GENETIC STUDIES ON THE SIMULTANEOUS IMPROVEMENT OF GRAIN YIELD AND GRAIN PROTEIN CONTENT IN WHEAT

(Triticum aestivum L. em Thell.)

A Thesis Submitted to the Faculty

of

Graduate Studies

The University of Manitoba

by

Solomon Kibite

In Partial Fulfillment of the Requirements for the Degree

of

Doctor of Philosophy Department of Plant Science October 1980

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ΒY

SOLOMON KIBITE

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 ©-1980

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ABSTRACT

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KIBITE, Solomon, Ph.D. The University of Manitoba, October, 1980. Genetic Studies on the Simultaneous Improvement of Grain Yield and Protein Content in Wheat (Triticum aestivum L. em Thell.).

Scope and Method of Study: The value of wheat is related to both grain yield (GY), and grain protein content (GPC), and therefore, the emphasis in most breeding programs is on the production of high yielding-high protein lines. Since in practice an increase in GY has been associated with a decrease in GPC, it has become an article of faith among wheat breeders that it would be very difficult to improve both GY and GPC simultaneously. The genetic basis of this problem is not clearly defined, but several theories and hypotheses have been provided by various workers.

The objectives of this study were: (i) to study more closely the nature and basis of the inverse relationship between GY and GPC: (ii) to investigate the effectiveness of selection for GY and GPC on single plant performance basis; and (iii) to evaluate base populations of known differences in gene frequencies for their breeding values with special emphasis on the simultaneous improvement of both characteristics.

Two utility wheat cultivars, ('Glenlea' and 'NB131'), and two hard red spring wheat (HRSW) cultivars, ('Sinton' and 'Coteau'),

exhibiting wide differences in GY and GPC were used in this study. These cultivars were chosen because they represent key varieties used in bread wheat breeding programs. The four cultivars and 7 base populations generated from them (4 backcrosses, 2 F_2 's and an intermated F_2 population) were evaluated for various genetic and statistical parameters under space planted conditions during the summer of 1978 and under solid planted conditions the following year.

Observations and Conclusions of the Study: Phenotypic correlations between GY and GPC were most always negative and highly significant, but their intensities were too low to hinder simultaneous selection for both characteristics. Phenotypic correlations in segregating base populations were not greater than those found in parental populations, suggesting that environment greatly influenced the relationship between the two characteristics. Standardized partial regression analysis suggested that when the effects of morphological yield components were removed, the correlation between GY and GPC was not significant. The absence of significant genetic correlation between the two characteristics was indicated in 6 of the 7 base Path analyses indicated that the negative populations studied. correlation between GY and GPC emerged not because of direct relationships, but as a result of the opposite and joint dependence of both characteristics on the same set of primary characteristics. Intermating the F₂ population did not result in reduction of the

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strength of the negative relationship between GY and GPC. Contrary to genetic expectations, it intensified the genetic and phenotypic correlations and decreased the genetic and phenotypic covariances. From these observations, it was concluded that the correlation between GY and GPC are phenotypically real, but not genetic in origin. It is anticipated that environmental causes, source-sink relationships, and dilution of protein by non-protein compounds are responsible for the inverse relationship between the two characteristics.

Simulated selection studies showed that intense early generation selection (0.1 selection intensity) for any characteristic or groups of characteristics had little effect in improving GY and (or) GPC, but was also inexpedient because of its adverse effects such as: (1) severe reductions in genetic variances; (2) undesirable shifts in the means of the characteristics for which selection has not been practised; and (3) misclassification of genotypes and consequently, irretrievable losses of elite progenies. A relaxed selection pressure of between 0.4 and 0.6 for heavy kernel weight did not cause such adverse effects, and was beneficial in minimizing the number of lines advanced for testing in the next generation. Selection efficiency on single plant performance basis was enhanced by stratifying the breeding nursery. A 'rhombus grid' design which allowed for correction of environmental differences in the breeding nursery was more effective in this respect than the conventional mass (individual plant) selection or the method of Gardner (1961).

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The genetic architecture of the base population appeared to have definite effects on the simultaneous improvement of GY and GPC. Base populations derived by backcrossing to the utility cultivars produced a higher frequency of desirable genotypes than the corresponding F2's, intermated F2's, and populations synthesized by backcrossing to HRSW cultivars. Backcrossing to the utility cultivar increased the mean GY, but depressed the mean GPC of the population. However, the residual variability left in the population appeared to be sufficient to select for genotypes that combined both characteristics. The backcross method was more successful than other methods because it capitalized on both introgression and upgrading simultaneously, thus preserving the integrity of an already established cultivar while adding factors from another variety.

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1. INTRODUCTION

Wheat is the principal commodity of Canadian Agriculture. Statistical abstracts show large annual fluctuations in acreage, production and prices, but roughly 10 million hectares are allotted each year to produce about 14 million metric tonnes of grain at a total value of 2.6 billion dollars. The importance of wheat to the Canadian economy can be emphasized by the fact that it directly contributes to about 5% of the country's export earning. Most of the wheat produced in Canada is grown in the Prairie provinces and channeled into the international market where it commands the highest prices among the bread wheats of the world. Most of the wheat exported from Canada is used for making yeast leavened bread in the importing countries.

