

INDEX SELECTION FOR GENETIC IMPROVEMENT
OF YIELD, KERNEL WEIGHT AND
PROTEIN CONTENT IN WHEAT

A Thesis
Submitted to the Faculty
of
Graduate Studies
The University of Manitoba

by



Hailu Gebre-Mariam

In Partial Fulfillment of the
Requirements for the Degree

of

Doctor of Philosophy
Department of Plant Science

October 1981



*INDEX SELECTION FOR GENETIC IMPROVEMENT OF YIELD,
KERNEL WEIGHT AND PROTEIN CONTENT IN WHEAT.*

by

Hailu Gebre-Mariam.

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

DOCTOR OF PHILOSOPHY

© 1981

Permission has been granted to the LIBRARY OF THE UNIVER-
SITY OF MANITOBA to lend or sell copies of this thesis, to
the NATIONAL LIBRARY OF CANADA to microfilm this
thesis and to lend or sell copies of the film, and UNIVERSITY
MICROFILMS to publish an abstract of this thesis.

The author reserves other publication rights, and neither the
thesis nor extensive extracts from it may be printed or other-
wise reproduced without the author's written permission.

FOREWORD

This thesis is written in the paper style, specified in the 1976 Plant Science Thesis Preparation Guide, in accordance with the style manual of Crop Science Society of America. It contains three manuscripts numbered 1 to 3.

ACKNOWLEDGEMENTS

I wish to express my sincere gratitude to my advisor, Dr. E.N. Larter, for his help during the course of this study and reviewing the manuscripts. Grateful acknowledgement is also expressed to the following: Dr. R.J. Baker for reading and commenting on the second manuscript, Mr. M. Fruehm and his crew for their invaluable assistance in the field, Mr. P. Becker for his kind help in conducting the protein analysis, Dianne Lapsley for typing the thesis, and friends who made the period of the study enjoyable and fruitful.

This study was completed while receiving a scholarship from the International Development Research Centre. This financial assistance is gratefully acknowledged. I am also grateful to the Ethiopian Government Institute of Agricultural Research for granting educational leave.

Above all, I would like to thank my wife, Fekerte and my children, Daniel and Mikael, for their patience, understanding and love, without which the completion of this thesis would not have been accomplished.

TABLE OF CONTENTS

	PAGE
LIST OF TABLES	vii
LIST OF FIGURES	xii
ABSTRACT	xiii
GENERAL INTRODUCTION	1
LITERATURE REVIEW	4
Selecting Superior Crosses in Early Generations of Wheat	4
Early Generation Selection	4
Heterosis and Evaluation of F1 and F2 Performance in Wheat	6
Bulk Prediction of Line Performance	8
Selecting Superior Crosses	9
Genetic Improvement of Yield in Wheat	12
Genetics of Yield and Kernel Weight in Wheat	13
Breeding for Yield in Wheat	18
Genetic Improvement of Wheat Protein	23
Genetic Control of Protein Content in Wheat	23
Genetic Variability and Breeding for High Protein Content	27
Relationship of Grain Yield and Percent Protein	30
Heritability and Response to Selection	32
Heritability	32
Response to Selection	35
Selection Indices for Genetic Improvement of Quantitative Characters	39
Selection Index Theory	40
Heritability of an Index	41
Expected Gains in the Aggregate Genotype from Selection on an Index	43

	PAGE
Various Modifications and Application of Selection Index	45
Restricted and Optimum Selection Indices	45
Weight-Free Selection Index	46
Desired Gains Selection Index	48
Other Uses of a Selection Index	49
Practical Limitations of Selection Indices	51
Parameter Estimations and Sampling Errors	51
Assignment of Relative Economic Weights	52
MANUSCRIPT 1. SELECTING SUPERIOR WHEAT CROSSES IN EARLY GENERATION	54
INTRODUCTION	55
MATERIALS AND METHODS	57
Crosses	57
F1 Yield Test	57
F2 Populations	59
F3 Experiments	59
RESULTS AND DISCUSSION	61
Selection Based on Average Performance and Heterosis of F1 Hybrids	61
Selection Based on Offspring-Parent Regression and Intergeneration Correlations	68
Evaluation of F2 Individual Plant Productivity in Comparison with Average F3 Group Performance	71
CONCLUSION	80
MANUSCRIPT 2. INDEX SELECTION FOR SIMULTANEOUS IMPROVEMENT OF YIELD, KERNEL WEIGHT, AND PROTEIN CONTENT IN WHEAT	82
INTRODUCTION	83
MATERIALS AND METHODS	85
Experimental Procedures	85
F3 Generation	85
F4 Generation	86
Estimation of Parameters	87
Construction of Indices	91

	PAGE
Smith-Hazel Selection Index	91
Elston's Weight-Free Selection Index	92
Desired Gains Selection Index	93
RESULTS AND DISCUSSION	95
Variance, Heritability, Index and Correlation Coefficient Estimates	95
Individual Traits	95
Smith-Hazel Selection Index	103
Weight-Free Selection Index	105
Desired Gains Selection Index	106
Comparison of Various Single Trait and Index Selection	109
Selection Based on Individual Traits	109
Selection Based on Various Indices	120
CONCLUSION	134
MANUSCRIPT 3. EFFECTS OF EXPERIMENTAL VARIABLES ON THE ESTIMATES OF HERITABILITY AND RESPONSE TO SELECTION IN WHEAT	139
INTRODUCTION	140
MATERIALS AND METHODS	142
RESULTS AND DISCUSSION	144
Heritability Estimates	149
Expected Genetic Gains	155
CONCLUSION	163
GENERAL DISCUSSION	166
SUMMARY AND CONCLUSIONS	171
LITERATURE CITED	175
APPENDIX	191

LIST OF TABLES

TABLE		PAGE
MANUSCRIPT 1		
1.1	Pedigree and class of the six spring wheat cultivars used in the study	58
1.2	Mean grain yield (kg/ha), TKW (g), protein (%), lysine levels and ranks of F1 hybrids and their respective parents	62
1.3	Weight-free index coefficients and ranks of six wheat crosses for yield and TKW (I ₁), yield, TKW and protein content (I ₂) and yield, TKW, protein and lysine content (I ₃), respectively	65
1.4	Average percent heterosis of F1 hybrids in relation to the better parent (H1) and the mid-parent value (H2) and potence ratio for yield, TKW, protein content, lysine level and selection index coefficient in six wheat crosses	66
1.5	Offspring-parent regression coefficients and standard errors for grain yield, TKW and protein (%) for four wheat crosses tested in two environments	69
1.6	Intergeneration rank correlation coefficients for grain yield, TKW and protein (%) in four wheat crosses grown in one location in F2 and at two locations in F3	72
1.7	Mean of the top 20%, population mean, and range of single plant performance for yield (g/plant), TKW (g), and protein percent of four F2 wheat populations grown in Obregon, Mexico	74
1.8	Mean of the top 20%, population mean, and range for yield (kg/ha), TKW (g) and protein (%) of four F3 wheat populations grown at the Point	75
1.9	Mean of the top 20%, population mean, and range for yield (kg/ha), TKW (g) and protein (%) of four F3 wheat populations grown at Glenlea Research Station	76
1.10	Mean yield (kg/ha) of the top 20%, multiplicative index values, and corresponding ranks of eight F3 experiments grown at the Point and Glenlea	78

TABLE	PAGE
MANUSCRIPT 2	
2.1	Estimates of phenotypic and genotypic variances and covariances for grain yield, TKW and percent protein in cross 1 96
2.2	Phenotypic and genetic variance and covariance estimates for grain yield, TKW, and protein content in cross 2 97
2.3	Phenotypic and genetic variance and covariance estimates for yield, TKW and percent protein in cross 5 98
2.4	Phenotypic and genetic variance and covariance estimates for yield, 1000-kernel weight and protein content in cross 6 99
2.5	Genetic coefficient of variation (%) for yield, TKW and protein content in four wheat crosses 101
2.6	Means, estimates of heritabilities (diagonal), phenotypic (above diagonal) and genetic (below diagonal) correlation coefficients for grain yield, TKW and protein content of four wheat crosses 102
2.7	Selection index coefficients, heritability, phenotypic and genotypic standard deviations of Smith-Hazel index and the standard deviation of the aggregate genotype in four wheat crosses involving yield, TKW and protein ... 104
2.8	Desired gains (PD1) selection index coefficients, heritability, phenotypic and genotypic standard deviations of PD1 indices and aggregate genotypes in four wheat crosses involving three traits 107
2.9	Desired gains (PD2) selection index coefficients, heritability, phenotypic and genotypic standard deviations of PD2 indices and aggregate genotype in four wheat crosses involving three traits 108
2.10	Selection differentials (proportion selected = 10%) for yield, TKW and protein using various unit-trait and index selection procedures in four wheat crosses expressed as a percentage of single-trait selection differentials 110
2.11	Predicted direct and correlated responses from selection based on various single-trait and SH selection index for grain yield, TKW, protein percent and net merit in F ₃ populations of four wheat crosses 114
2.12	Means, expected gains (R) and relative efficiencies (RE) from selection on various single-trait and selection indices for grain-yield, TKW and protein content in F ₃ population of wheat cross 1 116

TABLE	PAGE
2.13 Means, expected gains (R) and relative efficiencies (RE) from selection on various single-trait and selection indices for grain yield, TKW and protein content in F3 population of wheat cross 2	117
2.14 Means, expected gains (R) and relative efficiencies (RE) from selection on various single-trait and selection indices for grain yield, TKW and protein content in F3 population of wheat cross 5	118
2.15 Means, expected gains (R) and relative efficiencies (RE) from selection on various single-trait and selection indices for grain yield, TKW and protein content in F3 population of wheat cross 6	119
2.16 Means, realized gains (Ra) and Ra/R ratios from selection on yield and various selection indices for grain yield, TKW and protein content in wheat cross 1	121
2.17 Means, realized gains (Ra) and Ra/R ratios from selection on yield and various selection indices for grain yield, TKW and protein content in wheat cross 2	122
2.18 Means, realized gains (Ra) and Ra/R ratios from selection on yield and various selection indices for grain yield, TKW and protein content in wheat cross 5	123
2.19 Means, realized gains (Ra) and Ra/R ratios from selection on yield, TKW and various selection indices for grain yield, TKW and protein content in wheat cross 6	124
MANUSCRIPT 3	
3.1 Mean squares for grain yield, kernel weight and protein percent of wheat F3 population 1 grown at two locations ..	145
3.2 Mean squares for yield, kernel weight and protein percent of F3 wheat population 2 grown at two locations	146
3.3 Mean squares for grain yield, kernel weight and protein percent of F3 wheat population 5 grown at two locations ..	147
3.4 Mean squares for grain yield, kernel weight and percent protein of F3 wheat population 6 grown at two locations ..	148
3.5 Mean squares for yield, test weight, kernel weight and protein percent of selected F4 bulks from cross 1 grown at two locations	150
3.6 Mean squares for yield, test weight, kernel weight and percent protein of selected F4 bulks from cross 2 grown at two locations	151

TABLE	PAGE
3.7 Mean squares for yield, test weight, kernel weight and percent protein of selected F4 bulks from cross 5 grown at two locations	152
3.8 Mean squares for yield, test weight, kernel weight and percent protein of selected F4 bulks from cross 6 grown at two locations	153
3.9 Estimates of heritability (h^2) and genetic advance (R) on the basis of single-plot (SP) and multiple-plot (MP) selection, offspring-parent regression and intergeneration correlation methods for yield, kernel weight and percent protein at two levels of selection intensity (P = 5% and 10%) in wheat F3 population 1	156
3.10 Estimates of heritability (h^2) and genetic advance (R) based on single-plot (SP) and multiple-plot (MP) selection, offspring-parent regression and intergeneration correlation methods for yield, kernel weight and percent protein at two levels of selection intensity (P = 5% and 10%) in wheat F3 population 2	157
3.11 Estimates of heritability (h^2) and genetic advance (R) based on single-plot (SP) and multiple-plot (MP) selection, offspring-parent regression and intergeneration correlation methods for yield, kernel weight and percent protein at two levels of selection intensity (P = 5% and 10%) in wheat F3 population 5	158
3.12 Estimates of heritability (h^2) and genetic advance (R) based on single-plot (SP) and multiple-plot (MP) selection, offspring-parent regression and intergeneration correlation methods for yield, kernel weight and percent protein at two levels of selection intensity (P = 5% and 10%) in wheat F3 population 6	159
 APPENDIX	
A-1 Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks and parents of wheat cross 1 grown at the Point	191
A-2 Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 1 grown in Glenlea	192
A-3 Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 2 grown at the Point	193

TABLE		PAGE
A-4	Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 2 grown in Glenlea	194
A-5	Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 5 grown at the Point	195
A-6	Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 5 grown in Glenlea	196
A-7	Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 6 grown at the Point	197
A-8	Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 6 grown in Glenlea	198

LIST OF FIGURES

FIGURE		PAGE
	MANUSCRIPT 2	
2.1	Response to selection in one generation	90
2.2	Means of the best F3 lines in grain yield and protein (%), respectively, their F4 bulks and parents in wheat popula- tion 1 grown at the Point	111
2.3	Means of the best F3 lines in grain yield and protein (%), respectively, their F4 bulks and parents in wheat population 6 grown in Glenlea	112

ABSTRACT

Early generation information, viz., F1 heterosis, F1, F2, and F3 average performances, offspring-parent regression, and intergeneration correlation were used to select among six wheat crosses.

The F1 tests were effective in classifying crosses as poor and promising. Both F1 yield evaluation and application of weight-free index identified two of the top hybrid populations. Although the cross (C2) that showed significant F1 heterosis for yield gave high yielding lines in F3 and F4, results in general indicated that F1 heterosis for yield is of no or little value in predicting the potential of crosses.

The low and inconsistent F3 on F2 regression and intergeneration rank correlation coefficients indicated that F3 yield performance cannot be predicted using F2 single plant productivity. The stability of kernel weight, however, suggested that it may be a better component trait for predicting the potential of crosses in later generations.

Grain yield and percent protein were found to be negatively correlated in all populations studied giving genetic correlation coefficients as high as -0.87.

The simultaneous improvement of yield and protein in wheat has been difficult mainly due to the existence of strong negative correlation between yield and protein and lack of proper selection method. The methods of quantitative genetic theory were used to investigate selection differentials, expected and observed direct and correlated responses to simultaneous improvement of yield, kernel weight and protein content in F3 and

F4 generations of four spring wheat crosses.

Selections based on the Smith-Hazel index and yield per se were found to be superior in identifying high yielding F3 lines but resulted in substantial decrease in grain protein level. Conversely, a 1.0% increase in protein from selection for protein per se depressed grain yield as much as 536 kg/ha below the population mean, reducing the expected yield gains by 250%. The weight-free indices, particularly EW3 and EW4, and the desired gains indices were effective in improving protein content but were less efficient in identifying high yielding lines. Selection in the opposite direction using EW2 reduced all the traits significantly compared to the mean of the unselected population indicating the effectiveness of the unweighted selection index.

The observed genetic gains from selection based on yield per se, the SH, EW3, and EW4 indices were slightly lower than the expected advances in populations C1, C2, and C6 ($R_a/R = 70\%$ to 85%) but were higher in C5 ($R_a/R = 126\%$ to 143%).

It was concluded that weight-free and the desired gains indices can be used to improve grain yield and grain protein simultaneously.

The study dealing with the effect of methods of parameter estimation on the estimates of heritability and expected genetic advance showed that the variance components method of estimating h^2 overestimated "true" heritability, whereas the O-P regression method underestimated the h^2 values. The intergeneration correlation procedure gave intermediate values of h^2 and expected genetic advance. Within the AOV procedures, estimation of h^2 and R based on single-plot measurement in two locations resulted in lower estimates of h^2 of yield, TKW and protein. It is suggested that the use of single plot reference unit of combined data or intergeneration

correlation method will give less biased and attainable levels of heritability and expected genetic progress.

GENERAL INTRODUCTION

"... we must recognize that knowledge itself - theory, invention, discovery, technology - and human skills must be shared globally if the world hunger problem is to be solved." C.R. Wharton, Jr. (1980)

As the population of the world continues to increase, the capability of man to harness nature effectively and to produce enough to meet his requirements will be challenged increasingly. And the need for more food in the world increases the importance of the major cereal crops. This requires an increasing body of knowledge and its application in the areas of genetics, plant breeding and physiology in a constant effort to develop crop varieties with greater photosynthetic efficiency, more efficient uptake of soil nutrients, as well as an increased genetic resistance to disease, pests, and environmental stress. It is only through such determined, constant effort and the employment of various scientific and technological innovations that the agricultural sector of any economy can continually increase food production to satisfy the needs of its population today and in the future.

Wheat is one of the most important sources of nourishment for millions of people in the world. Therefore, the development of productive wheat varieties with increased amount of protein and high nutritional quality has been the subject of several investigations (Briggs and Shebeski, 1971; Wallace et al., 1972; Donald, 1968; Evans, 1975; Johnson et al., 1979). The objective of many wheat breeding programs is the simultaneous improvement of the crop for several desirable complexly inherited quantitative traits such as yield, protein content and kernel characteristics.

The idea of this study originated from the wheat program in Ethiopia whose focus was on the simultaneous improvement of yield and adaptability, kernel size and color, and percent protein. In addition to yield, large and white kernel is desirable for a new variety to be acceptable by the farmer and the buyer. The need for improved level of protein quantity and quality is also widely felt because cereals contribute a significant proportion of the diet of the people. However, multiple trait selection methods have never been attempted and as a result, improvement in one trait has caused an undesirable shift in another.

The search for an objective method of selection which can provide the best criterion that will determine the aggregate performance of selection of lines has been going on for many years. The selection index method first proposed by Smith (1936) and later modified by others (Kempthorne and Nordskog, 1959; Tallis, 1962; Elston, 1963; Pesek and Baker, 1969) has been shown to be the most efficient procedure for maximizing aggregate genetic progress (Hazel and Lush, 1942; Young, 1961). This method is widely used by animal breeders and to a lesser extent by plant breeders in an attempt to improve several traits simultaneously. In wheat, index selection for simultaneous improvement of multiple traits would be valuable to investigate intergeneration comparisons, as among F₂, F₃ and F₄ in relation to early generation selection. These evaluations and comparisons enable the breeder to assess and select potentially promising crosses and to estimate genetic variances and covariances in early generations so that he can determine heritabilities and expected genetic advance at an early stage of the selection program.

For this study, six crosses were carried out in the greenhouse in 1978 and F₁ tests were made in the same year at the Point, Winnipeg. The

six populations were grown in Obregon, Mexico, in 1979 and four crosses were selected and advanced into F3. The F3 experiments, consisting of 100 lines, parents and standard checks in each cross, were replicated three times. The tests were grown at the Point and Glenlea, Manitoba, in the summer of 1979. After selection in the F3 using different single trait and index selection methods, F4 tests were carried out at both locations in 1980. In all the above-mentioned experiments, yield, 1000-kernel weight, protein percent, etc. were measured based on single plants in F2 and based on standard plots in F1, F3 and F4.

The objectives of the various genetic selection studies in the project were:

- 1) To measure the genetic parameters concerning yield, kernel weight and protein content in early generations (F1 to F4) of four wheat crosses,
- 2) To identify superior crosses using early generation information, namely F1 heterosis, F1, F2 and F3 average performances, offspring-parent regressions and intergeneration correlations based on unit-trait and index selection methods,
- 3) To measure and compare the expected genetic gain and realized genetic response to simultaneous improvement of yield, kernel weight, and protein content in F3 and F4 generations of four spring wheat crosses based on single trait selection and three classes of selection index,
- 4) To determine and assess the direct and correlated responses due to selection on various traits and indices and compare the relative efficiencies of selection methods, and
- 5) To study the effect of experimental variables, particularly various methods of parameter estimation on the estimates of heritability and predicted genetic advance in yield, kernel weight and percent protein.

LITERATURE REVIEW

Selecting Superior Crosses in Early Generations of Wheat

In this section, selected reports in the areas of early generation selection, heterosis, bulk prediction of line performance, and selecting potentially promising crosses will be reviewed.

Early Generation Selection

Selection for grain yield is the most important objective of many wheat breeding programs. Conventionally selection in early generations consists of eliminating only those lines with undesirable characters such as disease susceptibility, or selection on the basis of an indirect estimation of yield by observing morphological characters and measuring yield components. From time to time attempts have been made by many breeders to evaluate yield potential on the basis of early generation testing (Shebeski, 1967; De Pauw and Shebeski, 1973).

Shebeski (1967) and Snee (1977) stated that for quantitatively inherited characters such as grain yield the frequency of genotypes with all the more desirable genes in either the homozygous or heterozygous condition is highest in the F₂ generation. This frequency decreases rapidly with increased homozygosity. Therefore, they argue the probability of selecting the most desirable genotype(s) is highest in the F₂ generation. At this stage, selection is based on single plant performance. However, selection based on individual F₂ plant productivity is commonly reported to be ineffective (McGinnis and Shebeski, 1968; Knott, 1972;

Bell, 1963; Hamblin and Donald, 1974; De Pauw and Shebeski, 1973).

Allard (1960) states that this ineffectiveness is mainly due to the high proportion of environmental variability relative to additive genetic variance. Selection involving complex honeycomb layouts as proposed by Fasoulas (1973, 1979) to minimize competition and environmental variance is considered to be impractical.

Many workers have also studied the effectiveness of selection based on F3 yield testing (Shebeski, 1967; De Pauw and Shebeski, 1973; Knott and Kumar, 1975; Sneep, 1977). Although some of these workers have reported effective selection for yield in F3 generation, there are a few limiting factors to F3 yield testing. These include the limited quantity of seed produced from individual F2 plants, therefore limiting the number of replications. If on the other hand replication and number of test environments are increased, the tests require a considerable amount of seed, land and labor (O'Brien et al., 1977). To solve some of these problems, Townley-Smith and Hurd (1973) proposed the use of a rolling plot mean to minimize the effect of soil heterogeneity for those lines not replicated.

In line with previous reports, Sneep (1977) discussed the difficulty with self-fertilized crops in selecting the best possible genotype(s) for a trait controlled by many genes. He points out that the single seed descent (SSD) method as proposed by some breeders (e.g. Knott and Kumar, 1975) will result in the loss of many genotypes through genetic drift. Alternatively, he proposed that selection be based on unreplicated F3 yield tests with a check cultivar sown every fourth plot. The yield of the F3 lines would then be expressed as a percentage of the nearest two check plots. The validity of the proposal would then depend on the

effectiveness of F3 yield tests in identifying genetically superior F3 lines. The available evidence in this area is contradictory.

The procedure used by De Pauw and Shebeski (1973) is essentially similar to the one proposed by Sneeep (1977) except that they planted a check cultivar every third plot and harvested all the three rows rather than just the center one. The yields of F4 bulks and F5 lines derived from selected F3 lines were then measured. Regression and correlation coefficients between F4 and F3 and F5 and F3 were significant. Briggs and Shebeski (1971) carried out similar studies comparing F3 lines and F5 lines derived from them. They observed a high rank correlation in one year but no significant correlation in two additional years. O'Brien et al. (1978) used F3 yield tests with three replicates of three-row plots. They reported significant realized response to selection as measured in F4 and F5 bulks in two of four crosses. However, the number of replicates used require considerable amount of seed, land and labor.

On the other hand, Knott (1972) examined the offspring-parent (F3 on F2) regressions and concluded the size of the regression coefficients to be of little practical breeding value. Knott and Kumar (1975) compared a procedure involving F3 yield tests with single seed descent (SSD) method. The F3 tests consisted of single row plots with three replicates. The regression coefficients of F5 yields on F3 yields for two crosses were low (0.29 and 0.14 respectively). Therefore, they concluded that F3 yield testing was of doubtful value.

Heterosis and Evaluation of F1 and F2 Performance in Wheat

The genetic basis of heterosis in bread wheat has not been studied exhaustively and yet is one of the most important areas of knowledge in

understanding the nature and exploitation of heterotic vigor.

Knott (1965) examined yield of F1 hybrids from a wide range of parental types. Though heterosis was present, no hybrid exceeded the check cultivar. The F1 yields followed closely the mean yield of the respective parents. Later, Knott and Sindagi (1969) tested F1 and F2 hybrids of diallel crosses of six hard red spring wheat varieties. They reported that heterosis was not significant in either generation and therefore no cross appeared to be promising. Singh and Singh (1971) studied heterosis for yield and yield components in F1, F2 and F3 generations in ten crosses of wheat under normal seeding rate. They reported that 80% and 60% F1 hybrids outyielded the high parent and the standard check by up to 44.3% and 36.4%, respectively. Two complete diallel crosses with eight and five parents were used by Walton (1971) to study the expression of heterosis in spring wheat of Canadian, Mexican, and American origin. In both experiments general combining ability was important to yield and yield components. Specific combining ability for yield, however, was measurable only in the five-parent diallel cross.

Widner and Lebsack (1973) evaluated the parents and 45 F1 and F2 generations from a 10-parent diallel cross of durum wheat at two locations in the first season and 17 of the 45 crosses in one location in the second year. For the first season, F1 heterosis percentage for grain yield relative to the higher parent ranged from -19% to 84%. Although 17 hybrids showed significant heterosis for yield, none of them significantly excelled the standard check variety. The variances due to genotype x environment interactions were significant for F1 hybrids and parents, but this was not the case for F2 populations. The general combining abilities were significant among F1's and among F2's for all traits, whereas specific combining

abilities among F1's were significant only for kernel weight, test weight, and seedling vigor.

Bulk Prediction of Line Performance

Harrington (1940) studied F3 bulks of six wheat crosses and evaluated their predictive ability by testing F6 through F8 selected lines. His results indicated that replicated F3 tests could be valuable to predict the yielding potential of advanced lines. For winter wheat, Fowler and Heyne (1955) reported contrary results. They tested the parents, F3, F4 and F5 bulks of 45 crosses to predict the yield of randomly selected lines from each F5 bulk. The conclusion was that bulk and parental performance were of little value in predicting yield of selections in later generations. Later, Busch et al. (1974) investigated 25 populations developed from crosses among four high and four low-yielding parents of HRS wheat. After evaluating the F4 and F5 bulks, parents and 21 randomly selected F2-derived F5 and F6 lines from each cross, they observed that the average cross performance of the lines and the average of the top five lines were highly correlated with the mean of the F4 and F5 bulks ($r = 0.90$ and $r = 0.88$, respectively). They reached the conclusion that bulk yield testing at relatively advanced generations could be useful to identify crosses with high yielding potential lines and higher frequency of desirable genotypes.

Pederson (1969a, 1969b) used prediction equations for self-fertilizing species to determine efficient selection procedures. He found between family selection was more effective than either within family selection, individual selection or a more complex combined selection. Harlan (1940) using 390 barley crosses compared the pedigree and bulk methods and concluded no differences in the effectiveness of the procedures in isolating

high yielding lines. Torrie (1958), studying six soybean crosses, also reached the same conclusion. However, the work of Raeber and Weber (1953) indicated the pedigree method to be superior to the bulk approach in isolating productive soybean lines.

Voigt and Weber (1960) carried out a similar comparison of the efficiency of the bulk, pedigree and family (early generation selection) methods in soybean. Results showed the family method of selection to be more efficient than the other two procedures. In contrast, a comparison of the same procedures, namely bulk, pedigree and early generation testing, in soybean by another group of workers (Luedders et al., 1973) showed no significant yield differences among the lines obtained by the three selection methods.

To shed more light on the question of superiority of alternative selection methods, Boerma and Cooper (1975) designed a comparative study involving three selection procedures, namely modified early generation testing (EYT), pedigree (PS), and single seed descent (SSD). After evaluating four segregating soybean populations, they reported that the means of all selected lines, the means of the five top yielding selections, and the highest yielder from each population showed no consistent differences due to selection methods. As a result, these workers concluded the SSD procedure to be the most efficient because it required the least selection effort compared to the other approaches. It also permits a rapid advance of the segregating material, and expensive yield testing was not required until later generations.

Selecting Superior Crosses

A careful screening of parents before carrying out various crosses in

a breeding program is an essential component of developing productive varieties. Multivariate and diallel cross analyses have been shown to be useful tools in choosing proper parental combinations and evaluating crosses after hybridization (Bhatt, 1970, 1973; Lupton, 1965; Whitehouse et al., 1958; Curnow, 1980). However, these procedures are highly laborious and their predictive value in practical plant breeding is not fully established.

In most cereal breeding programs, a number of undesirable crosses are eliminated in early generations through visual evaluation of morphological characters. Recently, however, plant breeders have started evaluating crosses by using some sort of early generation testing.

Stoskopf and Fairey (1975) used a 10-parent diallel to carry out replicated F2 bulk yield experiments. Using this approach they were able to retain 10% to 15% of the top yielding crosses for single plant selection in F3. Keydel (1973) designed a graduated scale of values of inherent differences between the parental varieties of winter wheat and F1 individual plant performance and drilled F2 tests. The implication of this study was that it is possible to reliably select promising crosses by using such an approach.

Most recently, Nass (1979) evaluated the yields of F1, F2 and parents for the purpose of identifying potentially high-yielding crosses in wheat. He tested two sets of spring wheat crosses and parental cultivars in replicated single row (F1) and multi-row (F2) plots over five years. Two of the highest yielding and two of the lowest yielding crosses in each set were selected based on F1 yield performance for further evaluation in later generations. Lines from high-yielding crosses in F1 had significantly higher means in F4 than those from low-yielding crosses. The

The high-yielding crosses had three to four times as many lines yielding in top 10% in F4 compared to the low-yielding crosses. He also observed significant correlations for yield between F1 and F2, whereas F1 and mid-parent values were not correlated. He recommended the use of mid-parent, F1 and F2 yield tests as a useful set of observations to identify potentially superior crosses in wheat.

It is a common experience among wheat breeders that certain combinations of selected cultivars or genetic stocks combine well producing superior offsprings, whereas others involving equally productive parents give disappointingly poor crosses. Diallel crosses have been used extensively to determine the complex genetic interaction systems of combining ability of selected parents. However, the present knowledge on the repeatability of diallel estimates over various generations is not adequate.

In wheat, proper diallel analysis utilizing F1 seed has been difficult because of the small quantity of seed that could be produced by hand pollination. Therefore, Bhullar et al. (1979) suggested the use of later generations for diallel analysis. These workers used F1 to F5 generations to assess combining abilities for grain yield and yield components in a seven-diallel bread wheat cross. For most traits, both general and specific combining ability variances were significant in all generations. General combining ability estimates predicted promising F5 bulks than parental performance. Among segregating generations, F2/F3 estimates gave superior results than F1 measurements. As a result, they recommended to use the relative performance of F2 progeny bulks to study combining abilities and predict the potential of advanced generation bulk hybrids (F5).

Very recently, Gordon (1980) evaluated the incomplete partial diallel as a tool for parental selection using a simulation study. He stated that, in self-pollinating crops, 20% of the partial diallel could give adequate information to reliably rank the parental general combining abilities, if general combining ability contributions are equal or greater than specific combining ability effects. Thus, he projected that under circumstances where a trait has a significant additive genetic variance, general combining ability estimates may be beneficially employed to predict performances of crosses.

Curnow (1980) also reported the result of a theoretical and simulation study to compare the techniques of selecting crosses. He employed the yields of the individual crosses in comparison with the sum of the estimated general combining abilities of the two parents of each cross. The choice between these alternative procedures depended on the magnitude of the g.c.a. and s.c.a. variances. Selection based on general combining ability is superior unless the s.c.a. variance of the parents exceeds twice their g.c.a. variance in which case selection must be based on individual cross performance.

Genetic Improvement of Yield in Wheat

In breeding self-pollinating crops the objectives are to develop true breeding genotypes from hybrid progenies, and to select lines that have the desired combination of productivity and quality characters. To obtain such potentially promising hybrids, the genetic variability both in overall productivity and environmental adaptation of sub-populations that are scattered eco-geographically must be exploited. Accepting the suggestion that there is considerable genetic variation among populations

of self-pollinating agricultural species such as wheat, the challenge to the breeder is the incorporation of various useful alleles into potential cultivars. This has posed the major problem of identifying optimum and inexpensive methods for synthesizing populations that combine a high proportion of the favorable alleles that exist in several breeding populations. For the wheat breeder, the central problem has always been synthesizing the best possible homozygous genotype from the alleles present in different genetic stocks available to him.

Such an endeavor requires sufficient knowledge of the genetics of quantitatively inherited characters such as yield and component of yield, also understanding of the roles of linkage and genotype-environment interaction. The review of this section will deal with these subjects followed by alternative approaches of wheat breeding for yield.

Genetics of Yield and Kernel Weight in Wheat

The choice of efficient breeding methods depends primarily on knowledge of the genetic systems controlling the characters of interest. Presently, there is a general agreement that yield is controlled quantitatively and that it is a complex character whose expression is influenced by the functions and interactions of several physiological processes (see Von der Pahlter and Goldberg, 1971; McNeal et al., 1978). Hence, Wallace et al. (1972) suggest that the minimum number of genes controlling yield must be equal to the total number of 'physiological components', assuming that each physiological component is controlled by a single gene. This is interpreted to mean that all genes in the plant system affect yield because any gene which affects photosynthesis and related processes will have direct or indirect influence on yield. This generalization is in agree-

ment with the conclusions of Grafius (1959), Williams and Gilbert (1969) and Malborn (1969) that genes for yield do not exist as such. This leads to the alternative thesis that the genetic control of yield is indirect and it acts through the control of the physiological component processes (Adams and Grafius, 1971; Thomas et al., 1971).

Recently, research evidence has accumulated that the ability of the wheat plant to store assimilates in the grain may limit yields as much as the capacity of the crop to provide the assimilates during the grain filling stages (Evans, 1975). The storage capacity of the crop is mainly determined during the period between inflorescence initiation and anthesis. Therefore, the breeder must take into consideration all the three important stages in the plant's life cycle, viz. vegetative, reproductive and grain filling, because high productivity in terms of economic yield will be attained only when the yield determining processes operating in the whole life cycle are in balance with one another.

The use of simple additive-dominance models in genetic studies of quantitative characters could result in biased estimate of genetic parameters if epistatic interactions are present (Ketata et al., 1976a; Comstock and Robinson, 1952; Mather and Jinks, 1971). Ketata et al. (1976a) investigated the genetic systems controlling yield and other traits in a set of winter wheat cultivars with an objective of determining the presence and significance of epistasis. Their results showed that epistatic interactions affect the expression of grain yield. The same was true for kernel weight in one of two experiments. Consequently, they concluded that epistasis may be of importance in the genetic variation of yield and some agronomic traits in wheat and the inclusion of epistatic gene effects in genetic models will improve the accuracy of parameter

estimation.

In a related study, Ketata et al. (1976b) estimated heritability and gene effects for grain yield and other agronomic characters in a winter wheat cross. They used parental, F₁, F₂ and backcross generations. The narrow-sense heritability estimates for grain yield and kernel weight were 0.16 and 0.65, respectively. Significant epistasis was detected for grain yield while additive gene effects were the major source of genetic variation for kernel weight indicating that effective early generation selection for high kernel weight is possible.

The determination of the magnitudes of the various components of genetic variance has become a common practice in any inheritance study of quantitative characters. The occurrence of predominantly additive gene effects is useful to the wheat breeder, because the genetic advance that he expects from selection depends on this portion of the total genetic variation. From their studies with durum wheat, Amaya et al. (1972) found that dominance effects was the major component of genetic variation for grain yield. In contrast, Chapman and McNeal (1971) demonstrated that epistasis also contributed significantly to the expression of grain yield in a spring wheat cross.

Sidwell et al. (1976) used parents, F₁, F₂ and backcrosses derived from two HRW wheat cultivars to study the genetic control of grain yield, kernel weight and other yield-related traits. They observed significantly smaller additive and dominance effects than the environmental variance component for all characters studied except kernel weight. Kernel weight showed both high narrow-sense heritability (0.44) and high broad-sense heritability (0.43), whereas the values for grain yield were only 0.36 and 0.19 for broad- and narrow-sense heritabilities, respectively. Therefore,

they suggested that selection for kernel weight in early generations may be very effective in increasing grain yield in wheat. The range of heritability estimates reported for grain yield and kernel weight in wheat is wide. Johnson et al. (1966) using F2 and backcross populations of winter wheat reported narrow-sense heritability estimates of 0.55 and 0.10 for kernel weight and grain yield, respectively. On the other hand, Fonseca and Patterson (1968) obtained intermediate to low heritability estimates for both these traits. Their estimates were based on the regression of F1 and F2 means on mid-parent values of a seven-parent diallel cross.

Meanwhile Baker et al. (1968) concluded that selection on the basis of kernel weight is advantageous because of its significant positive correlation with yield. Conversely, Hsu and Walton (1971) found no association between kernel weight and grain yield in spring wheat. Baker et al. (1968) also reported heritability values ranging from 0.77 to 0.93 for 1000-kernel weight depending on numbers of replicates, test locations, and years. The equivalent heritability estimates for yield ranged from 0.28 to 0.74.

Reddi et al. (1969) using F3 and F4 generations of two wheat crosses obtained relatively high heritability estimates for kernel weight. Earlier, Worzella (1942) after investigating F3 and F4 generations of three crosses involving three spring wheat cultivars, reported that kernel weight, although significantly influenced by environmental conditions, was quantitatively inherited. Later, Jasnowski (1953) suggested that only three pairs of genes are involved in controlling kernel weight in wheat. Nevertheless, a study by Boyce (1948) demonstrated high kernel weight to be dominant over low kernel weight. Copp and Wright (1952) used a

wheat cross of widely different parents to study the inheritance of kernel weight. Based on their work they concluded that kernel weight was controlled by a few major genes.

