder	214.386	127.646	191.756	37.000	142.697 cde
5	9	Novice	111.208	88.952	141.102	127.375	117.159 de
6	10	Inexperienced	128.670	67.677	39.780	53.500	72.407 e
15	11	Random	-22.067	7.673	-58.245	-49.167	-30.451 f

[†] Duncan's multiple range test at $P=0.05$; values followed by the same letter are not significantly different.

ξ Response to selection.

Table 7. Comparison of the response to selection when selecting lines estimated (visually) to be $\geq$ the yield of the nearest check plot (1974).

Selector	Rank	Experience	R pop'n. #1 ξ (log)	R pop'n. #2 (log)	R pop'n. #3 (log)	R pop'n. #4 (log)	Mean R
1	1	Plant breeder	0.589	0.702	0.440	0.268	0.499 a [†]
2	2	Plant breeder	0.426	0.676	0.399	0.267	0.442 ab
7	3	Novice	0.392	0.761	0.319	0.193	0.416 ab
5	4	Novice	0.454	0.432	0.372	0.185	0.361 ab
8	5	Novice	0.334	0.481	0.263	0.166	0.311 abc
3	6	Plant breeder	0.371	0.365	0.309	0.171	0.304 abcd
11	7	Novice	0.309	0.488	0.205	0.178	0.295 abcd
4	8	Inexperienced	0.305	0.392	0.300	0.726	0.267 abcd
14	9	Novice	0.293	0.325	0.276	0.114	0.252 bcde
12	10	Inexperienced	0.163	0.139	0.067	0.094	0.116 cde
13	11	Inexperienced	0.095	0.181	0.071	0.056	0.101 de
15	12	Random	-0.119	0.093	-0.115	-0.150	-0.043 f

[†] Duncan's multiple range test at $P=0.05$; values followed by the same letter are not significantly different.

ξ Response to selection.

≥ the yield of the nearest check plot (1973).

Selector	Rank	Experience	h^2 pop'n. A	h^2 pop'n. B	h^2 pop'n. C	h^2 pop'n. D	Mean h^2
2	1	Plant breeder	0.732	0.505	0.712	0.612	0.639 a [†]
10	2	Novice	0.635	0.478	0.532	0.657	0.576 ab
4	3	Inexperienced	0.499	0.413	0.616	0.757	0.571 ab
3	4	Plant breeder	0.522	0.530	0.538	0.549	0.535 ab
9	5	Novice	0.743	0.214	0.639	0.468	0.516 ab
8	6	Novice	0.583	0.330	0.421	0.430	0.441 ab
7	7	Novice	0.570	0.344	0.469	0.361	0.436 ab
1	8	Plant breeder	0.625	0.457	0.478	0.071	0.408 b
5	9	Novice	0.418	0.335	0.465	0.317	0.384 bc
6	10	Inexperienced	0.453	0.112	0.103	0.121	0.197 c
15	11	Random	-0.067	0.023	-0.127	-0.109	-0.070 d

[†] Duncan's multiple range test at $P=0.05$; values followed by the same letter are not significantly different.

Table 9. Comparison of selector efficiencies ($h^2 = R/i\sigma p$) when selecting lines estimated (visually) to be $\geq$ the yield of the nearest check plot (1974).

Selector	Rank	Experience	h^2 pop'n. #1	h^2 pop'n. #2	h^2 pop'n. #3	h^2 pop'n. #4	Mean h^2
2	1	Plant breeder	0.666	0.876	0.757	0.796	0.774 a [†]
3	2	Plant breeder	0.782	0.725	0.749	0.749	0.751 a
1	3	Plant breeder	0.766	0.664	0.821	0.537	0.697 a
5	4	Novice	0.752	0.659	0.770	0.579	0.691 a
8	5	Novice	0.671	0.686	0.714	0.483	0.686 a
7	6	Novice	0.627	0.916	0.588	0.592	0.681 a
14	7	Novice	0.591	0.461	0.784	0.613	0.612 ab
11	8	Novice	0.574	0.488	0.449	0.617	0.596 abc
4	9	Inexperienced	0.488	0.525	0.639	0.233	0.426 bcd
12	10	Inexperienced	0.531	0.381	0.245	0.504	0.415 cd
13	11	Inexperienced	0.386	0.449	0.298	0.334	0.367 d
15	12	Random	-0.039	0.153	-0.279	-0.105	-0.068 e

[†] Duncan's multiple range test at $P=0.05$; values followed by the same letter are not significantly different.

Table 10. Comparison of selector efficiencies ($h^2 = R/iop$) when selecting lines estimated (visually) to be within the top 20% (yield) of each population (1974).

Selector	Rank	Experience	h^2 pop'n. #1	h^2 pop'n. #2	h^2 pop'n. #3	h^2 pop'n. #4	Mean h^2
3	1	Plant breeder	0.729	0.819	0.741	0.705	0.749 a [†]
2	2	Plant breeder	0.775	0.728	0.699	0.671	0.418 ab
1	3	Plant breeder	0.802	0.657	0.744	0.653	0.714 ab
7	4	Novice	0.651	0.772	0.708	0.653	0.696 ab
5	5	Novice	0.655	0.683	0.804	0.609	0.688 ab
14	6	Novice	0.579	0.682	0.726	0.640	0.657 ab
8	7	Novice	0.666	0.766	0.614	0.352	0.599 ab
11	8	Novice	0.559	0.724	0.345	0.677	0.576 ab
4	9	Inexperienced	0.721	0.489	0.663	0.311	0.546 b
13	10	Inexperienced	0.217	0.404	0.410	0.328	0.339 c
12	11	Inexperienced	0.303	0.396	0.109	0.518	0.331 c
15	12	Random	-0.039	0.277	-0.149	-0.073	0.004 d

[†] Duncan's multiple range test at $P=0.05$; values followed by the same letter are not significantly different.

Table 11. Comparison of the mean yields of the top twenty lines in each population and twenty lines selected (visually) by individual selectors (1974).

Selector	Experience	Pop'n. #1		Pop'n. #2		Pop'n. #3		Pop'n. #4	
		Rank	Mean (log)	Rank	Mean (log)	Rank	Mean (log)	Rank	Mean (log)
Yield trial		-	0.030	-	0.172	-	0.036	-	0.197
1	Plant breeder	1	-0.021	7	-0.091*	3	-0.029	4	0.091
2	Plant breeder	2	-0.035	3	-0.039	7	-0.049	3	0.097
3	Plant breeder	3	-0.058	1	0.014	4	-0.030	1	0.108
4	Inexperienced	4	-0.062	9	-0.199*	8	-0.065	11	-0.020**
5	Novice	6	-0.095	5	-0.074	1	-0.002	7	0.077*
7	Novice	7	-0.097	2	-0.017	6	-0.045	5	0.091
8	Novice	5	-0.089	8	-0.118	2	-0.019	9	-0.007**
11	Novice	9	-0.143	4	-0.048	9	-0.153*	2	0.099
12	Inexperienced	10	-0.271**	11	-0.260**	11	-0.311**	8	0.050**
13	Inexperienced	11	-0.314**	10	-0.250**	10	-0.177**	10	-0.013**
14	Novice	8	-0.133	6	-0.075	5	-0.037	6	0.090*
	L.S.D. (P = 0.05)		0.178		0.253		0.137		0.107
	L.S.D. (P = 0.01)		0.235		0.333		0.183		0.141

* Significantly different from the mean yield of the top twenty lines (P=0.05).

** Significantly different from the mean yield of the top twenty lines (P=0.01).

selectors were superior to the inexperienced category ($P = 0.05$) moreover, all selector categories were significantly superior to the random sample ($P = 0.05$) in terms of selector efficiency.

Comparison of the selector efficiencies when selecting at 20 percent showed that efficiency rankings corresponded to the selector categories in 1974 (Table 10). In this case however, only the highest ranking experienced selector was significantly superior to the highest ranking inexperienced selector ($P = 0.05$). The random sample was significantly lower than all selector categories at $P = 0.05$.

Comparison of the mean yield of the top twenty lines (yield) in each population with the mean yield of lines selected by individual selectors indicated the superiority of the more experienced groups (Table 11). The mean yield of the top twenty lines selected (visually) by each of the experienced selectors did not deviate significantly from the mean yield of the top twenty lines selected by the yield trial in populations 1, 3 and 4 (LSD at $P = 0.05$ or $P = 0.01$). In population 2, two of the three selector mean yields did not deviate significantly from the mean yield of the top twenty lines selected on the basis of yield.

Discussion

In the past, the triticale breeding program at the University of Manitoba has involved an early generation yield trial as suggested by Shebeski (1967). Unfortunately, this method and modifications of it required the utilization of large quantities of land and labor. Consequently, any method which reduces land and labor requirements without an accompanying loss of efficiency would be welcomed in a

breeding program.

The results in 1973 and 1974 indicated that visual selection was in general significantly superior to random sampling in triticales. However, the ability to select lines greater than or equal to a check variety may depend on the populations evaluated (i.e. population variability). A small population sample size made evaluation more difficult and consequently may have increased the probability that selection appeared random in population 3 and 4 (1973).

Results of the present study are in contrast to results from previous studies conducted on this subject. Townley-Smith et al. (1973) concluded that no relationship occurred in wheat between experience and the ability to visually identify high yielding families in an F_3 early generation yield trial.

It would appear that experienced selectors with the ability to determine yield differences were more efficient than novice or inexperienced selectors in 1973 and 1974, whether selecting at comparable intensity levels or different ones. As a consequence, the more experienced selectors misclassified less of the low yielding lines than the less experienced selectors. This is more clearly shown when the selectors were selecting at equal intensities in 1974. In this case, selectors in the experienced category had the highest mean efficiencies, the novices were intermediate and the inexperienced selectors had the lowest efficiencies.

Observation of the response to selection showed that even the least experienced selector was superior at selecting higher yielding

lines than the random sample used, whether selecting lines greater than or equal to the check, or estimating the top twenty lines in each population. In addition, the plant breeders (experienced) and graduate students (novice) in general had a mean yield not significantly different from the yield trial when visually selecting the top 20 percent of the lines in each of the populations. Briggs and Shebeski (1970) found similar results but indicated that the ability to select the absolute highest yielding lines was limited. Similarly, Mundel (1972) found that lines selected visually in wheat were only slightly lower yielding than lines selected on the basis of plot yield.

It appears that visual selection may be a useful means of advancing triticales populations in terms of mean yield. At the present state of development in triticales, classical pedigree selection may be a means of selecting families and lines within families which have a high yield potential. However, to avoid misclassification of high yielding segregates, selection should not be conducted at a restrictively high level of intensity.

MANUSCRIPT III

A COMPARISON OF EARLY GENERATION (F_3) AND
PEDIGREE SELECTION METHODS IN HEXAPLOID TRITICALE

A COMPARISON OF EARLY GENERATION (F_3) AND
PEDIGREE SELECTION METHODS IN HEXAPLOID TRITICALE

Abstract

During the summer of 1974, four F_3 hexaploid triticales (X Triticosecale Wittmack) populations were evaluated for yield in an F_3 early generation yield nursery, involving systematically placed check plots, and concurrently in a headrow nursery. Ten high yielding, ten low yielding and ten random families along with ten families selected visually for yield in the headrow nursery were retained for further evaluation. Bults produced from each of the four selection groups in each population were compared in a 10-replicate yield trial at Glenlea and Carman, Manitoba during the summer of 1975 and in a 4-replicate yield trial at CIANO, Mexico during the winter of 1975-76. Yield comparisons at each location and over the two Manitoba locations combined were based on a fixed-effects factorial model. In addition, selection bults were compared for tiller production, test weight, 200-kernel weight, numbers of spikelets per spike, kernels per spike and kernels per spikelet at the two Manitoba locations. Combined analyses at each location and over the two Manitoba locations indicated that no significant difference occurred between bults produced from high yielding lines selected by the early generation yield trial and the headrow nursery. Both bults were superior to the random bults at all locations. Bults produced from the headrow selections had a significantly higher number of spikelets per spike than all other selection bults. The present results indicate that pedigree and early generation selection are equally efficient methods for yield selection.

Introduction

In a review of plant breeding methods in use throughout the world, Shebeski (1967) concluded that many were based on tradition rather than on the utilization of modern day concepts. Accordingly, he proposed a system of early generation yield testing involving systematically placed control plots. With this system, superior plots would be identified either by their plot yield in grams, or yield expressed as a percentage of the nearest check plot.

Salmon (1914) indicated that the use of check plots was advantageous in detecting variation due to soil heterogeneity but that they should not be used in place of replication for correcting plot yields. In contrast, Pritchard (1916) found that check rows in sugar beets were inadequate when used to compensate for variability caused by soil heterogeneity.

Yates (1936) and Baker and McKenzie (1967) stated that the use of control plots was a questionable practice on the basis of theoretical considerations unless an analysis of covariance was used rather than an analysis of variance. This was in agreement with Milton and Finkner (1967) who reported that check plots were advantageous in studies involving qualitative traits in alfalfa but found tests analysed by means of covariance to be more reliable. In that study, efficiency increases of 38 percent to 528 percent were found when both checks and replicates were used.

In 1953, Raeber and Weber reported that the greatest yield advance could be made by a combination of early generation selection and pedigree selection. They suggested that wherever possible, lines should be tested in a replicated F_3 yield test and simultaneously selected for

superior plants in a space-planted nursery.

Results of recent studies conducted in soybeans have supported the use of either early generation or pedigree selection methods. Recently, Cooper (1976) indicated that early generation selection, based on F_2 -derived F_3 and F_4 families, identified the most promising crosses and the best heterogeneous lines within crosses. However, Leudders et al. (1973) testing early generating selection, bulk and pedigree selection methods found no significant differences in mean yield of lines in the F_6 and F_7 which had been selected by either of these methods in the F_4 and F_5 . However, they found that early generation and bulk selection methods retained a greater number of high yielding lines than pedigree selection in soybeans.

Recent studies in wheat by DePauw (1970) and Briggs and Shebeski (1971) have indicated a lack of agreement between F_3 line yield and subsequent yield in the F_5 generation. They found however, on the basis of broad sense heritabilities, that early generation selection was effective in identifying lines superior for bread-making quality.