The production of yeast leavened bread usually requires flour with protein content of at least 11%, and to produce such flour, the grain must have a protein content of at least 12%. Climatic factors in many of the wheat importing countries are conducive for production of high yielding wheats, but the same climatic conditions make the production of wheat with high protein content impossible. As a result, bakeries in these countries usually import wheat of high protein content from Canada and the United States to blend with their local wheats. There is a growing concern that major changes in bread making technology, the increasing cost of Canadian wheat, and major plant breeding breakthroughs in increasing the protein content of local varieties in wheat importing countries would lower the demand for Canadian wheat on the world market. On the Canadian scene, the rising cost of production is forcing the wheat farmer to continously search for ways of making his operation more efficient. Application of a series of technological innovations such as generous application of fertilizers and pest controlling chemicals, higher plant densities, and improved farm husbandry techniques have made farm operations more efficient in the past. Anticipated shortages and (or) increases in the price of fuel, fertilizers and chemicals accentuate the need for other means of increasing farm efficiency which are not energy intensive. Already, the amount of energy now used to produce food in the more modern agricultural systems such as Canada and the United States, greatly exceed the amount of energy the crops themselves yield (Brown, 1974). The breeding of high yielding wheat cultivars which retain the traditional Canadian standards of quality would help to keep the commodity competitive on the World market, and would also help to increase farm efficiency.

Breeding efforts to produce such high yielding and high protein cultivars of wheat have been in progress for several decades and usually have utilized crosses between two different market classes of wheat such as Canadian Hard Red Spring Wheat and Utility Wheat. The Hard Red Spring Wheat cultivars are characterized by a relatively high percentage of protein that form a tenacious elastic gluten with good gas retention properties. The doughs of these cultivars also have excellent handling qualities, are not critical in their fermentation and mixing requirements, and most importantly, are capable of being baked into well risen loaves with good crumb and texture. Their major disadvantage is their low average yield which is considerably below

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that of Utility cultivars grown in the same area. The Utility cultivars, on the other hand, have good milling characteristics, adequate disease resistance, but are inferior in baking quality. Their major attribute is a distinct and significant yield advantage. In the past, attempts to combine in one genotype the good attributes from two such classes of wheat have met only limited success. Data from the Western Bread Wheat Co-operative test indicate only a small yield improvement has been made by recent releases over the variety 'Thatcher' when disease is not a limiting factor. Thatcher was released in 1934. The exact cause of this lack of progess is not clearly known, but possible reasons could be one or more of the following:

- Genetic causes of negative relationships between yield and protein content which would impede simultaneous improvement of these two characteristics;
- The increased difficulty of selecting individuals with the right combination of genes affecting both yield and protein content;
- the ineffeciencies of breeding methods currently used by plant breeders.

Plant breeders who are faced with problems of these nature have several alternatives such as: refining techniques to make selection more accurate; change the structure of the base populations so that desirable genotypes are more frequently found, or use a different method of selection.

This project attempts to modify and incorporate several procedures commonly used in breeding self-pollinated crops. Its general objective

is to identify some possible reasons why it has not been possible to combine in one genotype both high yield and high protein content. Specific objectives which it attempts to address are:

- To investigate the effectiveness of selection for grain yield and grain protein content on the basis of single plant performances in the earliest possible segregating generation;
- 2) To evaluate base populations of known differences in gene frequencies for their breeding values with special emphasis on the simultaneous improvement of grain yield and protein content in wheat; and
- 3) To study more closely the nature and basis of the negative correlation between grain yield and grain protein content often reported in wheat and other cereals.

2. LITERATURE REVIEW

Wheat (<u>Triticum aestivum</u> L.) is one of the most exhaustively studied cereal crops, and therefore the literature on it is quite extensive. It would be impossible to review all of the literature on this very important crop. This review is, therefore, restricted to those areas of research which are strictly pertinent to the present study. To simplify the presentation, and also to facilitate the continuity of ideas and views, the literature review is sub-divided into four sub-headings as follows:

- (1) Genetics and improvement of grain yield in wheat;
- (2) Genetics and improvement of grain protein content in wheat;
- (3) Early generation selection in wheat; and
- (4) Use of intermating to break undesirable linkage blocks.

2.1 Genetics and Improvement of Grain Yield and Yield Components

Grain yield in wheat is the end product of the interaction of a large number of physiological and biochemical processes in the plant, and therefore, should be genetically complex. Van der Pahlen and Goldberg (1971) classified yield as a character controlled by several genes. All chromosomes, except 1A, 2B, 2D, 4D and 7A, have been reported to be associated with yield (Ausemus et al., 1967). Since each gene in the plant in one way or another affects yield, Shebeski (1967) speculated that the maximum number of genes that govern yield equates to the total number of effective genes in the plant. Lelley

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(1976) based on an extensive literature review, stated that the multigenic inheritance of yield is accepted by all those who have attempted to study this character. However, contrary to the general belief that yield is a multigenic character, the individuality of genes for yield has been questioned by some workers. For example, Grafius (1959) and Williams and Gilbert (1969) are led to believe that yield is a genetic artifact arising from the interaction of several characters, and as such, there are no yield genes physically present on chromosomes.

Palmer (1952) proposed that yield increases may be achieved in breeding programs in two ways: (1) by removing or reducing the effect of factors which limit yield, which he called "resistance breeding", and (2) by direct selection for increased yield itself which he called "production breeding". Since most of the present day cultivars are well adapted to the environments in which they are grown, greater and more spectacular improvements in yield would be expected from the second approach than from the first.

Didactically, it is convenient to divide "production breeding" into two major classes: (1) improvement of yield through morphological components of yield, and (2) improvement of yield through genetic manipulation of physiological and biochemical processes that affect yield. The second class is not directly related to the present study, but in recent years, it has become the centre of considerable research attention (See the reviews by Wallace, et al., 1972; Evans and Wardlaw, 1976). In the present study improving morphological components of yield has been considered as a means of increasing yield potential in wheat. Therefore, it is on this aspect of yield improvement that this

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review will focus.

2.1.1 Relationships among yield and morphological components of yield

Engledow and Wadham (1923) are credited as the first to divide yield of cereals into component parts. They considered characters such as the number of plants per unit area, number of ears per plant, number of grains per ear, and weight per grain as the units from which higher yield might be developed. Since then, several studies have been conducted to study the relationship of yield with yield components and also among the yield components themselves. The literature is abundant with reports of interrelationships among yield and yield components, and it is therefore, impossible to cite every worker who has presented information on the topic. However, a summary of most of the published reports points to the following: (1) that each yield component is significantly correlated with yield, (2) that significant negative correlations occur among the yield components, and (3) that yield components compensate one another. An example of deviation from these general findings is a report by Austenson and Walton (1970) who observed no negative correlations among yield components in wheat.