Parental, F1, F2, F3 and backcross generations of a cross involving a large-kernelled parent, Selkirk, and a small-kernel parent, Chagot, were used by Sharma and Knott (1964) to study the inheritance of kernel weight in spring wheat. They estimated additive and dominance components of genetic variance and found that the additive effects was predominantly significant. The heritability estimates they obtained ranged from 0.37 to 0.69. On the basis of these observations they concluded that kernel weight was controlled by relatively few, possibly four, genes.

Sun et al. (1972) designed a diallel cross of four spring wheat cultivars to investigate the inheritance of kernel weight. They found that additive and dominance effects were predominant and more consistent than epistatic effects in determining kernel weight. As far as interaction effects were concerned, additive x additive and dominance x dominance types of epistasis were more important than the additive x dominance interaction. Estimated broad sense heritabilities ranged from 0.51 to 0.85 while heterosis in relation to mid-parent values ranged from -4.3% to 31.2%. The study of variation and covariation of agronomic traits in durum wheat (Lebsock and Amaya, 1969) revealed that the improvement of test weight and grain yield can be attained by selecting for high kernel weight in F2 and F3 generations. This conclusion was supported by their finding of high heritability estimate (0.72) for kernel weight. Knott and Talukdar (1971) transferred high kernel weight from 'Selkirk' to 'Thatcher' by backcrossing and obtained large-kernelled lines that out-yielded Thatcher. Nevertheless, yields fluctuated considerably depending

on the level of compensation in other yield components. In addition they reported significant positive correlation between grain yield and kernel weight.

Breeding for Yield in Wheat

In this section we do not intend to extensively review the area of wheat breeding for yield. The topic is far too large and complex to be adequately treated in this short review. However, selected papers in a few selected areas will be briefly covered.

Many researchers prefer, as covered in another section of this review, early generation selection for quantitatively inherited traits such as yield. But there are some pertinent difficulties ineffectively employing such an approach. These include limited quantities of seed and high number of entries limiting the extent of testing, the difficulty of separating genetic variation from non-heritable contributions, and extensive space and labor requirements. All conventional wheat breeding methods involve three stages: (1) creation of a population with adequate genetic variation, (2) selection and purification, and (3) maintenance of breeding lines. These stages influence the choice of breeding methods to be followed. Regardless of breeding methods used, the most significant contribution of plant breeding is the development of varieties with high physiological efficiency in terms of the final economic product. Frey (1971) and Russell (1974) have reported such achievements by breeders by significantly improving the yielding capacity of corn and other crops. Thus, the improvement of the architecture of the wheat and other plants and the application of yield component breeding techniques have been effectively used to a large extent to improve the physiologic productivity

and grain yield. Some of the extensive efforts directed at attempts to identify morphological characters correlated with yield are successfully exploited while some efforts did not contribute to breeding progress to the extent that some breeders thought it should (Rasmusson and Cannell, 1970; Grafius, 1960, 1965; Adams, 1967; Donald, 1968).

The application of yield component breeding to improve productivity would be more effective if the components under consideration are highly heritable and positively correlated with grain yield and with each other. To the contrary, however, negative correlations among the major components and other yield-related traits are not uncommon (Adams, 1967; Fonseca and Patterson, 1968; Hsu and Walton, 1971; Knott and Talukdar, 1971).

Hsu and Walton (1971) working on a diallel cross involving five spring wheat cultivars reported the relationship between yield and its components in that spike length, tiller number, and kernels/spike were significantly and positively correlated with yield, whereas kernel weight was not. They also found that tiller number and kernels per spike were positively correlated but the relationship between kernel weight and tiller/plant was negative. Adams (1967) in his studies with the field bean observed that yield components are independent characters that are free to fluctuate in response to environmental factors, and negative correlations among them are a widespread phenomenon. Earlier, Grafius (1965) attempted to use a geometrical concept of representing the three major yield components, tiller number, kernel weight, and kernels/spike, in various cereals. Based on observations that the individual yield components are more simply inherited than yield per se, he suggested practising selection on components in order to increase grain yield. The possibility of

improving yield by employing the major yield components is also supported by results from other workers (e.g. Hsu and Walton, 1971; Johnson et al., 1966; Knott and Talukdar, 1971).

The wheat breeder in his attempts to breed for improved yield while at the same time attempting to construct gene pools from which he can select high-yielding and better adapted lines, is faced with two important questions (Wright, 1976). Firstly, he has to decide whether to focus his efforts and resources on the production of a single productive variety with wide adaptation or to develop cultivars well-adapted to specific growing environments both in terms of location and management practices. This option is complicated by the occurrence of genotype-environment interaction. Secondly, the methodology of evaluating breeding material under the selected environments of growing conditions has to be determined.

Workers in the field have addressed these questions both when the environments are selected randomly (Dickerson, 1962) and non-randomly (Comstock and Moll, 1963). Finlay and Wilkinson (1963), and later Eberhart and Russell (1966), have developed methods of regression analysis whereby phenotypic values are regressed on to environmental effects. Finlay (1971) using their regression analysis technique reported that barley lines with significant increase in yield and adaptability were produced. Eberhart and Russell (1966) described the yield stability of a genotype to be the function of three parameters: (1) mean yield over a population of environments, (2) the regression coefficient that measures response over environments, and (3) the residual term. According to them a stable cultivar combines high mean yield with a unit regression coefficient and a minimum residual term. Several researchers have attempted

to apply the regression analysis technique proposed by Eberhart and Russell (1966) to study yield stability of various crops (Frey, 1972 in oats; Francis and Kannenberg, 1978 in maize; Jowett, 1972 in sorghum; Bains, 1976 in spring wheat). Bains (1976) working on spring wheat crosses found that the stability of progenies was closely correlated with that of their parents.

In contrast, other workers have carried out regression of phenotypic values on to genotypic effects (Wright, 1971). Recently, Wright (1976) examined regression analyses methods of genotype-environment interaction in relation to the relative efficiencies of selection for specific or general adaptation to growing environments. He looked at three alternative models: (1) the basic model on the AOV method, (2) a model basically similar to that of Finlay and Wilkinson (1963) and Perkins and Jinks (1968) involving the regression of an interaction component on to the environmental effects, and (3) the regression of the interaction term on to genotypic effects. As a result, he concluded that the two models involving the regression of the interaction term on to environmental effects or genotypic effects were equivalent when concurrence of the regression lines was observed. He pointed out that selection for general adaptation will result in more efficiency if the regression of the interaction term on to the genotypic effect is important. Conversely, if the regression does not hold, selection targeted at general adaptation will be less efficient and therefore selection should be based on grouped environments for the purpose of achieving a greater degree of homogeneity.

Falconer (1952, 1960) showed how the concept of correlated response between traits can be used to deal with selecting for a character under different environments. He suggested that results from different sites

be handled as if they were results from different traits and the method of correlated response be applied to analyze the data. Hence, the expected response in one environment to selection carried out in another can be estimated. Comstock and Moll (1963) warned that the estimated genotypic variance based on a single location test will be biased upward and thus influencing the magnitude of heritability and response to selection estimates. Baker (1968, 1969) working on small cereals stressed that the genotype-environment interaction variances are significant and important under most circumstances hence the breeder must take this into consideration. Later, Baker (1971a) investigated the effect of qualitatively inherited characters such as stem rust and leaf rust on the genotype-environment interaction variance of yield in wheat and concluded that a significant portion of the observed genotype-environment interaction effect may be caused by the influence of simply inherited traits such as leaf diseases.

Although the effect of linkage is of particular importance in plant breeding, most work in the area has been focused on the theoretical significance of linkage disequilibrium (Slatkin, 1975; Bulmer, 1976). Genetic linkage of quantitative characters affects the response expected from selection as measured by probabilities of fixation of favorable alleles in a genotype of interest. A simulation study by Bailey and Comstock (1976) confirmed that the probabilities of fixation of favorable alleles increased with coupling but decreased with repulsion. They observed that the significance of linkage on response to selection depends on the distribution of the desirable alleles between the two parents involved. This is interpreted to mean that if the parent lines are equivalent in genetic value, linkage will have little effect on fixation probabilities.

Nevertheless, coupling will be more effective than repulsion if one parent is significantly better than the other resulting in an increase in probability of fixation.

Genetic Improvement of Wheat Protein

Today wheat is one of the most important sources of nourishment for millions of people in the world (Inglett and Anderson, 1974). As the population of the world continues to increase, shortages in available food supplies will make it highly desirable that nutritional quality of various crops be improved. All presently used high-yielding cultivars around the world have protein levels less than desired amounts (Schmidt et al., 1974; Johnson et al., 1975). Therefore, the development of productive wheat varieties with an increased amount of protein and acceptable nutritional quality is an important but difficult challenge to plant scientists in the fields of genetics, plant breeding and physiology.

The effort to improve grain protein content will require the understanding of the genetical, physiological and environmental basis of its production. This section does not attempt to give an extensive review of the field but will try to summarize a few selected works. The review will include three specific topics: (1) genetic control of protein content in wheat, (2) relationship of grain yield and percent protein, and (3) genetic variability and breeding for high protein content.

Genetic Control of Protein Content in Wheat

The genetics of protein content in wheat, Triticum aestivum L., has been the subject of numerous investigations by plant geneticists, breeders and physiologists. Most of the studies lead to the general conclusion that the production of grain protein is genetically controlled and that

it is highly influenced by environmental variables.

Chapman and McNeal (1970) used parental, F₁, F₂, BC₁, BC₂ generations to study the inheritance of grain protein content in five spring wheat crosses. They reported that while epistatic interactions were absent, the additive component of genetic effect was highly significant in all five populations. However, they observed significant dominance effect in two of the five crosses. The F₁ and F₂ means were below the low-protein parent suggesting dominance of low-protein content. Based on the significance of the additive genetic effects, which are implied to be contributed by the parent with higher level of protein, they concluded that there is promising potential for improving percent protein through selection.

Haunold et al. (1962b) studied F₁, F₂, F₃ and F₄ generations of two crosses including Atlas 66 as a common parent. The distribution of F₂ and F₃ data showed no evidence of dominance for either the high or low protein. The mean grain protein content of F₂ plants and F₃ lines was intermediate to the parental cultivars. Using offspring-parent regression these workers obtained a heritability value as high as 0.65 for protein. In line with many previous reports, they concluded that protein in wheat is controlled multigenically (Ausemus et al., 1967; Worzella, 1942).

Diehl et al. (1978) used three wheat crosses involving three high-protein cultivars, namely 'April Bearded', 'Atlas 66' and 'Nap Hal' to determine the genetic differences in protein and lysine and to study the inheritance of protein and lysine concentration in the grain. The evaluation of spaced plants of the parental F₁, F₂ and backcross generations on each cross under two environments indicated the presence of additive gene effects for protein and lysine contents. Nevertheless, the

means of F1 hybrids were consistently lower than the mid-parent values and near or below the low-protein parent. Whereas the F2 means were approximately equal to the mid-parent protein level, backcross performances indicated that April Bearded and Nap Hal share common genes for protein content. In this study genotype x environment interactions for both protein and lysine were significant.

Since Middleton et al. (1954) first reported an elevated protein level in the soft red winter wheat 'Atlas 66', several workers have attempted to elucidate the genetic inheritance of protein content in this cultivar (Davis et al., 1961; Stuber et al., 1962; Sunderman et al., 1965; Lofgren et al., 1968). Middleton and his co-worker found Atlas 66 to produce 3.0% higher grain protein than the check cultivar they used. Greenhouse and field experiments by Haunold et al. (1962a) showed that Atlas 66 grain contained significantly elevated protein concentration supporting the results by Middleton et al. (1954).

Morris et al. (1973) using monosomic analyses found that chromosome 5D of Atlas 66 carries genes governing increased protein.

The inheritance of protein and sedimentation value was investigated by Hsu and Sosulski (1969) using diallel crosses involving four HRS wheat varieties. They reported an average broad sense heritability of 58% for protein. The heritabilities ranged from 42% to 71% for the six four-variety diallel crosses. Their genetic analysis showed that both dominant and recessive genes control the expression of high protein. Though they did not report F1 data, slight superiority of average F2 protein compared to the high-protein parent, indicated possible over-dominance for high protein.

To study the inheritance of high protein in 'Hand', Cowley and Wells

(1980) used parental, F1, F2, F3, BCF1 and BCF2 generations in a field (individual plant) experiment. They reported that Hand differed from Centurk and an experimental line for high protein by one dominant gene. They also found that high protein selections were not prevalent in crosses involving only high-protein parents.

On the other hand, Boyadjieva (1975), in a study of parental, F1, F2, BCF1 and BCF2 generations of three wheat crosses, found that high protein was recessive in the cross 'Panonja'/'Dardo' and 14% of the F2 population exceeded the high-protein parent. In another cross 'Valdichiana'/'San Pastore', high grain protein was recessive but no transgressive segregation was observed.

There are many reports dealing with heterosis and combining ability in the expression of wheat protein values. Mihaljev et al. (1979) investigated heterosis and combining ability in F1 hybrids of six crosses involving three winter and one spring wheat (Cajeme 71) varieties. Two of the six hybrids showed significantly higher percent protein than their respective better parent indicating positive heterosis. The other four crosses had no heterotic effect for grain protein. They suggested this to be due to considerable amount of environmental effect such as plant population density and recommended the evaluation of hybrids to be carried out under local environmental conditions. This result was in agreement with Griffing and Zsiros (1971) who reported that plant density and other environmental factors have an important influence on the magnitude of heterosis in wheat.

In the work of Mihaljev and co-workers, the analysis of variance for combining ability for percent protein showed both GCA and SCA to be highly significant. Nevertheless, the GCA was relatively larger in magnitude

than the SCA indicating the predominance of the additive gene effects in the genetic control of protein in the crosses used. Other workers (e.g. Chapman and McNeal, 1970; Ram and Srivastava, 1975; Ketata et al., 1976a; Bhullar et al., 1978) also reported significant additive gene effects for grain protein in wheat.

In contrast, Brown et al. (1966) reported non-additive gene effects to be significantly predominant.

Genetic Variability and Breeding for High Protein

Since Clark (1926) first reported on genetic investigations of grain protein in wheat, evidence for the existence of significant genetic differences in protein content in wheat and the potential for the exploitation of such inherent variability by breeding, has attracted much attention. Interest increased even more after the report of Middleton and co-workers in 1954. The two cultivars, Atlas 50 and Atlas 66, developed by Middleton carried genes for elevated grain protein from 'Fronodoso', a Brazilian cultivar. The high protein gene(s) in these two cultivars are closely linked with a gene for leaf rust resistance in Fronodoso (Johnson et al., 1968). Since this pioneering work, extensive efforts have been done in Nebraska and other parts of the world to improve the nutritional quality of wheat both in terms of protein quantity and amino acid balance. At present, the Nebraska group has systematically screened more than 25,000 wheats in the USDA World Wheat Collection for protein and lysine (Johnson et al., 1979). This work showed the existence of a range of variability for protein and lysine. Nonetheless, the success of producing high protein/lysine commercial varieties with high yielding capacity has been rather discouraging (Loffler and Busch, 1980; Baker

et al., 1968; Bhatia and Rabson, 1976).

Total variability for grain protein among common wheats, based on the evaluation of the world wheat collection maintained by the USDA, has amounted to 16 percentage points, ranging from 6% to 22%. Unfortunately, however, the genetic component of this total variation was only about 5 percentage points (Johnson et al., 1973; Vogel et al., 1975). The data also showed that the genetic variation for lysine in wheat is only about 0.5 percentage points. This indicates that the non-genetic contribution to protein level is so high that any major genetic improvement seems improbable.

There are some known major genes for protein in the wheat cultivars Atlas 50, Atlas 66, and Nap Hal. In addition, the existence of minor genes and modifier genes seem to be widespread among wheat cultivars and related wild species (Johnson et al., 1979). Winter wheat hybrids which carry T. timopheevi cytoplasm are known to have consistently higher protein than common wheat cultivars (Schmidt et al., 1970). Feldman and Avivi (1978) evaluated 12 populations of wild emmer (T. dicoccoides) collected in Israel. All of their collections were significantly higher in protein than the cultivated tetraploid (T. dicoccum and T. durum) checks. These workers stressed the point that T. dicoccoides and other wild relatives of modern-day cultivated wheats may be a good source of genes for protein.

If genes for protein are widespread in Triticum aestivum L. and its wild relatives, then the next question is whether this variability can be incorporated into productive varieties in wheat breeding programs around the world. There are three major problems confronting the breeder: (1) the actual genetic variability of protein is relatively low because the

major portion of the total variation is contributed by environmental factors, particularly soil nitrogen, (2) in spite of positive progress in the field, proper and inexpensive methods of nitrogen determination and screening for wheat breeding programs is still lacking, and (3) although there are some reports to the contrary, the inverse relationship between grain yield and grain protein is significant and real.

Though the large effect of soil and other environmental factors on grain protein has been established (Miezan et al., 1977; Zeleny, 1964; Finney et al., 1957; McNeal et al., 1972; Schlehuber and Tucker, 1959), Johnson et al. (1973) reported that genes for high protein from Atlas 66, which presumably affect both nitrogen uptake and translocation, were effective under a wide range of environments and soil fertility levels. They compared a high protein Atlas 66-derived line with Lancer, a normal protein wheat under several rates of nitrogen fertilizer. They found that while both cultivars responded similarly in yield to nitrogen applications, the high protein line maintained two percentage points superiority in grain protein over Lancer throughout the range of fertilizer levels. Thus, Johnson et al. (1979), using the variety Lancota as an example, argued that elevated grain protein and high yield are not incompatible when we consider the yield range of bread wheat cultivars grown in the U.S.A. Lancota is a HRW wheat variety developed in Nebraska and is reported to combine high yield, high protein percent and resistance to leaf rust and stem rust. On the other hand, several workers have concluded that environmental variables have a strong influence on protein in wheat and stress the fact that soil and climatic factors are more important than genotype (e.g. Schlehuber and Tucker, 1959).

To circumvent the problem of the lack of an efficient and effective

method of protein scoring in wheat, Jain et al. (1973) suggested a protein percent determination method calculated on a per seed basis rather than as a percentage of seed weight. They reported a three-fold increase in the heritability estimate of protein content and a significant positive correlation with seed size when this proposed method was used. The correlation between high protein and seed size was negative in the population when percent protein was used to score protein content. However, the question of an efficient and inexpensive method of determining protein in wheat is yet unresolved.

The third problem, that negative correlation between grain yield and protein, has discouraged many wheat breeders as it appears to center around the major problem of improvement of the two traits simultaneously. It is to this problem that we turn our attention in the next section.

Relationship of Grain Yield and Percent Protein

Grain protein content in wheat is a function of genetic factors interacting with soil and other environmental variables. Based on field and greenhouse experiments involving four varieties of wheat including Atlas 66 and Wichita, Haunold et al. (1962a) found that when soil nitrogen was not a limiting factor, Atlas 66 had the highest and Wichita the lowest grain protein percentages. In addition, at low available soil nitrogen, grain yield was negatively correlated with grain protein content. The literature contains several reports of such inverse relationship between yield and protein concentration in the wheat grain (e.g. Grant and McCalla, 1949; Malloch and Newton, 1934; Schlehuber and Tucker, 1959; Sunderman et al., 1965; Hsu and Sosulski, 1969; Baker et al., 1968).

Baker et al. (1968), using random lines of spring wheat crosses,

reported highly significant negative correlation ($r = -0.92$) between yield and percent protein. Based on their results, they concluded that it is not practically possible to improve protein content without adversely affecting grain yield. The underlying cause for this inverse relationship, however, has not been clearly understood. Recently, Bhatia and Rabson (1976) examined the bioenergetic implications of modifying cereal grain protein concentrations by means of genetic manipulations. Earlier, Sinclair and de Wit (1975) calculated seed biomass yield and nitrogen requirement in four different crops with a wide range of protein concentrations (8% to 38%). Their results showed that in any species, simultaneous increases in grain protein concentration and grain yield are incompatible from an energetic point of view. Such simultaneous increments compete for both the available carbon skeleton and energy derived from photosynthates. To calculate the energetic cost of increasing the level of grain protein in bread wheat, Bhatia and Rabson (1976) used the results of Penning de Vries et al. (1974), who reported that plants utilize 1 g of glucose to produce either 0.83 g of carbohydrates, 0.40 g of proteins, or 0.33 g of lipids. They found that a 1% increase in protein would require about a 1% increment in net photosynthates. This introduces the central point that any increase in grain percent protein will be associated with a commensurate decrease in carbohydrate percentage. For instance, in a wheat cultivar with a composition of 82% carbohydrate, 14% protein, 2% lipids and 2% minerals, a 1% increase in protein will result in carbohydrate percentage of 81% (Bhatia and Rabson, 1976). This implies that if this additional requirement is not met, any increase in protein content will reduce grain yield.

Heritability and Response to Selection

The practice of selection involves traits such as yield that are complex and quantitatively inherited. The relative magnitude of allele substitution effects determines the basic difference between qualitative and quantitative traits. If the effect of substituting one allele for another is small it indicates that the character is controlled either by numerous genes or a portion of the total variation is caused by environmental factors. Thus, the concept of heritability was originated to measure the degree of resemblance between relatives and to determine the magnitude of genetic variance, particularly the breeding value, relative to the total phenotypic variation.

Fisher (1918) and Wright (1921) defined the three components of genetic variance as: (1) additive genetic variance, (2) dominance deviations, and (3) deviations due to non-allelic interactions. This concept of components of variance was later applied by Lush (1941), Hazel and Lush (1942), Robinson et al. (1949) and others to determine the proportion of the total variance that is attributable to the average effects of genes.

Heritability

There are several techniques of estimating heritability. If reliable estimates of components of variance can be derived, the most classical method of estimating heritability is the variance components procedure. There are many approaches to this method depending on the genetic population one is dealing with, and the mating design used. In addition to the method of estimation, the heritability ratio is the function of the specific genetic population under consideration, the unit of measurement,

and environmental conditions. On the basis of the numerator employed in calculating the heritability ratio, two types of heritability values are defined for the same population. The ratio of additive genetic variance to the phenotypic variance is called heritability in the narrow sense whereas broad sense heritability is the ratio of the total genetic variance to phenotypic variance.

Sidwell et al. (1976) used the method developed by Mather and Jinks (1971) and others to derive components of variance in winter wheat by employing parental, F₁, F₂, and backcross generations. They reported heritability values of 0.19 (narrow sense) and 0.36 (broad sense) for yield and 0.43 (narrow sense) and 0.50 (broad sense) for TKW. However, the variance components method whereby the components are derived from AOV estimates is more practical and widely used in plant species. The procedures of estimating the different variance components for this method have been worked out by Crump (1946, 1951), Comstock and Moll (1963), Gordon et al. (1972) and others. Sidwell et al. (1978) used two approaches of estimating heritability by the AOV method in wheat. The first approach was based on single-plot F₃ family performance while their second procedure was estimating heritability on the basis of a multiple-plot measurement. Their results showed higher heritability values for both grain yield and kernel weight when the unit of measurement consisted of three replicates. For grain yield, they obtained heritability values of 0.61 and 0.34 for multiple-plot and single-plot estimates, respectively. The equivalent values for TKW were 0.85 and 0.65.

The second common method of estimating heritability of quantitative traits is the regression of offspring on parental performance. Design of experiments to estimate heritability from offspring-parent regression

analysis and their relative efficiencies were investigated by several workers (Kempthorne and Tandon, 1953; Bohren et al., 1961; Hill, 1970, 1971; Latter and Robertson, 1960). Very recently, Cahaner and Hillel (1980) compared three procedures of estimating heritability in F₂ and F₃ generations of self-pollinating species. The methods they compared were: (1) subtracting the environmental variance estimated from purebred parental lines from the corresponding phenotypic variance, (2) the AOV procedure using intra-class correlation, and (3) the offspring-parent regression technique. Based on their comparative study, they concluded that the family-analysis method of using intra-class correlation may be superior to the other two because parameter estimates from this procedure were less affected by non-additive effects. Also, heritability can be defined in terms of correlation between breeding and phenotypic values (Falconer, 1960).

Realized heritability is calculated from selection differential and predicted response after selection is carried out. According to Hill (1972), there are four possible unbiased estimates of realized heritability. They are, (1) the regression of cumulative response on corresponding cumulative selection differential, (2) the regression of single generation response on individual selection differentials, (3) the ratio of the total response to selection to total selection differential, and (4) the maximum likelihood estimator. After comparing realized heritability estimates by offspring-parent regression, Hill (1971) concluded that the offspring-parent regression method is more efficient than a single generation selection experiment, provided the heritability values are high. Nevertheless, these differences were negligible when the heritability was low. In contrast, he found that a realized heritability estimate from a selection

experiment of more than three generations will always be better because it will have lower sampling variance than an estimate based on offspring-parent regression.

Heritability estimates, because they are obtained using estimated parameters, are subject to sampling errors (Hanson, 1963). Therefore, several workers have attempted to work out how to determine the variance of heritability ratios estimated from various methods. The variance of heritability estimated by regression is given by Kempthorne and Tandon (1953) whereas Kempthorne (1957) used the variance of the intra-class correlation for sampling variance of heritability estimates. More recently, Gordon et al. (1972) have considered the variance of heritability estimates calculated from data on genotypes tested under a set of environments and season, applying the AOV method. On the other hand, Prout (1962) and Soller and Genizi (1967) have worked out formulae for the sampling error of realized heritability estimates.

Response to Selection

The effectiveness of selection depends primarily on the selection differential and the magnitude of heritability for the trait under selection. When reliable estimates of genetic and environmental components of variance and selection differentials are available, genetic advance can be predicted which serves as a guide in making breeding decisions. Predicting the response to selection is one of the most useful concepts in quantitative genetics and in plant and animal breeding. The size of the expected response of a trait can be used to assess the efficiency of a selection scheme and to determine the optimum intensity of selection pressure. Stated differently, the choice of a population and a breeding

method to use in initiating a crop improvement program will depend on the mean performance of the population, the magnitudes of the different kinds of genetic variations present, and the estimated heritability.

Thus, the response to selection is the function of the selection differential and the heritability of a unit trait. The selection differential, which is in essence the mean of order statistics, is the difference between the performance of the selected individuals and the mean of the population before selection. Assuming that the character in the population under selection is normally distributed, we observe a useful relationship between the proportion selected and the selection differential. Thus, for a normal distribution, there is a relationship between the standard deviation of the mean of a population and the proportion of individuals having values exceeding such a deviation. The properties of the normal distribution show that the average deviation from the mean, in standard deviation units, of a proportion of individuals with extreme values above or below the mean is the product of the height of the ordinate at the point of truncation and the proportion selected from the population (Hazel and Lush, 1942). This results in the intensity of selection or the standardized selection differential being equal to the ratio of the height of the ordinate to the proportion selected. This gives the well known equation of response to selection as the product of the intensity of selection, the phenotypic standard deviation of the population before selection and the heritability estimate for the trait under consideration. Appropriate tables are available for the average deviation for a selected proportion of one tail of the normal curve.

Heritability estimates are influenced by the method of estimation used, the unit of measurement, and environmental factors. Such variability

in the heritability estimates affects the response to selection. Pesek (1972) described the consequence of an estimation of standard errors of predicted and observed responses to selection in wheat. The comparison of two methods of estimating heritability ratios indicated that the one from components of variance based on two years of data underestimated the heritability. On the other hand, the AOV method on the basis of one year of data overestimated the heritability value because of the genotype-year interaction effect. Therefore, he concluded that comparisons of procedures of estimating heritability are of reduced value unless the estimated heritability is significant, genotype-environment interaction effects are absent, and the standard error of the observed response to selection is small. Sidwell et al. (1978) more recently estimated genetic advance in wheat based on single-replication and multiple-replication selections. They reported higher yield expected response for multiple-plot selection (14.1) than for single-plot (10.4) selection using selection pressure of 10%. The equivalent responses for kernel weight were 3.1 (multiple-plot) and 1.0 (single plot). Working on random mating populations of sorghum, Ekebil et al. (1977) obtained genetic gains in yield per cycle of selection ranging from 8.7 to 16.3 q/ha for the three populations employing selection pressure of 20%. The equivalent ranges of expected genetic gains in TKW and protein percent were 2.8 to 3.6 and 0.5 to 0.7, respectively. Fanous et al. (1971) estimated heritability and genetic advance in sorghum using both the regression and the variance components methods, and reported that heritability percentages for kernel weight in five populations ranged from 13 to 47 using the regression method and from 66 to 87 using the variance components method. Similar differences were also observed for predicted genetic progress. For

kernel weight the expected gains ranged from 1 to 3 when the O-P regression method was used and from 3 to 5 using the AOV method. These discrepancies serve as a good example to show that heritability estimates are not stable population parameters but vary with methodology and population variables.

Frey and Horner (1955) after comparing heritability and response to selection results in F4 and F5 barley lines, found close agreement between the expected gains from the components of variance analysis, whereas the F5 on F4 regression procedure underestimated the true heritability. A relatively simple method of calculating the variance of heritability estimates was presented by Pesek and Baker (1971) and was applied in five wheat populations to compare observed and predicted responses. Although they found differences between predicted and observed gains were non-significant, they concluded that a significant discrepancy between these two values could be due to inadequate measurement of observed response. It does not necessarily indicate the inadequacy of quantitative genetics to reliably predict response to selection.

So far, our discussion has been restricted to point estimates of the expected response. Recently, however, Tai (1979) has derived an expression that will provide for an interval estimate of response to selection. His derivation was based on the simplest completely randomized experimental design for progeny testing on the basis of one-way AOV of a group of lines.

The variance of response to selection has been also the subject of many investigations (Prout, 1962; Soller and Genizi, 1967; Baker, 1971b; Hill, 1974). Prout (1962) derived the variance of the conditional response to selection for single generations and later this was extended for several generations by Soller and Genizi (1967). Baker (1971b, 1975)

obtained the unconditional variance for response to the modified pedigree selection method. Hill (1971, 1974) reported on both conditional and unconditional variances for response to selection.

Selection Indices for Genetic Improvement
of Quantitative Characters

The objective of many plant breeding programs is the simultaneous improvement of a crop for several complexly inherited quantitative traits. The search for an objective method of selection which can provide the best criterion that will determine the "genetic worth" of an individual or a population started many years ago.

Smith (1936) first proposed the use of Fisher's (1936) concept of discriminant functions as a procedure for the selection of plant lines to improve several quantitative traits simultaneously. This method which Smith first applied on wheat became to be known as index selection. Though it was initially developed for plant species, selection index has been used extensively by animal breeders as a result of further extension and development of its genetic construction by Hazel (1943) for the selection of individuals in animal populations. The significance of Hazel's (1943) work was that he described a method to estimate genetic variances and co-variances which are required to construct the index and that he defined an aggregate genotype as a linear combination of genetic values. Earlier, Hazel and Lush (1942) compared the selection efficiency of index selection, independent culling levels, and tandem selection when the traits involved are independent. For uncorrelated traits where the products of heritability, the relative economic values and the phenotypic standard deviation for each trait are equal, they showed that selection index gave greater expected genetic gain than did independent culling levels and, in turn,

independent culling levels was more efficient than tandem selection. Young (1961) evaluated the three selection methods when the traits are correlated and he found that the relative efficiency of these methods depends on the number of traits selected, selection intensity, relative economic values of the traits, heritabilities, and phenotypic and genetic correlations between traits. He ranked the methods more or less in the same order as did Hazel and Lush (1942) concluding that index selection is at least as efficient as independent culling levels which, in turn, is at least as efficient as tandem selection.

These theoretical developments and evaluation of the relative efficiency of the three selection methods were confirmed experimentally by many workers (e.g. Elgin et al., 1970; Sen and Robertson, 1964; Doolittle et al., 1972; Eagles and Frey, 1974).

Selection Index Theory

There are various modifications and applications of the original selection index as developed by Smith and Hazel. The theory of the Smith-Hazel selection index will be reviewed briefly.

The index and aggregate genotypes, in selection index theory, are defined as follows:

$$\text{Index : } I = \sum_{i=1}^n b_i X_i = \underline{P}'\underline{b},$$

where \underline{P} is a vector of n known phenotypic values for individual traits and \underline{b} is a vector of corresponding index coefficients to be calculated.

$$\text{Aggregate genotype: } H = \sum_{i=1}^n a_i g_i = \underline{g}'\underline{a},$$

where \underline{g} is a vector of n unknown unit-trait breeding values and \underline{a} is a vector of corresponding relative economic weights.

The index, I , is chosen so as to maximize its correlation with the net merit, H . This concept of maximization led to the equation

$$P\mathbf{b} = G\mathbf{a}, \text{ where}$$

P is the phenotypic variance - covariance matrix and G is the genetic variance - covariance matrix. This results in the solution $\mathbf{b} = P^{-1}G\mathbf{a}$.

The above definition also results in the following relationships (Nordskog, 1978):

$$V_p(I) = \mathbf{b}'P\mathbf{b} = \mathbf{b}'G\mathbf{a} = \text{COV}(H, I)$$

$$V_G(I) = \mathbf{b}'G\mathbf{b}$$

$$V(H) = \mathbf{a}'G\mathbf{a}$$

$$R_{HI}^2 = \frac{\text{COV}^2(H, I)}{V(H) V(I)} = \frac{V(I)}{V(H)} = \frac{\mathbf{b}'P\mathbf{b}}{\mathbf{a}'G\mathbf{a}} = B_{HI}B_{IH}$$

$$\text{and } B_{HI} = \frac{\text{COV}(H, I)}{V(I)} = 1, \text{ so that}$$

$$B_{IH} = R_{HI}^2$$

The statistical properties of the selection index of multiple traits were given in detail by Henderson (1952, 1963), Williams (1962a) and Nordskog (1978).

Heritability of an Index

The heritability of an index is required to predict the genetic response in the aggregate genotype or single trait when selection is on I . Earlier, some workers have misinterpreted the squared correlation between H and I , R_{HI}^2 , to be the heritability of the selection index (Willham, 1965; Pirchner, 1969). This interpretation is not in accord with the classical definition of heritability. Lin and Allaire (1977) showed that the heritability for an index is not R_{HI}^2 , indicating that the squared multiple correlation coefficient, though measures the relationship between H and I , is not equal to the ratio of the variance of the genetic



index to the total variance of the index. Instead, they defined the heritability of an index, h_I^2 , as the regression of genetic index (g^*) on the selection index (I). That is

$$h_I^2 = V(g^*)/V(I) = \underline{b}'\underline{G}\underline{b}/\underline{b}'\underline{P}\underline{b}$$

They obtained the genetic index (g^*) by substituting the genetic values of the index into the phenotypic values. The genetic index, defined as a linear combination of the genetic components of each phenotype weighted by corresponding index coefficients, weights each breeding value with respective coefficient of selection index.

Nordskog (1978) derived the same relationship by defining the quantity K as breeding value of a performance index or the selection index, I, when selection is based only on a single trait in the index. K is defined as a function of breeding values of a trait weighted by the index coefficient, b_i , instead of a_i .

$$K = \sum_{i=1}^n b_i g_i$$

$$V(K) = \text{COV}(K, I) = \underline{b}'\underline{G}\underline{b} = V_{G(I)}$$

$$\text{and } h_I^2 = V(K)/V(I) = V_{G(I)}/V_{P(I)} = \underline{b}'\underline{G}\underline{b}/\underline{b}'\underline{P}\underline{b}.$$

He stated that the true heritability of an index is the regression of the selection response in K to the response in H. That is, $h_I^2 = R(K)/R(H)$. This quantity, of course, is not equal to the multiple correlation coefficient, R_{HI}^2 . The multiple correlation coefficient only serves as a predictor of effected change in H as a result of selection on I. Thus, the heritability of an index, defined as the ratio of genetic index to the selection index, can also be estimated by the analysis of covariance among relatives where the index value is treated as a single trait.

The equality of the h_I^2 values estimated by the regression and analysis of variance methods was reported by Lin (1976). The estimation of heritability of an index from experimental data are subject to error. The sampling variance of heritability estimate of a single trait has been investigated by various workers (e.g. Osborne and Paterson, 1952; Dickerson, 1959; Swiger et al., 1964). The sampling variance of the heritability of an index estimated using the AOV method can be calculated as is done for a single character. To derive the sampling variance of the heritability of an index, $V(h_I^2)$, estimated by the regression method, Lin (1979) used the approximation formula for the variance of a ratio given by Kelly (1947).

Expected Gains in the Aggregate Genotype from Selection on an Index

When selection is based on an index the genetic response (R) in the aggregate genotype (H) is

$$\begin{aligned} R(H) &= \frac{i \text{COV}(H, I)}{\sigma_I} \\ &= \frac{i(\underline{b}'\underline{G}\underline{a})}{(\underline{b}'\underline{P}\underline{b})^{\frac{1}{2}}} = i\sigma_I \end{aligned}$$

and

$$\begin{aligned} R(K) &= \frac{i\text{COV}(K, I)}{\sigma_I} \\ &= \frac{i(\underline{b}'\underline{G}\underline{b})}{(\underline{b}'\underline{P}\underline{b})^{\frac{1}{2}}} \end{aligned}$$

Then

$$\frac{R(K)}{R(H)} = \frac{\underline{b}'\underline{G}\underline{b}}{\underline{b}'\underline{G}\underline{a}} = \frac{\underline{b}'\underline{G}\underline{b}}{\underline{b}'\underline{P}\underline{b}} = h_I^2$$

and

$$R(K) = i\sigma_I h_I^2$$

This explains the fact that when selection is based on an index giving a unit change in economic genetic value, H, the corresponding gain in

breeding value, K , is h_I^2 .