Seitzer (1974) compared early generation selection techniques which were based on replicated hill plots and a F_3 contiguous yield trial with concomitant pedigree selection. No significant difference was found in the F_5 generation, in terms of yield between the hill plot and contiguous methods of early generation selection and pedigree selection. However, he concluded that the contiguous method may be most beneficial when dealing with crosses of low yield potential.

To date, segregating populations of triticale (X Triticosecale Wittmack) have been handled by a variation of the early generation method suggested by Shebeski (1967). Gustafson (personal communication)

has proposed that obvious morphological deficiencies (i.e. fertility, spikelets per spike, etc.) may allow the use of visual selection techniques employed in the pedigree system. This statement is supported by Qualset et al. (1969) who found that one of the most obvious differences between high and low yielding triticales was reflected by a high variability in fertility. More recently, Lorenz (1974) has indicated that triticales also have a high degree of variability in characters such as head length and tillering capacity.

The use of early generation selection requires a large amount of land for evaluating a relatively small number of crosses and their progenies. The pedigree system on the other hand, has the potential for carrying a large number of crosses and their progenies through a breeding program. For these reasons, the present study was initiated to compare the effects of pedigree and early generation selection on yield and yield related components.

Materials and Methods

In 1973 four triticale populations of diverse origin, designated as 1 through 4, were sown in a space-planted nursery at the CIANO Research Station, Cd. Obregon in northwestern Mexico (Fig. 1). Single plants were selected which produced sufficient seed for both a 3-row F_3 yield plot (5.6 meters long, with a row spacing of 0.15 meters) and two headrows (3 meters in length). All plants were discarded which were late in maturing or which exhibited signs of aneuploidy.

In 1974, 98, 99, 100 and 98 families from populations 1 through 4 respectively, were sown in 3-row plots (250 seeds per row) at Winnipeg. Individual plots were separated by 0.60 meters to reduce interplot

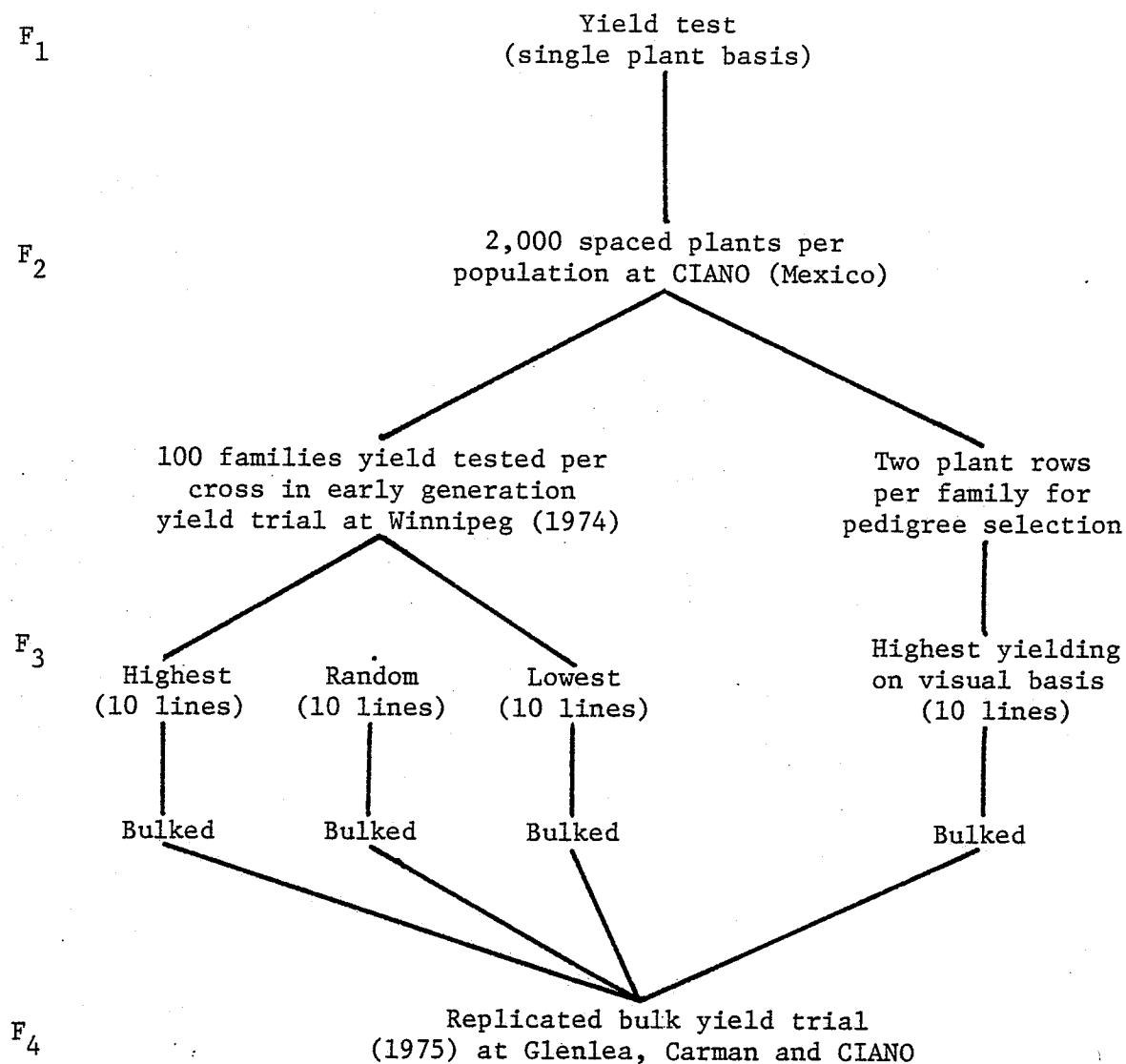


Figure 1. A schematic presentation of the advance of generations for the comparison of the pedigree and (F_3) early generation selection methods.

competition. Every seventh plot was seeded to the check variety 'Rosner'; similarly, every eleventh row of the headrow nursery was seeded to this same check variety. Headrows were seeded at a rate of 40 seeds per row.

The yield of each plot was expressed initially as a percentage of the nearest check. Using this basis for yield determination, each population was tested to determine if deviations from normal distributions occurred due to skewness. Where deviations occurred, F_3 analyses of variance were conducted on the basis of the transformation $\log \text{plot} \text{ minus } \log \text{check}$.

The ten highest yielding, the ten lowest yielding, also a random sample of ten families (yield as a percentage of the nearest check) in each population of the F_3 yield trial were retained for further evaluation. In addition, five superior plants were selected from ten of the best headrows (visual evaluation) in the F_3 . The average F_3 yield of each selection group within each population was compared by means of one-way analysis of variance. Within each population, a bulk was produced from each of the selection groups (Fig. 1).

In 1975, the four selection group bulks within each population were compared using a 10-replicate randomized complete block design at Glenlea and Carman, Manitoba. In addition, a 4-replicate yield trial was grown at CIANO during the winter of 1975-76. In Manitoba, individual bulks were grown in 3-row plots, 3 meters long with a row spacing of 0.15 meters. At CIANO, bulks were grown in 4-row plots, 3 meters long with 0.30 meters row spacing. Seeding rate was 50 kernels per row at Glenlea and Carman, whereas at CIANO the seeding rate was 40 kernels per row.

Prior to harvesting, a meter length was sampled from the center

row of 5-replicate plots in each treatment and population combination to determine the number of tillers per plant at Glenlea and Carman. A spike was retained from the primary tiller of each of five plants within each meter to determine the mean number of spikelets per spike, kernels per spike and kernels per spikelet. Two hundred-kernel weight and kilograms per hectoliter were obtained from bulk seed of the same five replicates after harvest. The treatment yield was determined on the basis of ten replicates.

Two-way analysis of variance was used to evaluate treatment differences in terms of yield and yield components within populations prior to combined analysis within each location and subsequently over both Manitoba locations. Combined analyses were conducted on the basis of a fixed-effects factorial model. Overall comparison of treatment group mean yields was based on single degree of freedom F-tests. Comparisons tested were: 1) yields from bulks of the headrows versus the bulks of the top ten families in each population in the F_3 early generation yield trial; 2) combined yields of the headrow and top ten F_3 yield trial bulks versus the yield of the random bulk; and 3) yield of the bulk produced from the lowest ten families in the F_3 early generation yield trial versus the combined yield of all other bulks. Duncan's multiple range test ($P = 0.05$) was used to evaluate the effects of selection on yield components in both individual and combined analyses.

Results

Yield

Observation of the degree of concurrence between selection on the

basis of yield and visual evaluation indicated little similarity between the two methods. Of 40 lines identified by each method as being the highest yielding, 13 were in common to both; three from population 1, five from population 2, four from population 3 and one from population 4. All populations showed a significant deviation from normality when yield was expressed as a percentage of the check. Results of the analyses of variance, based on the log plot minus log check transformation, indicated that the F_3 mean yield of the lowest ten families and the highest ten families (percentage of the check) deviated significantly ($P=0.05$) from the mean yield of the random sample (Table 12). F_3 families selected on the basis of headrow appearance yielded significantly superior to the random sample in populations 1 and 2 ($P=0.05$).

Results of individual analyses of variance conducted on selections grown at Glenlea in 1975 indicated that in populations 1 and 2, only bulks produced from the highest ten families in the F_3 were superior to a random sample at $P=0.05$ (Table 13). In population 4, the bulk formed from the lowest yielding ten families in the F_3 yield trial was the highest yielding at Glenlea, although differences were not significant.

At Carman (Table 13), both the headrow and the top ten family bulks were superior ($P=0.05$) to the random sample in population 1. In populations 2 and 3, the bulks from families selected as the lowest yielding in the F_3 early generation yield trial were significantly lower yielding ($P=0.05$) than the random bulk.

Individual analyses of the yields of the four populations in a 4-replicate test at CIANO indicated that both the headrow and top ten family bulks were significantly ($P=0.05$) higher yielding than the random sample (Table 13) in populations 1 and 2. In population 3, the

Table 12. Comparison of the mean F_3 plot yields of lines selected for the comparison of pedigree and (F_3) early generation selection.

Treatment	Pop'n. #1		Pop'n. #2		Pop'n. #3		Pop'n. #4	
	Mean % check ξ	Mean (log) $\S$	Mean % check	Mean (log)	Mean % check	Mean (log)	Mean % check	Mean (log)
Lowest ten	39.18	-0.9856 a [†]	28.75	-1.2146 a	38.37	-0.9125 a	58.60	-0.5387 a
Random ten	63.80	-0.5636 b	71.63	-0.4204 b	73.48	-0.3426 b	93.35	-0.0914 b
Headrow	87.30	-0.2171 c	114.48	0.0608 c	85.90	-0.2221 b	93.08	-0.0931 b
Highest ten	118.72	0.1663 d	140.42	0.3260 d	115.14	0.1380 c	130.89	0.2675 c

[†] Duncan's multiple range test at $P=0.05$; values followed by the same letter are not significantly different.

ξ Mean when plot yield was expressed as a percentage of the nearest check plot.

$\S$ Mean when plot yield was expressed as log plot minus log check plot yield in grams.

Table 13. Comparison of the mean yields (g) of pedigree and early generation selection bulks within individual populations at Glenlea, Carman and CIANO (Mexico).

Population	Treatment	Location		
		Glenlea	Carman	CIANO
1	Lowest ten	146.1 a [†]	124.7 a	426.7 a
	Random ten	182.0 a	107.7 a	445.7 a
	Headrow	206.2 ab	169.2 b	573.2 b
	Highest ten	255.0 b	168.1 b	563.5 b
2	Lowest ten	144.0 a	92.0 a	473.2 a
	Random ten	194.8 ab	180.9 b	512.0 a
	Headrow	256.3 bc	218.1 b	631.5 b
	Highest ten	272.4 c	193.7 b	668.7 b
3	Lowest ten	168.5 a	91.2 a	338.5 a
	Random ten	167.5 a	154.2 b	437.0 b
	Headrow	192.3 a	185.5 b	583.0 c
	Highest ten	199.0 a	173.0 b	497.2 b
4	Lowest ten	299.2 a	240.7 a	494.0 a
	Random ten	276.8 a	241.4 a	577.5 ab
	Headrow	277.0 a	265.4 a	651.3 b
	Highest ten	293.1 a	265.2 a	640.3 b

[†] Duncan's multiple range test at P=0.05; values followed by the same letter are not significantly different.

bulk produced from the lowest ten families in the F_3 early generation yield trial was significantly ($P=0.05$) lower yielding than the random bulk. At CIANO, population 4 showed no significant yield difference, based on selection group, although rankings were similar to those of other populations.

Combined analyses of population treatment effects at each of the locations (Table 14), based on a fixed-effects factorial model, indicated that no significant difference ($P=0.05$) occurred between the headrow and high yielding early generation bulks in all populations. At all locations, the random bulk was significantly lower yielding ($P=0.01$) than the headrow and early generation bulks combined. Similarly, the bulks produced from the lowest yielding lines in the F_3 early generation yield trial produced the lowest yield at all locations ($P=0.01$). Significant population differences occurred at all locations ($P=0.01$) but no significant population by treatment interactions occurred.

The results of combined analysis of the Glenlea and Carman locations showed similar significant differences ($P=0.01$) between treatments as obtained in the analysis of results at each location independently (Table 14). Significant population and location differences ($P=0.01$) occurred in the combined analysis but no significant interactions were obtained.

Yield Components

Tiller Per Plant. Comparison of treatment effects on tiller production within each population at Glenlea and Carman indicated no significant ($P=0.05$) differences between treatments (Tables 15 and 16).

Table 14. Treatment and error mean squares for single degree of freedom comparisons of early generation and pedigree selection for yield.