2.1.2 Causes of negative correlations among yield components

Since negative correlations among yield components could hinder progress from selection, the search for the genetic basis of these negative correlations has been carried out for many years and by many workers. Despite these efforts, an adequate explanation for the

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negative association among yield components has not been possible; but several hypotheses have been provided.

Grafius (1964) reasoned that since the development of component traits is separated in space and time, it is possible that they may be controlled by different genetic systems. Adams (1967) supported the proposal of Grafius (1964) that yield components are genetically independent characters, and further explained that yield component compensation occurs when two developing structures of a plant compete for a common nutrient supply. According to this theory, a strong negative correlation between components is an indication of competition between them, and occurs if one structure is favored over the other in the amount of nutrients received. In support of this view, Adams (1967) reported much reduced negative correlations between yield components for space planted than for solid planted crop and concluded that a strong negative correlation among yield components is an indication of competition between them. An observation that is not consistent with Adams (1967) view has been that by Grafius (1970) who reported that the negative relationship among yield components strength of the intensified as yield increased.

Rasmusson and Cannell (1970) studied the effects of selection for grain yield and yield components in barley and proposed that genetic linkage of the three yield components is the cause of the negative associations and yield component compensations frequently observed in cereals.

Brinkman and Frey (1977) suggested that yield components may not

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be inherited independently, and that the operation of a single pleiotropic gene may be reponsible for the negative correlations that exist among yield components. According to their hypothesis, a single gene may influence the timing of the sequence of yield component development. Thus, a genotype may have fewer spiklets per spike but heavier seeds, because its genetic message prevented the formation of a large number of spikelets per spike. This in turn leads to a situation where more substrate would be available to form heavy seeds. A theory very similar to this has also been advanced by Grafius and Thomas (1971).

2.1.3 Relative importance of the various yield components to yield

In recent years, the possibility of increasing yield through yield component selection has attracted the attention of several researchers. In most of the studies, that attention has centred on the identification of the most important yield component that affects yield, and the improvement of yield through selection for that character.

McNeal (1960) studied yield and yield components in the F_2 and F_3 generations of a wheat cross and observed that kernels per spike and spikes per plant were more highly correlated with yield than was kernel weight. He also found that no single component was correlated with yield in both generations, but kernels per plant (kernels per spike x spikes per plant) was highly associated with yield in both generations.

Johnson et al. (1966) studied four hard red winter wheat cultivars

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for yield and yield components at different locations in Colorado and Nebraska. The highest yielding cultivar produced more kernels per spike but its kernel weight and spike number were less than for the other three cultivars.

Fonseca and Patterson (1968) calculated correlation coefficients among yield components in the F_1 and F_2 generations of a seven parent diallel. Grain yield was positively correlated with number of spikes per unit area (r = 0.71), kernel weight (r = 0.41) and kernel number per spike (r = 0.18). Similarly, Austenson and Walton (1970) found spike number per plant was by far the most important component of yield; kernel number was the next important; and kernel weight was relatively unimportant. A finding consistent with this has also been reported by Hsu and Walton (1971) who, in their study of the relationships between yield and its components under field and greenhouse conditions found that the correlation between yield per plant and kernel weight was not significant. A report by Sikka and Maini (1962) considered the role of the number of productive tillers per plant to be more important than the number of kernels per ear or kernel weight; and according to Damisch (1971) 47.5%, 29.2% and 23.2% of the total variability in yield is accounted for by the number of productive tillers, the number of kernels per spike, and kernel weight, respectively.

The studies cited above represent a rather small but typical sample of the literature on wheat, and show that the sequence of relative importance of yield components with respect to total grain yield, in decreasing order of importance is: spikes per plant >

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kernels per spike > kernel weight. This sequence attests to the fact that characters developed early in the ontogeny of the plant are more important in determining yield than characters developed late in the plant's life cycle.

2.1.4 Heritability of yield and yield components

2.1.4.1 <u>Definition and uses of heritability</u>. The total (phenotypic) variability observed in a segregating base population results from (1) genetic differences, (2) environmental differences, and (3) genetic-environmental effects on individuals (Allard, 1960, Falconer, 1960). Since only the genetic differences are hereditary, the term "heritability" was coined to provide a quantitative measure of the relative importance of genes and environment to total variability. Falconer (1960) defined heritability as that fraction of the observed phenotypic variance which is caused by differences between the genes or the genotypes of individuals.

Heritability has two primary functions in a practical plant breeding program. As suggested by Hanson (1963), it can be used as a method of determining whether progress from selection for a character is relatively easy or difficult to make in a breeding program. Furthermore, it can be used as a very valuable tool for predicting the magnitude of the genetic gain that follows selection for a character (Falconer, 1960).

2.1.4.2 Estimates of heritability of yield and yield components in wheat. Published reports on estimates of heritability of yield and

yield components in wheat are abundant in the literature. Papers listed in Table 1 represent a small but representative sample of the literature on estimates of heritability of yield and yield components in wheat.

Estimates of heritability of yield, according to reports listed in Table 1, range from a low of 7.0% to a high of 101.0%. However, the mean heritability for yield is low (30.6%) which suggests that manipulation of this trait via selection in early generations should be difficult to accomplish. The three yield components have higher heritabilities than yield, but the heritability of spikes per plant is generally low with an average heritability of 33.8%, that of kernels per spike is intermediate (39.0%), and that of kernel weight is high (53.6%). It is interesting to note that the rank order of the heritability estimates of the three yield components as reported in the literature is the reverse order of the rank of the relative importance of each component to yield.