An important assumption in the theory of index selection is that the phenotypic and genetic population parameters, P and G , are taken to be known without error. This, of course, is never the case in practice; therefore, $R(H)$ is considered to be the optimum response. As a result, selection index coefficients and responses due to selection on I are estimated from samples and they are subject to estimation errors.

The effects of substituting estimates for population parameters have been investigated by several authors using different theoretical and experimental techniques (Tallis, 1960; Williams, 1962b; Harris, 1964; Heidhues, 1961; Sales and Hill, 1976a,b; Lin et al., 1979). The findings of these workers indicate the efficiency of selection index decreases with increase in the magnitude of random error due to parameter estimation. Furthermore, Lin et al. (1979) concluded that over-estimation of a parameter results in a more negative effect in the efficiency of selection index than does under-estimation.

To simplify the estimation of the variance of estimated index coefficients and facilitate the evaluation of the expectation of the realized response to selection, Hayes and Hill (1980) proposed a transformation (i.e. reparameterization) of the variables used to construct genetic selection indices.

To construct a selection index, three types of information are required for each trait: (1) phenotypic and genetic variances, (2) phenotypic and genetic covariances, and (3) relative economic weights. In addition to the problem of obtaining reliable estimates of phenotypic and genotypic parameters, one of the major difficulties in using selection index according to Smith (1936) and Hazel (1943) is that of determining the

relative economic weights of various traits. An objective estimate of relative economic weights for some important traits in plant breeding is practically impossible. Therefore, relative economic weights in most selection index constructions are subjective and sometimes arbitrary.

To circumvent the problem of determining relative economic weights, several modifications of the original Smith-Hazel theory of selection index have been proposed. In the following section, we will turn to some of these modifications and their applications.

Various Modifications and Application of Selection Index

Restricted and Optimum Selection Indices. Kempthorne and Nordskog (1959) derived the restricted selection index whereby an index is designed to genetically improve some traits while holding the response of some others to zero. This modified selection index helps to effect specific genetic changes in component traits in breeding while the unrestricted Smith-Hazel index deals with an aggregate genotype as a single trait and does not give the alternative of controlling component characters. Several researchers have applied and tested the validity of the restricted selection index experimentally (Abplanalp et al., 1963; Scheinberg et al., 1967; Okada and Hardin, 1967; Rosielle and Frey, 1975; Rosielle et al., 1977). Cunningham et al. (1970) derived a technique to simplify the solution to the restricted selection index.

Experimentally, Rosielle and Frey (1977) applied restricted selection indices to improve grain yield in oats with the response of heading data and height held to zero. They reported that the restricted selection index resulted in the elimination of correlated responses in heading date and height, but reduced the genetic advance for economic value.

Tallis (1962) extended the method by Kempthorne and Nordskog (1959) for selecting an optimum genotype. This modified restricted index is called optimum selection index. In this extension, Tallis (1962) set the genetic gain of some traits to be altered by a fixed optimum amount while allowing genetic advance in some others to be maximum possible. Lin (1978) discusses an extreme case of optimum index whereby the relative response in all traits included in the construction of the index is controlled thus eliminating the need to determine the relative economic weights and phenotypic variances and covariances.

Weight-Free Selection Index. Another modified selection index proposed to solve the problem of assigning relative economic weights was the weight-free selection index developed by Elston (1963). The index he proposed was

$$I = (X_1 - K_1) (X_2 - K_2) (X_3 - K_3)$$

for three traits.

Where K is the smallest sample measurement for the trait in question;

or

$$I = (X'_1 - K'_1) (X'_2 - K'_2) (X'_3 - K'_3)$$

where X' is log (X-K) and

K' is the smallest of the X''s in the group.

However, to rank all the individuals under investigation K and K' are given by

$$\frac{(n \min X - \text{Max } X)}{n-1}$$

and

$$\frac{(n \min X' - \text{Max } X')}{n-1}$$

respectively.

This selection index is appealing because it eliminates the need for estimating relative economic weights, genetic and phenotypic parameters required to construct a selection index. Baker (1974) compared Elston's method of constructing weight-free index with the index based on 'desired gains' proposed by Pesek and Baker (1969) and methods based on multivariate techniques. He pointed out the problem of calculating predicted gains due to selection because the multiplicative weight-free index is curvilinear. To avoid this problem, Baker (1974) suggested, in the case of two traits, the linear approximation of the multiplicative index by

$$I = X_1 V_{P(2)}^{\frac{1}{2}} + X_2 V_{P(1)}^{\frac{1}{2}}$$

where X_1 , X_2 , $V_{P(1)}^{\frac{1}{2}}$, and $V_{P(2)}^{\frac{1}{2}}$ are the means and the phenotypic standard deviations of the two traits, respectively. As a result, he came to the conclusion that the linear approximation of Elston's index was more efficient than the method of direct single trait selection. It gave similar results of expected response to the desired genetic gains method when he used a prechosen rate of genetic advance to be equal to the genetic standard deviations of the traits concerned. Because of its simplicity, also since it eliminates the need for estimating genetic and phenotypic parameters, Baker (1974) recommended Elston's (1963) selection index for animal breeding, particularly when the traits under consideration are nearly equal in importance.

Crosbie et al. (1980) compared the relative efficiencies of several selection indices constructed to select for improved cold tolerance in two maize populations. The indices included were the Smith-Hazel index, Elston's weight-free index, the linear approximation of the weight-free index, the rank summation index (Mulamba and Mock, 1978), the base index

(Williams, 1962b) and four desired gains indices. They concluded that the best predicted genetic gains for all traits were obtained by using multiplicative weight-free index, rank summation index and the base index. They stated that these indices combined the desirable properties of simplicity freedom from the requirement of estimating genetic parameters, and good selection differentials and predicted genetic gains for the individual traits and the aggregate genotype. Nevertheless, they did not mention how response to selection in the multiplicative index was predicted.

Desired Gains Selection Index. The desired gains index proposed by Pesek and Baker (1969) substitutes desired gains for relative economic weights. This method is basically similar with the extreme case of Tallis' (1962) optimum selection index, whereby all the traits are set at a desired optimum level of gains are incorporated in the index. The index coefficients are given by the following relationship:

$$\underline{b} = G^{-1}\underline{d}$$

where G^{-1} is the inverse of the genotypic variance-covariance matrix and \underline{d} is a vector of desired genetic gains.

As can be observed from the matrix formulation, this method also eliminates the need for assignment of economic weights which limits the practical use of selection index. And because it is simpler than the methods of Kempthorne and Nordskog (1959) and Tallis (1962), it can be used instead of the restricted index procedures. Pesek and Baker (1970) applied the index to select for days to head, maturity, height and yield from a wheat cross. Forty-eight F9 bulks generated using the single seed descent method were tested under two environments for two years. Employ-

ing AOV procedure of estimating genotypic and phenotypic parameters, the application of the desired gains selection index was explained in detail. However, they reported expected response as a result of their selection to be proportional to the desired gains set. In addition, their realized gains showed significant departure from those predicted.

On the other hand, Rosielle and Frey (1975) criticized the method proposed by Pesek and Baker on the grounds that secondary traits for which improvement is not desired cannot be included in the index to aid in selection. To solve this shortcoming, Tai (1977) proposed a procedure in which secondary traits can be included in the index to aid selection for those characters of economic importance in which the breeder is interested to effect genetic advance.

Other Uses of a Selection Index. Several researchers have applied the theory of selection index for various objectives. Henderson (1963) used a selection index procedure to combine information from sources of individuals and all their relevant relatives. He called the technique the 'best index'. In animal breeding it is a common practice to use information on relatives to help increase accuracy of selection. Earlier, Lush (1935, 1944) used the relationship of relatives in predicting breeding values of individuals. In particular, Lush (1947) applied the family index by using the mean value of the family to evaluate the performance of progenies. Osborne (1957) combined individual, full-sib family, and half-sib family information in poultry to maximize the efficiency of selection.

Although it is possible to permit genotype by environment inter-

action, basically it is assumed in the theory of index selection that genotype and environment are independent (Kempthorne and Nordskog, 1959). James (1961) constructed a selection index to maximize the genetic progress across environments in the presence of genotype by environment interaction. Henderson (1963) considered the theory in greater detail. According to him the selection index method should not be limited to selection of individuals because the same approach can be used to discriminate among lines and crosses. Thus, he extended the theory for the application of selecting among lines, top or single crosses. Young and Tallis (1961) developed what they called 'performance index' to select for life time productivity. Their approach helps to predict production instead of breeding values. Young (1964) later suggested a multi-stage index selection method whereby one or more genetic traits observable during the life span of the individual are selected for at each of several stages.

In theory, a selection index can be considered as a linear or non-linear function of traits. Smith (1936), when he developed the selection index application, indicated that the accuracy of a selection function could be increased by employing higher orders and products of the variates involved. Nevertheless, it has been the general assumption that the aggregate genotype was a linear combination of genetic values each weighted by relative economic measure. There are cases where researchers have transformed products or ratios of component traits to logarithmic scale to effect linearity and to use the transformed scale to estimate phenotype and genetic parameters (Smith, 1967; Bohren, 1970; Kempthorne and Nordskog, 1959). In contrast, Wilton et al. (1968) developed the 'quadratic index' based on an aggregate genotype that included squares and

products of observable traits.

In selection theory, it is generally assumed that an interaction between genotypes within a group is absent. Griffing (1967) reported that selection for individuals with maximum genetic values may result in the reduction of progeny performance when what he called 'direct additive effect' and 'associative additive effect' are negatively correlated. To avoid this decrease in response he later suggested an index incorporating direct and associative phenotypic values to attain maximum aggregate progress (Griffing, 1969).

Practical Limitations of Selection Indices. Theoretically, a selection index is the most efficient method among the numerous available selection procedures. Therefore, it is expected that its use should result in maximum genetic advance in a selection program. However, there are basic genetic constraints common to any selection method. Firstly, in single character selection, a plateau of genetic change may be attained in an index selection whereby progress in some component characters are counter-balanced by losses in others resulting in no change in an aggregate value. Secondly, there are certain serious difficulties of the method which limits its application in animal and plant breeding. Some of these problems will be treated in the following paragraphs.

Parameter Estimations and Sampling Errors. Despite the theoretical assumption that phenotypic and genetic parameters must be measured without error, in practice the parameter required for index construction are estimated from samples. That is, these parameters are never known to the breeder. Hence, Williams (1962b) calls the Smith-Hazel index as an 'estimated index'. The effect of sampling errors associated with parameter

estimation and/or the reliability and efficiency of the selection index have been the concern of many workers. Brim et al. (1959) stressed the point that inaccuracies in estimating parameters might bias predicted genetic gains. As an alternative, they proposed an index based on a combination of traits each weighted by its relative economic value. Williams (1962b) later called this the 'base index'. The major difference between the Smith-Hazel and the base indices is that the former maximizes the correlation between H and I, while the latter maximizes the correlation of H and K (Nordskog, 1978) or g^* (Lin and Allaire, 1977). Experimental results of Elgin (1970) and Eagles and Frey (1974) showed the base index to be as efficient as Smith-Hazel index or Smith-Hazel index to be slightly superior.

The influence of sampling errors due to parameter estimation on the relative accuracy and efficiency of selection index has been the subject of many investigations (Heidues, 1961; Williams, 1962b; Harris, 1964; Pease et al., 1967; Lin et al., 1979; Thompson, 1977; Haynes and Hill, 1980). The general conclusion one can draw from a review of such extensive reports is that errors in parameter estimates result in a significant effect on the efficiency and overall accuracy of index selection. The types and magnitudes of the effects of such errors will, of course, depend on the number of traits under investigation, the relative economic weights, the levels of genetic and phenotypic components of parameters, and selection intensity. In addition, the method of parameter estimation and the experimental design may have important contributions.

Assignment of Relative Economic Weights

One of the major practical constraints to the application of a

selection index in plant and animal breeding is lack of a procedure to assign reliable economic weights objectively. In practice, economic weights can be calculated in two ways: (1) direct economic analysis based on market values of products (Hogsett and Nordskog, 1958), or (2) the application of the method of multiple regression analysis in which the ratio of estimates of profit to phenotypic traits is calculated (Andrus and McGilliard, 1975). Both methods have major shortcomings. In the economic analysis technique, some traits of breeding importance are practically impossible to give any objective economic value. The difficulty with the regression method lies in the fact that the relative economic weights vary with number of traits under selection, the definition of profit and sampling variability.

Finally, in the theory of index selection, the correlation between the net merit and the index are always maximized for any given set of corresponding economic weights. Therefore, because economic values may change from time to time and place to place, the breeder has to re-estimate his genetic and phenotypic variances and covariances and reconstruct the selection index every time there is change in economic values.

MANUSCRIPT 1

SELECTING SUPERIOR WHEAT CROSSES
IN EARLY GENERATIONS

INTRODUCTION

Wheat breeders are faced with the common problem of identifying potentially the most promising cross(es) among many alternative combinations developed by using various genetic stocks. This problem becomes more important when dealing with the improvement of complex quantitatively inherited characters such as yield.

Diallel analyses have been used extensively to determine the complex genetic interaction systems of combining ability of possible parents. However, the use of such statistical approach is not very appealing to many practical wheat breeders because the small quantities of seed produced by manual pollination prohibit adequate testing in F1 generation. It is also time-consuming and expensive. In addition, the estimates from F1 test results in a diallel analysis may not reflect the performance of later generations (Bhullar et al. 1979).

Conventionally, wheat breeders carry out several crosses and evaluate the material in F2 generations qualitatively; in most cases visually, in terms of morphological characteristics such as vigor, tillering capacity, disease resistance, etc. A few programs practice F1 yield testing and reduce the number of crosses while others carry all the crosses in the hope of isolating promising segregants even in the poor looking hybrids (Evans, personal communication).

Recently, Curnow (1980) compared alternative methods of selecting crosses employing the yields of individual crosses in comparison with the sum of the estimated general combining abilities of the two respective

parents. His theoretical and simulation study results indicate selection on the basis of general combining ability will be better unless the specific combining ability variance of the parents exceeds twice their general combining ability variance.

Bhatt (1970, 1973) has attempted to use multivariate analysis in comparing various systems of selecting parents for hybridization. He concluded the use of multivariate analysis to be more efficient than other conventional methods. On the other hand, the use of F1 heterosis to identify crosses with promising transgressive segregants has been reported by several workers (Nass, 1979; Singh and Singh, 1971). However, in conventional wheat breeding the correlation between such heterotic effects and the performance of later generations is lacking, or as suggested by Leffel and Hanson (1961) and Grafius et al. (1952), heterosis due to dominance or epistatic effects may impair selection in early generations. Nass (1979) after evaluating F1, F2 and mid-parental yields concluded that mid-parent, F1 and F2 yield tests could be useful tools to identify potentially superior crosses.

This study was designed to use early generation information in spring wheat populations, namely F1 heterosis, F1, F2 and F3 average performances, offspring-parent regressions and intergeneration correlations, to select potentially promising crosses in terms of yield, kernel weight and protein content.

MATERIALS AND METHODS

Crosses

In the winter of 1977, six crosses were carried out in the greenhouse and growth room involving six parents chosen for specific characteristics (yield, protein, kernel size, disease resistance, etc.). Approximately 100 seeds were produced per cross. The parents used and their pedigrees are given in Table 1.1. Sinton and Glenlea are varieties released in Canada while the rest are advanced non-bread wheat lines. The crosses included Sinton x Glenlea (C1), Glenlea x NB505 (C2), NB320 x Sinton (C3), Glenlea x NB603 (C4), NB505 x A2P5 (C5) and A2P5 x NB320 (C6).

F1 Yield Test

An F1 yield test consisting of the six hybrids and the parents was carried out at the Point Research Station, Winnipeg in the summer of 1978. The test was arranged as a randomized complete block design with three replications. Each one-row plot was 2.5 m long x 0.20 m wide. A planting rate of 20 seeds per row was used and rows were spaced 20 cm apart. The experiment was sown on May 4 and harvested on August 28, 1978. Yield, 1000-kernel weight, protein content and lysine percent were determined at harvest. Analysis of variance, correlations and other evaluations were calculated based on the performance of hybrid lines and parents. Percent heterosis and potence ratios (Wigan, 1944; Mather, 1949; Mather and Jinks, 1971) were computed on the basis of average performance of hybrids in relation to parent and mid-parent values. Crosses were eval-

TABLE 1.1. Pedigree and class of the six spring wheat cultivars used in the study.

Designation	Cultivar	Class	Pedigree
P1	Sinton	HRS	CT262 (= Tc*/KF/Lee*6/KF)/Manitou
P2	Glenlea	Utility	2*Pembina/Bage/2/CBI00 [†]
P3	NB320	"	Tobari/Romany
P4	NB603	"	NP/Norteno 67
P5	NB505	"	Lerma-Rojo/Inia 66
P6	A2P5	" (High Protein)	Glenlea/Kenya Cross 6106

[†]CBI00 = Sonora 64/Tezanos Pintos Precoz/2/Nainari 60.

uated and ranked according to individual trait average performance and their aggregate weight-free index values (Elston, 1963).

F2 Populations

Random samples of about 600 F2 bulk seeds per cross were space-planted in Obregon, Mexico in 1979. Each of the six populations was planted in a block flanked by the two parents. The block consisted of 37 rows, 11 m in length and plants were spaced at about 60 cm within the row.

Prior to harvest, the overall performance of crosses were evaluated in terms of height, vigor, tillering capacity, maturity, disease reactions and other agronomic characters. In April approximately 200 F2 plants per cross were selected at random with the exception that very poor, small and diseased plants were discarded; as were very late plants. Based on visual evaluation and number of selected F2 plants, four crosses (C1, C2, C5 and C6) were retained for further studies. The sample sizes for these four crosses were reduced later to 100 lines per cross on the basis of seed quantity. The minimum seed requirement for the F3 test in two locations in three replications was 1800 seeds per line.

For the 100 selected lines per cross, yield per plant, 1000-kernel weight (TKW) and protein content ($N \times 5.7$; 0% moisture basis) was determined. Offspring-parent regressions and intergeneration correlations were carried out between F2 performances and F3 results for grain yield, TKW and percent protein in the four crosses tested under two environments.

F3 Experiments

Four experiments were planted at both the Point and Glenlea Research Stations in Manitoba in the summer of 1979. Each experiment consisted

of 100 F3 lines, each line derived from a single F2 plant plus two parents and two standard checks. Hence, each experiment had 104 entries. The plot consisted of two 3 m rows, 30 cm apart with a seeding rate of 150 seeds per row. Each experiment was arranged as a RCB design with some blocking modifications in three replications. To reduce soil heterogeneity, each replication was reblocked into three sub-blocks. Plots were later trimmed to 2.5 m at the Point site and to 2.75 m at Glenlea so that the net harvest area was $0.6 \times 2.5 \text{ m} = 1.5 \text{ m}^2$ and $0.6 \times 2.75 \text{ m} = 1.65 \text{ m}^2$ at the two test sites, respectively.

To give each line a standard or equal competitive environmental effect, each plot was flanked by a common cultivar of triticale (cv. Welsh). This format provided a high level of uniformity of treatments to each line aiding in proper comparison among F3 lines for selection.

Crosses were evaluated based on the average performance of F3 lines relative to F2 single plant performance. Offspring-parent regressions (F3 on F2) and intergeneration correlations were computed to compare the relative performance of crosses and assess the predictive value of early generation evaluations in identifying superior crosses.

RESULTS AND DISCUSSION

Selection Based on Average Performance and
Heterosis of F1 Hybrids

The summary of mean grain yield, 1000-kernel weight, protein content and lysine levels and the rankings of the six F1 hybrids and six parents is given in Table 1.2. The only cross that produced progeny superior to Glenlea in yield was C2 (138%). No cross excelled either A2P5 in protein content, NB320 in lysine level, or Glenlea in kernel weight. The two crosses involving the common parent Glenlea (C1 and C2) gave exactly equal levels of protein and lysine. This pattern was also the same for the reciprocal cross of C1 which is not included in this report.

Based on the average yield performance, the F1 test identified two high yielding crosses (C2 and C1), two intermediates (C3 and C4), and two relatively low yielding crosses (C5 and C6). In the F1 test, part of the first replication was slightly water-logged, therefore, the yield results may not be reliable. Mean hybrid yields ranged from 6340 to 2793 kg/ha. Grain yield, being the end product of the interaction of several physiological biochemical and environmental factors, is considered as genetically a complex trait. Lelley (1976), after an extensive review of the literature, stated the universality of opinion on the premise that yield in wheat is multigenic in inheritance. Because of the complexity of its inheritance and its high gene x environment interaction, an F1 performance in yield may not indicate productive populations in later generations.

TABLE 1.2. Mean grain yield (kg/ha), TKW (g), protein (%), lysine levels and ranks of F1 hybrids and their respective parents.

Cross or var.	Grain yield (kg/ha)	Rank	TKW (g)	Rank	Protein (%) (0.0 m.b.)	Rank	Lysine (% of protein)	Rank
P1 x P2 (C1)	3800	3	37.5	5	16.8	5	2.74	9
P2 x P5 (C2)	6340	1	40.6	2	16.8	5	2.74	9
P3 x P1 (C3)	3127	5	32.7	9	15.8	8	2.91	3
P2 x P4 (C4)	3127	5	37.0	6	16.5	7	2.88	4
P5 x P6 (C5)	3031	7	36.2	7	17.7	3	2.68	11
P6 x P3 (C6)	2793	11	40.3	3	15.7	11	2.87	5
Sinton (P1)	3240	4	30.8	11	18.7	2	2.75	8
Glenlea (P2)	4593	2	48.4	1	15.8	8	2.77	7
NB320 (P3)	2653	12	29.8	12	15.0	12	3.01	1
NB603 (P4)	2980	8	35.8	8	17.0	4	2.91	2
NB505 (P5)	2872	10	31.5	10	15.8	8	2.84	6
A2P5 (P6)	2947	9	40.3	3	20.6	1	2.64	12
LSD 5%	760		4.1		1.0		0.13	
1%	1033		5.6		1.4		0.17	

The best cross as far as TKW was concerned was again C2, although averaging only 83.9% of the kernel weight of Glenlea. Kernel weights were intermediate between parental values in all crosses except C3 and C6. Cross 3 which involved parents with low kernel weight gave rise to progeny with TKW values greater than those of the better parent, whereas the kernel weight of hybrids from C6 was equivalent to the better TKW parent.

Progeny of C6, which involved the highest protein parent (20.6%), averaged only 15.7% protein, a value close to that of the low protein parent. This trend toward dominance of low protein was similar in all crosses except C2, in which the hybrid protein content (16.8%) was greater than that of either of the parents. The two parental cultivars (NB505 and Glenlea) were equal in protein content (15.8%). This result is in line with many reports indicating that protein means of F1 hybrids fall below mid-parent values and near or below the low protein content (e.g. Diehl et al., 1978; Chapman and McNeal, 1970), indicating dominance of low protein content. However, the detection of significant additive genetic effects for protein is also widespread (see Chapman and McNeal, 1970; Diehl et al., 1978). In addition to its complex nature of inheritance, the high environmental influence on protein expression and its negative association with yield makes it more difficult to assess populations in F1 and predict the merit of crosses in subsequent generations.

The lysine levels in the six hybrids ranged from 2.64 to 3.01. The best F1 hybrid in lysine content was C3 which had the lowest protein percent. This in turn showed highly significant negative correlation between protein content and lysine percent in the protein ($r = -.80^{**}$).

Analysis of variance of hybrids showed highly significant ($P \leq .01$)

differences among crosses in yield, protein content and lysine levels; whereas mean squares of TKW were not significantly different. When analysis included both hybrids and parents, all four traits were highly significant.

Weight-free index coefficients and ranks of the six wheat crosses are given in Table 1.3. Index 1 (I_1) involves only yield and TKW; Index 2 (I_2) consists of yield, TKW and protein and Index 3 (I_3) includes all four traits including lysine. When ranking and selection was based on an aggregate multiplicative index value, the relative positions of hybrids changed slightly, however, C2 was consistently the best cross overall followed by C1. Among the six populations, C2 gave the best grain yield, kernel weight and the second best protein content. Cross 3 was consistently the poorest for all three indices.

Percent heterosis in F1 hybrids was computed in relation to both the better parent (H1) and the mid-parent values (H2). Potence ratios, measuring the relative potence of parental gene sets, were also calculated. To observe the relative magnitude of the percent of heterosis of the aggregate index, arbitrary H1 and H2 values were computed using the Index 3 coefficient for each hybrid. Percent heterosis of F1 lines in relation to the better parent and mid-parent value, also the potence ratio for yield, TKW, protein content, lysine percent and multiplicative index coefficient, are given in Table 1.4.

For grain yield, the only positive and significant percent heterosis in relation to the better parent was in C2. The 38% heterosis observed in H1 increased to approximately 70% when the mid-parent value was used. C3 and C5 showed slight heterotic effect for yield in relation to the mid-parent value. C2 and C5 showed a potence ratio greater than zero,

TABLE 1.3. Weight-free index coefficients and ranks of six wheat crosses for yield and TKW (I_1), yield, TKW and protein content (I_2) and yield, TKW, protein and lysine content (I_3), respectively.

Cross	I_1	Rank	I_2	Rank	I_3	Rank
C1	0.408	2	0.298	2	0.154	2
C2	0.867	1	0.633	1	0.328	1
C3	0.050	6	0.013	6	0.012	6
C4	0.233	3	0.148	4	0.130	3
C5	0.185	4	0.173	3	0.027	4
C6	0.142	5	0.022	5	0.019	5

TABLE 1.4. Average percent heterosis of F1 hybrids in relation to the better parent (H1) and the mid-parent value (H2) and potence ratio for yield, TKW, protein content, lysine level and selection index coefficient in six wheat crosses.

Cross	Yield			TKW			Protein			Lysine			Index 3	
	H1	H2	Potence	H1	H2	Potence	H1	H2	Potence	H1	H2	Potence	H1	H2
	C1	-17.3	-3.0	-17.2	-22.6	-5.4	-0.2	-10.3	-2.7	-0.3	-1.2	-.8	-2.0	-13.9
C2	38.0	69.9	3.0	-16.2	1.6	0.1	6.3	6.5	(OO)	-0.6	-2.4	-1.9	57.3	181.7
C3	-3.5	6.1	0.6	6.3	8.0	4.8	-15.5	-6.2	-0.6	-3.4	1.0	0.2	-19.4	60.4
C4	-31.9	-17.4	-0.8	-23.6	-5.1	-0.8	-2.8	0.8	0.2	-1.6	1.0	0.5	-50.0	-29.9
C5	2.9	4.2	3.2	-10.2	0.8	0.1	-14.2	-2.8	-0.2	-5.6	-2.1	-0.6	-29.1	23.1
C6	-5.2	-0.2	-0.1	0.1	15.0	1.0	-23.9	-11.9	-0.8	-4.8	1.4	0.2	-73.0	-46.0

whereas in C3, C4 and C6 the ratios were approximately zero. Such observable potence of sets of genes indicates dominance of individual genes controlling the trait predominantly in the same direction. Zero or near zero potence ratios as observed in C3, C4 and C6 for yield, suggest that the F1 falls at about the mid-parent value. However, such zero observation does not necessarily imply absence of dominance (Mather and Jinks, 1971).

Only the C3 population exhibited positive H1 heterotic effect in TKW while most crosses had negative percentages for this trait. Populations C3 and C6 showed potence ratios greater than zero for TKW, whereas all the other crosses had ratios approximately zero.

The trend in protein content was more clearcut. The C2 population gave H1 percent heterosis of 6.3%; all other crosses had low or negative values. The potence ratio of C2 approached infinity demonstrating that the parents did not differ in mean protein values because the genes are dispersed. This is interpreted to mean that the genes affecting protein content in the cross are equally shared between the two parental cultivars rather than being carried predominantly in one.

The percent heterosis for the multiplicative index coefficient may not have any biological or genetic meaning, but it is used to serve as an indicator of an aggregate heterosis level. Firstly, if the index coefficients involving yield, TKW and protein content were used in computing H1 and H2; progeny from the C2 cross showed a 57.3% 'heterotic' effect. All the rest of the crosses had negative values. By using mid-parent values, the percentages of C1, C3 and C5 were changed into positive heterotic levels, the change in value in C3 being significant (-19.4% to 60.4%).

Selection Based on Offspring-Parent Regression
and Intergeneration Correlations

Offspring-parent regression studies were undertaken using F2 individual plant measurements and F3 mean performance. There was one shortcoming in this study; the F2 and the F3 tests were carried out in different environments and seasons. The F2 results were obtained from Obregon, Mexico and the F3 data were from Manitoba. The F3 on F2 regression coefficients for grain yield, TKW and protein (%) in four spring wheat crosses are given in Table 1.5.

The regression coefficients for yield were significant only for populations C1 and C6 at the Glenlea location. The regression coefficients were 0.76 ($P \leq 0.05$) and 0.42 ($P \leq 0.01$) for C1 and C6, respectively. As a result the regression analysis based on combined data of the two locations showed significant b-values for these two populations. Otherwise, there was very little or no indication of individual F2 plant yields being translated into F3 productivity. This finding confirms similar reports by other workers (McGinnis and Shebeski, 1968; Knott, 1972), substantiating the contention that F2 single plant productivity has no predictive value of the performance of later generations. Also, this result indicates the possible malpractice of selecting individual F2 plants in Obregon for wheat breeding programs in Canada.

The F3 on F2 regression analysis for 1000-kernel weight revealed a different picture. All the regression coefficients for the four crosses grown in two locations were highly significant (Table 1.5). The magnitude of the b-values which could be equated to heritabilities, vary from cross to cross and from location to location. The fact that they were consistently significant, however, strongly suggests that kernel weight

TABLE 1.5. Offspring-parent regression coefficients and standard errors for grain yield, TKW and protein (%) for four wheat crosses tested in two environments.

Trait & loc.	Crosses					
	C1	C2	C5	C6	C5	C6
Yield						
Point	0.33 ± 0.38	0.20 ± 0.22	0.05 ± 0.20	0.20 ± 0.19	0.05 ± 0.20	0.20 ± 0.19
Glen.	0.76* ± 0.29	0.09 ± 0.18	0.06 ± 0.19	0.42** ± 0.16	0.06 ± 0.19	0.42** ± 0.16
Comb.	0.53* ± 0.27	0.15 ± 0.18	0.05 ± 0.17	0.31* ± 0.15	0.05 ± 0.17	0.31* ± 0.15
TKW						
Point	0.49** ± 0.06	0.32** ± 0.06	0.21** ± 0.04	0.26** ± 0.05	0.21** ± 0.04	0.26** ± 0.05
Glen.	0.46** ± 0.06	0.30** ± 0.07	0.24** ± 0.05	0.34** ± 0.05	0.24** ± 0.05	0.34** ± 0.05
Comb.	0.47** ± 0.06	0.31** ± 0.07	0.23** ± 0.04	0.30** ± 0.05	0.23** ± 0.04	0.30** ± 0.05
Protein						
Point	0.01 ± 0.07	0.09 ± 0.06	0.23** ± 0.05	0.26** ± 0.06	0.23** ± 0.05	0.26** ± 0.06
Glen.	-0.17 ± 0.10	0.09 ± 0.07	0.18** ± 0.06	0.27** ± 0.07	0.18** ± 0.06	0.27** ± 0.07
Comb.	-0.08 ± 0.08	0.09 ± 0.06	0.21** ± 0.05	0.26** ± 0.06	0.21** ± 0.05	0.26** ± 0.06

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

N = 100.

is one yield component that can be used to evaluate individual plants in F2. Notwithstanding, the selective value of TKW depends on its positive relationship with grain yield. This problem will be treated in detail in later sections of this thesis.

For protein content the pattern was more distinct. The trend of the offspring-parent regression analysis depended on the background of the crosses. In the C1 and C2 populations all regression coefficients were non-significant indicating the absence of any relationship between F2 protein level and F3 protein content. On the other hand, in C5 and C6 populations b-values were highly significant at both locations (Table 1.5). Whether F2 protein level could be used to predict F3 protein percent will depend on the background of the parents selected and the overall protein distribution within the F2 population and F3 lines. The two crosses showing significant O-P regression coefficients for protein have a common high protein parent (A2P5).

The inter-generation rank correlation coefficients showed the same trend as the regression coefficients (Table 1.6). In the C2 and C5 there was no correlation between F2 individual plant yield and F3 mean yield per plot in both test locations. Yet in the C1 and C6 the correlation between F2 plant productivity and F3 mean yield was significant (0.30** and 0.27** for C1 and C6, respectively) at the Glenlea site. This was not the case for F3 tests at the Point site. This leads to the same conclusion made earlier that F2 plant yield does not indicate potential F3 performance.

The relationship of F2 and F3 kernel weight, as indicated by the O-P regression analyses showed a very high and positive consistency from cross to cross and from experiment to experiment. The inter-generation

correlation coefficients ranged from 0.41 to 0.65 (Table 1.6). In addition, the correlation coefficients were of the same magnitude in the two test locations for the same cross.

Despite the high positive correlation between F2 and F3 kernel weights, the rank correlation between F3 grain yield and F2 TKW was relatively low (Table 1.6). Positive and significant correlations were observed only in the C1 at both Point and Glenlea sites ($r = 0.30$ and 0.24 , respectively) and in the C6 grown at the Point ($r = 0.23$). All the other experiments showed near zero correlation between F2 TKW and F3 yield. Therefore, although kernel weight is a highly heritable trait as observed in F3 on F2 regression and intergeneration correlation analyses, its value as a yield selection criterion is still questionable.

The correlation between grain protein percent of F2 plants and F3 lines was lacking in the C1 and C2 populations, whereas C5 and C6 showed significant rank correlation in both locations. This may be explained by the influence of the high protein parent, A2P5, in the latter group of crosses or by the high yielding characteristic of the former two.

Within F2 populations, yield was positively and significantly correlated with kernel weight in C1 and C2, but there was no correlation in C5 and C6. In addition, yield and protein content were positively associated in the C1 and C6 groups. There was no correlation between protein percent and kernel weight in all of F2 populations (Table 1.6).

Evaluation of F2 Individual Plant Productivity in Comparison with Average F3 Group Performance

On the basis of visual evaluation of morphological characters before harvest, the six crosses were scored as follows: C1 - very good (plus two stars), C2 - very good (plus one star), C3 - fair (generally late),

TABLE 1.6: Intergeneration rank correlation coefficients for grain yield, TKW and protein (%) in four wheat crosses grown in one location in F2 and at two locations in F3.

Cross	Character ⁺	F2 Yld	F2 TKW	F2 Pro	F3 M Yld	F3 M TKW	F3 M Pro
C1 ⁺⁺	F2 Yld		0.38**	0.28**	0.18	0.09	-0.01
	F2 TKW			0.01	0.30**	0.65**	0.01
	F2 Pro				0.04	-0.01	0.03
	F3 M Yld	0.30**	0.24*	0.15			
	F3 M TKW	0.09	0.62**	-0.04			
	F3 M Pro	-0.06	-0.05	-0.13			
C2	F2 Yld		0.36**	0.14	0.09	0.08	-0.10
	F2 TKW			-0.14	0.06	0.46**	0.16
	F2 Pro				-0.01	0.00	0.08
	F3 M Yld	0.09	-0.06	-0.05			
	F3 M TKW	-0.05	0.41**	0.01			
	F3 M Pro	-0.15	0.14	0.06			
C5	F2 Yld		0.16	0.10	0.03	-0.07	0.12
	F2 TKW			0.03	0.06	0.41**	0.21*
	F2 Pro				-0.28**	-0.04	0.39**
	F3 M Yld	0.04	-0.09	-0.24*			
	F3 M TKW	-0.01	0.43**	-0.02			
	F3 M Pro	-0.08	0.21*	0.22*			
C6	F2 Yld		0.18	0.26**	0.08	0.03	-0.10
	F2 TKW			-0.01	0.23*	0.50**	0.19
	F2 Pro				-0.24*	-0.22*	0.38*
	F3 M Yld	0.27**	0.15	-0.29**			
	F3 M TKW	0.00	0.53**	-0.24*			
	F3 M Pro	-0.16	0.04	0.37**			

N = 100.

*,** Significant at the 5% and 1% level, respectively.

+ Yld = Yield; M Yld = Mean Yield; Pro = Protein; M Pro = Mean Protein.

++ For each cross, values above diagonal are for F3 data from the Point; below diagonal are for F3 data from Glenlea.

C4 - fair (generally poor), C5 - very good and C6 - very good. As a result, C3 and C4 were discarded reducing the number of crosses for further studies to four.

Table 1.7 gives the performance of the four selected populations in the F2 generation. F2 measurements revealed C6 to be superior to all others in both yield and kernel weight. This cross which has the high protein, poor grain type line, A2P5 as one of its parents, exhibited excellent productivity and kernel size in Obregon. The protein ranges among these four populations were similar.

For comparison, F3 group performances are given in Tables 1.8 and 1.9. The F3 group average performance of the four crosses varied significantly both among populations and between locations within a population.

At the Point the highest yielding cross was C6 (top 20% averaged 4661 kg/ha), followed by C2 (4541 kg/ha). In fact, the two crosses were similar in overall performance at this location. This was similar to the ranking of the four crosses based on F2 single plant productivity; i.e. C6 was the best in individual plant yield followed by C2. F3 yield ranking of these same crosses changed at Glenlea, however, at that site the best yielding cross on the basis of the top 20% of the population was C2 followed by C1. Also, yield levels were significantly lower at Glenlea; the four populations, C1, C2, C5 and C6, produced only 73, 81, 79 and 66%, respectively, of what they produced at the Point station. This observation demonstrates the importance of including several locations in early generation evaluation of breeding material.