Comparison	Location	Comparison mean square	Error mean square
Headrow vs. top ten	Glenlea	9,614.11	4,402.04
	Carman	1,805.00	2,339.25
	CIANO	2,450.00	4,453.89
	Glenlea + Carman	1,531.40	5,497.25
Random vs. positive [§]	Glenlea	39,809.50**	4,402.04
	Carman	30,285.07**	2,339.25
	CIANO	115,232.04**	4,453.89
	Glenlea + Carman	67,426.50**	5,497.25
Low ten [§] vs. rest	Glenlea	51,875.21**	4,402.04
	Carman	95,316.03**	2,339.25
	CIANO	240,408.52**	4,453.89
	Glenlea + Carman	143,962.01**	5,497.25

[§] Combined effects of headrow and top ten early generation selections.

[§] Combined effects of headrow, top ten and random selections.

** Significant F value at P = 0.01.

Similarly, combined analysis of populations (Table 17) resulted in no significant treatment differences, although the headrow bulks had the highest mean number of tillers. At Carman on the other hand, the bulks produced from the lowest yielding lines in the F_3 yield trial had a significantly lower ($P=0.05$) mean number of tillers per plant than the random bulk in the combined population analysis. However at Carman, the headrow bulks had a significantly higher number of tillers per plant than all other selection bulks ($P=0.05$). No significant interactions or population differences occurred in the combined analyses at either Glenlea or Carman.

Combined analysis of the locations (Table 17) indicated that selection of the lowest yielding lines resulted in a significant ($P=0.05$) reduction in the mean number of tillers per plant as compared to the random bulks. In this case, the headrow bulks had a significantly higher ($P=0.05$) mean number of tillers per plant than bulks produced from either the highest or lowest yielding lines in the F_3 early generation yield trial. No significant population differences or interactions were obtained in the combined location analysis. However, the mean tiller number at Glenlea was significantly higher than at Carman ($P=0.01$).

Kilograms Per Hectoliter. Individual population analyses at Glenlea and Carman showed that selection groups had no significant effect on kilograms per hectoliter (Tables 15 and 16). Similar results were obtained when populations were combined at Glenlea (Table 17), whereas at Carman, the random bulks had a higher mean number of kilograms per hectoliter than any of the other selection groups ($P=0.05$). Significant differences ($P=0.01$) occurred between populations at both locations

Table 15. Yield component means for pedigree and early generation selection bulks within individual populations at Glenlea.

Pop'n.	Treatment	Tillers	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
1	Lowest ten	3.64 a [†]	59.02 a	6.39 a	20.72 a	34.16 a	1.63 a
	Random ten	5.50 a	57.42 a	6.86 a	23.88 a	41.72 a	1.74 a
	Headrow	4.16 a	56.62 a	6.39 a	23.38 a	33.26 a	1.39 a
	Highest ten	4.64 a	57.44 a	6.61 a	20.80 a	35.14 a	1.39 a
2	Lowest ten	4.04 a	55.34 a	6.98 a	21.70 a	31.76 a	1.39 a
	Random ten	3.78 a	52.58 a	6.94 a	19.76 a	35.78 a	1.79 a
	Headrow	3.82 a	54.22 a	7.50 a	24.74 b	41.40 a	1.66 a
	Highest ten	3.62 a	57.20 a	7.03 a	20.80 a	42.04 a	2.01 a
3	Lowest ten	4.10 a	59.44 a	7.49 a	20.70 ab	30.10 a	1.42 a
	Random ten	4.18 a	61.16 a	6.79 a	18.64 a	33.16 a	1.77 a
	Headrow	4.16 a	61.96 a	7.19 a	23.60 b	41.50 a	1.73 a
	Highest ten	3.78 a	63.20 a	7.12 a	23.18 b	35.34 a	1.52 a
4	Lowest ten	3.79 a	62.64 a	6.85 a	18.30 a	34.36 a	1.85 a
	Random ten	4.24 a	63.38 a	6.53 a	18.54 a	34.92 a	1.88 a
	Headrow	5.82 a	58.82 a	6.13 a	18.02 a	34.12 a	1.84 a
	Highest ten	5.26 a	61.62 a	5.90 a	18.68 a	35.52 a	1.90 a

[†] Duncan's multiple range at P=0.05; values followed by the same letter are not significantly different.

Table 16. Yield component means for pedigree and early generation selection bulks within individual populations at Carman.

Pop'n.	Treatment	Tillers	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
1	Lowest ten	1.80 a [†]	57.82 a	6.84 a	17.92 a	21.20 a	1.16 a
	Random ten	2.50 a	61.74 a	7.01 a	19.52 a	24.82 a	1.28 a
	Headrow	2.38 a	57.06 a	6.47 a	19.04 a	25.02 a	1.29 a
	Highest ten	2.08 a	59.50 a	6.85 a	18.86 a	31.12 a	1.64 a
2	Lowest ten	2.16 a	56.94 a	7.45 a	19.14 a	32.86 a	1.63 a
	Random ten	2.20 a	62.94 a	7.33 a	17.44 a	25.96 a	1.45 a
	Headrow	3.26 a	57.50 a	7.75 a	20.18 a	30.46 a	1.53 a
	Highest ten	1.88 a	56.00 a	7.32 a	19.78 a	25.00 a	1.27 a
3	Lowest ten	2.06 a	60.68 a	7.92 a	19.60 a	25.96 a	1.32 a
	Random ten	2.26 a	59.58 a	7.48 a	20.96 a	31.02 a	1.46 a
	Headrow	2.88 a	61.50 a	6.64 a	22.10 a	33.16 a	1.50 a
	Highest ten	2.88 a	59.34 a	7.44 a	19.96 a	31.04 a	1.57 a
4	Lowest ten	2.32 a	62.06 a	7.07 a	18.10 a	38.06 a	2.11 a
	Random ten	2.66 a	63.16 a	6.66 a	17.70 a	36.10 a	2.01 a
	Headrow	2.86 a	61.72 a	6.70 a	17.20 a	31.60 a	1.84 a
	Highest ten	2.44 a	63.72 a	6.36 a	17.62 a	32.06 a	1.80 a

[†] Duncan's multiple range test at P = 0.05; values followed by the same letter are not significantly different.

Table 17. Yield component means for pedigree and early generation selection bulks within individual locations and over the two Manitoba locations combined.

Location	Treatment	Tillers	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
Carman	Lowest ten	2.05 a [†]	59.37 a	7.33 a	18.69 a	29.52 a	1.59 a
	Random ten	2.40 b	61.86 b	7.12 a	18.90 a	29.47 a	1.56 a
	Headrow	2.84 c	59.44 a	7.15 a	19.63 a	30.08 a	1.54 a
	Highest ten	2.32 b	59.64 a	6.99 a	19.06 a	29.81 a	1.57 a
Glenlea	Lowest ten	3.89 a	59.12 a	6.94 a	20.36 a	32.59 a	1.58 a
	Random ten	4.43 a	58.64 a	6.78 a	20.21 a	36.40 a	1.81 a
	Headrow	4.49 a	57.91 a	6.80 a	22.44 b	37.57 a	1.67 a
	Highest ten	4.33 a	59.87 a	6.38 a	20.87 a	37.01 a	1.78 a
Glenlea + Carman	Lowest ten	2.97 a	57.70 a	7.14 a	19.53 a	31.06 a	1.59 a
	Random ten	3.42 bc	60.22 a	6.95 a	19.55 a	32.94 a	1.68 a
	Headrow	3.67 c	58.78 a	6.97 a	21.03 b	33.82 a	1.61 a
	Highest ten	3.32 b	59.60 a	6.68 a	19.96 a	33.41 a	1.68 a

[†] Duncan's multiple range at P=0.05; values followed by the same letter are not significantly different.

but no significant interactions were obtained in either individual or combined analyses.

Combined analysis of locations indicated no significant differences between selection groups (Table 17). No significant location differences, in terms of kilograms per hectoliter, or interactions were obtained in the combined location analysis.

Two Hundred-Kernel Weight. Comparison of selection effects on mean 200-kernel weight in each population at each location indicated no significant differences (Tables 15 and 16). Similar effects were obtained when selection bulks were compared in the combined analysis at each location and over the two locations (Table 17). Population differences ($P=0.01$) occurred at both locations and in the combined location analysis. Carman had a significantly ($P=0.01$) higher mean 200-kernel weight than Glenlea. No significant interactions were obtained when comparing selection effects on 200-kernel weight.

Spikelets Per Spike. Selection of the top ten headrows in populations 2 and 3 (Table 15) resulted in a significant ($P=0.05$) increase in spikelets per spike at Glenlea. Selection of the ten highest yielding families in population 3 also resulted in a significant ($P=0.05$) increase in spikelets per spike. At Carman however, no significant treatment differences occurred in the individual population analyses. Although the results of the combined analysis at Glenlea indicated that headrow selection resulted in a significant increase ($P=0.05$) in the number of spikelets per spike, no significant differences were obtained at Carman (Table 16). Significant population differences occurred at both locations ($P=0.05$), however, a significant

($P=0.05$) population $\times$ treatment interaction was obtained at Glenlea.

Combined location analysis (Table 17) of the effect of selection on spikelets per spike showed that selection on the basis of headrows resulted in a significant ($P=0.05$) increase in spikelets per spike. Significant ($P=0.05$) population differences were obtained in the combined analysis. At Glenlea, populations exhibited a significantly higher ($P=0.01$) mean number of spikelets per spike than they did at Carman. However, combined analysis over locations indicated that a significant ($P=0.05$) population $\times$ location interaction occurred.

Kernels Per Spike. Analysis of selection effect on kernels per spike indicated no significant differences between selection groups in the individual populations at either Glenlea or Carman (Tables 15 and 16). Similarly, no significant treatment differences occurred in the combined analysis at each location or over both locations (Table 17). A significant ($P=0.01$) population difference occurred only at Carman. Combined analysis of the two Manitoba locations resulted in no significant treatment differences. However, the Glenlea location had a higher mean number of kernels per spike than Carman ($P=0.01$). In addition, a significant ($P=0.05$) genotype $\times$ location interaction was obtained in the combined analysis.

Kernels per Spikelet. No significant difference occurred in terms of kernels per spikelet between treatments at Glenlea or Carman (Tables 15 and 16). Combined analysis at each location indicated no significant treatment differences but significant ($P=0.01$) population differences occurred at Carman. No significant treatment differences (Table 17) were obtained in the combined location analysis, however,

significant ($P=0.01$) population differences were obtained. Populations at Glenlea had a significantly ($P=0.01$) higher number of kernels per spikelet than those at the Carman location.

Discussion

Results of the present study conform with those obtained by Leudders et al. (1973), Seitzer (1974) and Boerma and Cooper (1975) comparing pedigree and early generation selection for yield. Combined analysis at each location and over the two Manitoba locations indicated that the two methods were about equally efficient in the identification of high yielding material. In addition, bulks produced from lines selected as low yielding by the early generation yield trial had a lower mean yield in the F_4 replicated yield trial than all other selections.

A common method for evaluating visual and yield plot selection has been to compare the mean yield of plots selected visually with yields from plots selected on the basis of a yield trial. Briggs and Shebeski (1971), Townley-Smith et al. (1973) and Mundel (1972) found that visual selection in an F_3 yield trial resulted in an increased yield but the yield increase was small compared to selection on the basis of plot yield. Similar results were found in the present case when the yield of F_3 lines selected in the headrows was compared to the yield of lines selected on the basis of a yield trial. In two of the populations, the mean yield of F_3 plots corresponding to selected headrows did not differ significantly from the random sample. However, in population 4, five of the top ten lines selected by the yield trial suffered water damage in the headrow nursery resulting in

a possible underestimation of true yielding ability. Although lines selected on the basis of plot yield had a significantly higher mean F_3 yield than families selected on the basis of visual criteria, the equality of the F_3 early generation yield selection and headrow selection methods in the F_4 yield trial indicated that visual selection retained high yielding segregates normally discarded on the basis of F_3 plot yield.

One major disadvantage of yield testing F_2 -derived progenies (Whitehouse, 1953) is that the number of progenies which can be tested is limited. A second criticism which should be considered is the importance of interplant competition within yield plots. Allard and Adams (1969) studying this problem in wheat and barley, found that high yielding lines of poor competitive ability suffered severe reduction in productivity in mixtures. Similarly, Khalifa and Qualset (1975) found that short-statured segregates were lost if populations of high yielding semi-dwarfs and low yielding tall-statured varieties were grown for several generations in bulks. Consequently, they concluded bulks should not be used to reduce the risk of losing desirable semi-dwarfs.

One of the major objectives in the development of triticale as a commercial crop species has been the synthesis of semi-dwarf strains (Salmon et al. 1975). Until recently, triticales emanating from the various programs throughout the world were characteristically tall and subject to lodging (Zillinsky and Borlaug, 1971). Salmon et al. (1975) noted the common occurrence of low fertility in wheat and triticale semi-dwarfs. As a consequence, rejection of lines solely on the basis of yield as in the F_3 early generation yield trial, may result in the loss of desirable semi-dwarfs. Similarly, interplant competition within F_3 yield plots may reduce the number of semi-dwarf segregates in future generations.

Meiotic instability, a common occurrence in present day triticales, is an additional factor which should be taken into account when determining when and how to select within triticales. Merker (1974) noted that high meiotic instability may result in production of aneuploids which in turn exhibit poor vigor and reduced yield. According to Merker (1974), early studies proposed that meiotic instability was directly related to poor fertility. However, studies conducted by Riley and Chapman (1957), Riley and Bell (1959), Muntzing (1966), Muntzing et al. (1963), Tsuchya (1927), Hsam and Larter (1973, 1974), Merker (1973) and Gustafson and Qualset (1975) revealed no concrete relationship between fertility and meiotic instability. Tsuchya (1972) qualified his statement by proposing that poor fertility may be related to meiotic instability when instability is severe.

In addition to natural meiotic instability in triticales containing a full complement of wheat and rye chromosomes, recent studies have shown a high frequency of wheat-rye chromosome substitution. Gustafson and Zillinsky (1973), Gustafson and Qualset (1974, 1975), Darvey and Gustafson (1975), Merker (1975), Gustafson and Bennett (1976) and Gustafson and Zillinsky (1976) have identified changes in heterochromatin content in rye chromosomes. Gustafson and Qualset (1975) concluded that crosses produced from parents differing in rye chromosomes should not be discarded on the basis of fertility in the F_1 and early generations. This could result in the loss of material which, although poor in early generations, could produce desirable segregates in subsequent generations.