Further examination of the data presented in Table 1 will reveal that the estimates of heritability were dependent on (1) the method used to calculate them (2) the parental combination used, and (3) the generation in which the estimates were determined.

Three general methods of estimating heritability namely: (1) the component of variance method (2) the offspring-parent regression, and (3) the diallel analysis have been used by most plant breeders. The literature indicates that each of these methods has its own merits and demerits.

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		CI	HARACTER		
Authors, method of calcula- tion and generation studied	Yield	Spikes/ Plant	* Kernels/ Spike	Kernel weight	Protein Content
Davis et al. (1961), Comp. Var. (F4 and F5)	14-53				54-69
Stuber et al. (1962), Comp.Var(F2 & B.C.)N.S. Comp.Var(F2,P1,P2)B.S. Comp.Var(F2,P1,&P2)B.S.	53 35 43	63 39 41			82 83 68
Haunold et al. (1962b), Reg.Conv.(F3 on F2) Reg.Stand.Unit (F3 on F2)					25-36 41-82
Lebsock et al. (1964), Reg.Conv.(F6 on F3) Reg.Conv.(F5 on F3)	70 37				
Sunderman et al. (1965), Comp.Var. (F3) Reg.Conv.F3 on F2 Reg.Stand. F3 on F2	7 7				26 15 24
Johnson et al. (1966), Comp.Var. (F2) B.S. Comp.Var. (F2 and B.S.) N.S.	10 2	3 3		55 61	
Fonseca and Patterson (1968), Diallel(F ₁ & F ₂ on M.P.)N.S.	17-49	34-80	47-89	15-55	
Frohberg et al. (1968), Comp.Var.(F3 & F4)	Low			48-65	Low
Anwer and Chowdhry (1969), Comp.Var.(F2 &B.C.)N.S. Comp.Var.(F2,P1,P2,F1)B.S. Baker et al (1968).	12-41 61-70				
Comp.Var. $(F_7 \& F_8)$ N.S. Reddi et al. (1969)	28-74			77-93	47-82
Reg.Conv.(F4 on F3) Reg.Stand.Unit (F4 on F3)		0-20 0-17		15-48 22-48	
Khadar (1971)				70	
Sun et al. (1972)				51-85	
Ketata et al. (1976) Comp.Var.(F2 & B.C.)N.S.	16	36	15	51- 85 65	
Sidwell et. al. (1976) Comp.Var(F2,P1,P2,F1)B.S. Comp.Var(F2 & B.C.)N.S.	36 19	44 25	27 17	50 43	
Over all mean	30.6	33.8	39.0	53.6	49.1

Table 1. Summary of heritability estimates (in %) of yield, yield components and protein content in wheat as reported by various authors.

* Spikes/plant also includes spike/unit area. Comp.Var = Component of Variance; N.S. = narrow sense; B.S. = broad sense; Reg. Conv. = conventional regression analysis; Reg. Stand. Unit = Standardized regression analysis.

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The variance component method has been extensively used by Mather and Jinks (1963) and generally utilizes data collected on an individual plant basis. Hanson (1963) has questioned the value of describing genetic variability based on individually spaced plants, because estienvironmental variability are not entirely reliable. mates of Recently, Baker (1978) evaluated the diallel analysis and its several He doubted the usefulness of the diallel method in modifications. estimating genetic parameters because of difficulties caused by correlation of genes in the parents. He suggested that the method should not be used unless the parents of the diallel cross have been produced by a laborious and time consuming process of random mating followed by non-selective inbreeding. Lush (1940) emphasized that the most realistic method of calculating heritabilities would be the offspring-parent regression technique. It more closely represents what plant breeders practice when selecting within segregating populations. An apparent problem with this method is that the parents are grown in one year and the offspring in the following year, and differences in environmental variances in the two years may sometimes be large resulting in unrealistic estimates. An objective evaluation of the different methods of estimating heritability has not been generally available, and therefore some confusion exists as to which gives the most realistic and reliable estimate of heritability.

2.1.5 Utilization of yield components for indirect selection for yield The observations: (1) that yield components have higher

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heritabilities than yield, and (2) that yield components have strong positive correlation with yield, stimulated interest among plant breeders to investigate the usefulness of yield components as indirect selection criteria for grain yield.

Grafius (1956) introduced a geometric concept of yield components in oats and suggested that it would be easier to increase total yield by selecting for yield components which are presumably more readily inherited than yield per se. He indicated that maximum yield is obtained at intermediate levels of the three yield components. In a subsequent paper, Grafius (1964) suggested that when the components are correlated and their heritabilities are not zero, one should select for (a) one component if the relationships are positive, (b) all components if the relationships are negative, and (c) total yield per se if the expected genetic gain for all components is high. Contrary to the proposal advanced by Grafius (1956, 1964), Hayman (1960) and Moll et al. (1962) profess the view that yield is inherited as an overall character, and therefore, component analysis is ineffective and at times confusing.

Examples where components of yield have been helpful in breeding for yield are sporadic, but do appear in the literature. Lebsock and Amaya (1969) and Knott and Talukdar (1971) suggested that indirect selection for yield through seed weight could increase yield in wheat. McNeal et al. (1978) observed that selection for yield components in the F_2 and F_3 generations was effective, with minimal improvements thereafter. They also observed that kernel weight and number of

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kernels per spike were effective characters for indirect selection for yield.

Yield component selection has also been applied to bulk populations via mechanical means with positive results. For example, Derera and Bhatt (1972) mass selected for kernel size in three heterogeneous wheat populations and improved yield by an average of 33.0% per cycle over a two year period. Frey (1967) conducted mechanical mass selection for seed width in oats populations, and after five cycles, the resulting F7 populations had heavier seed weight and about 9.0% greater yield.