Kernel weight was the least variable trait both among crosses and between environments. The population means ranged from 41.5 g to 42.4 g at the Point and from 41.6 g to 43.8 g at Glenlea. However, the range

TABLE 1.7. Mean of the top 20%, population mean, and range of single plant performance for yield (g/plant), TKW (g), and protein percent of four F2 wheat populations grown in Obregon, Mexico.

Cross	Yield		TKW		Protein				
	Mean of top 20%	Pop. mean	Range	Mean of top 20%	Pop. mean	Range			
C1	171	123	85-235	44.6	40.0	32.5-47.5	16.4	15.0	12.6-17.6
C2	187	139	90-257	44.4	39.8	31.5-50.6	15.1	13.5	10.9-16.6
C5	176	128	90-250	47.1	41.0	29.0-51.0	16.2	14.0	11.0-18.5
C6	217	157	106-309	50.2	44.4	34.3-56.8	15.7	14.1	11.0-16.6

TABLE 1.8. Mean of the top 20%, population mean, and range for yield (kg/ha), TKW (g) and protein (%) of four F3 wheat populations grown at the Point.

Cross	Yield			TKW			Protein		
	Mean of top 20%	Pop. mean	Range	Mean of top 20%	Pop. mean	Range	Mean of top 20%	Pop. mean	Range
C1	4502	3836	1505-4900	45.5	42.1	35.2-47.6	19.1	18.1	16.3-20.5
C2	4541	3961	2288-5383	45.9	42.4	35.6-50.0	17.7	16.7	14.0-19.2
C5	4165	3622	2268-5076	44.5	41.5	36.0-48.6	18.9	17.7	15.1-20.8
C6	4661	3891	2068-5763	45.5	42.2	36.5-48.4	18.1	17.0	14.9-19.3

TABLE 1.9. Mean of the top 20%, population mean, and range for yield (kg/ha), TKW (g) and protein (%) of four F3 wheat populations grown at Glenlea Research Station.

Cross	Yield			TKW			Protein		
	Mean of top 20%	Pop. mean	Range	Mean of top 20%	Pop. mean	Range	Mean of top 20%	Pop. mean	Range
C1	3414	2789	1137-3787	45.4	42.0	35.6-47.9	19.6	17.8	15.9-21.4
C2	3633	3213	2006-4406	45.5	42.0	34.8-49.6	17.7	16.5	14.6-19.9
C5	3312	2844	1563-4200	44.9	41.6	34.7-49.6	19.7	18.4	15.7-21.0
C6	3160	2569	812-4575	47.6	43.8	35.2-50.6	19.5	18.3	15.5-20.4

in variability within a population was significant. For instance, in the C2 population, TKW ranged from 35.6 g to 50.0 g at the Point and from 34.8 g to 49.6 g at Glenlea. This trend was similar to all crosses. The high kernel weight of C6 in F2 generation was retained in F3 and C6 was the best in TKW based on two locations.

Similarly, differences in mean protein among populations and between locations were small. At the Point the highest population mean for protein was 18.1% compared to 16.7% for the lowest protein cross (C2). Correspondingly, in Glenlea the range was between 16.5% and 18.4%. Within populations, however, significant percent protein variabilities were observed with average percent proteins ranging from 4.7 (C6) to 5.5 (C5) percentage points. This range was slightly wider in F2 generations where a range of 5.0 (C1) to 7.5 (C5) percentage points was recorded.

To identify the superior cross(es) in terms of an aggregate merit, Elston's (1963) index selection was applied using the mean of the top 20% trait performance for each experiment of each cross. The experiment mean yield index values and the corresponding ranks of the tests of each cross are given in Table 1.10.

In this section each of the eight tests (four crosses each grown in two locations) are assumed to be different populations. When handled as such and different selection criteria are applied, the rankings of some populations changed significantly. When selection was on the basis of yield per se and Index 1 (involving only yield and TKW) the same top three populations were selected with minor changes in their actual standings (Table 1.10). Nevertheless, when protein was included in the index (Index 2), there were some important changes in rankings. The C2-2 test fell from second and first position into sixth and C1-1 became

TABLE 1.10. Mean yield (kg/ha) of the top 20%, multiplicative index values, and corresponding ranks of eight F3 experiments grown at the Point and Glenlea.

Cross - expt. no.	Location	Mean yield of top 20%	Rank	Index 1 ⁺	Rank	Index 2 ⁺⁺	Rank
C1-1	Point	4502	3	0.638	3	0.570	1
C2-2	"	4541	2	0.751	1	0.096	6
C5-3	"	4165	4	0.114	8	0.096	7
C6-4	"	4661	1	0.665	2	0.336	2
C1-5	Glen.	3414	6	0.287	5	0.289	3
C2-6	"	3633	5	0.409	4	0.053	8
C5-7	"	3312	7	0.148	6	0.152	4
C6-8	"	3160	8	0.133	7	0.132	5

⁺ Index 1 is based on yield and TKW.

⁺⁺ Index 2 involves yield, TKW and protein percent.

number one. However, C6-4 maintained its first and second position despite changes in selection criteria. This shows the significant problem encountered by the plant breeder attempting to include protein content in his selection program. A selection index involving percent protein in wheat, while it may be applied to select an intermediate population or lines with reasonably optimum overall merit, could misclassify high yielding crosses or lines. This also depends on the breeding objectives and the nature of population under consideration. In this study C6-4 was constantly high yielding, high TKW and high protein, whereas C2 was high grain yield but low in protein content.

CONCLUSIONS

In broad terms, F1 tests may be useful to identify poor crosses of wheat and to select relatively better ones. Nonetheless, because of the complexity of the inheritance of yield and its interaction with the environment, the utilization of F1 yield performance to predict the potential of productive populations is doubtful. Our F1 evaluation identified some of the best and poorest groups of hybrids but misclassified one of the most promising crosses on the basis of yield. The same conclusion was reached for kernel weight. Similarly, the high environmental influence on protein expression and the complex nature of its genetic control made it more difficult to use F1 protein measurements in extrapolating protein levels to F3.

By evaluation of the F1 based on grain yield and the application of multiplicative index to select the best overall cross, it was possible to identify two of the productive populations.

The significant percent heterosis observed for yield and for index coefficient in C2 was shown later (F2 and F3) in the high productivity of the population.

The F3 on F2 regression analyses for yield confirmed the contention that there is very little or no indication of F2 single plant yield being translated into F3 performance in wheat. In contrast, same analyses showed kernel weight, as one of the important components of yield in wheat, to be of high value in predicting the potential productivity of subsequent generations. But the selective value of this component will

be limited by the lack of strong correlation between F2 kernel weight and F3 yield.

As far as protein is concerned, we conclude that whether F2 protein level can be used to predict F3 protein content will depend on the genetic background of the parents chosen and the overall protein distribution in F2 and F3 populations.

Inter-generation rank correlation studies also led to the conclusions that F2 plant measurements have little value in predicting F3 plot yield. While F2 results and F3 data from the Point indicated C6 to be the best cross, C2 was more stable in productivity from environment to environment. Thus, it was concluded that although specific crosses may be evaluated more accurately in an environment most favorable for them, segregating populations must be tested and selected under variable environments to measure stability in early generations. Kernel weight was found to be the most stable character across environments tested in the present study.

The application of a weight-free selection index on F3 group data identified consistently the two or three outstanding crosses, however, when protein was included in the index one of the top crosses was misclassified. Therefore, it is our contention that the inclusion in the multiplicative index of traits that are negatively correlated with productivity, such as grain protein, may result in erroneous ranking of breeding material. This was dependent on distribution of each trait in the population. In populations with reasonably high ranges of protein content, promising crosses with optimum overall performance could be identified using the weight-free selection index technique.

MANUSCRIPT 2

INDEX SELECTION FOR SIMULTANEOUS
IMPROVEMENT OF YIELD, KERNEL
WEIGHT, AND PROTEIN
CONTENT IN WHEAT

INTRODUCTION

Plant and animal breeders are often concerned with multiple trait rather than single trait selection. Several wheat breeding programs have multiple objectives of producing high yielding varieties with other desirable characters such as wide adaptability and high nutritional and industrial qualities.

Kernel size is one of the major components of grain yield in wheat. There are numerous reports indicating that wheat kernel weight, controlled quantitatively by relatively few genes, is positively correlated with yield and can be used to select for high yield (Knott and Talukdar, 1971; Fonseca and Patterson, 1968; Sharma and Knott, 1964; Lebsock and Amaya, 1969). On the other hand, many reports on the inheritance of grain protein in wheat and its association with productivity have shown that it is negatively correlated with yield (Chapman and McNeal, 1970; Diehl et al., 1978; Haunold et al., 1962b; Cowley and Wells, 1980; Hsu and Sosulski, 1969). There is, however, no sufficient knowledge as to the nature of this negative correlation.

In selection, unless appropriate multiple-trait selection procedure is applied, such inverse relationship between characters results in an undesirable shift in one trait as progress is attained in the other. The method of a selection index was first proposed by Smith (1936) using Fisher's (1936) concept of discriminant function for the selection of plant lines for the purpose of improving several quantitative traits simultaneously. The theory of selection was further extended and deve-

veloped by Hazel (1943) for the selection of individuals in animal populations. Since then the Smith-Hazel index and its various modifications (Kempthorne and Nordskog, 1959; Tallis, 1962; Elston, 1963; Pesek and Baker, 1969) have been shown to be the most efficient procedures in achieving aggregate genetic progress compared to any other direct single-trait selection methods (Hazel and Lush, 1943; Young, 1961; Sen and Robertson, 1964; Eagles and Frey, 1974; Elgin et al., 1970). Though it was originally developed for plant species, selection indices have been used more extensively by animal breeders than plant breeders.

In wheat, selection for simultaneous improvement of multiple traits would be valuable for comparisons of overall performance between F3 and F4 populations relative to early generation selection. These types of comparisons enable the breeder to estimate the genetic and phenotypic variances and covariances in early generations so that he can assess the potential of his populations and success early in the program.

The objectives of this study were to measure and compare the expected genetic gain and realized genetic response to simultaneous improvement of grain yield, kernel weight and percent protein in F3 and F4 generations of four spring wheat crosses based on single trait selection and three classes of selection index.

MATERIALS AND METHODS

Experimental Procedures

F3 Generation

Four experiments were carried out at each of the Point and Glenlea Research Stations in Manitoba in the summer of 1979. Each experiment or population consisted of 100 F3 lines, each derived from a single F2 plant, plus two parents and two standard checks. The four wheat populations were Sinton x Glenlea (C1), Glenlea x NB505 (C2), NB505 x A2P5 (C5) and A2P5 x NB320 (C6). Hence, each experiment had 104 entries.

The plot size was 3 m in length, each plot consisting of two rows 30 cm apart laid out in RCB design with some blocking modifications. Each test had three replications. To reduce soil heterogeneity each replication was reblocked into three sub-blocks. Later, plots were trimmed to 2.5 m at the Point and 2.75 m in Glenlea. Thus, the net harvest area was $0.6 \times 2.5 \text{ m} = 1.5 \text{ m}^2$ at the Point and $0.6 \times 2.75 \text{ m} = 1.65 \text{ m}^2$ at Glenlea. Seeding rate was 150 seeds per 3 m row and 300 seeds per plot.

To give each line a standard or equal competitive environmental effect, each plot was flanked by a common cultivar of triticale (Welsh). This arrangement gave an excellent uniformity of treatments to each line aiding in proper comparison among F3 lines for selection.

Relevant agronomic data such as disease scores, days to maturity and plant height were recorded before harvest. Grain and protein yields were evaluated on plot basis and converted to kg/ha at approximately 12.0%

moisture. Kernel weight was determined at the same moisture level from random samples from each plot by counting 500 seeds and calculating for 1000-kernel weight. The percent protein ($N \times 5.7$) was determined on whole flour samples from each plot by the Kjeldahl procedure on 0.0% moisture basis. Test weights were measured only for those lines retained after selection.

F4 Generation

The F4 bulk tests consisted of four experiments each carried out in the Point and Glenlea in 1980. Each experiment included (1) the top 10% of population selected based on the mean yield of two locations, (2) the best 10% in net merit (involving grain yield, TKW and protein) based on weight-free multiplicative index, and the Smith-Hazel index, (3) the lowest 10% of the population based on weight-free multiplicative index, (4) the top 10% of cross based on weight-free multiplicative index involving only yield and TKW, and (5) the top 10% selected based on the linear approximation of the multiplicative index for grain yield and TKW. Based on these six selection criteria, 30, 30, 29, and 27 F3 lines were retained from populations C1, C2, C5 and C6, respectively, for F4 testing. Some lines were common to different selection methods. In addition, a few of the highest protein lines and a composite made up of equal proportions of randomly measured samples from each of the 100 F3 lines were retained from each cross. Thus, each experiment consisted of 31 F4 bulks, one composite, two parents and two standard checks.

The plot size in each experiment at each location consisted of four 3 m rows sown 20 cm apart (2.4 m^2) and arranged in a RCB design with three replications. One blank row was left between plots. A seeding rate of 200 seeds per 3 m row or 800 seeds per plot was used. Tests were

planted on May 5 and 9 in the Point and Glenlea, respectively, and plots were harvested in the last week of August at the Point and the first week of September at Glenlea. Shortage of soil moisture was experienced in the initial stage of the tests both at the Point and at Glenlea; the Point plots were later irrigated.

Before harvest, field records such as disease reactions, maturity, height and lodging were observed. Grain yield, TKW, test weight and protein yield were evaluated at approximately 12.0% moisture on a plot basis. Percent protein ($N \times 5.7$) determined by Kjeldahl method, is expressed on 0.0% moisture basis. Grain yield and protein yield are reported in kg/ha, and TKW was calculated based on the weight of 250 seeds.

Estimation of Parameters

Combined analyses of variance and covariance were performed on F3 generation data collected from four populations grown under two environments. Estimations were based on the assumption that all effects were random. Mean squares for each trait and mean cross-products for pairs of traits were computed for locations, genotypes, genotype x location interaction, and error for each cross. Components of variance and covariance were estimated following the methods of Comstock and Moll (1963) and Gordon et al. (1972).

The components of variance and covariance were estimated by equating mean squares and mean cross products to their corresponding expectations and solving the resulting equation. For each trait in each population the following variances and covariances were estimated:

$$V_G = \text{genotypic component of variance due to genetic differences among F3 lines}$$

V_{GS} = variance component due to genotype by location
interaction

V_e = component due to plot-to-plot environmental variation

COV_G = genotypic covariance component due to genetic
covariation between traits

COV_{GS} = covariance component due to genotype by location
interaction

COV_e = error covariance effect

From these estimates, phenotypic variances and covariances of F3 lines means were calculated as follows:

$$V_p = V_G + \frac{V_{GS}}{s} + \frac{V_e}{rs} \quad (1)$$

$$\text{and } COV_p = COV(G) + \frac{COV_{GS}}{s} + \frac{COV_e}{rs} \quad (2)$$

where r and s are the number of replications and locations, respectively.

In the populations used in the study, the assumption of consistency of genotypes between F3 and F4, and of the genetic value being composed of entirely additive effect of genes are not strictly valid. There will be still some degree of segregation and the component estimates may be biased by the contribution of non-additive gene effects. The sampling variance of estimated variance components were calculated following procedures by Comstock and Moll (1963) and Crump (1946, 1951).

The phenotypic correlation between traits 1 and 2 was estimated as

$$r_p = \frac{COV_p(1,2)}{\sqrt{V_{p.1} \cdot V_{p.2}}} = \frac{MCP(1,2)}{\sqrt{M_1 \cdot M_2}} \quad (3)$$

where $MCP(1,2)$ is the line mean cross product and M_1 and M_2 are the line mean squares for traits 1 and 2, respectively. The genotypic correlation between two traits, 1 and 2, was estimated by:

$$r_G = \frac{\text{COV}_{G(1,2)}}{\sqrt{V_{G1} \cdot V_{G2}}} \quad (4)$$

where $\text{COV}_{G(1,2)}$ is the line component of covariance between traits 1 and 2 and V_{G1} and V_{G2} are the line components of variance for traits 1 and 2, respectively.

Standard errors of estimated genetic correlations were obtained using derivation by Robertson (1959).

Heritability in each population was estimated by the analysis of variance method as

$$h^2 = \frac{V_G}{V_p} \quad \text{for each trait.} \quad (5)$$

The variance of heritability estimates was calculated following Gordon et al. (1972).

The mean expected genetic response, due to selection of the top 10% of the F3 population was predicted for each of the three characters using the following relationships:

$$R = iV_p^{\frac{1}{2}}h^2 \quad \text{or} \quad R = Sh^2 \quad (6)$$

where i is the standardized selection differential, or selection intensity, $V_p^{\frac{1}{2}}$ is the phenotypic standard deviation of the single trait and h^2 is its heritability. S is the selection differential, while R is reported in the units of measurement for each trait (see Figure 2.1). The variance of predicted response to selection was calculated according to Hill (1974).

The expected correlated response in trait 1 to F3 selection for trait 2 was calculated according to the formula:

$$\text{CR}_{(1.2)} = i h_1 h_2 r_G V_p^{\frac{1}{2}}(1) \quad (7)$$

where h_1 and h_2 are the square roots of the heritabilities of traits 1 and 2, respectively. The expected correlated response in yield (YD) for selection on Index I was obtained by:

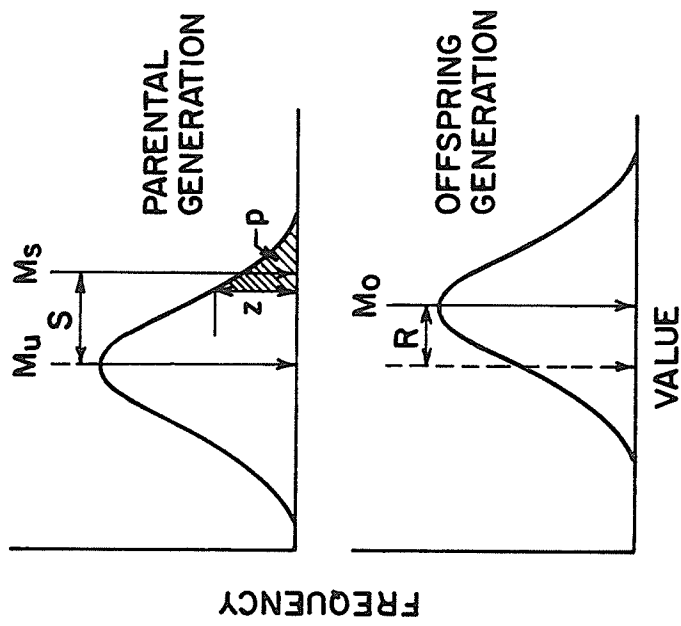


Fig. 2.1. Response to selection in one generation.

$$CR_{(YD \cdot I)} = \frac{i \text{ COV}_G(YD, I)}{V_P(I)} \quad (8)$$

$$\text{and } \text{COV}_G(YD, I) = b_{TK} \text{COV}_G(YD, TK) + b_{PR} \text{COV}_G(YD, PR) \quad (9)$$

etcetera.

Realized heritability, h_a^2 , of each trait after selection was estimated by the ratio of estimated response to selection differential, S .

That is,

$$h_a^2 = \frac{R}{S} \quad (\text{Falconer, 1960}). \quad (10)$$

The realized genetic gain was computed as the difference between the mean of selected F4 lines and the mean of the composite created by mixing equal quantities of random samples of F4 seed before selection. This entry represented the mean of the unselected F4 population.

Construction of Indices

Smith-Hazel Selection Index

The phenotypic and genotypic variance and covariance estimates were used to solve for the Smith-Hazel (SH) index coefficients (b 's) using the equation,

$$\underline{b} = P^{-1}G\underline{a} \quad (11)$$

where P and G are phenotypic and genotypic variance-covariance matrices, respectively, and \underline{b} and \underline{a} are vectors of index coefficients and relative economic weights, respectively. In the SH index, relative economic weights of 1.0, 0.0 and 0.2 were assigned for grain yield, 1000-kernel weight and protein content, respectively. The phenotypic and genotypic variances ($V_{P(I)}$ and $V_{G(I)}$) of the SH index I , and the variance of the aggregate genotype ($V_{(H)}$) were computed by the following matrix formulations (Nordskog, 1978):

$$V_{P(I)} = \text{COV}(H, I) = \underline{b}'\underline{P}\underline{b} \quad (12)$$

$$V_{G(I)} = \underline{b}'\underline{G}\underline{b} \quad (13)$$

$$V_H = \underline{a}'\underline{G}\underline{a} \quad (14)$$

where H is the aggregate genotype when selection is based on I.

The heritability of the index (h_I^2) was estimated by

$$h_I^2 = \frac{\underline{b}'\underline{G}\underline{b}}{\underline{b}'\underline{P}\underline{b}} \quad (15)$$

while the expected responses in the aggregate genotype, H, and aggregate breeding value K, were estimated based on the formulae:

$$R_{(H)} = i \frac{(\underline{b}'\underline{P}\underline{b})}{(\underline{b}'\underline{P}\underline{b})^{\frac{1}{2}}} = i V_{P(I)}^{\frac{1}{2}} \quad (16)$$

$$\text{and } R_{(K)} = i \frac{(\underline{b}'\underline{G}\underline{b})}{(\underline{b}'\underline{P}\underline{b})^{\frac{1}{2}}} = i V_{P(I)}^{\frac{1}{2}} h_I^2 \quad (17)$$

where i is the standardized selection differential and the vectors and matrices are as explained above. The selection intensity i, is equal to 1.76 for the selection of the top 10% of the population.

Elston's Weight-Free Selection Index

To calculate the weight-free index (EW) according to Elston (1963), the K for each trait was determined as follows:

$$K = \frac{(n \text{ Min } X - \text{Max } X)}{n-1} \quad (18)$$

where Min X and Max X were the lowest and the largest mean value respectively for each trait and n was the total number of lines in the group before selection. The actual index for each line was estimated for EW1 and EW2 by the formula:

$$I = (X_1 - K_1) (X_2 - K_2) (X_3 - K_3) \quad (19)$$

for the three traits considered. This index ranks all the n lines according to their overall merit. EW1 was a truncated selection of the

top 10% whereas EW2 was a truncated selection of the lowest 10% of the population. A third multiplicative index (EW3) was constructed involving only yield and kernel weight.

To be able to estimate the response to selection on an index, Baker (1974) suggested a procedure to approximate the multiplicative index of Elston (1963) for two traits by a linear index derived from multiplying the mean value of the first trait by the phenotypic standard deviation of the second trait and vice versa and adding to obtain the approximate linear index. For the purpose of comparing this linear approximation with the multiplicative index, this author has used Baker's (1974) suggestion to calculate a linear index for yield and kernel weight. This value will be called EW4. An approximate expected response (R) for EW4 was estimated by the usual procedure using the phenotypic standard deviations as index coefficients.

Desired Gains Selection Index

The index coefficients for the desired gains selection indices (PD) were obtained by the procedure described by Pesek and Baker (1969):

$$\underline{b} = G^{-1} \cdot \underline{d} \quad (20)$$

where \underline{d} is the vector of desired gains, G is the genotypic variance-covariance matrix and \underline{b} is the vector of index coefficients.

Two sets of desired gains were considered. In PD1 the genotypic standard deviations of each trait were taken as the desired gains and in PD2 the desired gains were calculated from the population mean before selection. The desired genetic gain for grain yield was set as 20% of the population mean (μ). The desired gain for kernel weight was held at zero, whereas for protein content 10% of the population mean was desired. These desired gains were used to calculate the index coefficients

and other parameters using the methods indicated in the Smith-Hazel index.

RESULTS AND DISCUSSION

Variance, Heritability, Index and Correlation Coefficient Estimates

Individual Traits

Estimates of phenotypic and genotypic covariances between traits and phenotypic and genetic variances of grain yield, 1000-kernel weight and protein content of four wheat crosses are given in Tables 2.1 to 2.4. The parameter estimates are based on combined analyses of F3 tests grown in two environments. Cross 1 showed the highest genetic variability in all three traits. Because we are dealing with F3 populations, the genetic variances of the three traits might have been biased upward because of the contribution of dominance and epistatic interactions. Genetic coefficient of variation was used to compare the relative magnitude of genetic variability among the four populations. The genetic coefficients of variation in the four crosses for yield, TKW and protein percent are given in Table 2.5.

Means, phenotypic and genetic correlation coefficients and estimates of heritabilities are given in Table 2.6. Heritability estimates for grain yield, as determined by the variance component method, ranged from 0.64 to 0.85 in the four crosses. The heritabilities for 1000-kernel weight were consistently high (0.86 to 0.96) while heritability estimates for protein percent ranged from 0.75 to 0.88. As indicated for the genetic variance, these high values of heritability could be an indication of

TABLE 2.1. Estimates of phenotypic and genotypic variances and covariances for grain yield, TKW and percent protein in cross 1.

Trait	Phenotypic variances and covariances			Genetic variances and covariances		
	Yield	TKW	Protein (%)	Yield	TKW	Protein (%)
Yield	270455.3 ± 38440.8	78.77 ± 11.20	-351.97 ± 50.03	230912.7 ± 38849.5	81.54 ± 11.20	-324.30 ± 50.18
TKW	78.77 ± 11.20	5.88 ± 0.84	0.34 ± 0.05	81.54 ± 11.20	5.62 ± 0.84	0.29 ± 0.05
Protein	- 351.97 ± 50.03	0.34 ± 0.05	0.75 ± 0.11	- 324.30 ± 50.18	0.29 ± 0.05	0.61 ± 0.11

TABLE 2.2. Phenotypic and genetic variance and covariance estimates for grain yield, TKW, and protein content in cross 2.

	Phenotypic variances and covariances			Genetic variances and covariances		
	Yield	TKW	Protein (%)	Yield	TKW	Protein (%)
Yield	<u>119909.2</u> ± 17043.2	172.19 ± 24.47	-152.07 ± 21.62	<u>79330.7</u> ± 17992.6	160.41 ± 24.53	-158.84 ± 21.64
TKW	172.19 ± 24.47	<u>5.74</u> ± 0.82	0.52 ± 0.07	160.41 ± 24.53	<u>5.26</u> ± 0.82	0.47 ± 0.07
Protein (%)	- 152.07 ± 21.62	0.52 ± 0.07	<u>0.51</u> ± 0.07	- 158.84 ± 21.64	0.47 ± 0.07	<u>0.45</u> ± 0.07

TABLE 2.3. Phenotypic and genetic variance and covariance estimates for yield, TKW and percent protein in cross 5.

Trait	Phenotypic variances and covariances			Genetic variances and covariances		
	Yield	TKW	Protein	Yield	TKW	Protein
Yield	107070.0 ± 15218.3	100.89 ± 14.34	-102.88 ± 14.62	76551.3 ± 15824.4	88.95 ± 14.44	-91.26 ± 14.72
TKW	100.89 ± 14.34	4.18 ± 0.60	-0.01 ± 0.00	88.95 ± 14.44	3.83 ± 0.60	-0.06 ± 0.01
Protein	-102.88 ± 14.62	-0.01 ± 0.0	0.56 ± 0.08	91.26 ± 14.72	-0.06 ± 0.01	0.41 ± 0.08

TABLE 2.4. Phenotypic and genetic variance and covariance estimates for yield, 1000-kernel weight and protein content in cross 6.

Trait	Phenotypic variances and covariances			Genetic variances and covariances		
	Yield	TKW	Protein	Yield	TKW	Protein
Yield	<u>169578.2</u> ± 24102.8	370.94 ± 52.72	-177.09 ± 25.17	<u>108170.1</u> ± 25634.5	381.05 ± 52.74	-165.10 ± 25.23
TKW	370.94 ± 52.72	<u>5.49</u> ± 0.78	- 0.17 ± 0.02	381.05 ± 52.74	<u>4.73</u> ± 0.79	- 0.24 ± 0.03
Protein	- 177.09 ± 25.17	- 0.17 ± 0.02	<u>0.58</u> ± 0.08	- 165.10 ± 25.23	- 0.24 ± 0.03	<u>0.51</u> ± 0.08

upward bias of estimates by non-additive components of genetic variance. This might have been contributed by both the nature of the F3 population and the method of estimation.

There were slight variations in realized heritabilities (h_a^2) calculated after selection using the predicted responses and selection differentials for each trait. Realized heritabilities for yield were 1.0, 0.79, 0.76 and 0.60 in C1, C2, C5 and C6, respectively. Correspondingly, h_a^2 values for TKW ranged 0.84 (C6) to 1.0 (C1), while the realized heritabilities for percent protein in the four crosses were 0.65 (C1), 0.82 (C2), 0.69 (C5) and 0.98 (C6).

The phenotypic and genetic correlations between yield and TKW were significant and positive in C2, C5 and C6. Grain yield and protein content were highly and negatively correlated ($r_G = -0.51^{**}$ to -0.87^{**}) in all four populations. The pattern of the correlation between TKW and protein content was not consistent across populations. In populations C1 and C2 these traits were positively correlated, whereas correlation coefficients were negative or zero in the other two crosses (Table 2.6).

The environmental correlation, r_E , can be defined by

$$r_E = \frac{(r_p - r_G \sqrt{h_1^2 h_2^2})}{\sqrt{(1-h_1^2)(1-h_2^2)}}$$

where r_p , r_G and r_E are the phenotypic, genetic and environmental correlation coefficients, respectively, and h_1^2 and h_2^2 are the heritability estimates of the two traits (Searle, 1961). The environmental correlation coefficients include random errors and may also contain genetic variation over and above additive genetic contribution. In the present study, the genetic correlation coefficients were relatively larger than their respective phenotypic correlation coefficients for most correlations in all

TABLE 2.5. Genetic coefficient of variation (%) for yield, TKW and protein content in four wheat crosses.

Cross	Yield	TKW	Protein
C1	14.5	5.6	4.4
C2	7.9	5.4	4.1
C5	8.6	4.7	3.6
C6	10.2	5.1	4.0

TABLE 2.6. Means, estimates of heritabilities (diagonal), phenotypic (above diagonal) and genetic (below diagonal) correlation coefficients for grain yield, TKW and protein content of four wheat crosses.

Cross	Trait	Means	Yield	TKW	Protein (%)
C1	Yield	3312 ± 35	<u>0.85</u> ± 0.03	0.06 ± 0.10	-0.78** ± 0.01
	TKW	42.1 ± 0.1	0.07 ± 0.10	<u>0.96</u> ± 0.01	0.16** ± 0.02
	Protein (%)	17.9 ± 0.05	-0.87** ± 0.01	0.16** ± 0.02	<u>0.81</u> ± 0.04
C2	Yield	3587 ± 35	<u>0.66</u> ± 0.07	0.21** ± 0.03	-0.61** ± 0.02
	TKW	42.2 ± 0.1	0.25** ± 0.03	<u>0.92</u> ± 0.02	0.30** ± 0.01
	Protein (%)	16.6 ± 0.05	-0.84** ± 0.01	0.30** ± 0.01	<u>0.88</u> ± 0.02
C5	Yield	3233 ± 38	<u>0.71</u> ± 0.11	0.15** ± 0.04	-0.42** ± 0.06
	TKW	41.6 ± 0.1	0.16** ± 0.04	<u>0.92</u> ± 0.02	-0.01 ± 0.03
	Protein (%)	18.0 ± 0.07	-0.51** ± 0.05	-0.05 ± 0.03	<u>0.75</u> ± 0.05
C6	Yield	3230 ± 39	<u>0.64</u> ± 0.07	0.38** ± 0.04	-0.56** ± 0.02
	TKW	43.0 ± 0.1	0.53** ± 0.03	<u>0.86</u> ± 0.03	-0.10 ± 0.02
	Protein (%)	17.7 ± 0.05	-0.70** ± 0.02	-0.15** ± 0.02	<u>0.88</u> ± 0.02

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

four crosses. Theoretically, such relationship between the magnitude of r_G and r_P implies negative environmental correlations, particularly so if the ratio of phenotypic correlation to the genetic correlation is less than the geometric mean of the heritabilities (Searle, 1961). However, this was not always the case in the present results. The environmental correlations between yield and TKW ranged from slightly negative value (-0.05, C6) to slightly positive coefficient (0.12, C5). The r_E values between yield and protein content were -0.37*, 0.13, -0.18 and -0.18, whereas the environmental correlations between TKW and protein percent were all positive with values of 0.24, 0.29*, 0.23 and 0.30* in C1, C2, C5 and C6, respectively.

Smith-Hazel Selection Index

Using the relative economic weights of 1.0, 0.0 and 0.2 for grain yield, TKW and protein content, respectively, index coefficients were computed following the procedures of Smith (1936) and Hazel (1943). The estimated SH index coefficients, heritability, phenotypic, and genotypic standard deviations of SH index, and the standard deviation of the aggregate genotype for the four crosses are given in Table 2.7. The relatively high level of genetic coefficient of variation observed in C1 was also shown in the high genetic standard deviations in the SH index and the aggregate genotype of same cross. The h^2_I 's were high in all crosses ranging from 74% (C5) to 91% (C2). The selection indices, when standardized by dividing each by the coefficient for yield in each population, were as follows:

$$C1 : (SH)I = MYD + 13.328 MTK - 131.783 MPR$$

$$C2 : (SH)I = MYD + 216.400 MTK - 1329.166 MPR$$

TABLE 2.7. Selection index coefficients, heritability, phenotypic and genotypic standard deviations of Smith-Hazel index and the standard deviation of the aggregate genotype in four wheat crosses involving yield, TKW and protein.

Cross	Trait	Index coeff. (b's)	h_I^2	$SD_{P(I)}$	$SD_{G(I)}$	$SD(H)$
C1	Yield	0.7262	0.87	446.6	416.6	480.4
	TKW	9.6788				
	Protein	- 95.7009				
C2	Yield	0.2207	0.91	267.8	256.2	281.5
	TKW	47.7594				
	Protein	-293.3470				
C5	Yield	0.6722	0.74	235.6	202.0	276.6
	TKW	4.9157				
	Protein	- 39.5556				
C6	Yield	0.3962	0.85	287.0	264.0	328.8
	TKW	37.9078				
	Protein	-151.8740				

$$C5 : (SH)I = MYD + 7.313 MTK - 58.845 MPR$$

$$C6 : (SH)I = MYD + 95.678 MTK - 383.327 MPR$$

where MYD, MTK and MPR are pooled means of grain yield, 1000-kernel weight and protein percent, respectively.

The top 10% of each population was selected using the above indices. Both the high negative genetic correlation between grain yield and percent protein and the negative index coefficient for mean protein indicate a major problem in attaining a reasonable level of simultaneous genetic progress of grain yield and protein content in wheat.

Weight-Free Selection Indices

Three weight-free selection indices were used in this study. First, selection was based on the multiplicative index involving yield, TKW and protein. To compare the relative progress in grain yield, the top 10% (EW1) and the lowest 10% (EW2) of each population was retained on the basis of this index. Second, weight-free multiplicative index (EW3) involving only grain yield and TKW was used to observe the effect on genetic progress of grain yield of including protein content in the construction of the index. This will shed some light on the degree of reduction from the attainable advance in yield due to the negative correlation between yield and protein content. The third weight-free index (EW4) was based on Baker's (1974) suggestion to approximate the index for grain yield and TKW by its linear equivalent by multiplying the mean yield by the phenotypic standard deviation of TKW, and vice versa, and adding. The weight-free indices obtained for each cross were as follow:

$$C1 : (EW1)I = (MYD - 1308.9) (MTK - 35.7) (MPR - 16.0)$$

$$(EW3)I = (MYD - 1308.9) (MTK - 35.7)$$

$$(EW4)I = MYD + 214.4 MTK$$

$$\begin{aligned}
 \text{C2 : (EW1)I} &= (\text{MYD} - 2482.6) (\text{MTK} - 36.3) (\text{MPR} - 15.4) \\
 (\text{EW3)I} &= (\text{MYD} - 2482.6) (\text{MTK} - 36.3) \\
 (\text{EW4)I} &= \text{MYD} + 144.5 \text{ MTK} \\
 \text{C5 : (EW1)I} &= (\text{MYD} - 2522.8) (\text{MTK} - 36.6) (\text{MPR} - 16.6) \\
 (\text{EW3)I} &= (\text{MYD} - 2522.8) (\text{MTK} - 36.6) \\
 (\text{EW4)I} &= \text{MYD} + 160.0 \text{ MTK} \\
 \text{C6 : (EW1)I} &= (\text{MYD} - 2246.5) (\text{MTK} - 37.3) (\text{MPR} - 15.4) \\
 (\text{EW3)I} &= (\text{MYD} - 2246.5) (\text{MTK} - 37.3) \\
 (\text{EW4)I} &= \text{MYD} + 175.8 \text{ MTK}
 \end{aligned}$$

Desired Gains Selection Indices

Two desired gains selection indices were constructed; one (PD1) based on desired gains equal to the genetic standard deviation of each trait and the second, (PD2), using 20% of F3 population mean as the desired gains for yield, zero for TKW and 10% of F3 population mean for protein. The resulting index coefficients, heritability and phenotypic and genetic standard deviations for PD1 and PD2 are shown in Tables 2.8 and 2.9, respectively. The desired gains indices in both procedures were standardized by dividing each coefficient by the index coefficient for yield. The indices for two approaches are listed below:

$$\begin{aligned}
 \text{C1 : (PD1)I} &= \text{MYD} - 22.2051 \text{ MTK} + 619.7746 \text{ MPR} \\
 (\text{PD2)I} &= \text{MYD} - 48.0161 \text{ MTK} + 641.6105 \text{ MPR} \\
 \text{C2 : (PD1)I} &= \text{MYD} - 66.8200 \text{ MTK} + 425.6389 \text{ MPR} \\
 (\text{PD2)I} &= \text{MYD} - 68.3750 \text{ MTK} + 425.7157 \text{ MPR} \\
 \text{C5 : (PD1)I} &= \text{MYD} + 58.8726 \text{ MTK} + 454.9284 \text{ MPR} \\
 (\text{PD2)I} &= \text{MYD} - 15.5890 \text{ MTK} + 447.7652 \text{ MPR} \\
 \text{C6 : (PD1)I} &= \text{MYD} - 17.5982 \text{ MTK} + 438.3061 \text{ MPR} \\
 (\text{PD2)I} &= \text{MYD} - 60.2845 \text{ MTK} + 398.4038 \text{ MPR}
 \end{aligned}$$

TABLE 2.8. Desired gains (PDI) selection index coefficients, heritability, phenotypic and genotypic standard deviations of PDI indices and aggregate genotypes in four wheat crosses involving three traits.