As a result of trials conducted throughout California, Qualset

et al. (1969) concluded that one of the most obvious causes of low yield capacity in triticale was poor fertility. Lorenz (1974) summarizing the literature on triticale research, observed that triticale exhibited a wide degree of variability for such characters as head length and tillering capacity, as well as fertility. However, as in other cereal crops, a wide degree of variability occurs in yield components in triticale. Sethi and Singh (1972) found a strong positive correlation between tillering and yield. Gustafson (1972), Barnett et al. (1973), Gebremariam (1974) and Chen (1974) have noted a strong correlation between yielding ability, kernels per spike and kernels per spikelet. Gebremariam further indicated that tillering capacity was negatively correlated with yield but that late maturity and plant height were positively related to yield.

Based on results from combined locations in the present study, it appears that yield improvement due to visual selection was accompanied by an increase in tiller number and spikelets per spike. In this case, a significant increase was found only for spikelets per spike. Selection of the highest yielding lines in the F_3 yield trial resulted in a reduced number of tillers per plant, a reduced 200-kernel weight, reduced kilograms per hectoliter but an increase in numbers of spikelets per spike and kernels per spike. However, selection of the highest yielding F_3 lines did not result in a significant increase over random for any of the yield components. Selection of the lowerst ten lines in the yield trial resulted in reduced tillering, reduced numbers of spikelets and kernels per spike, but an increase in 200-kernel weight.

Only the reduction in kilograms per hectoliter was significant.

However, when considering these results for yield components it must be noted that analyses were conducted on either a small number of plants or replicates in each case.

Although both the F_3 yield trial and the headrow selection methods resulted in equal and significant yield increases over random selection, the two methods differed in terms of lines retained. Selection in the F_2 generation is usually conducted on the basis of single plant fertility. However, plants showing desirable agronomic characteristics but which are cytologically unstable may also be selected and included in the F_3 yield and headrow nurseries. Subsequent production of aneuploids, resulting in reduced yield (Merker, 1974) may cause these lines to be discarded on the basis of the yield trial. In cases where meiotic stability is a problem, a reduced level of selection pressure, as made possible by the use of the pedigree selection method, may be more advantageous until meiotic stability has been achieved.

MANUSCRIPT IV

THE EFFECT OF SELECTION UNDER DIVERSE ENVIRONMENTAL
CONDITIONS ON THE YIELD AND YIELD RELATED
COMPONENTS IN HEXAPLOID TRITICALE

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Abstract

During the summer of 1973, four F_3 hexaploid triticales (X Triticosecale Wittmack) populations were evaluated for yield in an F_3 early generation yield nursery involving systematically placed check plots. In each population, families yielding 25 percent greater than the nearest check plot were retained. Each family was represented in a space-planted nursery at CIANO, Mexico during the winter of 1973-74 and at Winnipeg during the summer of 1974. All families and lines within families in each population which were light insensitive at CIANO were retained for bulk evaluation. Similarly, an equal number of families and lines within families were selected for yield on the basis of visual criteria and at random at Winnipeg. Within each population, a bulk was produced from each of the insensitive, random and visual selection groups. During the summer of 1974, selection bulks were grown in a 10-replicate yield trial at Glenlea and Carman, Manitoba. In addition, selection bulks were represented in a 4-replicate yield trial at CIANO during the winter of 1975-76. Bulks were compared for yielding ability at each location and over the two Manitoba locations by a fixed-effects factorial model. Similarly, bulks were compared for test weight (kg/hl), 200-kernel weight, numbers of spikelets per spike, kernels per spike and kernels per spikelet at the two Manitoba locations (5-replicates) and at CIANO (4-replicates). In addition, bulks were compared for tillering at the two Manitoba locations. Combined analysis over the two Manitoba locations indicated that the insensitive bulks had a

significantly lower yield and test weight than the random bulks. No significant differences occurred in terms of yield between bulks at CIANO. However, the insensitive bulks had a significantly higher 200-kernel weight but a lower number of spikelets per spike than either the random or visual bulks in the combined analysis. These results indicated that valuable high yielding triticale lines may be lost due to selection for light insensitivity in early generations.

Introduction

The first large scale triticale (X Triticosecale Wittmack) breeding program on the North American continent was initiated at the University of Manitoba in 1954. In 1964, a cooperative program was established with CIMMYT (International Center for Maize and Wheat Improvement) in Mexico. This program has facilitated the selection of triticale lines under two widely diverse environments.

Lebsock et al. (1973) noted that most spring wheats developed in the northern latitudes have a long-day requirement and consequently have limited adaptation to other parts of the world either as commercial varieties or as parental stocks. Similarly, many of the early primary and secondary triticales produced at the University of Manitoba are sensitive to short-day conditions (Qualset et al. 1969). In contrast, however, Krull et al. (1968) stated that problems of sensitivity to day-length have been removed from the CIMMYT breeding program by the selection of light insensitive genotypes. Intercrossing of Mexican and Canadian triticales has, consequently, allowed the incorporation of light insensitivity in triticales being produced at the University of Manitoba.

With the development of an F_3 early generation yield testing system by Shebeski (1967), the utilization of winter nurseries in northwestern Mexico has become an important means of rapid advancement from hybridization to preliminary yield testing in both the wheat and triticale programs at the University of Manitoba. Up to the present time, both F_2 and F_4 space-planted nurseries were grown at the CIANO Research Station, Cd. Obregon, during the winter months. It has

generally been considered that selection is random for yield but two types of selection may be occurring: 1) selection of plants sufficiently mature for harvesting in March at CIANO for planting at Winnipeg in May; and 2) selection of plants which will produce sufficient viable seed for a single test plot 5.6 meters long (750 kernels). Consequently, lines selected for yield testing in Canada contain a high proportion of light insensitive genotypes.

Studies conducted on common wheats have shown that a large proportion of the genotype by environment interaction may be attributed to complex interactions between vernalization (genes for winter habit), temperature during early stages of development and photoperiod response. Syme (1968), Pugsley (1970), Halse and Weir (1970) and Levy and Peterson (1972) have found that vernalization of photoperiod insensitive spring wheats resulted in reduced numbers of tillers per plant and spikelets per spike. Heiner (1971) explained this phenomena on the basis that some of the common bread wheats have genes for low temperature response which when combined with light insensitivity may cause abnormally rapid development. This in turn may result in reduced tillering, shorter straw and earlier maturity than temperature responsive light sensitive genotypes. Alternatively, Hurd-Karrer (1933), Syme (1968) and Lebsack et al. (1973) proposed that a similar effect may occur if light insensitive genotypes are exposed to high atmospheric temperatures and long-day periods during early plant development.

Studies conducted on the effect of short day-length on the development of cereal crops have indicated that increased exposure to short-day conditions results in a significant increase in magnitude of

specific components. In particular, Rawson (1971) studying the effect of photoperiod on day-length sensitive wheat and triticale lines found that both species showed a dramatic increase in the number of spikelets per spike under short-day conditions. The most extreme effect was observed in the triticale line which continued to respond after the wheat lines had reached an apparent maximum number of spikelets.

Zillinsky and Borlaug (1971) also noted that a short photoperiod had a dramatic effect on the number of tillers produced by light sensitive genotypes. They observed that light sensitive genotypes required at least two weeks longer to reach maturity but produced twice as many tillers as light insensitive genotypes.

Lebsock et al. (1973) conducted a study on the yielding ability of near-isogenic light sensitive wheat lines to determine the effect of selection for light insensitivity on the yielding ability of durum wheat lines in a series of yield trials throughout the northern United States. Results indicated that sensitive and insensitive F_6 lines differed little in yielding ability when analysis was based on all locations combined. Analysis of the individual locations showed that F_6 insensitive lines yielded as high or higher than sensitive lines at two of three locations but were 40 percent lower yielding than the sensitive lines at the third location. Lebsock et al. (1973) concluded that high atmospheric temperatures, along with the long-day environment, was responsible for reduced yield at this one location. In addition, they concluded that with selection of stable lines, light insensitivity would not adversely affect the yielding ability of lines selected for testing in the northern United States.

As in many other areas of research, little information is available

on the influence of selection for light insensitivity on the yielding ability of triticale lines grown in northern latitudes. Concern has developed at the University of Manitoba that imposed selection of light insensitive types by the use of space-planted F_2 and F_4 nurseries at CIANO, Mexico may be reducing the chance of obtaining a commercially viable triticale for use in Canada. Consequently, this study was initiated to determine the influence of selection between and within high yielding F_3 -derived F_4 families selected from crosses of light sensitive and insensitive triticale lines at CIANO and Winnipeg.

Method

During the summer of 1973, four populations designated as A through D were grown in an F_3 early generation yield trial (Shebeski, 1967) at Winnipeg, Manitoba. A total of 381, 207, 50 and 34 F_2 -derived families within each population, respectively were seeded in 3-row plots, 5.6 meters in length with 0.15 meter row spacing. Plots were separated by a space of 0.60 meters. The seeding rate of all plots was 250 seeds per row. Every seventh plot was seeded to the check cultivar 'Rosner'.

Individual plot yield was expressed as a percentage of the nearest check plot yield (in grams). In each cross, lines exceeding the check variety by at least 25 percent were retained for further evaluation. A total of 10, 20, 2 and 6 families were retained from populations A through D, respectively (Fig. 2).

Each family was represented by 200 plants in a space-planted nursery at CIANO, Mexico during the winter of 1973-74 and by 100 plants in a space-planted nursery at Winnipeg during the summer of 1974.

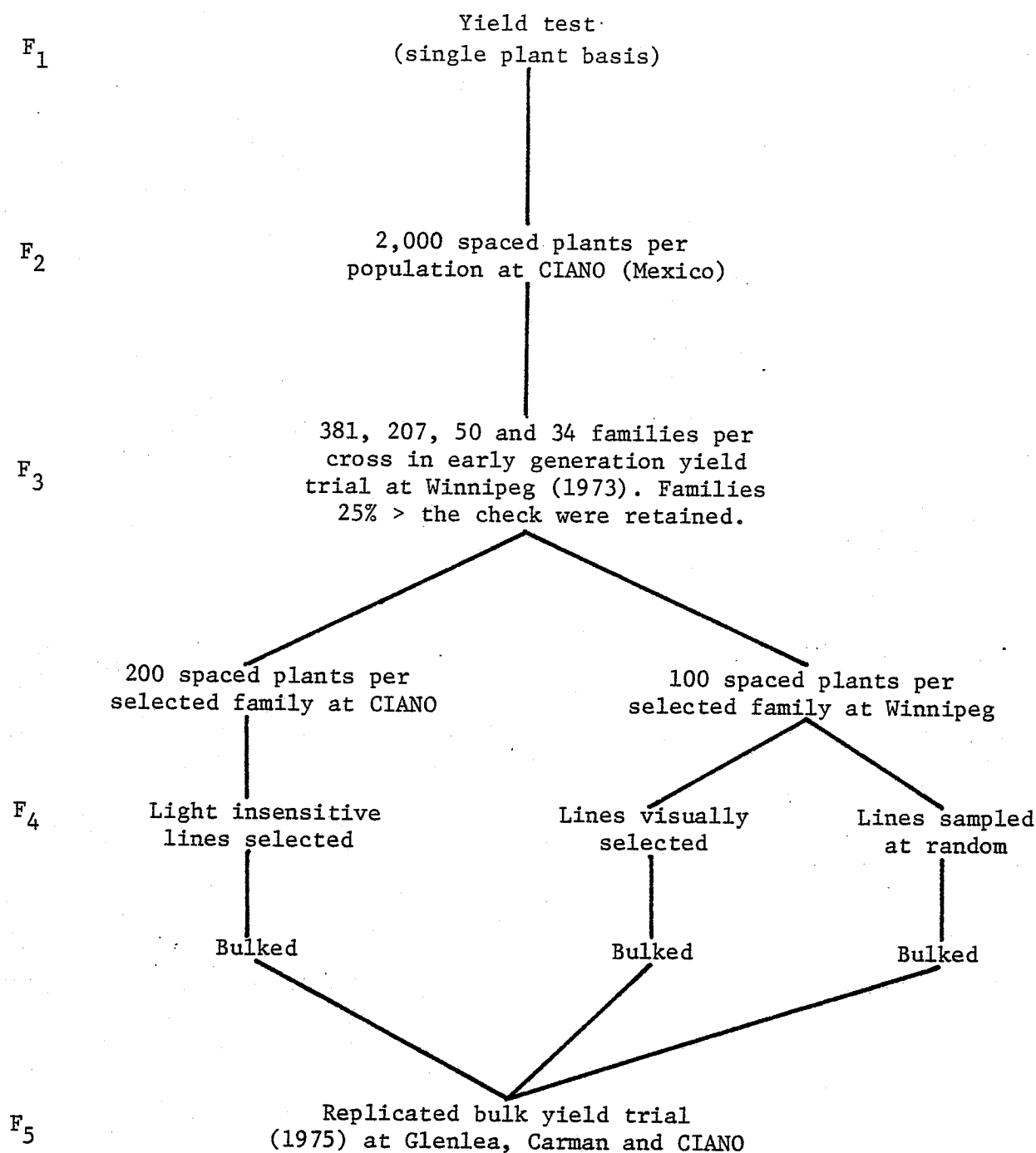


Figure 2. A schematic presentation of the advance of generations for the comparison of random, Mexican (insensitive) and Winnipeg (visual) selections.

Families were selected at CIANO which were sufficiently mature (light insensitive) to allow harvesting in the Mexican nursery (March) and planting (May) in Winnipeg and contained twenty plants with sufficient seed to produce a single plot equal in size to those used in the F_3 early generation yield trial (750 kernels). An equal proportion of lines were visually selected at Winnipeg during the summer of 1974. Within each family, ten plants were retained on the basis of desirable agronomic characteristics (fertility, tillering, etc.). In addition, within each population families were retained at random in Winnipeg. Each population was represented by a bulk population produced from the Mexican (insensitive), random and Winnipeg (visual) selection groups in a 10-replicate yield trial of randomized complete block design grown at Glenlea and Carman, Manitoba during the summer of 1975. Bulks were grown in 3-row plots, 3 meters long with 0.15 meter row spacing and 0.60 meter spacing between plots. Plots were seeded at a rate of 50 kernels per row.