Nickell and Grafius (1969) partitioned yield into simpler components for insight into genotype x environment interactions. They concluded that although the components of yield are assumed to be oenetically independent, under stress conditions, they may interact with each other and with the environment. Therefore, selection for yield while ignoring the components may end up with negative results. Also the converse appeared to be true; that is, selection for components while ignoring the complex trait (yield) may be disastrous. They emphasized that yield component compensation illustrates that selection for yield in one environment does not necessarily mean that the same performance will be obtained under another environment. The authors further suggested that the plant breeder should consider the joint manipulation of genotype and environment to get maximum gain from a given gene pool.

2.2 Genetics and Improvement of Protein Content

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2.2.1 Functional importance of protein content in wheat

Protein content of the grain is a major quality factor in wheat. Although grain protein content has been used as a measure of baking quality since the turn of the century, it was only in 1935 that crude protein content was accepted as a measure and definition of "flour strength" (Blish and Sandstedt, 1935). By and since then, the relationships between grain protein content and bread-making qualities have become firmly established. Grain protein content has been shown to be positively correlated with loaf volume (Finney and Barmore, 1948), and with bread grain and texture (Sunderman et al., 1965). In addition, wheat proteins are known to largely govern the flour water absorption (Finney, 1945); and also oxidation requirement and mixing and fermentation tolerance (Pyler, 1967). In grain with protein content of the same quality, an increase in protein content was shown to result in flour with better baking characteristics (Bushuk et al., 1969).

2.2.2 Factors that affect protein content

Environmental factors are known to largely affect grain protein content in wheat. Abundant rainfall during the period of kernel development usually results in low protein content, whereas dry conditions during that period favors high protein content (Zeleny, 1964). Finney et al. (1957) and McNeal et al. (1972) observed increased protein levels when nitrogen fertilizer was applied in amounts over and above the requirements for maximum yield expression. Schlehuber and Tucker (1959) have suggested that the major factors responsible for grain protein content, in order of importance are environment, soil and cultivar. More recently Miezan et al. (1977) studied effects of environmental and genetic factors on grain protein content in 12 environments, and concluded that the genetic effects influenced grain protein content as effectively as the environment.

2.2.3 Genetics of protein content in wheat

The first published report on the genetics of protein content in wheat is that of Clark (1926). In that paper, Clark showed that protein was inherited as a complex trait, and that it was often negatively associated with yield. Clark also concluded that phenotypic variability of protein in the F_2 of a cross of two wheat varieties he studied was no greater than that found in the parental population, although the parental varieties differed in protein content. This led him to believe that environment greatly influenced protein content.

Because of strong environmental influence, and the ploidy nature of the plant, protein content in wheat has not been amenable to simple gene analysis. However, various workers have postulated the genetic control of protein by gene numbers from one (Worzella, 1942) to eight (Haunold et al., 19625). These differences in estimated number of genes are apparently due to differences in environments, in sizes of populations, in parental combinations, and in techniques used. An extensive literature review by Ausemus et al. (1967) indicates the acceptance of the multigenic hypothesis by most workers who have studied the genetics of protein content in wheat. According to Lelley (1976) genes on 19 chromosomes (except 2A and 4D) are known to control protein content in wheat.

The mode of action of genes that control protein content is not very clear. Chapman and McNeal (1970) observed that epistasis for protein content was absent in five crosses they investigated. However, additive genetic effect was significant in all cases and dominance was effective in two of the five crosses studied. Diehl et al. (1978) observed that gene action for protein content was predominantly of the additive type while Clark et al. (1928) observed a preponderance of dominant genes for low protein content. Lebsock et al. (1964) reported that low protein content was partially dominant over high protein content.

Despite sizeable environmental effects, published reports summarized in Table 1 indicate heritability percentages for grain protein content in wheat ranged from 15 - 82% for F_2 plants and F_2 derived families. Presumably, these heritability estimates indicate significant potential for improving grain protein percentages in wheat through breeding.

2.2.4 Improvement of protein content through plant breeding

Early plant breeding efforts to improve protein content in wheat were discouraging. Johnson et al. (1963) attributed these difficulties to two problems: (1) known genetic differences in grain protein content among varieties of common wheat were small, and (2) environmental effects were comparatively large.

In 1950, Middleton et al. (1954) discovered a distinctly superior genetic source of high protein content in two Mexican wheats, 'Frondoso' and 'Frontiera', and opened new vistas for grain protein Several years later, Johnson et al. (1973) improvement in wheat. screened close to 13,000 genetic lines of wheat in the USDA World Wheat Collection, and reported that grain protein content among these lines varied from 6.0% to 22.0% with a mean of 13.0%. Johnson et al. (1973) also reported that the correlation for yield versus protein in the World Wheat Collection ranged from -0.43 to 0.0. However, the correlation for yield versus protein for varieties not known to be genetically different were from -0.61 to +0.65. Furthermore, they observed that very little variation in protein content was accounted for by differences in grain yield even when there was a large negative correlation. Their report renewed the hope and interest among plant breeders for improving protein content by genetic means.

The major problem of improving yield and protein content simultaneously is attributed to the negative correlation between these two characteristics as reported by Baker et al., 1968; McNeal et al., 1972; Meizan et al., 1977; and many others.

Stuber et al. (1962) studied F_1 , F_2 , BC_1 , and BC_2 generations of Winter Wheat crosses and reported phenotypic correlation between protein content and yield to be significant, but too low to

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hinder simultaneous selection for both characters. They also reported that phenotypic and genotypic correlations agree in sign, but genotypic correlations were greater in magnitude.

In contrast to those workers who have noted that grain yield of wheat is negatively correlated with the grain protein content, Dyck and Baker (1975) observed that there was no significant phenotypic, genetic or environmental correlations between yield and protein content in two wheat crosses they studied. Shebeski (1966), Schlehuber et al. (1967) and Clark et al. (1928) have reported significant positive relationships between yield and protein content in wheat.