Cross	Trait	Index coeff. (b's x 1000)	h^2_I	SDp(I)	SDg(I)	SD(H)
C1	Yield	0.0356	0.47	0.0119	0.0082	480.5
	TKW	- 0.7900				
	Protein	22.0491				
C2	Yield	0.9955	0.03	0.2360	0.0384	281.7
	TKW	- 66.5175				
	Protein	423.7120				
C5	Yield	0.0248	0.65	0.0097	0.0078	276.7
	TKW	1.4619				
	Protein	11.2966				
C6	Yield	0.0344	0.46	0.0118	0.0079	328.9
	TKW	- 0.6047				
	Protein	15.0616				

TABLE 2.9. Desired gains (PD2) selection index coefficients, heritability, phenotypic and genotypic standard deviations of PD2 indices and aggregate genotype in four wheat crosses involving three traits.

Cross	Trait	Index coeff. (b's x 1000)	h^2_I	$SD_{P(I)}$	$SD_{G(I)}$	$SD(H)$
C1	Yield	0.0528	0.46	0.0178	0.0120	480.5
	TKW	- 2.5375				
	Protein	33.9070				
C2	Yield	1.3456	0.03	0.3190	0.0517	281.7
	TKW	- 92.0054				
	Protein	572.8430				
C5	Yield	0.0291	0.62	0.0103	0.0081	276.7
	TKW	- 0.4545				
	Protein	13.0537				
C6	Yield	0.0515	0.39	0.0166	0.0104	328.9
	TKW	- 3.1037				
	Protein	20.5117				

Comparison of Various Single Trait and Index Selections

Selection Based on Individual Traits

Selection differentials of unit-trait and index selections were expressed as percentages of the single trait selection differential (Table 2.10).

The significant negative genetic correlation between yield and protein observed in the crosses (Table 2.6) resulted in substantial reduction in the selection differential (S) for protein when the selection criterion was grain yield per se. In all four crosses used in the present study, selection for yield resulted in about -50% of the selection differential if selection was based on protein per se. In contrast, the reduction in grain yield S when selection was on the basis of protein was very dramatic and variable. Selection differentials for yield ranged from -40% (C5) to -150% (C1). This means that in C1, for example, the selection differential for grain yield will be reduced by about 250% when selection is based on protein instead of yield. This makes it extremely difficult to maintain an acceptable level of percent protein if the breeders' sole objective is grain yield. The reverse is also true, i.e. the impracticability of maintaining yield if selection is based solely on protein content (see Figures 2.2 and 2.3).

The effect on TKW of selection based on yield also varied from cross to cross. In C1 selection differential was reduced by about 93% of what it would have been had selection been based on TKW, whereas in C6 this reduction was only 40%. On the other hand, when selection was based on TKW, the reduction in grain yield selection differential ranged from 24% (C6) to 120% (C5). Selecting for TKW also affected the selection differential for protein level differently but with less magnitude, ranging

TABLE 2.10. Selection differentials (proportion selected = 10%) for yield, TKW and protein using various unit-trait and index selection procedures in four wheat crosses expressed as a percentage of single-trait selection differentials.

Selection method	Cross 1*			Cross 2			Cross 5			Cross 6		
	YD	TK	PR	YD	TK	PR	YD	TK	PR	YD	TK	PR
SH	100.0	19.5	- 52.1	83.1	42.9	- 61.8	99.0	21.1	- 54.5	91.2	81.4	- 73.4
EW1	27.5	75.6	19.2	31.4	83.3	41.9	38.2	60.6	39.9	76.9	83.7	- 11.7
EW2	- 21.8	- 97.6	- 14.7	0.1	- 78.6	- 50.0	- 54.2	- 47.4	- 8.4	- 46.3	- 72.1	- 28.1
EW3	62.8	82.9	- 17.4	68.8	81.0	- 5.9	69.2	76.3	- 14.7	84.2	97.7	- 55.5
EW4	62.8	82.9	- 17.4	61.7	88.1	- 4.4	61.0	84.2	- 10.5	84.2	97.7	- 55.5
PD1	22.8	2.4	34.5	56.6	- 7.1	15.4	54.5	32.6	46.4	66.2	22.2	14.8
PD2	30.3	- 24.4	26.9	56.6	- 7.1	15.4	28.5	7.9	69.9	58.5	- 12.6	12.5
YD	100.0	7.3	- 50.5	100.0	23.8	- 47.8	100.0	7.9	- 51.0	100.0	60.5	- 66.4
TK	- 8.4	100.0	18.9	29.9	100.0	21.3	- 20.0	100.0	0.0	75.8	100.0	- 43.0
PR	-149.6	0.0	100.0	- 98.5	26.2	100.0	- 39.9	- 13.2	100.0	- 60.6	- 25.6	100.0

*YD = Yield (kg/ha); TK = TKW (g); and PR = Protein (%).

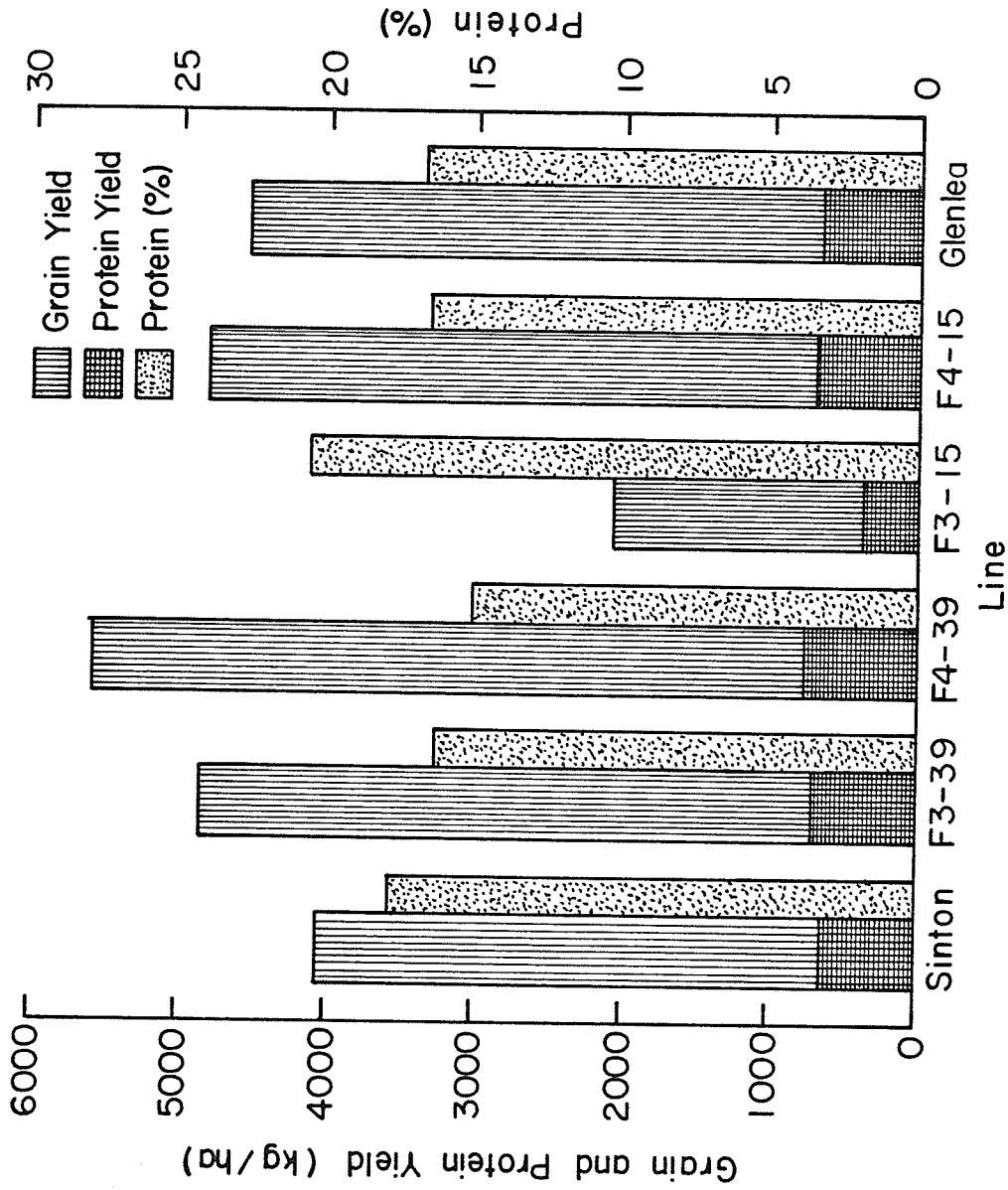


FIGURE 2.2. Means of the best F3 lines in grain yield and protein (%), respectively, their F4 bulks and parents in wheat population 1 grown at the Point.

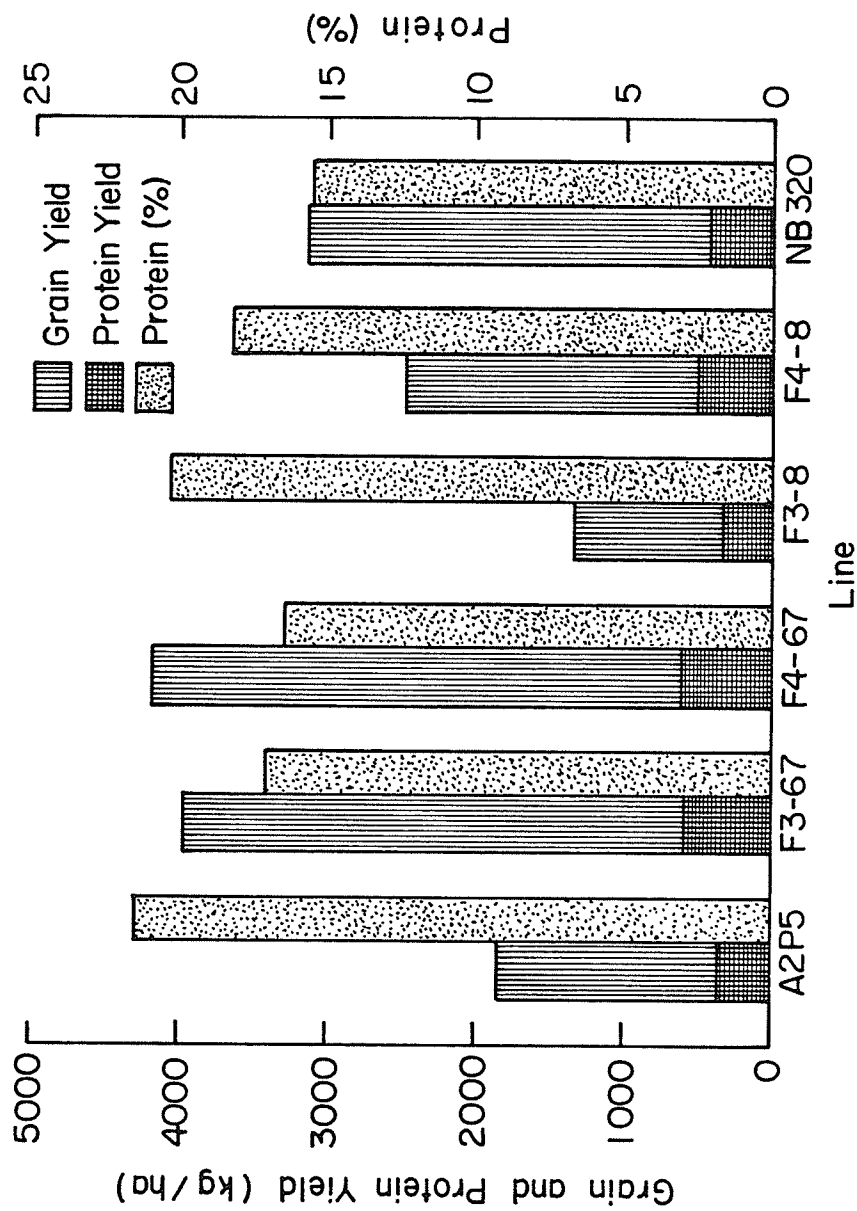


FIGURE 2.3. Means of the best F3 lines in grain yield and protein (%), respectively, their F4 bulks and parents in wheat population 6 grown in Glenlea.

between 79% and 143%. Inversely, selection on the basis of protein reduced the TKW selection differential from 74% to 126%.

These results for selection differentials are translated into predicted direct and correlated genetic response due to selection. Table 2.11 gives predicted direct and correlated responses due to unit-trait and SH index selections. The highest expected direct response for yield (778 kg/ha; C1) resulted in only a 0.28 g correlated response in TKW and a -1.1% response in protein (Table 2.11). The reverse was even more marked. In the same cross, selection on the basis of protein gave an expected gain in protein of 1.23% while the same selection resulted in a correlated response in yield of -659 kg/ha. This indicates that in the C1 population, at least, a 1.0% increase in protein through selection ($i = 1.76$) will depress grain yield by 536 kg/ha below the mean of the unselected population. These reductions due to correlated response were less in magnitude in the other three crosses but were still significant. The predicted correlated responses due to selection on TKW were relatively intermediate. The predicted CR for yield when selection was based on TKW per se ranged from 59 kg/ha (C1) to 286 kg/ha (C6). The implication of this result is that although genetic gains will be relatively low, progress in grain yield is possible in wheat by selecting for high kernel weight. This relationship was also true for protein. The CR of protein content when selection was for high kernel weight ranged from -.19% to .34%.

Expected gains from selection on various unit-trait and indices are given in Tables 2.12 to 2.15. Also, shown are the means of selected (P = 10%) F3 lines from each selection method and the relative efficiencies (RE %) of the methods. Relative efficiency values were determined in relation to expected gains from single trait selection. Some differences

TABLE 2.11. Predicted direct and correlated responses from selection based on various single-trait and SH selection index for grain yield, TKW, protein percent and net merit in F3 populations of four wheat crosses.

Cross and basis of selection*	Direct and Correlated Predicted Responses				
	YD (kg/ha)	TK (g)	PR (%)	H	K
C1 YD	778 ± 103	0.3	-1.10		
TK	59	4.1 ± 0.5	0.21		
PR	-659	0.6	1.23 ± 0.17		
SH	125	0.1	-0.92	786	684
C2 YD	403 ± 69	0.8	-0.81		
TK	118	3.9 ± 0.5	0.34		
PR	-391	1.1	1.11 ± 0.14		
SH	357	-0.7	-0.08	471	429
C5 YD	412 ± 65	0.5	-0.49		
TK	76	3.3 ± 0.4	-0.06		
PR	-216	-0.1	0.98 ± 0.15		
SH	30	0.5	-0.46	415	307
C6 YD	462 ± 80	1.6	-0.75		
TK	286	3.6 ± 0.5	-0.19		
PR	-381	-0.5	1.26 ± 0.15		
SH	242	1.1	-0.46	505	429

*YD = Yield; TK = TKW; PR = Protein; H = Aggregate genotype; K = Aggregate breeding value.

were observed between predicted direct and indirect responses in Table 2.11 and expected gains in Tables 2.12 to 2.15. This resulted from the fact that the expected gains in Tables 2.12 to 2.15 were calculated using selection differentials after selection.

Expected gains in yield for the four crosses when the selection criterion was yield per se, ranged from 335 (C2) to 596 (C1) kg/ha. These gains were significantly reduced when selection was based on either kernel size or protein content. The reduction in efficiency varied from population to population (Tables 2.12 to 2.15). When selection was based on TKW, the expected gain in yield was reduced by about 120% in cross 5 while this loss was only 24% in cross 6. The reduction in expected yield gain was rather dramatic when the selection criterion was protein percent. Expected gains were reduced by as much as 250%. This corroborates other reports on the difficulty of improving wheat grain yield and protein content simultaneously.

On the other hand, selection based on yield caused a moderate progress in kernel size but significantly reduced the potential advance in percent protein. The average relative efficiency for expected protein gain was -57% when selection was based on yield.

Means of selected F4 bulks and realized gains from various criteria of selection are given in Tables 2.16 to 2.19. In addition, the ratio of the actual gain (R_a) to the expected gain (R) from each method of selection is calculated and expressed in percent (Tables 2.16 to 2.19).

The actual yield gains from selection on grain yield were lower than expected estimates in three of the four populations. In C1 and C2, 75% of the expected yield gain was realized whereas in C6 the actual yield gain was only 60% of the expected progress. In contrast, the actual

TABLE 2.12. Means, expected gains (R) and relative efficiencies (RE) from selection on various single-trait and selection indices for grain yield, TKW and protein content in F₃ population of wheat cross I.

Basis of selection	Yield (kg/ha)			TKW (g)			Protein (%)		
	Means of sel. F ₃ lines	Exp. gain	RE (%)	Means of sel. F ₃ lines	Exp. gain	RE (%)	Means of sel. F ₃ lines	Exp. gain	RE
SH	4014	596	100.0	42.9	0.8	19.5	16.9	-0.80	- 52.1
EW1	3506	164	27.5	45.2	3.0	75.6	18.3	0.30	19.2
EW2	3160	-130	- 21.8	38.1	-3.8	- 97.6	17.7	-0.23	- 14.7
EW3	3753	374	62.8	45.5	3.3	82.9	17.6	-0.27	- 17.4
EW4	3753	374	62.8	45.5	3.3	82.9	17.6	-0.27	- 17.4
PD1	3473	136	22.8	42.2	0.1	2.5	18.6	0.53	- 34.5
PD2	3525	181	30.4	41.1	-1.0	- 24.6	18.4	0.41	26.9
YD	4014	596 ± 74	100.0	42.4	0.3	7.7	17.0	-0.78	- 50.6
TK	3254	- 50	- 8.4	46.2	3.2 ± 0.3	100.0	18.3	0.29	18.8
PR	2263	-892	-149.6	42.1	0.0	0.0	19.8	1.54 ± 0.13	100.0

TABLE 2.13. Means, expected gains (R) and relative efficiencies (RE) from selection on various single-trait and selection indices for grain yield, TKW and protein content in F3 population of wheat cross 2.

Basis of selection	Yield (kg/ha)			TKW (g)			Protein (%)		
	Means of sel. F3 lines	Exp. gain	RE (%)	Means of sel. F3 lines	Exp. gain	RE (%)	Means of sel. F3 lines	Exp. gain	RE
SH	4010	279	83.1	44.0	1.7	42.9	15.7	-0.74	- 61.8
EW1	3747	105	31.4	45.7	3.2	83.3	17.2	0.50	41.9
EW2	3588	0	0.0	38.9	-3.0	- 78.6	15.9	-0.60	- 50.0
EW3	3937	231	68.8	45.6	3.1	81.0	16.5	-0.07	- 5.9
EW4	3901	207	61.7	45.9	3.4	88.1	16.5	-0.05	- 4.4
PD1	3875	190	56.7	41.9	-0.3	- 7.7	16.8	0.18	15.4
PD2	3875	190	56.7	41.9	-0.3	- 7.7	16.8	0.18	15.4
YD	4096	335 ± 57	100.0	43.2	1.0	23.8	15.9	-0.57	- 47.8
TK	3739	100	29.9	46.4	3.9 ± 0.3	100.0	16.9	0.26	21.3
PR	3087	-330	- 98.5	43.3	1.0	26.2	17.9	1.20 ± 0.10	100.0

TABLE 2.14. Means, expected gains (R) and relative efficiencies (RE) from selection on various single-trait and selection indices for grain yield, TKW and protein content in F3 population of wheat cross 5.

Basis of selection	Yield (kg/ha)			TKW (g)			Protein (%)		
	Means of sel. F3 lines	Exp. gain	RE (%)	Means of sel. F3 lines	Exp. gain	RE (%)	Means of sel. F3 lines	Exp. gain	RE
SH	3767	379	98.9	42.4	0.7	20.8	17.3	-0.59	- 54.5
EW1	3439	146	38.2	43.9	2.1	59.9	18.6	0.43	39.9
EW2	2941	-208	- 54.2	39.8	-1.7	- 46.9	17.9	-0.09	- 8.4
EW3	3606	265	69.2	44.5	2.7	75.6	17.8	-0.16	- 14.7
EW4	3562	234	61.0	44.8	2.9	83.4	17.9	-0.11	- 10.5
PD1	3527	209	54.5	42.8	1.1	32.3	18.7	0.50	46.4
PD2	3387	109	28.5	41.9	0.3	7.8	19.0	0.76	71.3
YD	3773	383 ± 52	100.0	41.9	0.3	7.8	17.3	-0.55	- 51.0
TK	3125	- 77	- 20.0	45.4	3.5 ± 0.3	100.0	18.0	0.00	0.0
PR	3018	-153	- 39.9	41.1	-0.5	- 13.0	19.5	1.07 ± 0.12	100.0

TABLE 2.15. Means, expected gains (R) and relative efficiencies (RE) from selection on various single-trait and selection indices for grain yield, TKW and protein content in F3 population of wheat cross 6.

Basis of selection	Yield (kg/ha)			TKW (g)			Protein (%)		
	Means of sel. F3 lines	Exp. gain	RE (%)	Means of sel. F3 lines	Exp. gain	RE (%)	Means of sel. F3 lines	Exp. gain	RE
SH	3933	450	91.2	46.5	3.0	81.4	16.7	-0.83	- 73.4
EW1	3822	579	76.9	46.6	3.1	83.7	17.5	-0.13	- 11.7
EW2	2873	-228	- 46.3	39.9	-2.7	- 72.1	17.3	-0.32	- 28.1
EW3	3878	415	84.2	47.2	3.6	97.7	17.0	-0.62	- 55.5
EW4	3878	415	84.2	47.2	3.6	97.7	17.0	-0.62	- 55.5
PD1	3740	326	66.2	44.0	0.8	22.2	17.9	0.17	14.8
PD2	3681	288	58.5	42.5	-0.5	- 12.6	17.8	0.14	12.5
YD	4000	493 ± 68	100.0	45.6	2.2	60.5	16.8	-0.75	- 66.4
TK	3814	374	75.8	47.3	3.7 ± 0.3	100.0	17.1	-0.48	- 43.0
PR	2763	-299	- 60.6	41.9	-0.9	- 25.6	18.9	1.13 ± 0.10	100.0

advance in yield in C5 was 137% of the expected value. When selection was based on yield, the actual correlated responses in TKW and percent protein also varied from cross to cross (Tables 2.16 to 2.19). In the high-protein parent cross (C6), the actual reduction in protein content due to selection for yield was 159% of the expected decrease. In the same population, the actual loss in protein when selection was based on TKW was 200% of the predicted estimate.

Lack of the relative fit between the expected and the actual gain might have resulted from one or more of several factors: (1) seasonal variation, (2) methods of parameter estimations, (3) the genetic structure of the segregating F3 and F4 populations, or (4) the mean of the unselected F4 population which is assumed to be the mean of a random sample composite of the unselected population for each trait.

Selection Based on Various Indices

The resulting selection differentials of the SH index were relatively consistent from cross to cross as far as yield and protein were concerned (Table 2.10). The percent selection differentials for yield when selection was on SH index were high ranging from 83 (C2) to 100 (C1). This is a measure of the high relative economic weight assigned to grain yield in the construction of the index. On the other hand, percent selection differentials for protein were consistently low ranging from -52 (C1) to -73 (C6). In spite of the fact that TKW was given zero relative economic weight in SH, its selection differential in C6 was relatively high (Table 2.10).

In general, the weight-free indices resulted in the least reduction in protein selection differential. In particular, based on selection differential values, EW1 was one of the best indices for improving protein

TABLE 2.16. Means, realized gains (Ra) and Ra/R ratios from selection on yield and various selection indices for grain yield, TKW and protein content in wheat cross I.

Basis of selection	Yield (kg/ha)		TKW (g)		Protein (%)	
	Means of sel. F4 bulks	Realized gain	Means of sel. F4 bulks	Realized gain	Means of sel. F4 bulks	Realized gain
SH	4159	443	42.0	0.3	15.8	-0.59 (73.7)*
EW1	3776	60	44.0	2.3	16.9	0.49 163.3
EW2	3837	121	37.7	-4.0	16.3	-0.11 (47.8)
EW3	3964	248	44.4	2.7	16.3	-0.13 (48.1)
EW4	3964	248	44.4	2.7	16.3	-0.13 (48.1)
YD	4163	446	41.6	-0.2	15.8	-0.62 (79.5)

* Ratios in parenthesis show percent reduction.

TABLE 2.17. Means, related gains (Ra) and Ra/R ratios from selection on yield and various selection indices for grain yield, TKW and protein content in wheat cross 2.

Basis of selection	Yield (kg/ha)			TKW (g)			Protein (%)		
	Means of sel. F4 bulks	Realized gain	Ra/R (%)	Means of sel. F4 bulks	Realized gain	Ra/R (%)	Means of sel. F4 bulks	Realized gain	Ra/R (%)
SH	4937	236	84.6	41.2	1.0	58.8	14.5	-0.54	(73.0)*
EW1	4584	-118	-112.4	43.9	3.7	115.6	15.4	0.42	84.0
EW2	4645	- 57	--	38.0	-2.2	(73.3)	14.4	-0.59	(98.3)
EW3	4894	192	83.1	43.1	2.9	93.5	14.9	-0.11	(157.1)
EW4	4959	257	124.2	43.4	3.2	94.1	14.9	-0.17	(340.0)
YD	4952	250	74.6	41.2	1.0	100.0	14.7	-0.29	(50.9)

* Ratios in parenthesis indicate percent decrease.

TABLE 2.18. Means, realized gains (Ra) and Ra/R ratios from selection on yield and various selection indices for grain yield, TKW and protein content in wheat cross 5.

Basis of selection	Yield (kg/ha)			TKW (g)			Protein (%)		
	Means of sel. F4 bulks	Realized gain	Ra/R (%)	Means of sel. F4 bulks	Realized gain	Ra/R (%)	Means of sel. F4 bulks	Realized gain	Ra/R
SH	4259	543	143.3	38.8	0.7	100.0	15.6	-0.86	(145.8)*
EW1	3709	-7	4.8	41.1	3.0	142.9	16.9	0.35	81.4
EW2	3613	-103	(49.5)	36.6	-1.4	(82.4)	16.3	-0.17	(188.9)
EW3	4049	334	126.0	40.9	2.8	103.7	16.2	-0.26	(162.5)
EW4	4049	334	142.7	40.9	2.8	96.6	16.2	-0.26	(236.4)
YD	4221	505	131.9	38.6	0.5	167.9	15.7	-0.79	(143.6)

* Ratios in parenthesis show percent loss.

TABLE 2.19. Means, realized gains (Ra) and Ra/R ratios from selection on yield, TKW and various selection indices for grain yield, TKW and protein content in wheat cross 6.

Basis of selection	Yield (kg/ha)			TKW (g)			Protein (%)		
	Means of sel. F4 bulks	Realized gain	Ra/R (%)	Means of sel. F4 bulks	Realized gain	Ra/R (%)	Means of sel. F4 bulks	Realized gain	Ra/R
SH	4172	346	76.9	43.2	3.0	100.0	15.0	-1.32	(159.0)*
EW1	3976	150	39.6	43.8	3.7	119.4	15.8	-0.58	(446.2)
EW2	3667	-159	(69.7)	37.6	-2.5	(92.6)	15.6	-0.80	(250.0)
EW3	4096	270	65.1	43.7	3.6	100.0	15.3	-1.04	(167.7)
EW4	4096	270	65.1	43.7	3.6	100.0	15.3	-1.04	(167.7)
YD	4124	298	60.4	42.6	2.5	113.6	15.2	-1.19	(158.7)
TK	4022	196	52.4	43.9	3.8	102.7	15.4	-0.96	(200.0)

* Ratios in parenthesis show percent loss.

next to selecting direct for protein percent per se. EW1 and the PD's were the only indices that gave positive selection differential for protein. Selection differential percentages for EW1 were 19, 40 and 42 for C1, C5 and C2, respectively. On the other hand, EW1 was relatively inferior for identifying high yielding lines. Nevertheless, among the weight-free indices EW1, EW3 and EW4 tend to identify lines with high TKW. EW3 and EW4 showed very close agreement in all respects. Both these indices isolated relatively high yielders (S = 61% to 84%), lines having high kernel weight (S = 76% to 98%), and resulted in the least reduction in protein percent (S = -4% to -50%). Comparatively, EW2 resulted in significant decrease in selection differentials of yield, TKW and percent protein.

The two desired gains indices gave slightly different selection differentials across the four populations and the three traits. For yield, the percent selection differential from PD1 ranged from 23 (C1) to 66 (C6), whereas the equivalent range from PD2 was 29 (C5) to 59 (C6) (Table 2.10). In general, however, with the exception of C5, the two indices resulted in similar levels of percent yield selection differentials. On the other hand, the PD1 showed relatively higher selection differential in kernel size than PD2 in most cases. Nevertheless, the percent S for TKW from both PD1 and PD2 were very low. As far as protein content was concerned, all the selection differential estimates were positive and in some cases highly significant. The highest percent S values were 46 and 70 for PD1 and PD2, respectively. Both these values were recorded for population C5.

Based on selection differential values, the various indices used can be ranked as follows: for grain yield, the SH index was the most efficient

in identifying high yielding lines followed by EW3 and EW4 in a second position. The PD1, PD2 and EW1 were third as a group. The weight-free indices were superior in identifying large-kernelled lines followed by the SH index. The desired gains indices were the least in TKW S values. For protein content, the desired gains were found to be the most efficient methods followed by the weight-free indices, particularly EW1. Conversely, the SH index resulted in highly significant reduction in percent protein advance.

As the relative economic weights have important effects on the SH index, the assignment of appropriate and realistic levels of desired gains were important in the desired gains index. In this study, the use of genotypic standard deviations of each trait as desired gains was slightly more efficient than the second set of desired gains used.

In contrast, compared to EW1, selection in the direction of the low tail of the curve using the weight-free index (EW2) resulted in significant and approximately equal amounts of negative selection response (in the opposite direction) for most traits and crosses.

In the Smith-Hazel index predicted aggregate genotype values (H) for grain yield ranged from 415 (C5) to 786 (C1). The corresponding K values were 307 to 684 (Table 2.11). These results depict the high heritability and phenotypic standard deviation estimates of the index. The expected indirect responses for yield when selection was based on SH were low in populations C1 and C5 but comparatively high in C2 and C6. The corresponding estimates for TKW also varied from slightly negative response to positive gains. In contrast, the predicted correlated responses for protein when selection was based on this index were significantly and consistently negative (Table 2.11).

The expected gains shown in Tables 2.12 to 2.15 were calculated using the selection differentials obtained after selection, therefore there are some differences from the predicted gains in Table 2.11. In the C1 population, SH gave high expected yield gain (596 kg/ha), whereas the effect on TKW was non-significant. However, the expected selection response for protein content was reduced significantly (-52%). The relative efficiency results in the three traits of populations were more or less similar with that of C1. This explains that while the relative efficiency of selecting for high yield on this index was as good as direct selection for yield, the negative effect on protein improvement can be significant.

This same general trend was seen in the other two populations with minor differences. In the C2 population, the relative efficiencies of SH for yield, TKW and protein were 83%, 43% and -62%, respectively. In C6, however, these relative efficiencies were significantly different, viz., 91% (yield), 81% (TKW) and -73% (protein). These results indicate the effectiveness of selecting for high protein using the SH index is rather very low and approximately equal to selection based on yield per se. In all four crosses the expected gain in protein content was predominantly negative. For instance, in C6 the efficiency of selecting for elevated protein lines based on the Smith-Hazel index in relation to direct selection for protein percent was -73%. Therefore, as far as improving grain protein level is concerned, direct selection for high protein is superior to using the SH index by 173%. In other words, unless the breeder is willing to sacrifice grain protein level for genetic progress in yield and kernel size in wheat, the application of the Smith-Hazel index may not be the right choice of breeding method. Conversely,

increasing the relative economic weight assigned to protein content will result in yield reduction. In addition, the magnitude of such a reduction in expected protein improvement was similar when selection was based on grain yield per se.

Among the weight-free indices, EW3 and EW4 were similar in most respects across the four populations. The multiplicative weight-free index (EW3) and its linear approximation (EW4) were found to be better choices when protein improvement is one of the objectives of a selection program. These methods showed reasonable levels of relative efficiency for expected gains in yield (61% to 84%) and also resulted in a significantly high efficiency in the selection progress of kernel size. The expected gains in kernel weight ranged from 2.7 g to 3.6 g with RE varying from 76% to 98%. As far as protein content was concerned, the loss in expected gain in relation to direct selection for protein was minimal in three of the four crosses. The average RE values were -17%, -5% and -11% in the C1, C2 and C5 populations, respectively.

The multiplicative weight-free index (EW1) involving yield, TKW and percent protein was of particular interest. This index resulted in relatively low to intermediate levels of efficiency in identifying high yielding lines compared to selecting for yield per se. Relative efficiencies for yield ranged from 27% to 77%. Nevertheless, the low yield gains were compensated by the relatively high genetic advance in TKW, and moderate levels of positive progress in percent protein. The expected gains in TKW ranged from 2.1 g to 3.2 g with RE values ranging from 60% to 84%. Concurrently, the expected gains in protein percent were positive in all crosses except in C6. Relative efficiency values were as high as 42%. Conversely, EW2 resulted in significant negative selection effect

in all the traits studied.

More comparison of the expected selection responses from EW1 and EW2 is pertinent. The expected yield gains from EW1 ranged from 105 (C2) to 379 kg/ha (C6), whereas the equivalent expected yield gains from EW2 varied from zero to -228 kg/ha. The relative efficiency for yield response in EW1 averaged 43.5% compared to -30.6% for EW2. This pattern was similar for kernel size with average RE values of 75.6% for EW1 versus -73.8% for EW2. Thus, EW1 tended to identify high kernel weight lines, whereas selection in the opposite direction was also equally effective in identifying small-kernelled lines. The relative efficiency of EW1 in expected advance in protein content is of particular interest. EW1 gave significant positive RE values in three of the four crosses. Relative efficiency values as high as 41.9% were recorded for EW1, while EW2 gave significant percent efficiency values in the opposite direction ranging from -8.4% to -50.0%. These results support our hypothesis that the unweighted multiplicative index, although relatively less efficient in identifying high yielding lines, can be an efficient selection index in improving grain protein in wheat.

On the other hand, when protein percent was eliminated from the index to measure the effect of the negative correlation between grain yield and grain protein on the response to selection, the relative efficiency in yield progress increased significantly ranging from 62.8% (C1) to 84.2% (C6). In addition the efficiency of EW3 in selecting large-kernelled lines was better than EW1 (75.6% to 97.7%). However, the expected genetic progress in protein content when selection was based on EW3 became negative with RE values varying from -5.9% to -55.5%. This indicates that the inclusion of protein in the unweighted index does adversely affect the

genetic advance in grain yield but aids in improving protein content.

The expected genetic gains obtained for the two desired gains indices were similar with minor differences across populations. The expected yield gains ranged from 109 (C5 - PD2) to 326 kg/ha (C6 - PD1). The relative efficiencies of these indices in relation to direct selection for yield were 27%, 57%, 41% and 62% in populations C1, C2, C5 and C6, respectively. Thus, for the desired gains and populations used in the study, the use of the desired gains selection index may not result more than 50% of the expected yield gain under direct selection for yield. In addition, because of both the properties of the index and the desired gains assigned for each trait, the expected gains in TKW were low or negative in all crosses. However, the desired gains were found to be the best index in improving grain protein in wheat in the present study. Relative efficiency values of as high as 59% were recorded for protein content.

In general, these estimates of expected gains from selection on the basis of different indices indicate that although the Smith-Hazel index procedure was superior in identifying high yielding lines, the weight-free multiplicative index or preferably the linear approximation of the weight-free index would prove superior overall. This results from the fact that the former indices resulted in substantial negative effect on selection response of protein, whereas the latter group identified reasonably high yield and large kernel lines with the least decrease in protein content.

The realized gains in the three traits studied from selection on Smith-Hazel and weight-free indices and yield per se are given in Tables 2.16 to 2.19. When selection methods were compared in regard to the means of selected lines in F3 and F4 generations, the SH index and direct

selection for yield consistently gave higher yield means across populations in F3 and F4. The actual gains in yield compared to the expected gains, however, were variable from cross to cross and procedure to procedure. The realized gains in grain yield from selection based on the Smith-Hazel and weight-free indices were lower than the expected advance in populations C1, C2 and C6 but were higher in C5. The average actual yield gains in these three populations were 79%, 72% and 85% of the expected values for SH, EW3 and EW4, respectively. In populations C1, C2 and C6 the actual yield gain from selection for yield per se averaged 70% of the expected genetic advance. The realized gains in C5 from all the selection criteria used were higher than the expected yield progress. The Ra/R ratios for yield in this cross were 143%, 126%, 143% and 132% for SH, EW3, EW4 and yield per se, respectively. The results observed for this cross may be due to the general low level of productivity of the population during the 1979 season and its better performance during the F4 generation. On the other hand, the actual yield gain from EW1 varied inconsistently from cross to cross with Ra/R ratios ranging from -112% to 40%.