A 4-replicate yield trial of the same material as tested at the two Manitoba sites was also grown at CIANO, Mexico during the winter of 1975-76. The test consisted of 4-row plots, 3 meters long with 0.30 meter plot and row spacing. The seeding rate was 40 kernels per row.

Prior to harvesting, a meter length was sampled from the center row of each plot over five replicates, in order to determine tiller number per plant at Glenlea and Carman. A head was retained from the primary tiller of each of five plants within the meter sample to determine the mean numbers of spikelets per spike and kernels per spike. Two hundred-kernel weight (in grams) and kilograms per hectoliter were obtained from bulk seed of the same five replicates after harvest. The

treatment mean yield (in grams) was determined by the harvesting of all plots in their entirety.

At CIANO, the numbers of spikelets per spike and kernels per spike were determined by sampling five plants from the outer two rows of each of the 4-replicate plots per treatment. Two hundred-kernel weight (in grams) was determined from a sample of the five plants retained per plot. Kilograms per hectoliter was measured from a sample of seed obtained from the two center rows of each plot harvested for yield determination. Mean tiller number per treatment was not determined at CIANO.

Two-way analysis of variance was used to evaluate treatments in terms of yield and yield components within populations prior to combined analysis. Combined analysis of treatment groups was conducted at each location separately, and subsequently over the two Manitoba locations by using a fixed-effects factorial model. Overall comparison of treatment groups was based on single degree of freedom F-tests. Comparisons tested were: 1) bulks from Mexican selections (insensitive) versus bulks produced from random sampling at Winnipeg; and 2) bulks produced from visual selections at Winnipeg versus the combined effects of Mexican and random bulks. Duncan's multiple range test ($P = 0.05$) was used to evaluate the effects of selection on yield components in both individual and combined analyses.

Results

Yield

No apparent difference occurred in mean F_3 yield between the F_3 -derived F_4 families which were selected either visually or at random

in Winnipeg and those selected for light insensitivity at CIANO (Table 18). In populations A and B, approximately 40 percent and 60 percent, respectively of the families grown at CIANO were discarded on the basis of height and lodging. In populations C and D, however, all families were retained at CIANO.

Individual treatment comparisons within populations at Glenlea, Carman and CIANO (Table 19) indicated in general that the F_5 bulk with the lowest yield was the light insensitive type. At Glenlea, the light insensitive selections were significantly lower yielding than the random or visual bulks ($P = 0.05$) in populations B, C and D. At Carman, the visual selections were significantly higher yielding than the random and light insensitive selections ($P = 0.05$) in populations A and B but differed only from the light insensitive bulk in population C. At CIANO on the other hand, the highest yielding bulk in populations A through C was that produced from randomly sampled families. In population D, however, the random bulk was the lowest yielding treatment in terms of rank. Although significant differences ($P = 0.05$) were found between treatments within populations at Glenlea and Carman, no significant differences were obtained between treatments at CIANO.

Combined analysis of treatment effects over populations (Table 20) showed that the light insensitive Mexican bulks were significantly lower yielding than were the random samples ($P = 0.01$ and $P = 0.05$) at Glenlea and Carman, respectively. The mean yield of the bulks produced from visually selected material was significantly higher than the combined effects of the light insensitive and random bulks

Table 18. The number, F_3 mean yields and standard errors of families (25% > the check yield) selected from the F_3 early generation yield trial and subsequently from the F_4 space-planted nurseries at CIANO, Mexico (light insensitive) and Winnipeg (random and visual).

Pop'n.	Selected F ₃ families			Selected F ₄ families						
	Number selected	F ₃ mean yield		Number selected	Mean F ₃ yield					
		% check	Plot - check (g)		Light insensitive		Random		Visual	
					% check	Plot - check (g)	% check	Plot - check (g)	% check	Plot - check (g)
A	10	140.87	304.09	6	142.45	303.16	141.05	303.17	144.27	318.83
	SE ^ξ	4.33	17.30		6.69	25.73	6.95	25.73	6.10	18.19
B	20	147.02	346.50	7	146.17	309.57	148.03	366.86	144.75	332.43
	SE	3.15	24.51		4.49	25.71	6.55	42.27	5.02	27.41
C	2	145.95	257.50	2	145.95	257.50	145.95	257.50	145.95	257.50
	SE	7.05	39.50		7.05	39.49	7.05	39.49	7.05	39.49
D	6	148.07	409.83	6	148.07	409.83	148.07	409.83	148.07	409.83
	SE	2.85	34.14		2.85	34.14	2.85	34.14	2.85	34.14

^ξ SE refers to the standard error of the mean immediately above.

Table 19. Comparison of the mean yields (g) of random, Mexican (insensitive) and Winnipeg (visual) bulks within individual populations at Glenlea, Carman and CIANO (Mexico).

Population	Treatment	Location		
		Glenlea	Carman	CIANO
A	Mexico	202.00 a [†]	168.20 a	473.00 a
	Random	224.50 a	177.30 a	514.50 a
	Winnipeg	305.10 b	232.80 b	508.00 a
B	Mexico	198.30 a	182.00 a	553.50 a
	Random	292.00 b	211.80 a	623.00 a
	Winnipeg	305.00 b	282.80 b	603.25 a
C	Mexico	229.00 a	171.60 a	515.50 a
	Random	266.30 b	191.60 ab	592.75 a
	Winnipeg	296.00 b	220.30 b	541.75 a
D	Mexico	227.80 a	166.60 a	568.00 a
	Random	272.90 b	204.70 a	473.25 a
	Winnipeg	278.40 b	180.30 a	579.00 a

[†] Duncan's multiple range test at $P=0.05$; values followed by the same letter are not significantly different.

Table 20. Treatment and error mean squares for yield comparisons of random, Mexican (insensitive) and Winnipeg (visual) selection bulks.

Comparison	Location	Comparison Mean square	Error Mean square
Mexico vs. random	Glenlea	49,252.81**	4,830.53
	Carman	11,858.45*	2,370.00
	Glenlea + Carman	54,575.00*	8,724.99
Winnipeg vs. rest ^ξ	Glenlea	86,678.00**	4,830.53
	Carman	53,700.42**	2,370.00
	Glenlea + Carman	138,278.35**	8,724.99

* Significant F value at $P=0.05$.

** Significant F value at $P=0.01$.

^ξ Rest refers to the mean of the Mexican and random bulks.

($P=0.01$) at both locations. At CIANO on the other hand, no significant difference occurred between treatments. Although significant population differences occurred only at Carman ($P=0.05$), no significant interactions were obtained at any of the three locations.

In the combined analysis of the two Manitoba locations (Table 20), the light insensitive treatment was significantly lower yielding than the random treatment at $P=0.05$. The visual treatment was significantly superior ($P=0.01$) to the combined effect of the insensitive and random treatments. The mean yield over all treatments indicated that the yield at Glenlea was significantly superior to yields at Carman ($P=0.01$). No significant interactions were found for the combined analysis over the two Manitoba locations ($P=0.05$).

Yield Components

Tillers Per Plant. Although the visual bulk had a significantly higher number of tillers per plant than the light insensitive Mexican bulk in population A at Carman ($P=0.05$), no significant differences occurred between treatments in either the remaining populations at Carman or in all populations at Glenlea (Table 21). Combined analysis at each location and over the two Manitoba locations (Table 24) indicated that no significant differences existed between populations or treatments ($P=0.05$). Glenlea-grown material was significantly higher in tiller production than material at Carman ($P=0.01$). No significant interactions occurred within each location or the combined location analysis.

Kilograms Per Hectoliter. At both Manitoba locations, the visually selected bulks and random bulks had the highest test weight (kg/hl).

Table 21. Yield component means for random, Mexican (insensitive) and Winnipeg (visual) bulks within individual populations at Glenlea.

Pop'n.	Treatment	Tillers	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
A	Random	4.24 a [†]	60.30 ab	7.37 a	16.06 a	27.90 a	1.74 a
	Mexico	3.92 a	57.22 a	7.50 a	16.38 a	31.18 a	1.90 a
	Winnipeg	3.28 a	63.04 b	7.35 a	16.80 a	36.26 a	2.06 a
B	Random	3.04 a	61.94 a	7.00 a	16.62 a	30.64 a	1.87 a
	Mexican	4.70 a	61.76 a	6.72 a	14.36 a	25.26 a	1.62 a
	Winnipeg	2.96 a	62.96 a	6.91 a	17.56 a	37.10 a	2.12 a
C	Random	4.24 a	58.72 a	6.88 a	17.90 a	39.70 a	2.08 b
	Mexican	4.14 a	54.14 a	7.53 a	18.88 a	33.80 a	1.86 ab
	Winnipeg	3.48 a	61.32 a	7.11 a	17.18 a	31.78 a	1.37 a
D	Random	2.74 a	61.78 a	6.84 a	16.96 a	31.94 a	1.87 b
	Mexican	3.36 a	59.96 a	6.76 a	17.32 a	24.38 a	1.59 a
	Winnipeg	3.36 a	63.56 a	6.54 a	17.52 a	33.82 a	1.90 b

[†] Duncan's multiple range test at P=0.05; values followed by the same letter are not significantly different.

Table 22. Yield component means for random, Mexican (insensitive) and Winnipeg (visual) bulks within individual populations at Carman.

Pop'n.	Treatment	Tillers	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
A	Random	2.20 ab [†]	54.64 a	7.83 a	14.70 a	26.12 a	1.79 a
	Mexico	1.66 a	57.48 a	7.27 a	16.18 b	22.80 a	1.42 a
	Winnipeg	2.56 b	60.04 a	7.17 a	15.46 ab	26.58 a	1.73 a
B	Random	2.24 a	60.54 ab	6.96 b	16.62 a	33.44 b	2.05 a
	Mexico	2.46 a	58.20 a	6.38 a	15.50 a	30.74 b	1.72 a
	Winnipeg	2.38 a	61.40 b	7.07 b	16.13 a	22.20 a	2.00 a
C	Random	1.80 a	59.08 b	6.98 a	16.14 a	28.38 a	2.08 b
	Mexico	1.80 a	55.80 a	6.80 a	16.58 a	32.40 a	1.86 ab
	Winnipeg	1.74 a	62.62 c	7.40 a	15.46 a	32.00 a	1.37 a
D	Random	2.66 a	61.90 b	6.49 a	16.52 a	34.28 a	1.75 a
	Mexico	2.50 a	59.56 a	6.76 a	16.10 a	26.90 a	1.97 a
	Winnipeg	2.04 a	60.00 ab	6.54 a	15.96 a	32.42 a	1.99 a

[†] Duncan's multiple range test at P=0.05; values followed by the same letter are not significantly different.

Table 23. Yield component means for random, Mexican (insensitive) and Winnipeg (visual) bulks within individual populations at CIANO (Mexico).

Pop'n.	Treatment	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
A	Random	67.03 a [†]	6.61 a	28.00 b	53.23 a	1.91 a
	Mexico	69.53 a	10.07 b	22.00 a	49.48 a	1.99 a
	Winnipeg	70.60 a	7.43 a	25.20 b	48.55 a	1.94 a
B	Random	70.83 a	7.90 b	28.60 b	44.35 a	1.54 a
	Mexico	70.47 a	8.69 b	22.40 a	60.20 a	2.73 b
	Winnipeg	71.33 a	6.79 a	28.20 b	53.63 a	1.90 a
C	Random	71.83 b	8.63 a	22.40 a	55.50 a	2.54 b
	Mexico	66.75 a	9.33 a	26.10 a	58.40 a	2.25 ab
	Winnipeg	68.68 ab	6.67 a	26.20 a	46.03 a	1.78 a
D	Random	71.10 a	8.97 a	23.80 a	59.75 a	2.52 a
	Mexico	72.01 a	9.19 a	20.80 a	55.02 a	2.70 a
	Winnipeg	71.20 a	8.82 a	22.80 a	52.75 a	2.37 a

[†] Duncan's multiple range test at P = 0.05; values followed by the same letter are not significantly different.

Table 24. Yield component means for random, Mexican (insensitive) and Winnipeg (visual) bulks within individual locations and over the two Manitoba locations combined.

Location	Treatment	Tillers	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
Glenlea	Random	3.57 a [†]	60.69 a	7.09 a	16.89 a	30.77 a	1.90 a
	Mexico	4.03 a	59.27 a	7.07 a	17.98 a	28.53 a	1.72 a
	Winnipeg	3.27 a	62.67 a	6.98 a	17.45 a	34.75 a	1.98 a
Carman	Random	2.23 a	59.79 b	7.08 b	16.00 a	30.55 a	1.92 a
	Mexico	2.11 a	56.11 a	6.76 a	16.04 a	28.23 a	1.75 a
	Winnipeg	2.18 a	60.99 b	7.08 b	15.75 a	28.30 a	1.77 a
CIANO	Random	-	70.19 a	8.03 a	25.70 b	53.21 a	2.15 a
	Mexico	-	69.71 a	9.33 b	22.83 a	55.78 a	2.43 a
	Winnipeg	-	70.45 a	7.43 a	25.49 b	50.24 a	2.04 a
Glenlea + Carman	Random	2.90 a	60.24 b	7.08 a	16.44 a	30.66 a	1.91 a
	Mexico	3.07 a	57.69 a	6.92 a	16.51 a	28.38 a	1.73 a
	Winnipeg	2.73 a	61.83 b	7.04 a	16.60 a	31.52 a	1.88 a

[†] Duncan's multiple range test at P=0.05; values followed by the same letter are not significantly different.