Despite the negative correlation between yield and protein content, some plant breeders have obtained protein and yield increases in wheat simultaneously. For example, Middleton et al. (1954) reported that cultivars 'Atlas 50' and 'Atlas 66' were equally as productive as traditional cultivars in extensive yield tests over a three year period at many sites. These two cultivars exhibited from 0.9 to 3.2 percentage points more protein in the grain. Johnson et al. (1973) using 'Atlas 66' as a source of genes for high protein have isolated several 'second cycle' hard red winter wheat types which combined high grain yield with a 2.5% increase in protein content. Substantial increases as a result of selective breeding for grain protein content have also been reported by Davis et al. (1961).

Since 'Atlas 66' has consistently produced progenies with high protein content, it has attracted the attention of several physiological studies. Haunold et al. (1962a) compared space planted 'Atlas

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66' with 'Wichita' (a low protein cultivar) under nitrogen fertilized and unfertilized conditions in a greenhouse study. They concluded that under conditions of adequate nitrogen supply, Atlas 66 exhibited a protein threshold 3% higher than Wichita. The term 'protein threshold' was coined to represent the zone of protein-yield interaction at which the inverse relationship between protein content and yield of the grain becomes effective. Brunori et al. (1977) were interested as to whether the rate or the duration of protein synthesis was more important in the high protein content of Atlas 66. They concluded that the increased protein content of this cultivar was due to an extended period of protein synthesis in the grain rather than higher protein accumulation rates.

Johnson et al. (1968) attributed the high protein content of Atlas 66 to the greater ability of the cultivar to translocate amino acids from the leaves to the developing grain.

2.2.5 Causes of negative correlation between yield and protein content

The tendency for high yielding lines to express low protein content has attracted the attention of several researchers. In general that attention has centred on: (1) nitrogen uptake from the soil, (2) the nitrate reductase system, (3) remobilization of amino acids and protein from the leaves to the developing grain and (4) source sink relationships of the plant.

Hutcheon and Paul (1966) using greenhouse facilities demonstrated that the protein content of wheat can be effectively controlled by adjusting the nitrogen supply and soil moisture stress. They showed that in the lower protein range (11-16%) concomitant increments of yield and protein content can be obtained, while above the 16% protein level, increase in protein content could only be obtained by keeping a growth factor such as moisture below the optimum level for maximum yield expression. Haunold et al. (1962a) indicated that the negative relationship was stronger for wheats grown in areas of soil nitrogen deficiency.

Frey (1951) proposed a 'Universal nitrogen constant' or a ceiling on nitrogen absorption at 318 kg/ha as the cause of the negative relationships between yield and protein content in cereals. White and Black (1954) using pot cultured plants showed that cereals can absorb much more nitrogen than the equivalent of 318 kg/ha and concluded that the negative relationships between yield and grain protein could be attributed to the amount of available nitrogen in the soil at different stages of crop development in relation to soil moisture, mineral nutrients in the soil, and environmental factors that determine yield.

Williams (1966), and Eilrich and Hageman (1973) suggested that limitation of NO₃ supply during grain development may be responsible for the negative correlation between grain protein concentration and grain yield often reported in the literature. Croy and Hageman (1970) proposed that low nitrate reductase activity in wheat late in the growing season limits protein production by the plant. By sequentially sampling shoots of wheat plants, Simmons and Moss (1978) demonstrated that about 90% of the total nitrogen is accummulated before anthesis and suggested that minimal accumulation of reduced N after anthesis is not primarily the result of limiting levels of nitrate reductase. Their data suggested that during much of the sampling period, substantial levels of nitrate reductase were present in the tissues but insufficient nitrate was being supplied to the enzyme.

It has also been suggested that protein content of wheat depends not only on the relative amounts of carbohydrates and nitrogenous compounds made available to the developing grain, but also on the source sink relationships of the plant. For example, Rooney et al. (1969) reported that grain from male sterile wheat was lower in test weight and produced flour higher in protein content than grain from fertile wheat of the same cultivar. They suggested that the higher protein content was associated with the lower seed set (40%) and test weight of the male sterile line. McNeal and Davis (1954) found that the earliest formed and matured kernels contained the highest protein content; and in a more recent study McNeal and Davis (1966) noted that kernels from the top third of the spike were significantly lower in protein content than those from the middle and bottom parts. These studies suggested that the supply of nitrogeneous products needed for protein production may become limiting before the additional kernels produced by the high yielding cultivars mature; thereby causing inverse relationships between yield and protein content.

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2.3 Early Generation Selection

Early elimination of experimental lines which do not possess the desirable yield potential and quality characteristics of an acceptable wheat cultivar is a matter of concern to wheat breeders.

According to Allard (1960) many simply inherited characteristics such as disease and insect resistance, lodging and plant height are rapidly fixed and can be selected for in early generations. Selection for characteristics which are quantitatively inherited such as yield and protein content are normally deferred until the segregating lines have approached homozygousity. Recent theoretical considerations of complexly inherited characteristics by Shebeski (1967) and Sneep (1977) have suggested that selection for such characters should be started in the earliest possible generation, preferably in the F_2 if maximum selection efficiency is required. Their argument is that individual plants possessing all of the desired genes in the homozygous or heterozygous condition occur most frequently in the F_2 , with the frequency declining in later generations.

Selection for quantitative characters can be justified to some extent in either early or late generations, but disadvantages appear to exist for both systems. Early generation selection for characters controlled by a large number of genes permits comparison between plants or lines at a stage when the total genetic variability from the cross is at a maximum, and the frequency of the most desirable genotypes is at its greatest as proposed by Shebeski (1967) and Sneep (1977).

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Identification of superior genotypes in the initial stages of the breeding program would also allow a more efficient and judicious allocation of plant breeding facilities. The disadvantage of early generation selection is that it would be very easy to mis-classify genotypes due to the masking effects of environment on genotypes. When such a method is used, valuable combinations may be classified as 'poor types' and might irretrievably be lost (Seitzer and Evans, 1978).