The comparison of EW1 and EW2 in relation to actual gains observed showed that realized yield gains fluctuated inconsistently from cross to cross while the kernel size and protein content results were consistent with expected gains across populations. The actual yield gains from EW1 were low but positive in population C1, relatively high in C6, negative in C2 and near zero in C5. In parallel, the observed yield gains from EW2 were positive in C1 and negative in the other three crosses. Nevertheless, EW2 gave consistent negative realized gains in TKW (-1.4 g to -4.0 g) and protein percent (-0.11% to -0.80%), whereas EW1 gave con-

sistent and relatively high genetic progress in TKW (2.3 g to 3.7 g) and protein (0.5%, C1; 0.4%, C2; 0.4%, C5).

The efficiency of EW1 in identifying high yielding lines was substantially improved by using EW3. The actual yield gains from EW3 ranging from 192 to 334 kg/ha were accompanied by corresponding significant observed gains in kernel weight (2.7 g to 3.6 g). However, the realized gains in percent protein tended to be slightly negative (0.1% to -1.0%). Therefore, while the application of the unweighted index (EW1) aids in genetic improvement of protein content and kernel size with relatively less gain in yield, EW3 may be a better choice if the breeding objective includes increase in yield with minimum reduction in protein content.

The picture of the realized gains in kernel weight was different from that of grain yield. The SH index gave Ra/R ratios of 37%, 59%, 100% and 100% for C1, C2, C5 and C6, respectively. In parallel, the results in EW3 and EW4 were 82%, 94%, 100% and 100%, whereas the actual gains in TKW from selection on EW1 were higher than expected gains in most cases. In both F3 and F4 generations, selections based on kernel weight, EW1, EW3 and EW4 gave high mean kernel weight of selected lines. In contrast, EW2 gave the lowest mean values for all traits studied in both F3 and F4 generations of the four populations. This indirectly supports the suggestion that the weight-free index does effectively separate poor lines from superior genotypes.

In populations C1 and C2, the actual reductions in protein percent due to selection on the various indices with the exception of EW1 in C1 and EW3 in C2 were less than expected, whereas in populations C5 and C6, the actual decrease increased significantly for all indices (Tables 2.16

to 2.19). As indicated for single trait selection, these fluctuations might have been caused by various factors. The seasonal variation, in addition to population variables, could be an important contributor. Such a possibility is indicated by the relatively low levels of F4 protein means compared to F3 means in all the crosses (Tables 2.16 to 2.19). Generally, when means of yield, TKW and protein percent of F3 and F4 selected lines are compared, a slight increase in F4 yield is observed while decreases in TKW and protein is evident. In particular, the reduction in the mean protein levels of F4 selected lines is prevalent (Appendix Tables A-1 to A-8).

CONCLUSIONS

The genetic variances estimated by the AOV method might have been biased upward because of dominance and epistatic effects and the limited number of testing seasons and environments. Cross 1 with the highest genetic coefficient of variation for grain yield resulted in higher heritability estimates than the other populations and gave the highest predicted yield gain from selection. The relatively high heritability values generally observed for all the three traits studied might have also been caused by the nature of the F3 partially segregating populations investigated.

While grain yield and TKW were positively correlated in three of the four populations, yield and protein percent were highly negatively correlated giving genetic correlation values as high as -0.87. In the present study, the genetic correlation coefficients in most cases were relatively larger than their respective phenotypic correlation coefficients. However, the environmental correlation coefficients were not consistently negative despite theoretical expectations.

The relatively high level of the genetic coefficient of variation observed in cross 1 was also shown in the high genetic standard deviation in the Smith-Hazel index and the high standard deviations of the aggregate genotype of this cross in the SH and PD indices. In addition, as observed for the individual traits, the heritability estimates for the SH index were high. The negative genetic correlation between yield and percent protein together with the high negative index coefficients for mean pro-

tein in the SH index indicated the presumably unsurmountable problem of improving wheat grain yield and protein content simultaneously by employing conventional selection index procedures.

The construction of desired gains indices based on gains equal to the genetic standard deviation of each trait and using 20% of F3 population mean for yield, zero for TKW and 10% of F3 population mean for protein, resulted in essentially similar index coefficients within a population, identifying more or less the same sets of genotypes for selection.

The significant reduction in the selection differential for yield when selection was based on high protein content and vice versa again revealed the extreme difficulty in maintaining an acceptable level of percent protein if the breeder's main objective and basis of selection is grain yield. Consequently, a 1.0% increase through selection in protein depressed grain yield by up to 536 kg/ha below the mean of the unselected population. In contrast, the predicted correlated response in yield and protein content due to selection on kernel weight showed that although genetic gains will be relatively low, progress in both grain yield and percent protein is possible in wheat by selecting for high TKW. However, the expected direct gains in yield which ranged from 335 to 596 in the four populations were reduced by up to 120% and 250% when selections were based on kernel weight and protein content, respectively.

Lack of similarity between expected and actual gains in the three traits is assumed to be caused by either methods of parameter estimation, the genetic structure of the F3 and F4 populations, seasonal variation, or the use of the mean performance of the composite as the mean of the unselected population. Realized gains as high as 505 kg/ha together with

the means of individual groups, effectively indicated the potentially promising populations among the crosses studied and identified the highly productive F3 and F4 lines for further selection.

When selection methods were compared in regard to the means of selected F3 and F4 lines, the SH index and direct selection for yield gave higher yield means across populations than the other methods studied. The realized gains in yield from selection based on yield per se, the SH index, EW3 and EW4 were lower than expected advance in populations C1, C2 and C6 (Ra/R ratios ranging from 70% to 85%) but were higher in C5 (Ra/R = 126% to 143%).

The relatively high percent selection differential for yield and the significantly negative selection differential for protein when selection was on the basis of Smith-Hazel index point out the shortcoming of this index if used for improving both grain yield and protein percent. In contrast, the weight-free and desired gains indices were better choices when the protein level was an important component in a wheat breeding program. Particularly, EW1 was relatively the best index in attaining both a certain level of progress in grain yield and significant increase in kernel size and protein content. EW3 and EW4, which were very similar, identified relatively high yielding lines with high kernel weight and caused the least reduction in protein content. Conversely, EW2 identified very poor sets of lines in regard to all the traits studied, substantiating the value of the weight-free index as a selection tool to improve both protein and overall productivity.

The desired gains selection indices used were more or less similar in efficiency with minor superiority of PDI in predicting genetic progress in the populations studied. The SH index was superior in identifying

high yielding lines with relatively above average kernel size but the desired gains indices were superior than the SH index for selecting lines with higher percent protein. Results showed that the use of genetic standard deviations of each trait as desired gains was appropriate and effective for the desired gains index.

Comparison of expected gains in the three traits as a result of selection based on yield per se, and the SH and EW indices revealed that while the relative efficiencies of selection on the SH index were close to direct selection for yield, the negative effects on protein improvement were significant and of equal magnitude as in direct selection for yield. Thus, we conclude that unless the breeder is willing to sacrifice in the level of grain protein for genetic progress in yield and kernel size in wheat, the application of the Smith-Hazel index may not be the best choice of breeding methods. Among the weight-free indices, the linear approximation of the multiplicative index (EW4) and its multiplicative equivalent (EW3) were found to be superior when simultaneously selecting for high grain yield, large kernel size, and minimum reduction in protein percent. EW1, PD1 and PD2 were the only indices which resulted in positive genetic advance in protein through selection but it was accompanied by a slight loss in yield gain compared to selection based on SH index or yield per se.

In general, our results lead to the conclusion that although the Smith-Hazel index procedure is superior in identifying high yielding lines within the range of populations and relative economic weights used, the weight-free indices are better overall. The former index and selection based on yield per se equally caused substantial negative effect on protein improvement while the latter group isolated lines with reasonably

high yield and large kernel with positive progress or the least negative effect on protein.

When selection methods were compared in relation to the means of selected F3 and F4 lines identified by these procedures, the Smith-Hazel index and direct selection for yield consistently gave higher yield means across populations. Similar comparison for kernel weight showed that selection based on TKW, EW1, EW3 and EW4 gave high mean TKW values. As far as protein is concerned, however, selections on the basis of protein content per se, kernel size, EW1, PD1 and PD2 resulted in higher protein means.

MANUSCRIPT 3

EFFECTS OF EXPERIMENTAL VARIABLES
ON THE ESTIMATES OF HERITABILITY
AND RESPONSE TO SELECTION
IN WHEAT

INTRODUCTION

Heritability estimates are useful to predict the genetic advance from various selection schemes. Therefore, the knowledge of the magnitude of the ratio of the additive genetic variance to the total phenotypic variance is essential in any selection program. It is used to evaluate the relative degree to which a trait is transmitted from parent to offspring. On the other hand, heritability estimates depend on several variables so that it varies significantly with the structure of the specific genetic population under consideration, the reference unit of measurement, the precision with which the environmental variance is estimated, and the method of estimation. Because the response to selection is the function of the heritability of a character, any variation in the heritability estimates of a unit trait affects the reliability of the predicted genetic advance from selection.

The two most commonly used procedures of estimating heritability in plant and animal breeding and genetic studies are the variance components and offspring-parent regression methods (Comstock and Moll, 1963; Gordon et al., 1972; Kempthorne and Tandon, 1953; Bohren et al., 1961). The effect of these various methods of estimation on heritability ratios and the relative efficiencies of the different techniques of measuring heritability were the subject of investigation by several workers (Hill, 1971; Latter and Robertson, 1960). Sidwell et al. (1978) used two approaches of estimating heritability by the AOV method in winter wheat. They used F3 family performance based on single plot and multiple-plot

measurements to estimate heritabilities for several characters. They reported that heritability values increased by up to 62% when the units of measurement consisted of three replicates rather than single replicate. Recently, Cahaner and Hillel (1980) compared three procedures including AOV, offspring-parent regression, or intergeneration correlation methods in F2 and F3 generations of self pollinating crops. They concluded that the variance components family-analysis method based on intra-class correlation was superior to the other two because this procedure was less affected by non-additive contributions.

This study was designed to compare heritability estimates based on various approaches of variance components, offspring-parent regression, and intergeneration correlation methods, and to determine predicted genetic advances in yield, kernel weight and percent protein of four wheat crosses at two levels of selection intensity.

MATERIALS AND METHODS

Experimental details of F2, F3 and F4 generation tests were given in manuscripts 1 and 2. Individual and combined analyses of variance were performed on F3 and F4 generations data collected from four populations grown under two environments. F3 measurements included yield, kernel weight and protein content, whereas yield, test weight, kernel weight and percent protein were measured in F4. F3 on F2 regression analyses were computed for yield, kernel weight and percent protein for each test in each location and combined means of results from two locations. Also, moment correlation between F2 single plant measurements and F3 mean performance from two sites was carried out for the three traits in four populations.

Three classes of methods of estimating heritability were used, namely the variance component method, offspring-parent regression method and intergeneration correlation (Cahaner and Hillel, 1980). Under the AOV method, heritability values for yield, kernel weight and percent protein were determined using two types of reference units (Sidwell et al., 1978): single replication and multiple replications. Thus, heritability estimates were determined on the basis of single-plot and multiple-plot measurements on tests in each location, and single-plot (one plot per location) and multiple-plot measurements of combined data.

In determining the genetic variance estimates for a one location test, the error mean squares was used as the interaction residual to be subtracted from F3 lines mean squares (Sidwell et al., 1978), while the location x F3 lines interaction mean squares were employed in the

combined analysis. Predicted genetic gain from the various methods of estimating heritability was computed using the selection differential of each trait in each cross and its corresponding heritability at two levels of selection intensity ($P = 5\%$ and 10%). The ratio of the expected genetic gain from selecting 5% of the population to the mean of the population before selection is given in percent.

RESULTS AND DISCUSSION

Mean squares from individual and combined analyses for grain yield, kernel weight and protein content of the four F3 populations are given in Tables 3.1 to 3.4. F3 lines of all four populations were significantly different in yield, TKW, and percent protein in both test locations. This was also true for the combined analyses. Locations effect was also highly significant ($P \leq 0.01$) in all three traits of the four crosses. The results of the F3 lines-locations interaction were variable. In populations C1 and C4 interaction mean squares of all three characters were highly significant. The genotype-environment interaction mean squares for protein in C2 and yield in C5 were non-significant. However, the interaction effects for yield and TKW in population C2 and TKW and protein in C5 were significant.

Tables 3.5 to 3.8 give mean squares for yield, test weight, kernel weight and percent protein measured on selected F4 bulks grown under two environments. The bulks included in the F4 tests were significantly different in all four traits studied. These results were expected because the F4 entries included a certain proportion of the top lines truncated using various selection criteria and also a certain proportion of the lowest in aggregate performance on the basis of weight-free selection index involving yield, TKW, and protein content (Elston, 1963). On the other hand, differences were less significant among those lines in the top truncated segment (see Appendix Tables A1 to A-8). Locations effect were also highly significant in all traits of the four crosses. Never-

TABLE 3.1. Mean squares for grain yield, kernel weight and protein percent of wheat F3 population 1 grown at two locations.

Point	Source	df	Mean Squares		
			Yield (kg/ha)	TW (g)	Protein (%)
<u>Point</u>	Reps.	2	348,582*	17.3**	1.2**
	F3 lines	99	947,079**	19.0**	1.5**
	Error	198	100,381	0.6	0.2
<u>Glenlea</u>	Reps.	2	176,815	2.6	1.7**
	F3 lines	99	912,909**	17.8**	3.9**
	Error	198	133,908	1.0	0.3
<u>Combined</u>	Locations	1	164,333,993**	0.1	10.9**
	Reps.	2	29,253	15.0**	1.2**
	F3 lines	99	1,622,732**	35.3**	4.5**
	Locations x F3 lines	99	237,256**	1.5**	0.9**
	Error	398	119,049	0.8	0.2

*,** Significant at the 5% and 1% level, respectively.

TABLE 3.2. Mean squares for yield, kernel weight and protein percent of F3 wheat population 2 grown at two locations.

Source	df	Mean Squares		
		Yield (kg/ha)	TKW (g)	Protein (%)
<u>Point</u>				
Reps.	2	234,123	4.5**	4.5**
F3 lines	99	624,526**	17.4**	1.5**
Error	198	107,880	0.9	0.3
<u>Glenlea</u>				
Reps.	2	447,206**	3.3	0.4
F3 lines	99	338,400**	20.0**	1.9**
Error	198	117,172	1.2	0.2
<u>Combined</u>				
Locations	1	83,927,096**	27.6**	5.6**
Reps.	2	2,848,717**	7.0**	1.9**
F3 lines	99	719,455**	34.4**	3.1**
Locations x F3 lines	99	243,471**	2.9**	0.3
Error	398	121,295	1.1	0.3

** Significant at the 1% level.

TABLE 3.3. Mean squares for grain yield, kernel weight and protein percent of F3 wheat population 5 grown at two locations.

Source	df	Mean Squares		
		Yield (kg/ha)	TKW (g)	Protein (%)
<u>Point</u>				
Reps.	2	509,227	45.2**	16.2**
F3 lines	99	477,045**	12.6**	1.8**
Error	198	178,472	1.1	0.6
<u>Glenlea</u>				
Reps.	2	1,342,041**	0.2	0.5
F3 lines	99	348,487**	14.7**	2.4**
Error	198	113,098	0.8	0.2
<u>Combined</u>				
Locations	1	90,679,825**	0.2	67.2**
Reps.	2	1,732,361**	25.6**	5.7**
F3 lines	99	642,420**	25.1**	5.3**
Locations x F3 lines	99	183,112	2.1**	0.8**
Error	398	145,650	1.0	0.4

** Significant at the 1% level.

TABLE 3.4. Mean squares for grain yield, kernel weight and percent protein of F3 wheat population 6 grown at two locations.

Source	df	Mean Squares		
		Yield (kg/ha)	TKW (g)	Protein (%)
<u>Point</u>				
Reps.	2	2,418,752**	2.4	11.7**
F3 lines	99	853,469**	15.3**	1.7**
Error	198	164,120	0.8	0.2
<u>Clenlea</u>				
Reps.	2	1,287,800**	8.4**	0.2
F3 lines	99	532,448**	22.2**	2.2**
Error	198	114,667	1.2	0.2
<u>Combined</u>				
Locations	1	262,149,946**	427.6**	236.9**
Reps.	2	1,910,280**	9.0**	5.1**
F3 lines	99	1,017,469**	32.9**	3.5**
Locations x F3 lines	99	368,448**	4.5**	0.4**
Error	398	149,568	1.0	0.2

** Significant at the 1% level.

theless, the genotype-environment interaction effects were significant only in test weight and TKW across the four crosses. The F4 bulks-locations interaction mean squares for yield were significant only in C1 and C6, while the genotype-environment interaction effects for protein were non-significant in all crosses.

Heritability Estimates

The various methods of estimating heritability ratios resulted in significantly different estimates for each trait. This, in turn, affected the magnitude of the expected gains from selection substantially. Observed heritability values for some traits ranged from approximately zero to 0.92.

The heritability ratios estimated based on the variance components method will be considered first. Comparatively, the heritability estimates based on the AOV method were predominantly higher than those from the regression or correlation procedures. For yield, for instance, the least heritability observed across the four populations was 0.36 when the AOV approach was used, whereas values as low as 0.03 were obtained using the correlation or regression methods (Table 3.11). Within the AOV method the estimations based on the measurements of three replications were larger, as expected, than those estimates on the basis of single-plot observations. This may be caused by the reduction in the residual error effect as the number of replications increased from one to three. Nevertheless, this change in heritability varied from trait to trait and from population to population. For yield the highest percent increase in heritability estimates as the reference unit changed from one replication to three replications were 22, 41, 43 and 42 for populations C1, C2, C5 and C6, respectively. Because the heritability estimates for kernel

TABLE 3.5. Mean squares for yield, test weight, kernel weight and protein percent of selected F4 bulks from cross 1 grown at two locations.

Source	df	Mean Squares			
		Yield (kg/ha)	Test wt. (kg/hl)	TKW (g)	Protein (%)
<u>Point</u>					
Reps.	2	358,133	0.9	1.1	12.0**
F4 bulks	31	409,638**	2.8**	37.7**	1.2**
Error	62	195,042	0.2	0.8	0.2
<u>Glenlea</u>					
Reps.	2	1,199,067**	0.0	0.6	0.0
F4 bulks	31	461,400**	2.9**	26.0**	1.4**
Error	62	131,937	0.1	0.5	0.2
<u>Combined</u>					
Locations	1	189,232,048**	396.7**	492.8**	25.2**
Reps.	2	1,281,105**	0.4	0.2	5.5**
F4 bulks	31	555,838**	5.3**	62.2**	2.2**
Locations x F4 bulks	31	315,201**	0.4**	1.6**	0.4
Error	126	165,277	0.2	0.7	0.3

** Significant at the 1% level.

TABLE 3.6. Mean squares for yield, test weight, kernel weight and percent protein of selected F4 bulks from cross 2 grown at two locations.

Source	df	Mean Squares			
		Yield (kg/ha)	Test wt. (kg/hl)	TKW (g)	Protein (%)
<u>Point</u>					
Reps.	2	854,799	1.2	0.9	4.3**
F4 bulks	31	498,433*	5.2**	24.1**	1.5**
Error	62	249,877	0.4	1.2	0.2
<u>Glenlea</u>					
Reps.	2	124,258	0.0	2.8	0.1
F4 bulks	31	675,369**	5.3**	27.1**	1.9**
Error	62	184,848	0.4	0.8	0.5
<u>Combined</u>					
Locations	1	170,733,922**	358.1**	185.1**	7.7**
Reps.	2	284,391	0.6	0.7	1.9**
F4 bulks	31	872,482**	10.1**	49.2**	2.9**
Locations x F4 bulks	31	301,320	0.4**	1.9**	0.4
Error	126	224,939	0.4	1.0	0.3

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

TABLE 3.7. Mean squares for yield, test weight, kernel weight and percent protein of selected F4 bulks from cross 5 grown at two locations.

Source	df	Mean Squares			
		Yield (kg/ha)	Test wt. (kg/hl)	TKW (g)	Protein (%)
<u>Point</u>					
Reps.	2	1,428,323**	0.3	10.1**	6.6**
F4 bulks	31	778,046**	4.0**	17.1**	2.1**
Error	62	189,500	0.3	1.5	0.3
<u>Glenlea</u>					
Reps.	2	793,740*	2.0**	0.4	0.8*
F4 bulks	31	531,611**	3.4**	21.5**	3.0**
Error	62	177,111	0.2	0.8	0.2
<u>Combined</u>					
Locations	1	116,349,939**	199.7**	288.4**	122.4**
Reps.	2	1,025,899**	1.2*	5.0*	5.0**
F4 bulks	31	1,143,675**	6.7**	36.4**	4.6**
Locations x F4 bulks	31	165,981	0.7**	2.2**	0.4*
Error	126	199,383	0.3	1.2	0.3

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

TABLE 3.8. Mean squares for yield, test weight, kernel weight and percent protein of selected F4 bulks from cross 6 grown at two locations.

Point	Source	df	Mean Squares			
			Yield (kg/ha)	Test wt. (kg/hl)	TKW (g)	Protein (%)
<u>Point</u>	Reps.	2	1,198,050*	3.0	10.8**	11.5**
	F4 bulks	31	868,873**	3.5**	33.5**	3.4**
	Error	62	276,373	1.2	1.9	0.7
<u>Clenlea</u>	Reps.	2	268,339	0.3	1.8	1.3*
	F4 bulks	31	620,605**	3.7**	29.2**	2.7**
	Error	62	164,663	0.2	0.8	0.2
<u>Combined</u>	Locations	1	51,200,647**	137.2**	216.7**	109.5**
	Reps.	2	1,240,479*	2.6	2.8	6.7**
	F4 bulks	31	1,182,557**	5.8**	60.0**	5.7**
	Locations x F4 bulks	31	306,922	1.4**	2.7*	0.4
	Error	126	220,604	0.7	1.5	0.5

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

weight were consistently high, the changes due to the increase in the number of replications were relatively low ranging only from 5% to 21% among the four populations. The equivalent changes for heritability of protein were intermediate between kernel weight and yield.

The actual magnitudes of the heritability estimates of a trait on the basis of the AOV procedure showed slight variation from population to population. The heritability of yield in population C1 ranged from 0.66 to 0.89 while the same range for C5 was from 0.36 to 0.71. In contrast, the heritability values for kernel weight were consistently high across the four populations. In C2 the Glenlea test and the combined analysis on the basis of single-plot measurement resulted in relatively low heritability estimates (0.39). Similarly, single-plot observation gave the lowest heritability estimates for yield in the C5 and C6 populations, respectively. On the other hand, the application of the multiple-plot approach gave high heritability estimates when both single location data or combined analysis were considered. This resulted in an over-estimation of the parameter. For instance, the average heritability for TKW based on various reference units from the AOV procedure were 0.92, 0.88, 0.87 and 0.86 for populations C1, C2, C5 and C6, respectively. The heritability estimates for protein, however, using the same AOV method were lower than those for kernel weight. In the C5 population, heritability for protein ranged from 0.39 to 0.93 depending on the reference unit used. These same estimates averaged 0.79, 0.76, 0.67 and 0.81 in populations C1, C2, C5 and C6, respectively. All estimates showed significant upward bias which will indirectly affect the reliability of the expected response to selection.

Thus, whereas the heritability values and expected genetic gains

from the AOV method were overestimated, the offspring-parent regression and intergeneration correlation methods underestimated these parameters in all the populations studied. The F3 on F2 regression coefficients for grain yield were significant only in populations C1 (0.76) and C6 (0.42) grown at the Glenlea location. As a result, the heritability estimates from these tests were relatively higher (Tables 3.9 and 3.12). On the other hand, the estimates for the heritability of yield on the basis of offspring-parent regression for populations C2 and C5 were approximately zero. The results from the intergeneration correlation also showed similar results. The results obtained for TKW was rather different. Both the F3 on F2 regression and correlation showed significant levels of heritability estimates. In addition, the intergeneration correlation coefficient for each trait was larger than the corresponding regression coefficient for all populations. Therefore, for TKW it is suggested that the intergeneration correlation may give a better estimate of heritability than either the AOV method which may overestimate the parameter or the offspring-parent procedure which may underestimate the values. For protein content the heritability estimates using the O-P regression and correlation were low and non-significant for populations C1 and C2. However, in populations C5 and C6 these values were relatively high and again the correlation method gave larger estimates than the O-P regression method.

Expected Genetic Gains

The expected genetic gains from selection estimated using the heritability values from the AOV method were significantly higher than predicted gains from the other two procedures (Tables 3.9 to 3.12). In

TABLE 3.9. Estimates of heritability (h^2) and genetic advance (R) on the basis of single-plot (SP) and multiple-plot (MP) selection, offspring-parent regression and intergeneration correlation methods for yield, kernel weight and percent protein at two levels of selection intensity (P = 5% and 10%) in wheat F3 population 1.

Method	Yield (kg/ha)			TKW (g)			Protein (%)					
	h^2	R		h^2	R		h^2	R				
		10%	5%		10%	5%		10%	5%			
AOV SP - Point	0.74	625	715	18.6	0.92	3.8	4.2	10.0	0.72	1.0	1.3	7.1
AOV MP - Point	0.89	752	860	22.4	0.97	4.0	4.5	10.7	0.89	1.2	1.6	8.8
AOV SP - Glenlea	0.66	492	546	19.6	0.85	3.6	4.0	9.5	0.79	1.8	2.2	12.4
AOV MP - Glenlea	0.85	634	704	25.2	0.94	3.9	4.4	10.5	0.92	2.1	2.6	14.4
AOV SP - Combined	0.66	463	499	15.1	0.88	3.6	4.1	9.7	0.59	1.1	1.4	7.6
AOV MP - Combined	0.85	596	643	19.4	0.96	3.9	4.5	10.7	0.81	1.5	1.9	10.5
Regression - Point	0.33	279	319	8.3	0.49	2.0	2.3	5.5	0.01	0.0	0.0	0.0
Regression - Glenlea	0.76	567	629	22.6	0.46	1.9	2.2	5.2	0.17	0.4	0.5	2.8
Regression - Combined	0.53	372	401	12.1	0.47	1.9	2.2	5.2	0.08	0.2	0.2	1.1
Correlation - Combined	0.20	140	151	4.6	0.66	2.7	3.1	7.4	0.10	0.2	0.2	1.3

TABLE 3.10. Estimates of heritability (h^2) and genetic advance (R) based on single-plot (SP) and multiple-plot (MP) selection, offspring-parent regression and intergeneration correlation methods for yield, kernel weight and percent protein at two levels of selection intensity (P = 5% and 10%) in wheat F3 population 2.

Method	Yield (kg/ha)			TKW (g)			Protein (%)					
	h^2	R		h^2	R		h^2	R				
		10%	5%		10%	5%		10%	5%			
AOV SP - Point	0.61	412	461	11.6	0.87	3.8	4.7	11.1	0.56	0.7	0.9	5.6
AOV MP - Point	0.83	560	627	15.8	0.95	4.2	5.1	12.0	0.79	1.0	1.3	8.0
AOV SP - Glenlea	0.39	205	234	7.3	0.83	3.7	4.6	11.0	0.73	1.1	1.4	8.5
AOV MP - Glenlea	0.65	342	390	12.1	0.94	4.2	5.2	12.4	0.89	1.4	1.7	10.3
AOV SP - Combined	0.39	198	231	6.4	0.78	3.3	4.1	9.7	0.72	1.0	1.3	7.8
AOV MP - Combined	0.66	335	392	10.9	0.92	3.9	4.8	11.4	0.88	1.2	1.6	9.5
Regression - Point	0.20	135	151	3.8	0.32	1.4	1.7	4.0	0.09	0.1	0.2	0.9
Regression - Glenlea	0.09	47	54	1.7	0.30	1.3	1.6	3.8	0.09	0.1	0.2	1.1
Regression - Combined	0.15	76	89	2.5	0.31	1.3	1.6	3.8	0.09	0.1	0.2	1.0
Correlation - Combined	0.09	46	53	1.5	0.43	1.8	2.2	5.2	0.13	0.2	0.2	1.4

TABLE 3.11. Estimates of heritability (h^2) and genetic advance (R) based on single-plot (SP) and multiple-plot (MP) selection, offspring-parent regression and intergeneration correlation methods for yield, kernel weight and percent protein at two levels of selection intensity (P = 5% and 10%) in wheat F3 population 5.

Method	Yield (kg/ha)			TKW (g)			Protein (%)					
	h^2	R		h^2	R		h^2	R		% of mean		
		10%	5%		10%	5%		10%	5%			
AOV SP - Point	0.36	231	259	7.2	0.78	2.9	3.5	8.4	0.39	0.6	0.8	4.3
AOV MP - Point	0.63	404	453	12.5	0.91	3.4	4.0	9.6	0.66	1.0	1.3	7.2
AOV SP - Glenlea	0.41	246	291	10.2	0.86	3.6	4.2	10.1	0.82	1.3	1.4	7.8
AOV MP - Glenlea	0.68	408	482	16.9	0.95	4.0	4.7	11.3	0.93	1.4	1.6	8.9
AOV SP - Combined	0.46	248	302	9.3	0.78	3.0	3.6	8.7	0.50	0.7	0.9	4.9
AOV MP - Combined	0.71	383	466	14.4	0.92	3.5	4.3	10.3	0.75	1.1	1.3	7.4
Regression - Point	0.05	32	36	1.0	0.21	0.8	0.9	2.2	0.23	0.3	0.4	2.5
Regression - Glenlea	0.06	36	43	1.5	0.24	1.0	1.2	2.9	0.18	0.3	0.3	1.7
Regression - Combined	0.05	27	33	1.0	0.23	0.9	1.1	2.6	0.21	0.3	0.4	2.1
Correlation - Combined	0.03	16	20	0.6	0.47	1.8	2.2	5.3	0.39	0.6	0.7	3.8

TABLE 3.12. Estimates of heritability (h^2) and genetic advance (R) based on single-plot (SP) and multiple-plot (MP) selection, offspring-parent regression and intergeneration correlation methods for yield, kernel weight and percent protein at two levels of selection intensity (P = 5% and 10%) in wheat F3 population 6.

Method	Yield (kg/ha)			TKW (g)			Protein (%)					
	h^2	R		h^2	R		h^2	R				
		10%	5%		10%	5%		10%	5%			
AOV SP - Point	0.58	516	642	16.5	0.86	3.7	4.1	9.7	0.68	0.9	1.0	5.8
AOV MP - Point	0.81	720	897	23.1	0.95	4.1	4.5	10.7	0.86	1.1	1.2	7.3
AOV SP - Glenlea	0.55	414	508	19.8	0.85	4.1	4.8	11.0	0.82	1.2	1.3	7.4
AOV MP - Glenlea	0.78	587	721	28.1	0.95	4.6	5.3	12.1	0.93	1.3	1.5	8.4
AOV SP - Combined	0.37	285	335	10.4	0.68	2.9	3.4	7.9	0.71	0.9	1.1	6.0
AOV MP - Combined	0.64	493	579	17.9	0.86	3.7	4.3	10.0	0.88	1.1	1.3	7.5
Regression - Point	0.20	178	221	5.7	0.26	1.1	1.2	2.8	0.26	0.3	0.4	2.2
Regression - Glenlea	0.42	316	388	15.1	0.34	1.6	1.9	4.3	0.27	0.4	0.4	2.5
Regression - Combined	0.31	239	281	8.7	0.30	1.3	1.5	3.5	0.26	0.3	0.4	2.2
Correlation - Combined	0.20	154	181	5.6	0.55	2.4	2.7	6.3	0.39	0.4	0.6	3.3

yield, the least expected gains were obtained from combined data of one plot per location, whereas the highest expected gain in each cross was from the Point test using three replications. This trend was similar across populations with minor variation in population C5. However, the magnitude of predicted yield gains were high in populations C1 and C6, but relatively low in C2 and C5 within the AOV method. The percent expected yield gains on top of the population mean using the AOV method when 5% of the population was truncated varied from population to population. In the C1 population this increase ranged from 15% to 25% of the mean, whereas such improvements were up to 16%, 17% and 28% for populations C2, C5 and C6, respectively.

In contrast, the expected yield gains using the offspring-parent regression and correlation procedures were low, particularly in populations C2 and C5. However, the expected progress from the Glenlea tests of C1 and C6 were relatively high. Although this depended on the structure of the specific population, the variability of the offspring-parent regression and correlation results was accentuated by differences in testing environments of the F2 and F3 populations contributed by both seasonal variations and location effects.

In populations C1 and C2 the genetic gains in TKW followed a similar pattern with that of the yield response; the highest expected gain was from replicated tests at the Point and the least expected progress was from combined analysis with single-replicate tests. Conversely, the trend in the C5 and C6 populations was that the maximum expected gain in kernel weight was obtained from multiple-plots at Glenlea and the minimum improvement was observed from single-plot measurements in the combined analysis. The maximum expected gains in TKW using multiple-plot

criterion were 4.0 g and 4.6 g, respectively, whereas the minimum gains were 3.0 g and 2.7 g for C5 and C6, respectively at 10% selection pressure (Tables 3.11 and 3.12). These results based on the regression and correlation procedures were significantly lower than from the variance components method.

The expected gain in percent protein showed consistent trend across the four populations. The maximum expected gains were obtained from the Glenlea tests using both single and multiple plots. However, the expected gains based on multiple plots as reference units were larger. Conversely, the least expected progress was observed from the Point experiment, particularly those based on single-plot observations (Tables 3.9 to 3.12).

The general trend based on the results of these four populations grown under one relatively optimum environment and another relatively sub-optimum growing environment clearly indicated that selection using multiple-plot measurements under optimum or near optimum environment results in maximum genetic advance from selection. Conversely, the least progress may be expected from selection when more than one testing locations are combined and particularly when some of these environments have sub-optimal growing conditions. This brings out the important problems of genotype-environment interaction and the need for a decision on the objective of a selection scheme in terms of adaptability and stability of varieties. That is, although the breeder may be able to identify genotypes that are relatively stable across environments, he will be forced to sacrifice maximum productivity and rapid genetic advance compared to selecting under specific optimum growing environments.

In general, the heritability estimates and the expected responses from selection in all the three traits were significantly lower when

offspring-parent regression and correlation procedures were used than the AOV method. With the relative exception of yield gains in C1 and C6, predicted levels of yield gains were under-estimated considerably. The results of this study substantiates the well-known fact that heritability estimates are not stable population parameters but fluctuates depending on the nature of a specific population, reference units, and methods of estimation.

CONCLUSIONS

The present study has shown that, depending on specific genetic material and availability of resources, the testing of early generation wheat breeding material across various growing environments must be an important component of any selection scheme. This conclusion was reached based on the significant F3 lines-locations interaction obtained in this study.

The comparisons of heritability estimates determined on the basis of the three procedures, namely the variance components method, the offspring-parent regression, and intergeneration correlation techniques showed that the AOV method considerably overestimated heritabilities in all three traits studied. Conversely, the offspring-parent regression tended to predominantly underestimate the heritability values. The intergeneration correlation, on the other hand, gave intermediate values resulting in more conservative but realistic heritability estimates for TKW and protein in all populations. Therefore, it is suggested that the correlation method, particularly when parents and the corresponding offsprings can be tested under the same environments, may be a better choice of method for estimating heritability.

When heritability estimates were relatively low, the AOV method based on three replications increased the value by more than 40% compared to single-plot measurement in certain traits. But the change decreases as the levels of heritability increases. The proportionately very high heritability estimates observed based on multiple-plot measurements in

one or more locations led to the conclusion that tests in two or more locations with single plot observation may give lower but more realistic estimates of heritability for the three traits studied.

The fluctuations in heritability estimates obtained when various estimation methods were applied resulted in corresponding variation in expected gains due to selection in all traits and populations studied. Because the expected genetic advances were overestimated by estimation procedures involving AOV methods, particularly those involving multiple-plot measurements, and significantly underestimated by the offspring-parent regression procedure, it is concluded that depending on the trait, the single plot reference unit of the combined data would be more applicable to estimate attainable levels of genetic gains. The general levels of heritability and expected gains estimates based on offspring-parent regression and correlation coefficients and their variations, were accentuated by differences in testing conditions of the F2 and F3 populations thus were affected by both the seasonal and locational variations. Therefore, the testing of genetic material under similar growing conditions may give more stable results.

Depending on the genetic structure of the population under consideration, the presence of genotype-environment interaction, and the objective of a selection scheme, selection based on multiple-plot measurements under one or more optimum growing environment(s) may result in maximum genetic advance from selection. However, because most breeders are interested in cultivars with high stability and wide adaptability in overall productivity, selection based on optimum number of replications under wide range of environments would be recommended to attain more realistic and stable progress. In addition, depending on the specific trait and

population, the use of intergeneration correlation may be a better method of estimating heritability to predict response to selection in wheat.

GENERAL DISCUSSION

The cereal breeder today is interested in developing varieties that have a combination of desirable productivity and quality characters. Such a far reaching goal also includes wide range of environmental adaptation, requiring the availability of a considerable amount of genetic variation in productivity, resistance or tolerance to environmental and pest stress conditions, and nutritional and industrial qualities. The effort in this area in the last few years has accomplished significant progress in the field of efficient testing, screening, and selection techniques to create and identify productive genotypes more prudently.

The findings of the present investigation dealing with selecting promising crosses during early generations in a wheat selection program corroborates the contention that the breeder must make use of all relevant information in F₁, F₂ and F₃ generations in terms of their performances, offspring-parent regression, and intergeneration correlation (Nass, 1979). However, results of the specific crosses studied indicated that early generation evaluation such as F₁ hybrid performance can be used only to separate poor crosses from highly promising ones but minor differences among populations cannot be discerned. Generally, the information in the area of early generation yield testing in wheat is still incomplete and evidence in most cases are inconsistent and contradictory (Knott and Kumar, 1975; Briggs and Shebeski, 1971).