In populations A at Glenlea (Table 21), the visual bulk was significantly higher in kilograms per hectoliter than the light insensitive (Mexican) bulk ($P=0.05$). Similarly, at Carman (Table 22) the visual bulk was superior to the light insensitive bulk in populations B and C, whereas only the random bulk was superior to the light insensitive bulk in population D ($P=0.05$). Combined analysis at Glenlea showed no significant difference between the test weight (kg/hl) of the random and light insensitive (Mexico) selections (Table 24). However, the visual bulk (Winnipeg) had a higher mean test weight than any other selection group. At Carman (Table 24) both the random and visual selections were superior to the light insensitive (Mexico) selections ($P=0.05$). No significant differences were obtained at CIANO. No significant interactions occurred at any of the three locations but significant ($P=0.01$) population differences were found at Glenlea.

Combined analysis over the Glenlea and Carman locations (Table 24) indicated that the light insensitive (Mexico) treatment had a significantly lower ($P=0.05$) test weight than either the random or Winnipeg selection groups. No significant population differences or interactions were obtained; however, a significantly higher mean test weight ($P=0.05$) was found at Glenlea.

Two Hundred-Kernel Weight. Individual analysis at Glenlea indicated no significant difference for 200-kernel weight (Table 21) between treatments in any of the populations ($P=0.05$). At Carman, the light insensitive bulk had a significantly lower 200-kernel weight than either the random or visual bulks ($P=0.05$) in population B. Combined population analysis (Table 24) indicated no significant differences

between treatments at Glenlea, but at Carman the light insensitive bulks were significantly lower in 200-kernel weight than the random sample ($P=0.05$). Combined analysis over locations, however, indicated no significant treatment differences. No significant interactions or location differences occurred between populations in the combined location analysis ($P=0.01$).

Comparison of treatments, on the basis of 200-kernel weight (Table 23) at CIANO, showed that the light insensitive bulks were higher ranking than the random and visual bulks. In population A, the insensitive bulk was significantly superior to random and visual bulks ($P=0.05$). In population B, the visually selected bulk was significantly lower in 200-kernel weight than either the random or light insensitive bulks ($P=0.05$). Combined analysis (Table 24) indicated that the light insensitive bulks had a mean 200-kernel weight superior to both the random and visual selections ($P=0.05$). No significant difference occurred between the random and visual bulks. Similarly, no significant population differences or interactions were obtained at CIANO.

Spikelets Per Spike. Analysis of data on spikelets per spike (Tables 21 and 22) at Glenlea and Carman showed a significant difference ($P=0.05$) between selection bulks only in population A at Carman. In this case, the light insensitive bulk had a higher number of spikelets per spike than either the random or visual bulks. Combined analysis (Table 24) at each location and over both locations indicated neither significant treatment and population differences nor interactions ($P=0.05$). However, the bulks grown at Glenlea had a

significantly higher number of spikelets per spike than when grown at Carman ($P = 0.05$).

In populations A and B at CIANO, the random and visual bulks had a significantly higher number ($P = 0.05$) of spikelets per spike than the light insensitive bulks (Table 23). In the remaining two populations (C and D) the insensitive bulk had the lowest number of spikelets per spike. Combined analysis (Table 24) indicated that the insensitive bulks had a mean spikelet number significantly lower than either the random or visual bulks ($P = 0.05$). The comparison of the visual bulks and the random bulks indicated no significant difference at the 5 percent level. Significant population differences ($P = 0.01$) and a significant population x treatment interaction ($P = 0.05$) were obtained at CIANO.

Kernels Per Spike. Individual population analyses (Tables 21, 22 and 23) of data on kernels per spike of material tested at Glenlea, Carman and CIANO indicated that the only significant difference between bulks was obtained at Carman. In this case, the visual bulk in population A was significantly lower ($P = 0.05$) than either the light insensitive or random bulks. Combined analysis (Table 24) at each location and over the two Manitoba locations indicated no significant treatment or population difference in kernel number ($P = 0.05$). At Carman, however, a significant population x treatment interaction was obtained ($P = 0.05$).

Kernels Per Spikelet. Population analysis of data pertaining to kernels per spikelet (Tables 21 and 22) showed that in populations B, C and D at Glenlea, and A and B at Carman, the insensitive bulk was the lowest ranking. In population C at Glenlea, the random bulk

had a significantly higher number of kernels per spikelet than either the insensitive or visual bulks ($P=0.05$). In population D, both the random and visual bulks were significantly superior to the insensitive bulk at the 5 percent level. At Carman, the random bulk was significantly superior ($P=0.05$) to the visual selection bulk in population C. Combined analysis (Table 24) at each location and over the two Manitoba locations indicated no significant treatment, population or location differences at the 5 percent level. However, a significant population x treatment interaction was obtained at Carman ($P=0.05$).

At CIANO, the light insensitive bulks had a higher mean number of kernels per spike in populations A, B and D than in either the random or visual bulks (Table 23). In population B, the light insensitive bulk was significantly higher ($P=0.05$) than both the random and visual bulks. In population C on the other hand, the random bulk was significantly superior only to the visual bulk ($P=0.05$). Combined analysis showed significant population ($P=0.05$) difference but no significant treatment or population x treatment interactions were obtained at CIANO ($P=0.05$).

Discussion

The present study, based on four genetically diverse triticales populations, showed that selection of light insensitive genotypes in the F_4 generation from high yielding F_3 -derived families resulted in significant yield reduction in F_5 tests grown at Glenlea and Carman, Manitoba. Observation of all populations at both locations indicated that the light insensitive bulks had the lowest yield, the random bulks were intermediate and the visually selected bulks were

the highest yielding. On the average, over all locations in Manitoba, selection of light insensitive families and lines resulted in a yield reduction of approximately 15 percent. The visually selected bulks, on the other hand, had a 14 percent yield advantage over the random bulks. Lebsock et al. (1973) found similar results in durum wheat at only one location. Consequently, they concluded that selection of stable light insensitive lines would not cause significant yield reduction at higher latitudes and would result in varieties with wide range adaptability.

Observation of treatment means at CIANO indicated that the light insensitive bulks had the lowest yield in three of the four populations. The random bulks, on the other hand, were the highest yielding in three of four populations. In this case, no significant differences were found between treatments within populations or in the combined analysis.

In addition to differences between yields, combined analysis of the two Manitoba locations indicated that the light insensitive bulks had the lowest test weight (kg/hl), 200-kernel weight, number of kernels per spike and kernels per spikelet. Similarly, the visual bulks had the highest mean value for test weight and spikelets per spike and kernels per spike numbers. Combined analysis, however, showed that the insensitive bulks were significantly inferior to random selection in test weight. No significant difference was found in tiller number between the insensitive and random bulks.

At CIANO, the light insensitive genotypes had the lowest mean test weight (kg/hl), the lowest number of spikelets per spike, the highest mean number of kernels per spikelet and the highest 200-kernel weight. Combined analysis indicated that the light insensitive bulks

had a significantly higher 200-kernel weight than the random sample, but a significantly lower number of spikelets per spike.

Literature on yield components shows that a wide degree of variability occurs in the expression and importance of yield components in relation to yield. Negative correlations and yield component compensation are common-place. Rasmusson and Cannell (1970) have explained these factors on the basis of linkage. Adams and Grafius (1971), on the other hand, have explained the interrelationship of yield components as being due to a balance between sequential components achieved by an oscillating response to resources. This is exemplified in the present study by the fact that although the visual selection of lines was conducted partially on the basis of tillering capacity in the space planted nursery at Winnipeg, differences in tillering were not found within populations grown in densely planted yield plots.

Studies conducted on light insensitive genotypes have shown that many of the yield components are drastically influenced by temperature. Syme (1968), Pugsley (1970), Halse and Weir (1970), Heiner (1971) and Levy and Peterson (1972) have noted that vernalization of light insensitive spring wheats frequently caused a reduction in the degree of expression of a yield component. Heiner (1971) has explained this result as being due to the presence of temperature responsive genes (winter habit) which in combination with light insensitivity, results in abnormally rapid plant development. Alternatively, Hurd-Karrer (1933) and Syme (1968) have shown that similar results may be obtained if light insensitive genotypes are subjected to high atmospheric temperatures during early development and long day-length.

Studies conducted on long-day cereals under short-day conditions

have indicated that many of the yield components may be amplified. Zillinsky and Borlaug (1971) found that late-maturing light sensitive genotypes frequently have a lower number of tillers relative to light insensitive material. Rawson (1971) indicated that light sensitive triticales show a drastic increase in spikelets per spike when grown for prolonged periods under short-day conditions. Under extreme conditions, a higher proportion of the terminal spikelets are infertile.

Lebsock et al. (1973) noted that the light insensitive lines were the lowest yielding at only one location. These researchers then concluded that abnormally high temperatures and long-day conditions were responsible. It appears that this may be the most obvious reason for the low yield of light insensitive triticales grown under Manitoba conditions. Thus, the rapid development converts resources from the production of the yield components to the reproductive phase, resulting in reduced yields when compared to random and visually selected lines.

Under short-day conditions, it appears that a prolonged period for development in light sensitive lines is responsible for the observed increases in spikelets per spike (Rawson, 1971) and tillers per plant (Zillinsky and Borlaug, 1971).

The present study indicated that selection of light insensitive genotypes from high-yielding F_3 -derived families resulted in a significant yield reduction in four triticales populations grown at two locations in Manitoba. The size of the population sampled had no apparent effect on the response obtained. Consequently, it appears that single plant selection for insensitivity in two of the four populations, had the

same effect on yield reduction as family and within family selection in the remaining two populations. Intensive selection for light insensitivity in early generations may be reducing the total number of high yielding progenies involved in F_3 early generation yield trials at the University of Manitoba. The fact that some high yielding F_3 families contained light insensitive genotypes may lead to a suggestion that high yielding light insensitive genotypes may be obtained. Subsequent analyses should be conducted on the possible effect of single plant selection for light insensitivity on the yielding abilities of families derived from plants selected as early as the F_2 generation. It may be more realistic to select for adaptation and yield under Manitoba conditions prior to selection of lines for light insensitivity under short day conditions if a high proportion of lines with high yielding ability are to be retained.

GENERAL DISCUSSION

GENERAL DISCUSSION

Studies evaluating F_1 selection as a means of predicting potential yielding ability have concluded that heterosis is a major limiting factor. Briggs and Knowles (1967) summarized problems in F_1 yield evaluation as follows: 1) seed quantities are frequently too small for adequate testing; 2) the yield of widely-spaced F_1 plants is not correlated with the yields of more closely spaced plants; and 3) F_1 heterosis is a major concern in predicting the yield potential of hybrids in subsequent generations.

The present study was based on the premise that triticale F_1 hybrids which show poor fertility and yield have a low potential for producing desirable segregates in subsequent generations. In both years, the highest yielding F_1 's produced the highest yielding individual families in the F_3 yield trial. However, the number of lines in each population which were among the top twenty-five or top ten lines in the yield trial showed no relationship with F_1 yield. Reversal of yield ranking between the F_1 and F_3 generations was taken as an indication that F_1 selection was not a reliable basis for the discarding of hybrids.

Numerous studies have compared visual selection and yield selection on the basis of yield plots. Using this method in soybeans (Hanson et al., 1962; Kwon and Torrie, 1964) and in wheat (Briggs and Shebeski, 1970; Mundel, 1972; Townley-Smith et al., 1973), it was found that visual selection was effective in increasing yield but was not as efficient as selection on the basis of plot yield. Townley-Smith et al. (1973)

further concluded that no difference occurred between the selecting abilities of experienced and inexperienced selectors.

In the present study, experienced (plant breeders), novice (graduate students) and inexperienced (summer students) selectors were in general able to retain a higher ratio of superior to low yielding lines than dictated by the population structure in both 1973 and 1974. However, in the two small populations (1973) only the experienced and novice selector categories contained individuals who retained a higher ratio of superior yielding to low yielding families relative to a random sample. The present study did not determine if visual selectors were able to select a higher proportion of lines significantly superior to the check than if sampling had been conducted at random. When selecting the top twenty lines in each population, all selector categories were able to select a significantly higher number of the top ten lines in each population than expected at random. However, the experienced category was the only group in which all individuals selected more of the ten highest yielding lines than would be represented by a random sample.

In both years, visual selection resulted in a higher yield increase (response) and was more efficient than a random sample. The selector with the highest mean response and selection efficiency in each year was an experienced selector. Visual selection conducted by visual selectors, at an intensity of 20 percent, resulted in a mean response and efficiency which was superior to that gained by random sampling.

In 1974, the mean yield of the best yielding twenty lines visually selected by each selector was compared to the mean of the best twenty

lines in each population. Under these circumstances, experienced selectors selected lines equal in yield to the best twenty lines in each population.

A more adequate test of visual versus yield selection was the comparison of headrow (pedigree) and F_3 early generation yield selection. Previous studies in soybeans (Leudders et al., 1973; Boerma and Cooper, 1975) and in wheat (Seitzer, 1974) have found little difference in yield resulting from use of the two methods.

Results of the present study conformed with those of previous studies. No significant differences occurred between the mean yield of lines selected by the pedigree and F_3 early generation selection method. However, lines used to produce the bulks differed for the two methods. Part of this discrepancy can be explained by the fact that five of the highest yielding lines in population 4 were damaged by water in the headrow nursery. Even so, selection of superior plants within headrow lines, rejected on the basis of plot yield in the F_3 early generation yield trial, resulted in an increase in yield not significantly different from selection on the basis of F_3 plot yield.

Studies conducted on wheat have indicated that the crosses involved in a breeding program may reflect on the type of selection method used. Khalifa and Qualset (1974) have noted that the productivity of high yielding wheat semi-dwarfs is frequently reduced when grown in combination with tall, low yielding genotypes. They concluded that the use of bulks for several generations should not be considered if selection of high yielding semi-dwarfs is a major goal of the breeding program. Salmon et al. (1975) concluded that at least one semi-dwarf triticales (semi-dwarf mutant of 6TA204) showed a close

relationship between short stature and low seed-set. Gebremariam (1974) noted that height and yield are related in triticales. Under these conditions, selection of families on the basis of bulk F_3 family yield may result in the loss of valuable semi-dwarfs.