The ability of the plant breeder to select for quantitatively inherited characters is also impaired by several environmentally produced variabilities. Leffel and Hanson (1961) cited heterosis, due to dominance or epistasis, which cannot be fixed in heterozygous lines as one cause which may reduce efficiency in early generation selection. Grafius et al. (1952) proposed that heterozygosity may impair selection, and demonstrated that selection efficiency would increase as homozygosity was approached and dominance and epistatic effects are minimized. Brim and Cockerham (1961) showed that the progress expected from selecting among progenies of soybean lines increased as inbreeding increased and the progenies approached homozygousity. Lupton and Whitehouse (1957) concluded that selection for characters such as yield and grain quality in self-pollinated crops should be delayed until a fair degree of homozyzousity has been reached.

According to Khalifa and Qualset (1975) the manner in which the F₂ nurseries are grown also affects the efficiency of selection in that generation. Usually reasons such as maximum single plant seed production, selection for highly heritable and easily identified

characters, and convenience of observation of single plant performances, justify the need for space planted F_2 nurseries. This arrangement, however, does not correspond to commercial practices wherein the cultivars are grown in solid stand, and as result, selection for quantitatively inherited characteristics in widely spaced F_2 nurseries may not favor the desirable genotypes. As a means of avoiding this problem Nass (1978) proposed that individual plant selections should be practiced at high population densities if the selected lines are to be evaluted at high population densities comparable to commercial planting.

On the other hand, selection in later generations between relatively homozygous lines allows comparison of genotypes in which the additive genetic variance has been fixed and provisions for replicating in space and (or) time of the test material could be provided. Its major disadvantage as cited by Shebeski (1967) is that the delay in testing reduces the probability of the presence of the best genotypes, for a population of a given size. Plant breeders who delay selection until later generations are also forced to produce and test a large number of lines at an advanced stage only to find a great percentage of them deficient for important characteristics.

One of the most important problems hindering effectiveness of selection in early generation is the inability to select single plants for wide range adaptability in one generation. As a means of solving this problem, Shebeski and Evans (1973) proposed a hill test technique which requires only a small amount of seed, thus allowing more thorough testing and selection for wide range adapatability. O'Brien et al. (1977) compared the hill plot technique with row plots for F_3 yield testing. The results of their experiment indicated that selection based on a single hill plot basis was 50-75% as efficient as selection based on a single three row plot. They concluded that two to four replicates of hill plots would be required to give the equivalent information of one three row plot. Earlier reports by Torrie (1962) showed that to obtain comparable experimental precision for yield, the required number of replications for rows and hills would be 4 and 9 respectively.

Soil heterogeneity is also acknowledged to be a major environmental factor which minimizes efficiency of early generation selection. Fisher (1931) stated that soil fertility cannot be regarded as being distributed at random, but that plots located in close proximity generally are more alike than those further apart. The findings of Briggs and Shebeski (1967) who used many bread-making quality characteristics in their soil uniformity analysis were consistent with the view that the similarity of soils decreased as the distance between them increased.

2.3.3 Methods of increasing efficiency of early generation selection

Several studies have been devoted to the study of increasing efficiency in early generation selection out of which three general methods have evolved.

One of these methods requires that selection nurseries be

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conducted under optimum conditions of moisture and fertility so that the plants are able to express their full genetic potential, and thus plant breeders could easily discriminate among different genotypes. For example, Gotoh and Osanai (1959) grew winter wheat crosses under different fertilizer levels to measure the efficiency of selection for yield. They found higher selection efficiency for yield under high fertility levels than under low fertility levels. Frey (1964) found that the mean heritability was 45% in the non-stress and 32% under stress condition for grain yield in F4 generations of oats. He also showed that selection for yield capacity was more effective when practised under non-stress conditions than when under stress environments. Johnson and Frey (1967) reported higher selection efficency in oat populations grown in non-stress environments than populations grown in stress environments.

Contrary to the above findings McVetty and Evans (1980) using a multiple regression approach observed that effectiveness of selection for high yieldings F_2 genotypes was not enhanced by growing the plants in near optimum stress-free environments. Their contrasting result from those previously reviewed could be due to differences in methods of measuring efficiency of selection. McVetty and Evans (1980) used the number of high yielding lines retained out of a total of 53 high yielding lines (lines that showed yield greater than the highest yielding parent) when an arbitrary selection intensity of 15% was applied as an indicator of selection efficiency. Other workers cited above, on the other hand, have used only single traits, and utilized

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heritability as an indicator of selection efficiency.

Stratification of environments has been used as a second means of reducing environmental variability. One such method is that proposed by Gardner (1961). In this method, the nursery is divided into several grids or sub-plots to minimize error variance. The sub-plots are used as selection units, and individual plant selection is practiced within them. Using this technique, Gardner (1961) has achieved an average yield improvement of 3.5% per year over a four year period. Lonnquist et al. (1966) have reported continued progress from mass selection using the same technique. Johnson (1963), using this technique in a tropical corn variety, reported yield increases of 33 percent in three cycles of selection.

Fasoulas (1973) suggested another method of stratifying environments which he called the "honey comb method of selection". In this method, plants are grown in an arrangement that resembles a honey comb. Consequently, each plant is surrounded by six other plants all spaced equidistant, and share a common environment. A given genotype is selected for advancement in a breeding program provided it yields better than its six immediate neighbors. From the data provided, the method appeared to have been used successfully although reports of its use by other workers have not appeared in the literature.