The intergeneration rank correlation and offspring-parent regression coefficients we found were relatively high in some crosses and traits but

low in some others. This indicates that F2 single plant performance cannot effectively predict F3 productivity. This supports the results of Knott (1972) who examined F3 on F2 regressions and concluded that the size of regression coefficients were non-significant and of little practical selection value. Results of a recent study by Nass (1979) who evaluated F1, F2, and parents to identify high yielding crosses in wheat agree, in broad terms, with findings of the present study. Therefore, the proper use of F1 heterosis, F1, F2 and F3 performance, intergeneration correlation and regression results will be valuable in aiding to identify promising crosses. This enhances the chances of isolating high yielding lines, also reduces the amount of cost involved through reducing the crosses to a manageable number.

The application of the unweighted index to select for the net merit of crosses in the F1 to F3 generations is very appealing and can be of high practical value in ranking populations or lines based on their aggregate performance.

The effort of simultaneous improvement of several traits in wheat requires the use of a proper selection index procedure to isolate genotypes with desirable overall merit. However, the existence of strong negative correlation between yield and protein content in wheat has been a major problem in the application of the conventional selection index theory to simultaneously improve these two characters. The existence of such strong negative correlation between grain yield and grain protein is confirmed by the results of this study.

The comparison of selection based on individual and various indices showed that the breeder must select the optimum selection criterion for the populations and traits of interest. In terms of selection differential,

expected and observed gains from selection, and relative efficiencies of various selection methods, selection on the basis of yield per se, and the Smith-Hazel index tended to be equally efficient in selecting for high yield but they were poor in improving kernel weight and grain protein. This is the function of the amount of relative economic weight assigned to yield compared to the other traits, and the magnitude of the genetic variance of each trait. Thus, the task of determining objective weights is one of the main constraints in the application of the Smith-Hazel selection index. This problem will slightly be ameliorated if the desired gains index is used in that the breeder will, from experience, assign desired levels of gains for each character. However, both the Smith-Hazel and desired gains indices are sensitive to relative magnitude of economic weights or desired gains assigned to each trait included in the index.

Our findings of selection based on desired gains index indicated that it is inferior in improving yield but is efficient in selecting for higher protein content than the other indices studied. Kauffmann and Dudley (1980), after evaluating different indices to select for yield, protein in corn came to similar conclusion that simultaneous improvement of grain yield and percent protein is possible using the desired gains index.

To circumvent the problem of determining relative economic weights and parameter estimation, we have focused on investigating unweighted indices in comparison with the Smith-Hazel and desired gains indices and unit trait selections. The unweighted index, because of its simplicity in that it does not need the estimation of genetic and phenotypic parameters and economic weights, can be a useful tool in improving protein

and kernel size while making modest progress in grain yield. The multiplicative weight-free index involving yield, TKW and protein percent was found to be good for this purpose except that it was inferior to the other unweighted indices in selecting high yielding lines, also its performance was inconsistent from population to population and generation to generation. Baker (1974) recommended the use of the weight-free index for animal breeding when the characters under consideration are equally important. Crosbie et al. (1980) also reported good predicted gains using the unweighted index and suggested that breeders should consider using this index. In the present study, the weight-free multiplicative index involving only yield and TKW (EW3) was better in improving yield but it had no effect on protein. Thus, EW3 may be a better choice in that it enables the breeder to maintain protein percent at a reasonable level while improving yield and kernel weight.

Based on theoretical considerations, Cahner and Hillel (1980) pointed out that because the O-P regression method under-estimates heritability as a result of differences in generation means and variances the use of the offspring-parent correlation procedure would give a better estimate of heritability. Our results support this general recommendation.

Comparisons within the AOV method showed that multiple plot measurements in two locations gave the highest expected gain. This expected advance and the heritability estimates decreased significantly when a single replicate was used. Sidwell et al. (1978) have reported similar results in winter wheat. To calculate realizable gains, however, single-plot measurement in two or more locations may be a better choice of an estimation method. Conversely, Pesek (1972) reported that using the AOV method on two-year data resulted in underestimation of the "true" heri-

tability, whereas the same procedure based on one-year data overestimated heritability as a result of genotype-year interaction.

SUMMARY AND CONCLUSIONS

The F1 hybrid tests were effective in broad terms, in classifying crosses as poor and potentially superior and in selecting hybrid populations with a high frequency of productive lines in later generations. However, because of the complexity of the inheritance of grain yield and protein content in wheat, also due to environmental effects, reliable prediction of the potential of specific crosses in later generations using F1 performance evaluation was not consistent unless the cross(es) selected were highly superior. In this study, it was found that both F1 yield evaluation and the application of weight-free multiplicative index to select the best aggregate genotypes identified two of the top hybrid populations (C1 and C2) but misclassified one cross (C6).

The cross (C2) that showed significant F1 heterosis for yield tended to give productive lines in F2 and F3, but in general F1 percent heterosis for yield was found to be of no or little value in predicting the potential of the crosses studied.

The F3 on F2 regression and the intergeneration rank correlation studies indicated that F2 individual plant productivity cannot serve as a measure of F3 line yield performance. F2 kernel weight, however, was found to be more stable across environments than yield and protein and therefore can be used to predict the productivity of F3 lines. However, the rank correlation between F3 yield and F2 kernel weight was not consistently high. The F3 mean TKW on F2 kernel weight regression coefficients were significant across populations and locations, whereas the equivalent b-values for protein were significant only on C5 and C6.

Although a better evaluation of a specific cross under a near-optimum environment was possible, it was concluded that segregating populations must be tested under a range of variable environments to increase stability of selected lines.

The use of unweighted index to rank crosses based on the net merit of the top 20% of the F3 lines identified consistently the two or three superior crosses. The inclusion of protein in the index, however, resulted in misplacing one of the productive crosses.

Grain yield and percent protein were negatively correlated in all populations giving genetic correlation coefficients as high as -0.87. In addition, the heritability estimates based on variance components procedure were high for all the traits studied. This might have been caused by upward bias of genetic variance due to dominance and epistatic effects, and a limited number of testing seasons and environments in F3 populations.

The strong negative genetic correlation between yield and protein and the results of selection based on the Smith-Hazel index and yield per se led to the conclusion that the problem of the simultaneous improvement of wheat grain yield and percent protein using conventional breeding methods seems real and unsurmountable.

A 1.0% increase in protein depressed grain yield up to 536 kg/ha below the mean of unselected population, whereas the expected direct gains in yield were reduced by as much as 250%, when selection was based on protein content. Based on these results, we conclude that the improvement of these two characters by directly selecting either for yield or protein is impossible.

On the basis of selection differential, expected and observed gains results from various individual trait and index selection procedures,

selections based on yield and the Smith-Hazel index were superior in identifying high yielding lines with above average kernel size but were poor selection criteria for improving protein percent. These methods of selection substantially reduced the mean protein level of the selected lines. In contrast, the unweighted and the desired gains indices were efficient in improving protein content but were less efficient in identifying high yielding lines. The weight-free indices particularly EW3, were suitable indices for modest genetic advance in grain yield with high kernel weight and slight positive progress or minimal reduction in protein content.

Conversely, selection in the opposite direction (the low tail of the curve) using the unweighted multiplicative index (EW2) resulted in very significant reduction in all traits. Thus, we conclude that the weight-free index can be a useful tool in improving grain yield, kernel weight and protein content in wheat. This is a simple selection index which does not require genetic and phenotypic parameter estimations and assignment of relative economic weights.

The two desired gain indices used were more or less similar in efficiency in predicting genetic progress in the populations studied. The use of genetic standard deviation of each trait as desired gains was found to be effective. This index was the most efficient in improving protein content but was relatively poor in selecting high yielding lines.

When selection methods were compared in regard to the means of selected lines in F3 and F4 generations, the SH index and direct selection for yield consistently gave higher yield means across populations than the other procedures used. The observed gains in grain yield from selection based on yield per se, the Smith-Hazel index, and the weight-free

indices (EW3 and EW4) were lower than expected advance in populations C1, C2 and C6 (average $Ra/R = 77\%$) but were higher in C5 (average $Ra/R = 136\%$).

The AOV and O-P regression methods either overestimated or underestimated, respectively, the "true" heritability. The intergeneration correlation, on the other hand, was found to estimate conservative but realistic heritability values for kernel weight and protein content. Therefore, the intergeneration correlation is suggested to be a better choice of method for estimating heritability.

Comparison of procedures within the AOV method showed that estimation heritability based on single-plot measurement in two or more locations may result in relatively low but more realistic estimates of heritability of yield, kernel weight and protein content.

The effect of the various methods of estimation on heritability correspondingly influenced the levels of the expected genetic advance in the three traits. The AOV method based on multiple-plots and O-P regression resulted in either upward or downward bias in estimated expected genetic gains. Therefore, it is suggested that the single-plot reference unit of combined data may be more applicable to estimate attainable levels of genetic advance.

In conclusion, depending on the genetic structure of the population, presence of genotype-environment interaction, and objectives of a selection program, selection based on multiple-plot measurements in one or more optimum environments may result in a maximum expected genetic advance from selection. Nevertheless, more objective selection for widely adapted and stable wheat varieties may be attained by testing early generation material across a wide range of variable environments.

LITERATURE CITED

- Abplanalp, H.F., F.X. Ogasawara, and V.S. Asmundson. 1963. Influence of selection for body weight of different ages on growth of turkeys. *Poul. Sci.* 4: 71-82.
- Adams, M.W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, *Phaseolus vulgaris*. *Crop Sci.* 7: 505-510.
- Adams, M.M., and J.E. Grafius. 1971. Yield component compensation - alternative interpretations. *Crop Sci.* 11: 33-55.
- Allard, R.W. 1960. Principles of plant breeding. John Wiley & Sons, Inc., N.Y.
- Amaya, A.A., R.H. Busch, and K.L. Lebsock. 1972. Estimates of genetic effects of heading date, plant height, and grain yield in durum wheat. *Crop Sci.* 12: 478-481.
- Andrus, D.F., and L.D. McGilliard. 1975. Selection of dairy cattle for overall excellence. *J. Dairy Sci.* 58: 1876-1879.
- Ausemus, E.R., F.M. McNeal, and J.W. Schmidt. 1967. Genetics and inheritance. *In* K.S. Quisenberry and L.P. Reitz (eds.) *Wheat and Wheat Improvement*. American Soc. Agron., Madison, Wisconsin.
- Bains, K.S. 1976. Parent dependent genotype x environment interaction in crosses of spring wheat. *Hered.* 36: 163-171.
- Bailey, Jr., T.B., and R.E. Comstock. 1976. Linkage and the synthesis of better genotypes in self-fertilizing species. *Crop Sci.* 16: 363-370.
- Baker, R.J. 1968. Genotype-environment interaction variances in cereal yields in western Canada. *Can. J. Plant Sci.* 48: 293-298.
- Baker, R.J. 1969. Genotype-environment interactions in yield of wheat. *Can. J. Plant Sci.* 49: 743-751.
- Baker, R.J. 1971a. Effects of stem rust and leaf rust of wheat on genotype-environment interactions for yield. *Can. J. Plant Sci.* 51: 457-461.
- Baker, R.J. 1971b. Theoretical variance of response to modified pedigree selection. *Can. J. Plant Sci.* 51: 463-468.
- Baker, R.J. 1974. Selection indices without economic weight for animal breeding. *Can. J. Anim. Sci.* 54: 1-8.

- Baker, R.J. 1975. Letter to the editors. *Can. J. Plant Sci.* 55: 355.
- Baker, R.J., V.M. Bendelow, and M.L. Kaufmann. 1968. Inheritance of and interrelationships among yield and several quality traits in common wheat. *Crop Sci.* 8: 725-728.
- Bell, G.D.H. 1963. Breeding techniques - general techniques, p. 285-302. In *Barley Genetics I. Proc. 1st Int. Barley Genet. Symp., Wageningen.*
- Bhatia, C.R., and R. Rabson. 1976. Bio-energetic considerations in cereal breeding for protein improvement. *Science* 194: 1418-1421.
- Bhatt, G.M. 1970. Multivariate analysis approach to selection of parents for hybridization aiming at yield improvement in self-pollinated crops. *Aust. J. Agric. Res.* 21: 1-7.
- Bhatt, G.M. 1973. Comparison of various methods of selecting parents for hybridization in common bread wheat (Triticum aestivum L.). *Aust. J. Agric. Res.* 24: 457-464.
- Bhullar, B.C., K.S. Gill, and G.S. Mahal. 1978. Genetic analysis of protein wheat. 5th Int. Wheat Genetics Symp., Abstr., New Delhi, India.
- Bhullar, G.S., K.S. Gill, and A.S. Khehra. 1979. Combining ability analysis over F1-F5 generations in diallel crosses of bread wheat. *Theor. Appl. Genet.* 55: 77-80.
- Boerma, H.R., and R.L. Cooper. 1975. Comparison of three selection procedures for yield in soybeans. *Crop Sci.* 15: 225-229.
- Bohren, B.B. 1970. Genetic gains in annual egg production from selection on early part records. *World's Poul. Sci.* 26: 647-657.
- Bohren, B.B., H.E. McKean, and Y. Yamada. 1961. Relative estimates based on regression of offspring on parent. *Biometrics* 17: 481-491.
- Boyadjieva, D. 1975. Inheritance of protein content in backcross hybrids of Triticum aestivum L. *Wheat Inf. Serv.* 40: 17-20.
- Boyce, S.W. 1948. A preliminary study of the inheritance of grain weight in wheat. *New Zeal. J. Sci. Tech. A. Agr. Res. Sec.* 30: 13-22.
- Briggs, K.G., and L.H. Shebeski. 1971. Early generation selection for yield and breadmaking quality of hard red spring wheat (Triticum aestivum L. em Thell.). *Euphytica* 20: 453-463.
- Brim, C.A., H.W. Johnson, and C.C. Cockerham. 1959. Multiple selection criteria in soybeans. *Agron. J.* 51: 42-46.
- Brown, C.M., R.O. Wiebel, and R.D. Seif. 1960. Heterosis and combining ability in common winter wheat. *Crop Sci.* 6: 382-383.
- Bulmer, M.G. 1976. The effect of selection on genetic variability: a simulation study. *Genet. Res., Camb.* 28: 101-117.

- Busch, R.H., J.C. Janke, and R.C. Frohberg. 1974. Evaluation of crosses among high and low yielding parents of spring wheat (Triticum aestivum L.) and bulk prediction of line performance. *Crop Sci.* 47-50.
- Cahaner, A., and J. Hillel. 1980. Estimating heritability and genetic correlation between traits from generations F2 and F3 of self-fertilizing species: a comparison of three methods. *Theor. Appl. Genet.* 58: 33-38.
- Chapman, S.R., and F.H. McNeal. 1970. Gene effects for grain protein in five spring wheat crosses. *Crop Sci.* 10: 45-46.
- Chapman, S.R., and F.H. McNeal. 1971. Gene action for yield components and plant height in a spring wheat cross. *Crop Sci.* 11: 384-386.
- Clark, J.A. 1926. Breeding wheat for high protein content. *J. Am. Soc. Agron.* 18: 648-661.
- Comstock, R.E., and R.H. Moll. 1963. Genotype-environment interactions. p. 164-196. In W.D. Hanson and H.F. Robinson (eds.) *Statistical Genetic and Plant Breeding*. Nat. Acad. Sci. NRC Publ. 982, Washington, D.C.
- Comstock, R.E., and H.F. Robinson. 1952. Estimation of average dominance of genes. p. 494-516. In J.W. Gowen (ed.) *Heterosis*. Iowa State College Press, Ames, Iowa.
- Copp, L.G.L., and G.M. Wright. 1952. The inheritance of kernel weight in a Triticum vulgare cross. *Hered.* 6: 187-199.
- Cowley, C.R., and D.G. Wells. 1980. Inheritance of seed protein in crosses involving 'Hard': a hard red winter wheat. *Crop Sci.* 20: 55-58.
- Crosbie, T.M., J.J. Mock, and O.S. Smith. 1980. Comparison of gains predicted by several methods of cold tolerance traits at two maize populations. *Crop Sci.* 20: 649-655.
- Crump, S.L. 1946. The estimation of variance components in analysis of variance. *Biometrics* 2: 7-11.
- Crump, S.L. 1951. The present status of variance component analysis. *Biometrics* 7: 1-16.
- Cunningham, E.P., R.A. Moen, and T. Gjedrem. 1970. Restriction of selection indices. *Biometrics* 26: 67-74.
- Curnow, R.N. 1980. Selecting crosses using information from a diallel cross. *Biometrics* 36: 1-8.
- Davis, W.H., G.K. Middleton, and T.T. Herbert. 1961. Inheritance of protein texture and speed in wheat. *Crop Sci.* 1: 235-238.

- DePauw, R.M., and L.H. Shebeski. 1973. An evaluation of an early generation yield testing procedure in Triticum aestivum. Can. J. Plant Sci. 53: 465-470.
- Dickerson, G.E. 1959. Techniques for research in quantitative animal genetics. p. 56-105. In Techniques and Procedures in Animal Production Research. Am. Soc. Anim. Sci., New York.
- Dickerson, G.E. 1962. Implications of genetic-environmental interactions in animal breeding. Anim. Prod. 4: 47-64.
- Diehl, A.L., V.A. Johnson, and P.J. Mattern. 1978. Inheritance of protein and lysine in three wheat crosses. Crop Sci. 18: 391-395.
- Donald, C.M. 1968. The breeding of crop ideotypes. Euphytica 17: 385-403.
- Doolittle, D.P., S.P. Wilson, and L.L. Hulbert. 1972. A comparison of multiple trait selection methods in the mouse. J. Hered. 63: 366-372.
- Eagles, H.A., and K.J. Frey. 1974. Expected and actual gains in economic value of oat lines from five selection methods. Crop Sci. 14: 861-864.
- Eberhart, S.A., and W.A. Russell. 1966. Stability parameters for comparing varieties. Crop Sci. 6: 36-40.
- Eckebil, J.P., W.M. Ross, C.O. Gardner, and J.W. Maranville. 1977. Heritability estimates, genetic correlations, and predicted gains from S₁ progeny tests in three grain sorghum random mating populations. Crop Sci. 17: 373-377.
- Elgin, J.H., R.R. Hill, and D.E. Zeiders. 1970. Comparison of four methods of multiple trait selection for five traits in alfalfa. Crop Sci. 10: 190-193.
- Elston, R.C. 1963. A weight-free index for the purpose of ranking or selection with respect to several traits at a time. Biometrics 19: 85-97.
- Evans, L.T. 1975. The physiological basis of yield. p. 327-355. In L.T. Evans (ed.) Crop Physiology, Cambridge Univ. Press, London.
- Falconer, D.S. 1952. The problem of environment and selection. Am. Nat. 86: 293-298.
- Falconer, D.S. 1960. Introduction to quantitative genetics. Oliver and Boyd, Edinburgh.
- Fanous, M.A., D.E. Weibel, and R.D. Morrison. 1971. Quantitative inheritance of some head and seed characteristics in sorghum (Sorghum bicolor L. Moench.). Crop Sci. 11: 787-789.

- Fasoulas, A. 1973. A new approach to breeding superior yielding varieties. Dept. Genet. Plant Breeding, Publ. No. 3, Aristotelian Univ., Thessaloniki, Greece.
- Fasoulas, A. 1979. The honeycomb field designs. Dept. Genet. Plant Bldg. Publ. No. 9, Aristotelian Univ., Thessaloniki, Greece.
- Feldman, M., and L. Avivi. 1978. Utilization of Israeli wild wheats in the improvement of the quality and quantity of grain protein of cultivated wheats. Report Weizmann Industrial Res. Liaison.
- Finlay, K.W. 1971. Breeding for yield in barley. p. 338-345. In R.A. Nilan (ed.) Proc. 2nd Int. Barley Genetics Symp., Pullman, Washington.
- Finlay, K.W., and G.N. Wilkinson. 1963. The analysis of adaptation in a plant breeding programme. Aust. J. Agric. Res. 14: 742-754.
- Finney, K.F., J.W. Meyer, F.W. Smith, and H-C Fryer. 1957. Effects of foliar spraying of Pawneer wheat with urea solution on yield, protein content, and protein quality. Agron. J. 49: 341-347.
- Fisher, R.A. 1918. The correlation among relatives on the supposition of Mendelian inheritance. Trans. Royal Soc., Edinburgh 52: 399-433.
- Fisher, R.A. 1936. The use of multiple measurements in taxonomic problems. Ann. Eugen. (London) 7: 179-189.
- Fonseca, S., and F.L. Patterson. 1968. Yield component heritabilities and interrelationships in winter wheat (Triticum aestivum L.). Crop Sci. 8: 614-617.
- Fowler, W.L., and E.G. Heyne. 1955. Evaluation of bulk hybrid tests for predicting performance of pure line selections in hardy winter wheat. Agron. J. 47: 430-434.
- Francis, T.R., and L.W. Kannenberg. 1978. Yield stability studies in short season maize. I. A descriptive method for grouping genotypes. Can. J. Plant Sci. 58: 1029-1034.
- Frey, K.J. 1971. Improving crop yields through plant breeding. p. 15-58. In Moving off the Yield Plateau. ASA Special Publ. 20, Madison, Wis.
- Frey, K.J. 1972. Stability indices for isolines of oats (Avena sativa L.). Crop Sci. 12: 809-812.
- Frey, K.J., and T. Horner. 1955. Comparison of actual and predicted gains in barley selection experiments. Agron. J. 47: 186-188.
- Gordon, G.H. 1980. A method of parental selection and cross prediction using incomplete partial diallels. Part 1: A simulation study. Theor. Appl. Genet. 56: 225-232.

- Gordon, I.L., D.E. Byth, and L.N. Balaam. 1972. Variance of heritability ratios estimated from phenotypic variance components. *Biometrics* 28: 401-415.
- Grafius, J.E. 1959. Heterosis in barley. *Agron. J.* 51: 551-554.
- Grafius, J.E. 1960. Does overdominance exist in corn? *Agron. J.* 53: 361.
- Grafius, J.E. 1965. A geometry of plant breeding. Michigan State Univ., Res. Bull. 7, 59 pp.
- Grant, M.N., and A.G. McCalla. 1945. Yield and protein content of wheat and barley. I. Interrelation of yield and protein content of random selections from single crosses. *Can. J. Res. C.* 27: 230-240.
- Griffing, B. 1967. Selection in reference to biological groups. I. Individual and group selection applied to populations of unordered groups. *Aust. J. Biol. Sci.* 20: 127-139.
- Griffing, B. 1969. Selection in reference to biological groups. IV. Application of selection index theory. *Aust. J. Biol. Sci.* 22: 131-142.
- Griffing, B., and E. Zsiroa. 1971. Heterosis associated with genotype-environment interaction. *Genetics* 68: 443-445.
- Hamblin, J., and C.M. Donald. 1974. The relationships between plant form, competitive ability and grain yield in a barley cross. *Euphytica* 23: 535-542.
- Hanson, W.D. 1963. Heritability. p. 125-140. In W.D. Hanson and H.F. Robinson (eds.) *Statistical Genetics and Plant Breeding*. Nat. Acad. Sci. NRC Publ. 982. Washington, D.C.
- Harlan, H.V. 1940. A study methods in barley breeding. USDA Tech. Bull. 720, Washington, D.C.
- Harrington, J.B. 1940. Yielding capacity of wheat crosses as indicated by bulk hybrid tests. *Can. J. Res.* 18: 578-584.
- Harris, D.L. 1964. Expected and predicted progress from index selection involving estimates of population parameters. *Biometrics* 20: 46-72.
- Haunold, A., V.A. Johnson, and J.W. Schmidt. 1962a. Variation in protein content of the grain in four varieties of Triticum aestivum L. *Agron. J.* 54: 121-125.
- Haunold, V., V.A. Johnson, and J.W. Schmidt. 1962b. Genetic measurements of protein in the grain of Triticum aestivum L. *Agron. J.* 54: 203-206.

- Hayes, J.F., and W.G. Hill. 1980. A reparameterization of a genetic selection index to locate its sampling properties. *Biometrics* 36: 237-248.
- Hazel, L.N. 1943. The genetic basis for constructing selection indices. *Genetics* 28: 476-490.
- Hazel, L.N., and J.L. Lush. 1942. The efficiency of three methods of selection. *J. Hered.* 33: 393-399.
- Heidhues, T. 1961. Relative accuracy of selection indices based on estimated genotypic and phenotypic parameters. *Biometrics* 17: 502-503.
- Henderson, C.R. 1952. Specific and general combining ability. p. 352-370. In J.W. Gowen (ed.) *Heterosis*, Iowa State College Press, Ames, Iowa.
- Henderson, C.R. 1963. Selection index and expected genetic advance. p. 141-163. In W.D. Hanson and H.F. Robinson (eds.) *Statistical Genetics and Plant Breeding*. Nat. Acad. Sci. - NRC Publ. 982, Washington, D.C.
- Hill, W.G. 1970. Design of experiments to estimate heritability by regression of offspring on selected parents. *Biometrics* 26: 566-571.
- Hill, W.G. 1971. Design and efficiency of selection experiments for estimating genetic parameters. *Biometrics* 27: 293-311.
- Hill, W.G. 1972. Estimation of realized heritabilities from selection experiments. II. Selection in one direction. *Biometrics* 28: 767-780.
- Hill, W.G. 1974. Variability of response to selection in genetic experiments. *Biometrics* 30: 363-366.
- Hogsett, M.C., and A.W. Nordskog. 1958. Genetic-economic value in selection for egg production rate, body weight and egg weight. *Poul. Sci.* 37: 1404-1419.
- Hsu, C.S., and F.W. Sosulski. 1969. Inheritance of protein content and sedimentation value in diallel crosses of spring wheat (Triticum aestivum L.). *Can. J. Genet. Cytol.* 11: 967-976.
- Hsu, P., and P.D. Walton. 1971. Relationships between yield and its components and structures above the flag leaf node in spring wheat. *Crop Sci.* 11: 190-193.
- Inglett, G.E., and R.A. Anderson. 1974. Flour milling. p. 186-198. In G.E. Inglett (ed.) *Wheat: Production and Utilization*. Avi Publ., Westport, Connecticut.

- Jain, H.K., N.C. Singhal, M.P. Singh, and A. Austin. 1975. An approach to breeding for higher protein content in wheat. p. 39. In Breeding for Seed Protein Improvement using Nuclear Techniques (Proc. Meeting Ibadan, 1973), IAGA, Vienna.
- James, J.W. 1961. Selection in two environments. *Heredity* 16: 145-152.
- Jasnowski, S. 1953. On the inheritance of some characters of the ear of wheat (in Polish). *Polon. Acad. Bull. Sci. Lettres Cracovie* 197-218. *Plant Bldg. Abstr.* 5: 217(#654), 1953.
- Johnson, V.A., P.J. Mattern, and S.L. Kuhr. 1979. Genetic improvement of wheat protein. In Seed Protein Improvement in Cereals and Grain Legumes. Vol. II, IAEA, Vienna, pp. 165-181.
- Johnson, V.A., P.J. Mattern, J.W. Schmidt, and J.E. Stroike. 1973. Genetic advances in wheat protein quantity and composition. p. 547-556. In E.R. Sears (ed.) Proc. 4th Inter. Wheat Genetics Symp., Columbia, Mo.
- Johnson, V.A., P.J. Mattern, and K.P. Vogel. 1975. Cultural, genetic and other factors affecting quality of wheat. p. 127-140. In A. Spencer (ed.) Bread: Social, Nutritional, and Agricultural Aspects of Wheat Bread. Applied Science Publ., London.
- Johnson, V.A., J.W. Schmidt, and P.J. Mattern. 1968. Cereal breeding for better protein impact. *Econ. Bot.* 22: 16-25.
- Johnson, V.A., J.W. Schmidt, and W. Mekaska. 1966. Comparison of yield components and agronomic characteristics of four wheat varieties differing in plant height. *Agron. J.* 58: 438-441.
- Jowett, D. 1972. Yield stability parameters for sorghum in East Africa. *Crop Sci.* 12: 314-317.
- Kauffmann, K.D., and J.W. Dudley. 1979. Selection indices for corn grain yield, percent protein, and kernel weight. *Crop Sci.* 19: 583-588.
- Kelly, T.L. 1947. Fundamentals of statistics. Harvard Univ. Press, Cambridge, Mass.
- Kempthorne, O. 1957. An introduction to genetic statistics. Wiley, New York.
- Kempthorne, O., and A.W. Nordskog. 1959. Restricted selection index. *Biometrics* 15: 10-19.
- Kempthorne, O., and B. Tandon. 1953. The estimation of heritability by regression of offspring on parent. *Biometrics* 9: 90-100.
- Ketata, H., E.L. Smith, L.H. Edwards, and R.W. McNew. 1976a. Detection of epistatic, additive, and dominance variation in winter wheat (Triticum aestivum L. em Thell.). *Crop Sci.* 16: 1-4.

- Ketata, H., L.H. Edwards, and E.L. Smith. 1976b. Inheritance of eight agronomic characters in a winter wheat cross. *Crop Sci.* 16: 19-22.
- Keydel, F. 1973. Investigations on the yielding properties of F1 hybrids of winter wheat. *Z. Pflanzenzuchtg.* 69: 239-255.
- Knott, D.R. 1965. Heterosis in seven wheat hybrids. *Can. J. Plant Sci.* 45: 499-501.
- Knott, D.R. 1972. Effects of selection for F2 plant yield on subsequent generations in wheat. *Can. J. Plant Sci.* 52: 721-726.
- Knott, D.R., and J. Kumar. 1975. Comparison of early generation yield testing and a single seed descent procedure in wheat breeding. *Crop Sci.* 15: 295-299.
- Knott, D.R., and S.S. Sindagi. 1969. Heterosis in diallel crosses among six varieties of hard red spring wheat. *Can. J. Genet. Cytol.* 11: 810-822.
- Knott, D.R., and B. Talukdar. 1971. Increasing seed weight in wheat and its effects on yield, yield components, and quality. *Crop Sci.* 11: 280-283.
- Latter, B.D.H., and A. Robertson. 1960. Experimental design in the estimation of heritability by regression methods. *Biometrics* 16: 348-353.
- Lebsock, K.L., and A. Amaya. 1969. Variation and covariation of agronomic traits in durum wheat. *Crop Sci.* 9: 372-375.
- Lin, C.Y. 1976. Comparison of selection indices for economic merit in dairy cattle. Ph.D. Thesis, Ohio State University.
- Lin, C.Y. 1978. Index selection for genetic improvement of quantitative characters. *Theor. Appl. Genet.* 52: 49-56.
- Lin, C.Y. 1979. The sampling variance of heritability of an index. *Can. J. Genet. Cytol.* 21: 273-276.
- Lin, C.Y., and F.R. Allaire. 1977. Heritability of a linear combination of traits. *Theor. Appl. Genet.* 51: 1-3.
- Lin, C.Y., I. Pevzner, and G.W. Friars. 1979. Experimental investigation of errors of heritability estimates in index selection. *Can. J. Genet. Cytol.* 21: 303-308.
- Loffler, C.M., and R.H. Busch. 1980. Selection for grain protein, yield, and N Partitioning in spring wheat. *Agron. Abstr.* p. 60, 72nd Ann. Meeting ASA, Detroit, Mi.

- Lofgren, J.R., K.F. Finney, E.G. Heyne, L.C. Bolte, R.G. Hosney, and M.D. Shogren. 1968. Heritability estimates of protein content and certain quality and agronomic properties of bread wheats (Triticum aestivum L.). *Crop Sci.* 8: 563-568.
- Luedders, V.D., L.A. Duclos, and A.L. Matson. 1973. Bulk, pedigree, and early generation testing breeding methods compared in soybeans. *Crop Sci.* 13: 363-364.
- Lupton, F.G.H. 1965. Studies in the breeding of self pollinating cereals. 5. Use of incomplete diallel in wheat breeding. *Euphytica* 14: 331-352.
- Lush, J.L. 1935. Progeny test and individual performance as indicators of an animal's breeding value. *J. Dairy Sci.* 18: 1-19.
- Lush, J.L. 1941. Intra-sire correlations or regressions of offspring on dams as a method of estimating heritability of characteristics. *Proc. Am. Soc. Anim. Prod.* 33: 293-301.
- Lush, J.L. 1944. The optimum emphasis on dam's records when proving dairy stress. *J. Dairy Sci.* 44: 937-951.
- Lush, J.L. 1947. Family merit and individual merit as basis for selection. *Amer. Nat.* 81: 241-261, 362-379.
- Malborn, S.O. 1966. Some aspects of studies of complex characters in the field of genetics. *Hereditas* 56: 109-112.
- Malloch, J.G., and R. Newton. 1934. The relation between yield and protein content of wheat. *Can. J. Res.* 10: 774-779.
- Mather, K., and J.L. Jinks. 1971. *Biometrical genetics*, 2nd ed. Chapman and Hall, London.
- McGinnis, R.C., and L.H. Shebeski. 1968. The reliability of single plant selection for yield in F₂. p. 110-115. In *Proc. 3rd Inter. Wheat Genet. Symp.*, Canberra, Australia.
- McNeal, F.H., M.A. Berg, C.F. McGuire, V.R. Stewart, and D.E. Baldrige. 1972. Grain and plant nitrogen relationships in eight spring wheat crosses, Triticum aestivum L. *Crop Sci.* 12: 599-602.
- McNeal, F.H., C.D. Qualset, D.E. Baldrige, and V.R. Stewart. 1978. Selection for yield and yield components in wheat. *Crop Sci.* 18: 795-799.
- Middleton, G.K., C.E. Bode, and B.B. Boyles. 1954. A comparison of the quantity and quality of protein in certain wheat varieties of soft wheat. *Agron. J.* 46: 500-502.
- Miezan, K., E.G. Heyne, and K.F. Finney. 1977. Genetic and environmental effects on grain protein content in wheat. *Crop Sci.* 17: 591-593.

- Mihaljev, I., B. Vulic, and M. Djolai. 1979. Expression of heterosis and combining ability for grain protein in a diallel wheat cross. *Wheat Inf. Serv.* 49: 1-4.
- Morris, M.R., J.W. Schmidt, P.J. Mattern, and V.A. Johnson. 1973. Chromosomal locations of genes for high protein in the wheat cultivar Atlas 66. *In Proc. 4th Int. Wheat Genetics Symp. (Missouri Agric. Exp. Stn.)*, Columbia, Mo, p. 715-
- Mulamba, N.N., and J.J. Mock. 1978. Improvement of yield potential of the Eto Blanco maize (*Zea mays* L.) population by breeding for plant traits. *Egypt J. Gen. Cytol.* 7: 40-51.
- Nass, H.G. 1979. Selecting superior spring wheat crosses in early generations. *Euphytica* 28: 161-167.
- Nordskog, A.W. 1978. Some statistical properties of an index of multiple traits. *Theor. Appl. Genet.* 52: 91-94.
- O'Brien, L., R.J. Baker, and L.E. Evans. 1977. Evaluation of F3 selection for yield. *Agron. Abstracts.* p. 66. 69th Ann. Meeting of ASA, Los Angeles, CA.
- O'Brien, L., R.J. Baker, and L.E. Evans. 1978. Response to selection for yield in F3 of four wheat crosses. *Crop Sci.* 18: 1029-1033.
- Okada, I., and R.T. Hardin. 1967. An experimental examination of restricted selection index using *Tribolium castaneum*. I. The result of two-way selection. *Genetics* 57: 227-236.
- Osborne, R. 1957. The use of sire and dam family averages in increasing the efficiency of selective breeding under a hierarchical mating system. *Heredity* 11: 93-116.
- Osborne, R., and W.S.B. Paterson. 1952. On the sampling variance of heritability estimates derived from variance analyses. *Proc. Royal Soc., Edinburgh, Sec. B.* 64: 456-461.
- Pease, A.H.R., G.L. Cook, M. Greig, and A. Cuthbertson. 1967. Combined testing. Report DA188 of the Pig Industry Development Authority. Hitchin, Herts, England.
- Pederson, D.G. 1969a. The prediction of selection response in a self-fertilizing species. I. Individual selection. *Aust. J. Biol. Sci.* 22: 117-129.
- Pederson, D.G. 1969b. The prediction of selection response in a self-fertilizing species. II. Family selection. *Aust. J. Biol. Sci.* 22: 1245-1257.
- Penning de Vries, F.W.T., A.H.M. Brunsting, and H.H. Van Laar. 1974. Products, requirements and efficiency of biosynthesis: A quantitative approach. *J. Theor. Biol.* 45: 339-377.