An additional problem in triticales which should be considered before deciding on the time and type of selection is the importance of meiotic instability. Merker (1974) stated that meiotic instability, although not directly related to infertility, results in a high frequency of aneuploidy which in turn contributes to poor plant vigor with an accompanying reduction in yield. Gustafson and Zillinsky (1973), Gustafson and Qualset (1974, 1975), Darvey and Gustafson (1975), Merker (1975), Gustafson and Bennett (1976), Gustafson and Zillinsky (1976) and Qualset et al. (1976) have reported that occurrence of substitution of wheat for rye chromosomes in hexaploid triticales. In addition, Darvey and Gustafson (1975), Gustafson and Bennett (1976) and Gustafson and Zillinsky (1976) have found evidence of the diversity of heterochromatin content in rye chromosomes. Factors such as these could further increase meiotic instability. Gustafson and Qualset (1975) concluded that crosses between triticales differing in wheat-rye substituted chromosomes may be similar to interspecific crosses and that hybrids and segregating populations should not be discarded on the basis of poor fertility per se. In subsequent generations, some of these crosses could produce highly fertile segregates due to selection for fertility in the F_2 to F_4 generations.

Observation of the pedigrees presented in Table 1 suggests that the parents involved in the present crosses may have differed in terms of substituted rye chromosomes. Gustafson and Zillinsky (1973) found

that the CIMMYT cultivar 'Armadillo' lacks rye chromosome 2R. More recently, Merker (1975) found that the Armadillo derivatives, Beaver, Maya II-Arm "S" and Bronco-90 also contained rye chromosome substitutions. These considerations may explain the unreliability of F_1 selection and the fact that high yielding lines were selected within headrows which corresponded to plots rejected in the F_3 early generation yield trial.

Sethi and Singh (1972) working with triticale, observed a strong positive correlation between tillering capacity and yield. Gebremariam (1974) on the other hand, reported a negative correlation between tillering and the yield of triticale lines. The number of kernels per spike has been indicated as an important yield-related factor by Gustafson (1972), Barnett *et al.* (1973), Gebremariam (1974) and Chen (1974). In addition, Gustafson, Gebremariam and Chen have indicated a positive relationship between yield and number of kernels per spikelet.

In the present study, comparing pedigree and early generation selection, pedigree selection resulted in a significant increase in the number of spikelets per spike. Selection of the lowest yielding ten lines in the F_3 early generation yield trial was manifested by a significant reduction in tiller number per plant. The fact that a relatively small amount of material was sampled may have reduced the validity of yield component analyses.

Qualset *et al.* (1969), evaluating the yielding ability of triticale in northern California, concluded that most of the early triticales produced at the University of Manitoba were tall and late-maturing due to their light sensitivity. Lebsock *et al.* (1973) noted similar problems in wheat developed in northern latitudes. An important component of recent breeding programs in triticale and wheat has been

the incorporation of light insensitivity from the CIMMYT wheat breeding program. Lebsock et al. (1973) studied the effect of light sensitivity on the yielding ability of durum wheat. They concluded that selection of stable light insensitive lines would not have a deleterious effect on durum wheat yields.

Results of the present study contrast with those obtained by Lebsock et al. (1973). In the combined analysis of the two Manitoba locations, light insensitive bulks had a significantly lower mean yield than a random sample. Similarly, they were lower yielding than the random bulk in three populations at CIANO, Mexico. Although populations were represented by an unequal number of F_3 families in the early generation yield trial and subsequent selection bulks contained differing numbers of families and lines within families between populations, no significant population x treatment interaction was obtained.

Studies conducted on light insensitive wheats have shown a response to temperature in terms of yield-related components. Syme (1968), Pugsley (1970), Halse and Weir (1970) and Levy and Peterson (1972) have concluded that vernalization results in a reduction in numbers of tillers per plant and spikelets per spike. Heiner (1971) has noted that vernalization also results in a shorter straw and earlier maturity due to abnormally rapid plant development. Alternatively, Hurd-Karrer (1933), Syme (1968) and Lebsock et al. (1973) have proposed that a similar effect will occur when light insensitive lines are subjected to warm temperature and long-day conditions during early plant development.

Similar studies have been conducted on light sensitive wheat and triticale lines under short-day conditions. Rawson (1971) found that

photosensitive lines of both species produced an increased number of spikelets per spike when grown under short photoperiods. However, triticale was more responsive than wheat, resulting in a high frequency of sterile terminal florets. Zillinsky and Borlaug (1971) observed that under short-day conditions in Mexico, light sensitive lines were late-maturing but produced a higher number of tillers per plant than light insensitive genotypes.

Unfortunately, only a small sample was used to evaluate yield components in the present study. Combined analysis of the two Manitoba locations indicated a significant reduction in 200-kernel weight in the light insensitive bulks as compared to the random and visual bulks. At CIANO, the insensitive bulks had a significantly higher 200-kernel weight, but produced a significantly lower number of spikelets per spike than the random and visually selected bulks. In this study, light insensitive lines were selected in the F_4 generation from families which were high yielding in the F_3 early generation yield trial, possibly limiting the amount of variability for yield and related components. It is suggested, therefore, that a similar study should be conducted on a larger number of crosses but selection should be conducted in the F_2 generation. Under these conditions it may be possible to determine if selection of light insensitive lines at CIANO, Mexico changes the yield potential of crosses grown in the F_3 early generation yield trials in Manitoba.

SUMMARY

SUMMARY

Recent studies have concluded that problems occur in the handling of triticales populations due to meiotic instability caused by the interaction of alien genomes and/or the intercrossing of parents differing for wheat-rye chromosomal substitutions. Observation of the pedigrees of the crosses involved in the present study indicates that the parents may have differed for substitutions. Since this condition may be considered a common occurrence within triticales populations, the following conclusions as drawn from the results of the present study may be applicable to all breeding programs. However, the fact that only a small number of crosses were evaluated and that analyses were based on a fixed-effects model restricts conclusions to the material analysed. As a consequence, it is suggested that subsequent studies be conducted to substantiate the present conclusions.

The following information was obtained in the individual manuscripts presented in this thesis:

Manuscript I. F_1 Evaluation of Yield Potential in Hexaploid Triticale.

- (1) No relationship exists between F_1 single plant yield and the number of superior segregates or mean yield of populations in the F_3 early generation yield trial.

Manuscript II. Visual Selection as a Basis for Yield Prediction in Triticale.

- (1) In the present study, superior lines ($\geq$ the nearest check plot) comprised a larger proportion of the visually

- selected lines in all selector categories than expected by random selection.
- (2) When selecting at an intensity of 20 percent, all selectors selected a larger proportion of the top ten lines within each population than would have been expected if selection was at random.
 - (3) All selector categories achieved a higher response and selection efficiency than was obtained from a random sample, whether selecting lines $\geq$ the nearest check plot or selecting the highest yielding twenty lines in each population.
 - (4) Selectors with the highest efficiency in visual selection were experienced selectors, whereas selectors with the lowest response or selection efficiency were inexperienced.
 - (5) Experienced selectors consistently selected twenty lines in each population with a mean yield which was not significantly different in yield than the top twenty lines identified on the basis of actual plot yield.

Manuscript III. A Comparison of Early Generation (F_3) and Pedigree Selection Methods in Triticale.

- (1) Combined analysis indicated no significant yield differences between bulks produced by either pedigree or early generation selection. However, pedigree selection retained a high proportion of families rejected by the early generation yield trial.

- (2) Combined location analysis showed that pedigree selection resulted in a significant increase in the number of spikelets per spike.
- (3) As shown by combined location analysis, selection of the lowest yielding lines in the early generation yield trial resulted in a significant reduction in tiller number.

Manuscript IV. The Effect of Selection under Diverse Environmental Conditions on the Yield and Yield Related Components in Triticale.

- (1) Combined analysis indicated that bulks produced from light insensitive selections had a significantly lower mean yield than either the random or visual selection bulks.
- (2) Light insensitive bulks had a significantly lower mean test weight (kg/hl) than either the random sample or visually selected bulks in the combined location analysis.
- (3) No significant yield differences occurred between either the insensitive, the random or visually selected bulks at CIANO, Mexico.
- (4) At CIANO, the light insensitive bulks had a significantly higher 200-kernel weight, but a significantly lower number of spikelets per spike than either the random sample or visual selected bulks.

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APPENDICES

Appendix 1-1. Degree of skewness using three methods of plot yield expression in the F_3 early generation yield trials.

Year	Pop'n.	N ξ	% Check	Plot check	Log plot - log check
1973	A	381	0.5483**	0.0483	-
	B	207	0.4206**	-0.0031	-
	C	50	0.2762	-0.1905	-
	D	34	0.1538	0.0572	-
1974	1	98	0.8036**	0.3499	-0.2285
	2	99	1.3814**	0.6904**	0.0555
	3	100	0.4155	0.1171	-0.3545
	4	98	0.4230	0.3059	-0.1358

ξ The number of families in each F_3 population.

** Significant degree of skewness at $P = 0.01$.

Appendix 1-2. Treatment and error mean squares for the comparison of the mean yielding abilities of F_3 populations in the F_3 early generation yield trials of 1973 and 1974.

Source	1973		1974	
	d.f.	Mean squares	d.f.	Mean squares
Treatment (populations)	3	137857.88**	3	2.78**
Error	668	52650.50	391	0.12

** Significant at $P = 0.01$.

Appendix 2-1. Total number of lines in each population, total number of lines $\geq$ the check (yield) and the total number of lines selected by each selector which were superior to the nearest check (1973).

Selector	Pop'n. A		Pop'n. B		Pop'n. C		Pop'n. D	
	Total lines selected	Total lines $\geq$ check	Total lines selected	Total lines $\geq$ check	Total lines selected	Total lines $\geq$ check	Total lines selected	Total lines $\geq$ check
1	59	35	55	36	10	4	3	2
2	32	23	23	18	5	4	5	5
3	46	24	14	12	4	2	5	5
4	101	43	40	30	15	5	12	9
5	102	36	58	33	18	9	8	6
6	95	36	49	32	11	5	6	4
7	51	29	31	22	3	2	7	6
8	49	30	37	20	3	2	5	4
9	48	32	10	6	5	3	2	2
10	63	34	30	22	7	4	9	8
N ^ξ =	381		207		50		34	
n [§] =	75		84		13		17	

^ξ The number of lines in each population.

[§] The number of lines in each population equalling or exceeding the yield of the nearest check plot.

Appendix 2-2. Total number of lines in each population, total number of lines $\geq$ the check (yield) and the total number of lines selected by each selector which were superior to the nearest check plot (1974).

Selector	Pop'n. 1		Pop'n. 2		Pop'n. 3		Pop'n. 4	
	Total lines selected	Total lines $\geq$ check	Total lines selected	Total lines $\geq$ check	Total lines selected	Total lines $\geq$ check	Total lines selected	Total lines $\geq$ check
1	4	2	3	1	10	7	4	3
2	9	4	12	7	10	7	17	13
3	22	8	33	14	24	10	37	22
4	10	3	13	5	18	7	23	10
5	11	5	19	9	16	7	22	11
7	10	4	8	8	12	5	20	12
8	20	5	16	8	30	11	17	10
11	16	3	13	4	25	8	22	17
12	45	7	50	14	48	11	49	20
13	56	7	45	12	59	11	55	21
14	20	5	37	13	32	10	50	25
N ^ξ =	98		99		100		98	
n [§] =	8		15		11		28	

^ξ Total lines in each population.

[§] Total lines in each population equalling or exceeding the yield of the nearest check plot.

Appendix 2-3. The mean yield (log.), intensity of selection (i) and expected response to selection ($i\sigma_p$) for selectors selecting lines estimated visually to be $\geq$ the nearest check plot (1974).

Selector	Pop'n. 1			Pop'n. 2			Pop'n. 3			Pop'n. 4		
	Mean (g)	$i^\dagger$	$i\sigma_p$	Mean	i	$i\sigma_p$	Mean	i	$i\sigma_p$	Mean	i	$i\sigma_p$
1	0.166	2.15	0.768	0.186	2.29	1.057	0.081	1.69	0.537	0.147	2.15	0.500
2	0.003	1.79	0.639	0.160	1.67	0.771	0.039	1.66	0.527	0.145	1.44	0.326
3	-0.052	1.33	0.475	-0.151	1.09	0.503	-0.049	1.30	0.413	0.049	0.98	0.228
4	-0.117	1.75	0.625	-0.123	1.62	0.748	-0.059	1.48	0.469	-0.050	1.32	0.307
5	0.032	1.69	0.604	-0.083	1.42	0.655	0.013	1.52	0.482	0.063	1.37	0.319
7	-0.030	1.75	0.625	0.245	1.80	0.831	-0.039	1.71	0.543	0.071	1.40	0.326
8	-0.089	1.39	0.497	-0.034	1.52	0.701	0.262	1.16	0.368	0.045	1.48	0.344
11	-0.112	1.51	0.540	-0.028	1.42	0.655	0.205	1.27	0.403	0.056	1.24	0.289
12	-0.259	0.86	0.307	-0.376	0.79	0.365	0.067	0.86	0.273	-0.028	0.80	0.168
13	-0.327	0.69	0.247	-0.335	0.87	0.401	0.076	0.66	0.210	-0.066	0.72	0.162
14	-0.129	1.39	0.497	-0.191	1.01	0.466	0.276	1.11	0.352	-0.007	0.80	0.186
15	-0.542	1.40	0.500	-0.422	1.32	0.599	-0.474	1.30	0.413	-0.151	1.20	0.279

† Approximate i as extrapolated from Fig. 11.3; D.F. Falconer, 1960. Introduction to Quantitative Genetics p. 193.

$\xi \sigma_p$ equals the phenotypic standard deviation for yield in each population.

Appendix 2-4. The mean yield (log.), intensity of selection (i) and expected response (g) to selection (io_p) for selectors selecting lines estimated visually to be $\geq$ the nearest check plot (1973).

Selector	Pop'n. A			Pop'n. B			Pop'n. C			Pop'n. D		
	Mean(g)	$i^\dagger$	io_p^ξ	Mean	i	io_p	Mean	i	io_p	Mean	i	io_p
1	20.09	1.57	342.78	92.06	1.26	279.03	-26.63	1.40	401.10	12.00	1.74	518.62
2	91.59	1.79	390.81	164.35	1.70	376.47	148.60	1.80	252.00	261.20	1.57	467.45
3	0.42	1.71	373.34	195.79	1.97	436.26	74.33	1.90	544.35	243.40	1.64	488.82
4	-58.07	1.25	272.91	83.16	1.30	287.89	-10.07	1.18	338.07	140.42	1.18	351.71
5	-82.79	1.19	259.81	53.36	1.20	265.74	-77.28	1.06	303.69	102.38	1.35	402.38
6	-65.33	1.30	283.83	32.09	1.30	287.89	-178.60	1.35	386.78	28.50	1.48	441.12
7	13.53	1.67	364.61	84.17	1.57	347.68	50.33	2.00	573.00	134.29	1.48	441.12
8	18.10	1.67	364.61	70.39	1.45	321.10	23.00	2.00	573.00	176.20	1.57	467.95
9	83.08	1.71	373.34	59.30	2.00	442.90	111.00	1.80	515.70	254.50	2.00	596.12
10	20.71	1.55	338.41	131.63	1.58	349.89	21.00	1.57	449.80	222.00	1.30	387.48
Random	-216.37	1.50	327.50	-27.92	1.20	265.74	-276.63	1.55	444.08	-74.17	1.52	453.05

† Approximate i as extrapolated from Fig. 11.3; D.F. Falconer, 1960. Introduction to Quantitative Genetics p. 193.

$^\xi$ σ_p equals the phenotypic standard deviation for yield in each population.

Appendix 2-5. Treatment and error mean squares for the comparison of selectors on the basis of response to selection and selection efficiency when selecting lines estimated to be $\geq$ the check yield or in the top 20% (yield) of each population.

Source	1973			1974				
	Mean squares ($\geq$ Check)			Mean squares ($\geq$ Check)			Mean squares (Top 20%)	
	d.f.	Response	Efficiency	d.f.	Response	Efficiency	d.f.	Efficiency
Treatment (Selectors)	10	32050.18**	0.16**	11	0.10**	0.22**	11	0.20**
Error	33	3326.28	0.02	36	0.02	0.02	36	0.02

** Significant at $P = 0.01$.

Appendix 2-6. Treatment and error mean squares for the comparison of the mean yield of the top 20 lines selected visually with the means of the top 20 lines (yield) in each population.

Source	d.f.	Mean squares			
		Pop'n. #1	Pop'n. #2	Pop'n. #3	Pop'n. #4
Treatments (Selectors)	13	0.205**	0.275**	0.182**	0.076**
Error	228	0.803	0.167	0.049	0.030

** Significant at $P = 0.01$.

APPENDIX 3. Average values of mean squares for factorial: the three factor fixed-effects model (1).

Source	d.f.	Average value of mean square
Blocks	$r-1$	$\sigma^2 + abc\sum\rho^2/(r-1)$
A	$a-1$	$\sigma^2 + rbc\sum\alpha^2/(a-1)$
B	$b-1$	$\sigma^2 + rac\sum\beta^2/(b-1)$
C	$c-1$	$\sigma^2 + rab\sum\gamma^2/(c-1)$
AB	$(a-1)(b-1)$	$\sigma^2 + rc\sum(\alpha\beta)^2/(a-1)(b-1)$
AC	$(a-1)(c-1)$	$\sigma^2 + rb\sum(\alpha\gamma)^2/(a-1)(c-1)$
BC	$(b-1)(c-1)$	$\sigma^2 + ra\sum(\beta\gamma)^2/(b-1)(c-1)$
ABC	$(a-1)(b-1)(c-1)$	$\sigma^2 + r\sum(\alpha\beta\gamma)^2/(a-1)(b-1)(c-1)$
Error	$(r-1)(abc-1)$	σ^2

Reference: Steele, R.G.D. and Torrie, J.H. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Company Inc. Table 11.8, pp. 210.

Appendix 4-1. Treatment and error mean squares for the comparison of the yielding abilities of early generation and pedigree selection bulks at Glenlea, Carman and CIANO (Mexico).

Location	Source	d.f.	Mean squares			
			Pop'n. # ₁	Pop'n. # ₂	Pop'n. # ₃	Pop'n. # ₄
Glenlea	Treatment	3	20880.09*	34784.76**	2624.89	1297.29
	Error	27	3914.02	5291.02	1916.69	6753.05
Carman	Treatment	3	9653.69**	30241.96**	17535.09**	1961.09
	Error	27	784.15	2275.42	1740.78	3943.41
CIANO	Treatment	3	23580.06**	35001.08**	42327.73**	21095.23**
	Error	9	1984.95	2594.58	1558.28	3538.67

* Significant at $P = 0.05$.

** Significant at $P = 0.01$.

Appendix 4-2. Mean squares for the comparison of the effect of early generation and pedigree selection on yield and related components at Glenlea, Carman, CIANO (Mexico), and in the combined analysis of the two Manitoba locations.

Location	Source	Yield mean square				Yield component mean squares				
		d.f.	Yield (g)	d.f.	Tillers	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
Glenlea	Population	3	85402.69**	3	3.73	213.31**	2.29	60.69**	37.11	0.29
	Treatment	3	33766.28**	3	1.44	13.57	1.18	20.84**	101.26	0.23
	A x B	9	8606.92	9	2.09	14.19	0.94	14.44*	69.99	0.14
	Error	135	4402.04	60	1.87	9.86	0.69	4.12	81.26	0.15
Carman	Population	3	102473.69**	3	0.61	72.15**	4.29**	30.49**	277.92**	1.35**
	Treatment	3	42508.83	3	2.20	28.42	0.33	3.24	1.56	0.01
	A x B	9	5627.67	9	0.49	17.17	0.25	4.45	82.61	0.15
	Error	135	2345.91	60	0.37	10.39	0.25	5.01	52.56	0.09
CIANO	Population	3	81151.35**	-	-	-	-	-	-	-
	Treatment	3	119363.52**	-	-	-	-	-	-	-
	A x B	9	3573.20	-	-	-	-	-	-	-
	Error	45	4453.89	-	-	-	-	-	-	-
Glenlea +Carman	Population	3	185365.15	3	2.49	281.89**	6.29**	74.35**	98.23	1.42**
	Treatment	3	71770.39	3	3.33**	47.67	1.39*	19.89*	59.59	0.10
	Location	1	135795.20	1	141.38**	6.01	7.18**	143.45**	1524.61**	0.85**
	A x B	9	10599.37	9	1.29	18.59	0.92	12.67	78.63	0.11
	A x C	3	2511.23	3	1.87	60.16	0.31	16.85*	216.80*	0.24
	B x C	3	4504.71	3	0.31	69.40	0.18	4.14	43.23	0.13
	A x B x C	9	3635.22	9	1.29	42.39	0.27	6.21	73.97	0.18
	Error	297	5497.86	124	1.14	32.52	0.51	5.25	76.07	0.13

* Significant at P = 0.05.

** Significant at P = 0.01.

Appendix 4-3. Population means for yields and yield related components in the comparison of bulks selected by pedigree and contiguous systems of yield selection (1975).

Location	Pop'n.	Yield	Tillers/ plant	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
Glenlea	1	197.33 ab [†]	4.49 a	57.63 b	6.57 a	22.20 b	36.07 a	1.63 a
	2	216.88 b	3.82 a	54.84 a	6.82 ab	21.75 b	37.75 a	1.72 a
	3	181.83 a	4.06 a	61.45 c	7.15 b	21.53 b	35.03 a	1.62 a
	4	286.53 c	4.78 a	61.62 c	6.37 a	18.38 a	34.73 a	1.88 a
Carman	1	142.43 a	2.19 a	59.04 a	6.81 ab	18.84 a	25.54 a	1.37 a
	2	171.18 b	2.34 a	58.35 a	7.46 bc	19.14 a	28.57 ab	1.46 a
	3	150.98 ab	2.52 a	60.28 a	7.63 c	20.66 b	30.30 bc	1.47 a
	4	253.18 c	2.57 a	62.67 b	6.70 a	17.66 a	34.47 c	1.95 a
CIANO	1	502.31 b	-	-	-	-	-	-
	2	625.81 d	-	-	-	-	-	-
	3	471.25 a	-	-	-	-	-	-
	4	582.75 c	-	-	-	-	-	-
Glenlea + Carman	1	169.88 a	3.34 a	57.11 a	6.69 a	20.52 b	30.81 a	1.50 a
	2	194.02 a	3.08 a	56.61 a	7.14 b	20.45 b	33.16 a	1.58 a
	3	166.40 a	3.28 a	60.45 b	7.39 b	21.09 b	32.66 a	1.54 a
	4	269.85 b	3.68 a	62.13 b	6.53 a	18.02 a	34.60 a	1.91 b

[†] Duncan's multiple range test at P=0.05; values followed by the same letter are not significantly different.

Appendix 5-1. Treatment and error mean squares for the comparison of the yielding abilities of the random, Mexican (insensitive) and Winnipeg (visual) selection bulks at Glenlea, Carman and CIANO (Mexico).

Location	Source	d.f.	Mean squares			
			Pop'n. A	Pop'n. B	Pop'n. C	Pop'n. D
Glenlea	Treatment	2	29387.03*	34090.00**	11132.10*	7707.70*
	Error	18	5595.63	3904.52	3534.69	1983.51
Carman	Treatment	2	12227.03**	26816.13**	5992.30	3724.43
	Error	18	1796.37	3983.24	2167.67	2606.80
CIANO	Treatment	2	1033.36	5130.25	7529.25	13521.08
	Error	6	4239.72	8019.92	4874.69	3449.97

* Significant at $P = 0.05$.

** Significant at $P = 0.01$.

Appendix 5-2. Mean square for the comparison of the effect of random, Mexican (light-insensitive) and Winnipeg (visual) selection on yield and related components at Glenlea, Carman, CIANO (Mexico) and in the combined analysis of the two Manitoba locations.

Location	Source	Yield mean square		Yield component mean squares						
		d.f.	Yield (g)	d.f.	Tillers	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
Glenlea	Population	3	2905.942	3	1.846	53.842*	0.404	6.747	122.745	0.062
	Treatment	2	67965.408**	2	2.936	58.162*	0.071	1.831	198.407	0.347
	A x B	6	4783.808	6	1.526	11.616	0.367	3.778	127.739	0.173
	Error	99	4830.535	44	1.761	13.810	0.482	3.205	62.258	0.141
Carman	Population	3	9920.289**	3	1.210	39.193	1.927	2.056	116.150**	0.259
	Treatments	2	32671.033**	2	0.074	129.240**	0.694	0.487	34.833	0.169
	A x B	6	5362.956	6	0.513	47.832	0.396	1.725	85.526	0.314
	Error	99	2370.924	44	0.287	20.105	1.887	1.846	30.313	0.108
CIANO	Population	3	16819.243	3	-	18.254*	3.229	36.828**	59.777	0.685*
	Treatment	2	3482.313	2	-	2.243	15.284**	41.066**	123.139	0.670
	A x B	6	7908.118	6	-	13.040	3.145	24.053	124.499	0.520
	Error	33	6418.060	33	-	3.334	2.334	7.510	90.043	0.229
Glenlea +Carman	Population	3	8706.981	3	0.261	32.750	2.150**	5.959	167.221*	0.072
	Treatment	2	96426.754**	2	1.173	174.214**	0.240	0.257	105.651	0.351
	Location	1	209037.038**	1	63.220**	109.634**	0.120	41.536**	161.564	0.094
	A x B	6	8014.565	6	0.948	16.554	0.541	4.600	87.256	0.331*
	A x C	3	4119.249	3	2.794	10.679	0.271	2.844	136.106	0.248
	B x C	2	4209.688	2	1.836	13.189	0.506	2.060	127.589	0.166
	A x B x C	6	2132.199	6	1.090	20.460	0.181	0.903	13.344	0.156
	Error	207	8724.998	92	1.056	15.179	0.267	3.023	61.791	0.125

* Significant at P = 0.05.

** Significant at P = 0.01.

Appendix 5-3. Population means for yield and yield components in the comparison of random, Mexican (insensitive) and Winnipeg (visual) selection bulks (1975).

Location	Yield (g)	Tillers	Kilograms/ hectoliter	200-kernel weight (g)	Spikelets/ spike	Kernels/ spike	Kernels/ spikelet
Glenlea	243.87 a [†]	3.81 a	61.52 b	7.25 a	16.67 a	31.78 a	1.89 a
	265.90 a	3.57 a	62.17 b	7.03 a	16.51 a	28.44 a	1.85 a
	263.90 a	3.95 a	58.06 a	7.05 a	17.98 a	35.12 a	1.94 a
	259.70 a	3.15 a	61.75 b	6.84 a	17.26 a	30.04 a	1.79 a
Carman	192.77 a	2.14 ab	58.35 a	7.42 c	15.38 a	25.17 a	1.64 a
	225.53 b	2.36 b	60.04 a	6.81 ab	16.08 a	31.20 b	1.93 a
	194.50 a	1.78 a	56.96 a	7.07 b	16.06 a	28.28 ab	1.77 a
	183.87 a	2.40 b	60.49 a	6.59 a	16.19 a	30.92 b	1.91 a
CIANO	502.42 a	-	69.05 a	8.99 a	25.06 b	50.42 a	2.01 a
	593.25 a	-	70.88 b	8.23 a	26.46 b	52.72 a	2.07 a
	552.50 a	-	69.09 a	7.80 a	24.88 ab	53.30 a	2.19 ab
	540.08 a	-	71.46 b	8.01 a	22.27 a	55.85 a	2.54 b
Glenlea + Carman	218.32 a	2.98 a	60.95 a	7.33 c	16.02 a	27.58 a	1.77 a
	245.42 a	2.96 a	60.02 a	6.92 ab	16.30 a	28.79 a	1.89 a
	229.20 a	2.87 a	60.23 a	7.06 bc	17.02 a	32.04 b	1.85 a
	221.78 a	2.78 a	58.46 a	6.69 a	16.73 a	32.33 b	1.85 a

[†] Duncan's multiple range test at P = 0.05; values followed by same letter are not significantly different.