- Perkins, J.M., and J.L. Jinks. 1968. Environmental and genotype-environmental components of variability. IV. Non-linear interactions for multiple inbred lines. *Hered.* 23: 525-535.
- Pesek, J. 1972. The reliability of estimates of grain from selection in self-pollinated cereals. *Genet. a Slecht. (Praha)* 8: 127-136.
- Pesek, J., and R.J. Baker. 1969. Desired improvement in relation to selection indices. *Can. J. Plant Sci.* 49: 803-804.
- Pesek, J., and R.J. Baker. 1970. An application of index selection to the improvement of self-pollinated species. *Can. J. Plant Sci.* 50: 267-276.
- Pesek, J., and R.J. Baker. 1971. Comparison of predicted and observed responses to selection for yield in wheat. *Can. J. Plant Sci.* 51: 187-192.
- Pirchner, F. 1969. Population genetics in animal breeding. W.H. Freeman & Co., San Francisco.
- Prout, T. 1962. The error variance of the heritability estimate obtained from selection response. *Biometrics* 18: 404-407.
- Raeber, J.G., and C.R. Weber. 1953. Effectiveness of selection for yield in soybean crosses by bulk and pedigree systems of breeding. *Agron. J.* 45: 362-366.
- Ram, H.H., and J.P. Srivastava. 1975. Inheritance of grain protein and sedimentation value in wheat. *Indian J. Genetics and Pl. Breeding* 35: 21-25.
- Rasmusson, D.C., and R.Q. Cannell. 1970. Selection for grain yield and components of yield in barley. *Crop Sci.* 10: 51-54.
- Reddi, M.V., E.G. Heyne, and G.H.L. Liang. 1969. Heritabilities and interrelationships of shortness and other agronomic characters in F3 and F4 generations of two wheat crosses (*Triticum aestivum* L. em Thell.). *Crop Sci.* 9: 222-225.
- Robinson, H.F., R.E. Comstock, and P.H. Harvey. 1949. Estimates of heritability and the degree of dominance in corn. *Agron. J.* 41: 353-359.
- Rosielle, A.A., H.A. Eagles, and K.J. Frey. 1977. Application of restricted selection indices for improvement of economic value in oats. *Crop Sci.* 17: 359-361.
- Rosielle, A.A., and K.J. Frey. 1975. Application of restricted selection indices for grain yield improvement in oats. *Crop Sci.* 15: 544-546.
- Russell, W.A. 1974. Comparative performance for maize hybrids representing different eras of maize breeding. p. 81-101. *In Proc. Ann. Corn and Sorghum Res. Conference, Vol. 29, Washington, D.C.*

- Sales, J., and W.G. Hill. 1976a. Effect of sampling errors on efficiency of selection indices. 1. Use of information from relatives for single trait improvement. *Anim. Prodn.* 22: 1-17.
- Sales, J., and W.G. Hill. 1976b. Effect of sampling errors on efficiency of selection indices. 2. Use of information on associated traits for improvement of a single important trait. *Anim. Prodn.* 23: 1-14.
- Scheinberg, E., A.E. Bell, and V.L. Anderson. 1967. Genetic gain in populations of Tribolium castaneum under uni-stage tandem selection and under restricted selection indices. *Genetics* 55: 69-90.
- Schlehuber, A.M., and B.B. Tucker. 1959. Factors affecting the protein content of wheat. *Cereal Sci. Today* 4: 240-242.
- Schmidt, J.W., V.A. Johnson, M.R. Morris, and P.J. Mattern. 1970. Cytoplasmic male sterility and fertility restoration. *Seiken Ziho.* 22: 113-118.
- Schmidt, J.W., P.J. Mattern, V.A. Johnson, and R.L. Morris. 1974. Investigations of the genetics of bread wheat baking quality. p. 83-101. In R. Bogart (ed.) *Genetic Lectures III.* Oregon State Univ. Press, Corvallis.
- Sen, B.K., and A. Robertson. 1964. An experimental examination of methods for the simultaneous selection of two characters using Drosophila melangaster. *Genetics* 50: 199-209.
- Sharma, D., and D.R. Knott. 1964. The inheritance of seed weight in a wheat cross. *Can. J. Genet. Cytol.* 6: 419-425.
- Shebeski, L.H. 1967. Wheat and breeding. p. 253-272. In K.F. Nielsen (ed.) *Proc. Canadian Centennial Wheat Symp.*, Modern Press, Saskatoon, Saskatchewan.
- Sidwell, R.J., E.L. Smith, and R.W. McNew. 1976. Inheritance and interrelationships of grain yield and selected yield-related traits in a hard red winter wheat cross. *Crop Sci.* 16: 650-654.
- Sidwell, R.J., E.L. Smith, and R.W. McNew. 1978. Heritability and genetic advance of selected agronomic traits in a winter wheat cross. *Cereal Res. Comm.* 6: 103-111.
- Sinclair, T.R., and C.T. de Wit. 1975. Photosynthate and nitrogen requirements for seed production by various crops. *Science* 189: 565-567.
- Singh, K.B., and J.K. Singh. 1971. Potentialities of heterosis breeding in wheat. *Euphytica* 20: 586-590.
- Slatkin, M. 1975. Gene flow and selection in a two-locus system. *Genetics* 81: 787-802.

- Smith, C. 1967. A note on the improvement of a trait by selecting on its components. *Anim. Prod.* 9: 127-130.
- Smith, H.F. 1936. A discriminant function for plant selection. *Ann. Eugen. (London)* 7: 240-250.
- Sneep, J. 1977. Selection for yield in early generations of self-fertilizing crops. *Euphytica* 26: 27-30.
- Soller, M., and A. Genizi. 1967. Optimum experimental designs for realized heritability estimates. *Biometrics* 23: 361-365.
- Stoskopf, N.C., and D.T. Fairey. 1975. Breeding schemes and procedures to obtain yield in cereals. *Proc. of the Eastern Wheat Workers' Conference, Wooster, Ohio.*
- Stuber, C.W., V.A. Johnson, and J.W. Schmidt. 1962. Grain protein content and its relationship to other plant and seed characters in the parents and progeny of a cross of Triticum aestivum L. *Crop Sci.* 2: 506-508.
- Sun, P.L.F., H.L. Shands, and R.A. Forsberg. 1972. Inheritance of kernel weight in six spring wheat crosses. *Crop Sci.* 12: 1-5.
- Sunderman, D.W., M. Wise, and E.M. Sneed. 1965. Interrelationships of wheat protein content, flour sedimentation value, farinograph peak time, and dough mixing and baking characteristics in the F2 and F3 generations of winter wheat, Triticum aestivum. *Crop Sci.* 5: 537-540.
- Swiger, L.A., W.R. Harvey, D.O. Everson, and K.E. Gregory. 1964. The variance of intra-class correlation involving group with one observation. *Biometrics* 20: 818-826.
- Tai, G.C.C. 1977. Index selection with desired gains. *Crop Sci.* 17: 182-183.
- Tai, G.C.C. 1979. An interval estimation of expected response to selection. *Theor. Appl. Genet.* 54: 273-275.
- Tallis, G.M. 1960. The sampling errors of estimated genetic regression coefficients and the error of predicted genetic gains. *Aust. J. Statis.* 2: 66-77.
- Tallis, G.W. 1962. A selection index for optimum genotype. *Biometrics* 18: 120-122.
- Thomas, R.L., J.E. Grafius, and S.K. Hahn. 1971. Stress: an analysis of its source and influence. *Hered.* 26: 423-432.
- Thompson, R. 1977. Estimation of quantitative genetic parameters. p. 639-657. In E. Pollak, O. Kempthorne and T.B. Bailey (eds.) *Proc. Inter. Conference on Quantitative Genetics.* Ames, Iowa.

- Torrie, J.H. 1958. A comparison of the pedigree and bulk methods of breedings soybeans. *Agron. J.* 50: 198-200.
- Townley-Smith, T.F., and E.A. Hurd. 1973. Use of moving means in wheat yield trials. *Can. J. Plant Sci.* 53: 447-450.
- Vogel, K.P., V.A. Johnson, and P.J. Mattern. 1975. Re-evaluation of common wheats from the USDA World Wheat Collection for protein and lysine content. *Nebraska Res. Bull.* 272. pp. 36.
- Voight, R.L., and C.R. Weber. 1960. Effectiveness of selection methods for yield in soybean crosses. *Agron. J.* 52: 527-530.
- Von der Pahl, A., and J.B. Goldenberg. 1971. Effects of individual genes on quantitative characters in barley. p. 434-442. In R.A. Nilan (ed.) *Proc. 2nd Inter. Barley Genetics Symp.*, Pullman, Washington.
- Wallace, D.H., J.C. Ozbun, and H.M. Munger. 1972. Physiological genetics of crop yield. *Adv. Agron.* 24: 97-146.
- Walton, P.D. 1971. Heterosis in spring wheat. *Crop Sci.* 11: 422-424.
- Wharton, Jr., C.R. 1980. Food, the hidden crisis. *Science* 208: 1415.
- Whitehouse, R.N.H., J.B. Thompson, and M.A.M. Do Vaille Ribeiro. 1958. Studies on the breeding of self-pollinating cereals. 2. The use of a diallel cross analysis in yield prediction. *Euphytica* 7: 147-169.
- Widner, J.N., and K.L. Lebsack. 1973. Combining ability in durum wheat: I. Agronomic characteristics. 13: 164-167.
- Willham, R.L. 1965. Animal breeding. Memo, Dept. of Animal Sci., Iowa State University.
- Williams, J.S. 1962a. Some statistical properties of a genetic selection index. *Biometrika* 49: 325-337.
- Williams, J.S. 1962b. The evaluation of a selection index. *Biometrics* 18: 375-393.
- Williams, W., and N. Gilbert. 1960. Heterosis and the inheritance of yield in the tomato. *Hered.* 14: 133-145.
- Wilton, J.W., D.A. Evans, and L.D. Van Vleck. 1968. Selection indices for quadratic models of total merit. *Biometrics* 24: 927-949.
- Worzella, W.W. 1942. Inheritance and interrelationship of components of quality, cold resistance, and morphological characters in wheat hybrids. *J. Agric. Res.* 65: 501-522.
- Wright, A.J. 1971. The analysis and prediction of some two factor interactions in grass breeding. *J. Agric. Sci., Camb.* 76: 301-306.

- Wright, A.J. 1976. The significance for breeding of linear regression analysis of genotype-environment interactions. *Hered.* 37: 83-93.
- Wright, S. 1921. Systems of mating. *Genetics* 6: 111-178.
- Young, S.S.Y. 1961. A further examination of the relative efficiency of three methods of selection for genetic gains under less restricted conditions. *Genet. Res.* 2: 106-121.
- Young, S.S.Y. 1964. Multi-stage selection for genetic gain. *Heredity* 19: 131-145.
- Young, S.S.Y., and G.M. Tallis. 1961. Performance index for lifetime production. *J. Anim. Sci.* 20: 506-509.
- Zeleny, L. 1964. Criteria for wheat quality. p. In Y. Pomeranz (ed.) *Wheat Chemistry and Technology.* Amer. Assoc. Cereal Chem., St. Paul, Mn.

TABLE A-1. Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks and parents of wheat cross 1 grown at the Point.

Selected line or variety	F3 Lines					F4 Bulks				
	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)	Yield (kg/ha)	TKW (g)	Test wt. (kg/ha)	Protein (%)	Protein yield (kg/ha)
49	4751	41.1	77.8	16.9	708	5403	43.7	80.5	14.8	707
76	4640	44.3	77.2	17.7	721	4544	45.5	78.7	15.2	607
57	4353	44.7	76.6	17.5	672	5410	44.9	78.9	15.7	748
73	4778	42.1	76.4	16.9	710	5670	43.0	79.2	14.7	735
39	4840	42.8	75.0	16.3	694	5587	42.8	78.2	15.0	740
61	4335	42.8	78.0	17.6	672	5454	44.8	79.6	16.5	793
48	4491	39.1	77.2	17.1	674	5101	40.6	79.0	14.9	667
81	4522	41.2	76.0	16.8	671	5377	41.1	78.7	15.9	750
82	4742	44.4	77.4	17.2	718	5288	45.7	79.6	15.7	726
64	4324	41.4	78.4	17.4	664	4807	42.1	79.6	15.7	665
65	4235	46.5	76.6	18.6	695	4552	46.7	78.9	16.5	662
59	3671	47.6	75.6	18.4	594	4875	48.1	78.9	16.8	723
89	4382	42.8	76.9	18.4	710	4769	44.7	79.0	16.4	690
38	3535	45.0	79.0	18.9	588	4800	46.5	79.9	16.5	702
10	3947	46.5	78.7	18.2	631	4696	46.8	80.5	16.8	696
77	4042	43.9	75.2	18.8	669	4953	45.1	78.2	16.3	709
67	4498	46.6	75.0	18.1	716	4937	47.3	77.8	16.0	698
41	3920	44.1	78.0	18.6	641	4796	43.1	79.9	16.6	700
28	4645	45.9	74.8	17.7	722	4804	47.0	77.7	16.3	690
18	4216	41.8	80.0	18.6	688	4856	42.6	81.6	16.5	703
16	3855	46.6	79.0	17.9	606	5303	48.9	80.1	15.9	741
94	3964	38.2	77.8	17.8	621	4468	40.0	80.3	15.8	623
91	2624	37.7	77.7	19.6	453	4248	39.1	79.1	17.2	641
79	3795	38.3	79.0	17.3	578	4952	38.9	81.1	15.4	670
72	3771	38.3	77.2	17.5	582	5060	38.0	78.5	16.0	713
45	3831	36.3	76.8	17.9	603	4358	37.6	79.6	16.4	628
25	3126	36.5	78.7	17.9	491	4636	38.8	80.5	16.0	652
14	3299	35.2	78.0	18.0	523	4718	36.4	80.7	16.4	678
7	1505	40.1	--	20.0	265	4392	42.2	81.0	15.5	598
96	4102	36.1	78.8	17.5	633	4930	35.8	80.3	15.6	678
15	2043	45.9	--	20.5	368	4803	45.2	80.0	16.5	696
Composite	--	--	--	--	-	4562	42.9	79.2	16.3	655
Sinton	4030	38.3	78.0	17.7	629	5003	39.1	78.9	16.2	716
Glenlea	4544	46.4	76.8	16.8	672	5812	48.1	78.7	15.0	767
CV (%)	8.3	1.8	--	2.3	8.4	8.8	2.3	0.6	2.9	10.1
LSD (5%)	513	1.2	--	0.8	83	710	1.6	0.8	0.7	115

TABLE A-2. Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 1 grown in Glenlea.

Selected line or variety	F3 Lines					F4 Bulks				
	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)
49	3581	41.5	80.8	16.2	511	2932	39.3	77.0	16.5	425
76	3523	42.3	80.6	16.6	514	2862	40.6	76.6	16.3	410
57	3787	45.6	80.8	17.3	577	3683	41.7	76.1	15.7	508
73	3258	43.4	80.4	16.9	485	2992	39.7	76.6	16.4	431
39	3178	42.6	79.6	15.9	445	2918	38.7	74.8	15.6	401
61	3642	41.8	80.2	16.8	538	3442	40.8	76.5	16.5	501
48	3460	41.4	80.4	16.2	491	2605	37.7	76.5	15.8	363
81	3418	39.8	79.6	16.5	494	3004	37.1	75.1	16.4	435
82	3145	44.2	80.4	17.5	483	3160	42.7	75.9	16.0	445
64	3507	40.9	80.6	18.1	555	3018	38.7	76.9	16.3	433
65	3436	46.3	80.8	17.5	530	2569	42.1	75.7	16.6	373
59	2915	47.9	79.9	18.2	467	1962	44.4	75.9	18.3	317
89	3024	43.9	80.4	18.7	498	2778	41.1	76.7	17.8	433
38	3064	45.5	81.0	18.1	489	3047	43.5	77.2	17.8	477
10	2785	46.5	81.7	18.0	441	3264	41.9	77.4	16.7	480
77	2685	44.9	81.0	18.0	428	1987	41.5	77.0	17.5	306
67	3329	45.8	79.0	17.0	497	2821	42.8	74.6	16.6	410
41	2244	44.2	80.8	19.6	385	3032	40.9	76.8	17.6	470
28	2780	46.4	78.6	17.6	431	2486	43.4	75.1	16.5	362
18	2757	42.8	82.6	19.0	461	3542	40.9	78.7	17.4	540
16	2731	47.2	81.7	17.5	422	3407	45.5	77.5	16.6	498
94	3276	37.8	81.0	16.5	476	3350	36.9	77.3	16.4	483
91	1527	37.9	78.7	20.2	272	2500	37.3	76.6	17.7	390
79	2652	37.9	81.0	17.3	405	3022	37.9	78.7	16.9	448
72	2818	37.4	79.4	17.0	421	2814	36.1	76.0	17.1	424
45	2764	38.0	80.8	17.5	426	2544	35.5	76.0	16.2	361
25	2822	37.9	81.0	17.4	432	2880	35.5	77.0	16.8	427
14	2519	37.2	80.8	18.9	419	2815	34.2	77.6	17.6	434
7	1170	39.7	--	21.0	216	3232	38.9	77.7	16.0	452
96	2741	35.6	81.0	16.9	406	3315	34.4	77.9	16.1	470
15	1137	44.6	--	21.4	213	2718	41.4	76.9	16.6	397
Composite	--	--	--	--	--	2871	40.6	76.8	16.5	416
Sinton	2974	37.8	81.7	17.9	470	3175	35.5	76.4	17.0	475
Glenlea	3005	45.2	80.8	17.0	450	3521	44.6	76.2	15.6	483
CV (%)	13.2	2.5	--	3.1	13.2	12.2	1.9	0.5	2.9	11.0
LSD (5%)	592	1.7	--	0.9	92	591	1.2	0.6	0.8	78

TABLE A-3. Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 2 grown at the Point.

Selected line or variety	F3 Lines					F4 Bulks				
	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)
60	4836	39.8	79.4	16.1	687	5356	39.7	79.9	14.2	669
58	4529	49.3	80.8	16.1	640	5908	47.7	80.1	15.4	802
64	4665	43.6	76.6	16.0	658	5665	41.6	77.6	14.4	717
80	4836	41.6	78.8	16.1	686	5866	41.4	80.5	14.8	766
79	4545	42.2	76.4	15.6	624	5575	38.8	77.0	14.2	700
73	4424	47.2	78.0	17.0	660	6576	43.3	79.4	13.4	778
66	4242	43.2	78.8	16.0	595	5574	41.5	79.9	14.8	725
41	4162	42.5	79.8	15.4	565	5764	40.1	78.6	13.8	701
65	4589	44.4	78.0	15.8	639	6144	42.1	79.2	14.1	763
100	4296	42.9	78.9	16.1	606	6011	41.0	80.5	14.4	764
6	4100	46.1	78.3	17.4	625	6037	47.3	80.0	15.2	807
12	4620	44.7	77.8	17.7	718	5533	43.0	79.2	15.3	741
98	3953	47.8	78.6	17.7	618	5734	46.4	79.4	15.9	800
13	3751	47.5	76.6	17.3	570	6238	45.8	78.8	14.3	788
57	4369	44.7	77.4	17.4	669	5729	44.1	78.8	14.8	746
18	4432	43.7	77.2	17.0	662	5195	42.6	78.1	15.3	699
84	3606	45.6	79.0	17.3	549	5408	44.3	80.5	15.9	757
46	4104	44.4	76.8	17.3	625	5821	44.2	78.3	15.2	780
7	4276	43.4	81.3	17.1	646	5348	42.7	80.7	15.6	736
97	4627	46.8	80.4	15.6	635	5773	45.3	80.3	14.3	726
43	4282	45.3	76.4	16.1	607	6459	41.0	76.3	13.7	779
15	3190	39.7	76.4	15.9	446	4939	40.4	76.7	14.7	636
1	4098	42.2	78.6	15.2	548	5488	41.7	79.6	13.7	661
69	3815	38.8	77.9	15.7	529	5774	40.0	78.6	13.9	704
49	4029	38.5	76.7	16.2	575	5804	37.0	77.6	14.5	740
63	4440	39.5	76.9	15.8	615	5819	37.7	77.5	14.1	720
93	3600	40.2	77.8	16.0	507	5061	40.8	78.3	14.6	649
78	3713	37.2	76.5	16.9	550	5056	37.5	78.7	14.9	660
3	2557	39.5	75.2	17.1	385	5168	39.6	77.9	14.3	651
87	3493	36.5	77.2	16.6	511	5629	37.2	77.1	14.1	696
90	2988	44.9	73.2	18.8	495	4887	43.6	75.8	16.1	692
Composite	--	--	--	--	--	5722	41.3	79.4	15.1	760
NB505	3767	38.3	77.0	16.0	531	5340	35.1	77.9	13.9	653
Sinton	4305	38.1	77.9	18.1	686	4557	37.6	78.9	16.3	655
Glenlea	4155	46.2	78.6	17.3	632	5977	47.3	79.6	15.4	811
CV (%)	8.3	2.2	--	3.3	8.3	8.8	2.5	0.8	2.7	8.8
LSD (5%)	528	1.5	--	0.9	78	809	1.7	1.1	0.7	105

TABLE A-4. Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 2 grown in Glenlea.

Selected line or variety	F3 Lines					F4 Bulks				
	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)
60	3705	37.9	80.4	15.1	490	3825	36.7	77.1	14.7	495
58	3901	48.4	79.8	16.3	560	4036	45.1	76.3	16.1	572
64	3751	43.6	77.4	15.4	507	4094	39.9	75.5	14.4	520
80	3450	41.0	80.6	15.4	468	4014	39.9	77.5	14.9	526
79	3589	42.3	77.8	15.2	481	4248	40.3	74.4	13.8	518
73	3656	43.0	79.2	16.0	514	4502	41.9	76.7	14.5	575
66	3838	41.7	80.2	15.9	537	3918	40.2	77.1	15.2	522
41	3858	40.5	78.6	15.4	522	4304	39.0	75.9	15.4	582
65	3406	43.5	79.2	15.7	469	4130	40.0	76.0	14.7	532
100	3634	41.1	80.2	15.4	492	4205	38.4	76.5	15.0	556
6	3333	47.6	80.0	17.3	507	3674	45.3	77.2	15.1	489
12	3311	44.2	79.6	16.0	489	4003	42.2	76.8	16.4	574
98	3246	45.4	79.8	16.9	484	3560	43.7	76.9	15.8	495
13	3123	48.2	78.5	17.2	472	3285	44.6	76.1	15.7	454
57	3460	43.9	79.6	17.0	519	3128	42.6	76.6	15.0	416
18	3157	46.5	78.8	17.1	474	3030	41.4	75.9	15.9	424
84	3242	44.8	81.4	17.9	511	2883	43.6	78.2	15.4	389
46	2866	44.6	78.0	17.6	445	3427	40.2	75.7	14.8	445
7	3559	43.5	81.9	16.9	530	3696	41.3	79.1	15.7	510
97	3236	46.8	80.0	16.6	471	3268	42.9	77.1	14.4	414
43	3521	43.9	77.0	15.8	491	4555	39.0	74.5	14.0	561
15	2911	39.8	77.2	16.1	413	3790	38.2	74.4	14.7	491
1	3695	43.0	79.6	15.8	514	3238	39.1	76.7	14.1	403
69	3006	39.6	79.0	15.9	420	4215	36.8	76.1	14.2	524
49	3422	38.0	77.2	15.3	461	4403	36.2	74.9	14.7	567
63	3416	37.0	76.8	15.6	469	3694	35.5	74.0	14.7	478
93	3210	37.4	77.4	15.3	433	4011	36.4	74.7	15.0	529
78	3058	35.6	78.5	16.6	448	3176	34.4	76.0	15.3	426
3	2444	39.4	76.4	16.6	357	3601	38.9	75.4	15.0	475
87	2858	36.3	78.5	15.6	390	4207	33.9	74.9	14.5	536
90	2260	42.7	75.0	19.4	386	2908	41.0	72.3	17.8	457
Composite	--	--	--	--	--	3681	39.1	76.0	15.0	486
NB505	3183	37.1	78.5	15.7	439	4258	34.8	75.9	14.8	554
Sinton	3131	36.3	--	18.1	499	2921	35.4	76.6	16.4	419
Glenlea	3151	46.0	80.6	16.5	458	3589	44.4	76.4	14.9	490
CV (%)	10.7	2.7	--	2.7	10.2	12.0	2.2	0.8	4.6	11.9
LSD (5%)	552	1.8	--	0.7	76	735	1.4	1.0	1.1	97

TABLE A-5. Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 5 grown at the Point.

Selected line or variety	F3 Lines					F4 Bulks				
	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)
65	4427	42.9	75.0	17.1	667	5039	41.5	76.6	15.5	686
53	4207	41.3	77.0	17.0	628	5066	39.1	79.1	15.2	677
72	4391	44.7	77.0	17.3	670	5175	40.1	79.0	14.5	658
42	4233	41.7	75.4	16.7	627	4518	39.4	76.6	15.4	612
40	3973	40.2	75.8	17.3	604	5285	37.8	77.4	14.4	671
18	4060	44.0	76.4	17.8	637	4705	41.3	78.8	15.2	631
56	4113	44.7	77.4	17.3	629	4547	41.1	77.6	15.9	636
66	4180	42.5	74.6	17.6	646	5180	39.5	76.2	15.0	685
85	4040	43.0	76.2	17.3	614	5669	40.0	78.5	14.5	718
80	3831	41.1	74.2	17.3	585	5060	37.9	75.4	15.4	688
94	4189	44.3	73.6	18.9	697	4998	43.0	76.5	16.6	733
11	3860	46.5	77.8	17.8	601	4662	44.3	77.1	16.3	670
68	4089	42.4	77.8	18.5	665	3911	4 . 5	77.0	16.4	565
75	3644	44.0	74.2	17.7	569	4622	42.5	75.7	15.6	633
64	3695	45.8	75.0	18.0	583	4261	44.5	77.9	15.8	593
31	3971	43.2	75.6	18.6	656	3656	40.1	76.4	16.2	523
43	3542	44.3	74.0	18.8	584	4352	45.1	78.7	16.7	638
13	3613	42.6	77.2	18.5	587	4502	39.8	76.3	16.4	650
6	3860	45.7	76.6	16.3	555	4977	42.2	76.1	14.2	621
4	4093	43.7	76.6	17.1	616	5415	39.2	77.7	14.6	697
71	3311	40.6	76.8	17.1	500	4860	38.7	79.5	14.2	610
96	2766	40.3	78.2	18.1	440	3963	39.1	78.5	15.6	547
99	3737	39.9	77.8	16.3	535	4573	37.3	78.7	14.4	578
32	3139	37.0	77.0	18.1	500	4143	35.1	76.1	15.8	575
97	2910	41.0	72.6	20.6	529	4175	39.3	76.2	16.8	616
91	3371	37.7	77.0	17.7	525	3973	38.3	77.5	16.5	576
17	3331	43.1	76.6	16.4	483	4619	39.7	80.0	14.8	600
58	2846	39.5	74.4	18.9	474	4299	40.5	78.0	16.1	607
26	3311	37.5	78.6	16.7	487	3839	34.7	77.6	15.8	535
89	3420	42.7	78.8	19.6	590	3951	39.3	77.8	16.9	588
93	2919	40.7	76.0	20.0	514	4092	37.3	77.7	16.8	602
Composite	--	--	--	--	--	4614	39.9	78.0	15.9	646
NB505	4104	38.3	76.6	16.1	579	5117	34.0	78.6	13.5	608
A2P5	2833	42.6	76.8	19.6	486	3951	42.3	76.5	17.3	602
Sinton	4071	39.2	--	17.8	639	4491	37.2	78.6	15.4	609
Glenlea	3933	45.7	--	16.4	570	5792	44.4	79.1	15.0	768
CV (%)	11.7	2.5	--	4.4	13.1	9.0	3.1	0.7	3.5	9.7
LSD (5%)	684	1.7	--	1.3	119	678	2.0	0.9	0.9	100

TABLE A-6. Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 5 grown in Glenlea.

Selected line or variety	F3 Lines					F4 Bulks				
	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)
65	3668	43.7	77.6	17.4	562	3487	38.5	76.7	15.7	482
53	3656	39.6	79.6	16.2	522	3454	36.9	76.9	15.7	477
72	3442	42.4	77.4	18.0	546	3418	37.6	76.3	16.2	487
42	3321	41.5	77.8	17.0	497	3107	35.6	73.8	16.7	455
40	3570	40.3	78.4	17.2	539	3238	35.6	76.0	16.3	463
18	3169	43.7	79.2	17.7	493	3567	39.3	76.1	17.0	533
56	3295	42.7	79.4	18.0	520	3544	38.8	75.9	17.5	545
66	3193	42.0	78.4	17.0	476	3305	38.6	74.0	15.7	460
85	3242	41.1	78.8	16.7	476	3878	37.3	76.3	15.8	540
80	3432	40.2	77.4	18.2	551	3176	35.5	73.2	16.8	471
94	2870	44.1	76.6	19.5	493	3089	39.4	74.7	18.1	491
11	2983	48.4	77.8	19.1	501	2829	43.1	74.3	18.6	464
68	2870	44.8	77.6	19.4	488	2941	40.9	74.3	18.2	472
75	3307	44.7	78.0	18.4	536	2875	40.1	74.3	17.5	445
64	2917	45.3	79.2	18.1	464	2886	42.5	75.2	17.8	452
31	2561	41.5	76.4	19.5	440	2680	38.0	75.1	18.7	441
43	2505	45.8	79.0	19.2	424	2476	40.8	76.0	17.9	391
13	3141	43.6	79.0	18.3	508	2576	38.9	75.3	17.5	396
6	3068	46.6	78.2	17.5	472	3312	40.1	74.9	16.2	471
4	3076	43.1	79.6	17.4	472	3579	39.0	75.9	16.3	514
71	2891	39.0	78.6	16.7	423	3593	33.9	76.3	16.1	511
96	2444	41.0	79.2	18.5	397	2551	36.7	76.3	17.7	398
99	2723	39.9	80.2	17.3	413	3343	35.5	77.1	16.6	488
32	2234	38.4	77.6	20.1	395	3197	33.2	74.7	17.9	503
97	2192	40.5	75.6	20.0	384	2566	37.0	74.3	18.3	414
91	2166	37.8	78.6	18.2	347	2388	33.3	74.7	17.6	370
17	3115	41.7	80.6	16.8	460	2813	37.8	77.8	16.5	407
58	2230	40.0	76.8	20.0	393	2304	35.5	75.5	18.2	370
26	2315	35.9	78.4	17.9	365	2539	31.4	74.7	17.0	379
89	2394	41.6	78.4	20.6	433	2759	38.2	76.2	19.0	462
93	2759	39.7	78.4	19.9	484	2592	35.2	75.9	18.4	420
Composite	--	--	--	--	--	2817	36.3	75.9	17.1	424
NB505	3311	37.2	80.0	15.2	442	2932	34.2	77.3	14.8	512
A2P5	1582	43.4	76.7	21.5	299	2375	38.9	73.9	20.1	419
Sinton	3339	37.3	--	17.8	523	2850	34.0	76.3	16.9	424
Glenlea	3234	46.0	--	16.6	472	3066	43.2	75.7	16.4	441
CV (%)	11.8	2.1	--	2.2	11.9	14.0	2.4	0.7	2.4	14.1
LSD (5%)	543	1.4	--	0.6	88	689	1.5	0.8	0.7	105

TABLE A-7. Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 6 grown at the Point.

Selected line or variety	F3 Lines					F4 Bulks				
	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)
67	5032	46.3	78.0	16.3	723	5249	44.0	76.8	13.9	646
73	4767	43.3	79.6	17.5	734	3876	40.7	78.6	15.8	541
60	4953	45.9	78.4	15.4	671	4430	44.2	78.1	13.1	512
22	4969	44.2	77.0	15.4	673	4705	40.2	75.4	14.0	578
48	4509	46.9	79.0	16.2	643	5833	47.1	79.6	14.2	726
85	4731	42.0	78.0	16.7	696	4394	41.6	78.3	14.1	552
75	4422	42.3	79.2	15.8	615	4661	41.7	78.8	13.6	557
28	4425	41.8	76.8	16.7	651	4290	42.2	78.5	14.9	565
51	5111	46.5	78.6	16.9	759	3835	47.4	77.6	15.7	526
30	4927	46.6	76.6	16.4	713	4379	48.3	77.9	14.5	559
55	4749	45.5	79.8	17.5	729	4313	43.6	78.6	16.1	612
36	4369	43.4	77.2	17.9	690	4334	44.3	78.3	15.1	578
9	4218	45.3	79.0	17.5	652	4433	45.4	79.0	15.7	616
25	4160	46.0	76.6	17.1	624	4485	44.9	78.1	14.7	588
35	4558	40.4	75.8	16.7	670	4645	42.6	78.4	13.7	567
2	4455	47.2	78.2	16.0	629	4268	44.5	76.9	14.5	545
46	4507	45.7	80.0	16.4	652	4496	44.9	77.5	14.6	583
86	3473	41.7	78.0	16.3	498	5105	41.1	79.2	14.4	649
77	3366	39.9	79.4	17.8	529	3686	37.6	80.2	16.9	545
96	4255	39.0	79.2	16.3	612	4714	37.1	79.3	14.0	580
20	3893	37.8	79.6	16.6	569	4978	37.1	80.8	14.7	642
61	3666	39.5	76.4	15.4	497	4436	38.9	78.1	13.8	540
68	3546	38.2	79.4	17.3	540	3739	38.4	78.4	16.2	533
52	2370	43.6	72.9	16.7	347	3900	46.3	79.3	14.7	504
40	3084	37.3	78.2	17.2	467	4138	37.3	79.7	14.9	543
64	2561	37.8	79.6	18.3	412	3126	35.5	80.7	16.2	449
65	3942	37.8	77.4	15.2	527	4547	38.5	78.8	13.6	545
4	3591	39.8	80.8	18.6	588	3899	40.3	78.8	16.0	548
8	4087	43.5	79.0	18.0	647	3747	42.1	78.7	16.2	540
21	3322	42.7	77.0	18.7	548	4015	41.7	78.5	16.8	592
94	3304	42.7	79.2	18.6	542	3515	40.5	77.7	16.6	513
Composite	--	--	--	--	--	4530	40.7	78.3	16.0	638
A2P5	3008	40.5	75.4	19.8	523	3154	42.2	76.1	17.1	485
NB320	5114	40.8	80.0	14.3	647	5328	41.6	79.5	12.6	588
Sinton	3906	38.5	--	17.0	584	4144	36.1	78.0	15.3	560
Glenlea	4204	46.4	--	16.4	605	4932	47.7	79.4	13.8	601
CV (%)	10.6	2.1	--	2.9	11.1	12.6	3.5	1.4	5.6	15.5
LSD (5%)	662	1.4	--	0.8	104	888	2.4	1.7	1.4	143

TABLE A-8. Mean grain yield, TKW, test weight, percent protein, and protein yield for selected F3 lines, F4 bulks, checks, and parents of wheat cross 6 grown in Glenlea.

Selected line or variety	F3 Lines					F4 Bulks				
	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)	Yield (kg/ha)	TKW (g)	Test wt. (kg/hl)	Protein (%)	Protein yield (kg/ha)
67	3957	47.9	78.8	17.0	593	4190	41.9	76.3	16.4	603
73	3416	43.1	80.4	18.1	542	3255	40.9	78.1	17.2	494
60	3175	48.2	80.2	16.6	465	4017	41.7	76.4	15.4	545
22	3127	45.6	78.6	16.6	456	4042	38.7	75.0	15.2	542
48	3450	49.7	81.0	17.7	537	3834	44.7	77.3	15.8	534
85	3133	44.2	80.0	17.2	475	3553	38.9	76.2	16.1	502
75	3335	43.2	80.6	16.2	474	4366	38.9	78.0	15.0	575
28	3307	44.2	79.8	17.5	510	2969	40.6	77.1	16.0	419
51	2594	50.2	78.4	18.5	425	3211	44.5	76.3	16.8	475
30	2670	49.2	78.2	17.7	415	3393	43.4	75.8	16.1	480
55	2604	47.2	80.4	18.5	425	3071	42.0	76.3	17.2	464
36	2941	45.7	78.2	19.1	493	3317	40.4	75.9	16.9	494
9	2373	46.2	79.8	19.3	402	2888	43.7	77.9	17.1	436
25	3022	47.4	79.0	17.4	463	3592	40.7	75.2	16.2	513
35	2981	48.2	78.8	18.4	481	3657	39.7	75.7	16.1	518
2	3123	47.8	78.8	17.7	486	3760	44.0	75.9	15.7	521
46	2474	49.9	78.6	17.9	390	2820	42.8	75.3	16.4	408
86	2222	42.5	81.1	17.3	339	3563	37.7	76.8	15.5	487
77	1820	40.1	80.8	19.5	312	2880	36.2	79.4	17.8	450
96	2917	39.3	80.8	16.9	433	3232	35.7	77.9	15.8	448
20	2683	39.3	81.8	17.8	420	3242	33.5	77.9	15.8	446
61	2747	42.2	79.6	16.7	405	3267	36.8	76.0	15.3	440
68	1915	37.3	80.0	18.4	310	2994	35.5	77.7	17.1	451
52	2168	47.3	79.6	18.1	346	2779	43.0	78.0	16.4	400
40	2527	37.5	79.6	18.3	408	2731	33.9	77.4	17.2	411
64	2339	37.2	81.1	19.1	392	2971	36.5	77.6	16.4	430
65	2444	40.9	79.4	15.7	337	3307	35.5	75.3	14.8	431
4	2210	43.0	80.0	20.0	388	2841	38.8	76.8	18.4	461
8	1319	44.8	77.7	20.3	236	2446	41.9	76.5	18.2	390
21	2321	45.8	80.0	19.6	400	3104	40.1	76.7	18.1	496
94	1869	45.4	78.7	20.1	329	3238	40.6	79.0	17.9	509
Composite	--	--	--	--	--	3122	39.5	77.1	16.8	460
A2P5	1834	43.1	78.0	21.5	347	2470	40.2	73.9	19.2	417
NB320	3137	43.3	81.0	15.4	426	3757	39.7	77.5	14.2	469
Sinton	2622	36.8	--	17.9	413	3136	34.9	76.4	17.5	483
Glenlea	2949	46.4	--	17.2	446	3835	43.5	76.9	16.2	546
CV (%)	13.0	2.5	--	2.1	12.9	12.1	2.2	0.6	2.9	11.9
LSD (5%)	273	1.8	--	0.6	85	649	1.4	0.7	0.8	93