Check varieties are also employed as means of measuring differences in environments within a breeding nursery and as a standard when making selection. Shebeski (1967) studied the possibility of reducing the effects of environmental heterogeneity by expressing the yield of

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each line as a percent of an adjacent control plot. According to him, this method has effectively eliminated influences of soil heterogeneity on selection resulting in a highly significant correlation (r = 0.84; p < 0.001) between the yield of F₂ derived F₃ lines and their respective F₅ means. Knott (1972) attempted to reduce environmental variability in the F3 generation by expressing yield in three different ways: (1) percent of adjacent checks, (2) percent of replicate means, and (3) percent of moving average. Plot yield expressed either as percent of adjacent checks or as percentage of a moving average resulted in significant reductions in error mean squares, but since the use of adjacent checks increased the size of the trial, he preferred the moving average procedure as the more efficient one. Baker and McKenzie (1967) took issue with the use of control plots as proposed by Shebeski (1967) and doubted the merit of the method unless an analysis of covariance is conducted to determine the reliability of the control plot yields.

The literature on early generation selection is rather extensive, but these few examples serve to show the necessity of improving environments and experimental designs if early generation selection for complexly inherited characters is to be effective.

2.4 Use of Intermating to Break Undesirable Linkage Blocks

Since the success of plant breeding programs depends upon obtaining desirable recombinants, the extent to which linkage blocks are broken is of prime importance to plant breeders. Hanson (1959)

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suggested that if intermating in a self-pollinated species is at all possible, at least one or more intermating cycles should preceed the selfing generation to insure a fair degree of breakup of linkage groups and to increase genetic recombination within the linkage group. Presumably, this procedure would increase the genetic potential of the population and would effect a greater reduction of intact linkage blocks as compared to a non-intermated population. Miller and Rawlings (1967) supported this view after observing the occurrence of non-parental types in the F₃ progenies of a cotton cross for which one parent was of interspecific origin. They found that six cycles of 50% outcrossing produced a better source of genetic material for selection. They attributed this to a partial breakup of linkage blocks in the original material.

Meredith and Bridge (1971) estimated the effect of intermating on the genetic correlations in cotton populations and found that the association between yield and fiber strength, as well as most other correlations were reduced in absolute values. Redden and Jensen (1974) investigated the effects of intermating both in absence and presence of selection on negative correlation in wheat and barley. They concluded that the intermated population should provide a better source of material for selection than the original F_2 population. Baker (1968) conducted a computer simulation study to establish the number of F_2 plants that would be required to approximate true random mating and at the same time assure that the advantages of intermating are not offset by genetic drift. This study led to the conclusion that mating as few as 20 to 30 pairs of randomly chosen F_2 individuals would serve to realize the expected results of random mating. He further suggested that recurrent selection would have to be used to take full advantage of the increase in selection potential attributable to random mating. Stam (1977), also based on computer simulation studies, concluded that the short term effect of intermating is negligible, but in the long run, random mating should be superior to selfing especially when many loci are involved.

The merits of intermating the F_2 generation for multi-locus system has been doubted by Pederson (1974) who concluded that, if all possible arrangement of alleles are equally likely, the effect of intermating in the F_2 must be dubious. The conclusion drawn from another computer simulation study by Bos (1977) appeared to support the views of Pederson (1974) that intermating before selection in selfpollinated species may not be helpful in providing desirable recombinants.

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3. MATERIAL AND METHODS

3.1 General Description

3.1.1 Description of parental lines and base populations synthesized

Data for this study were obtained from parental lines, F_2 's, backcrosses and an intermated F_2 population generated from four common wheat cultivars exhibiting wide differences in yield and protein content. The cultivars, their pedigrees together with information on market class, country of origin, and year of release are presented below.

Cultivar	Pedigree	Country of	Date of	Mark	et
		origin	release	cla	ISS_
Glenlea	Pembina 2*/Bage//CB100	Canada	1971	Util	ity
NB 131	Tobari 66/Gaines	Canada	Experimental	11	11
Sinton	CT262/Manitou	Canada	1975	Hard sprir	red Ig
Coteau	ND496 sib//ND487/Fletcher	United States	1978	11	11

These cultivars were chosen partly because they represent 'key' varieties used in bread wheat improvement programs in which attempts are made to combine in one genotype the high grain yielding ability of utility wheat cultivars, and the high bread-making qualities of hard red spring wheat cultivars; and partly because they represent unrelated groups of agriculturally successful cultivars. All four cultivars are well adapted to the agricultural conditions of Western Canada as indicated by their acceptable yield levels in Wheat Co-operative Tests.

3.1.2 Base populations synthesized

From the above four parental cultivars, seven base populations were synthesized as shown in Table 2. The direction of the crosses used to generate the base populations are indicated in the Table, and were chosen following a preliminary evaluation of the cultivars and hybrids for pollen production and ease of emasculation.

Table 2. Parental combinations and base populations generated.

Parental combinations	Direction of Cross	Base populations synthesized
Glenlea x Sinton	(Glenlea x Sinton) F ₂	F ₂ population
	Glenlea x (Glenlea x Sinton)	Backcross to Glenlea
	(Glenlea x Sinton) x Sinton	Backcross to Sinton
	(Glenlea x Sinton) F ₂ x (Glenlea x Sinton) F ₂	Intermated F ₂ population
NB131 x Coteau	(NB 131 x Coteau) F ₂	F ₂ population
	Coteau x (NB131 x Coteau)	Backcross to Coteau
	NB 131 x (NB131 x Coteau)	Backcross to NB131

3.1.3 Method of seed production

Seed of the F1, F2, the two backcrosses and the intermated F₂ population of the Glenlea x Sinton cross were produced under greenhouse conditions during the fall and winter seasons of 1977 and 1978, respectively. F2 seeds were produced by selfing about 20 F1 plants, and each of the backcrosses were produced using more than 50 F_1 plants. a minimum of 590 seeds were produced for each of these The manner in which the intermated F_2 seeds were populations. synthesized, is as follows: Two hundred and forty F2 seeds were planted in two greenhouse benches designated as bench I and bench II to produce about 120 plants in each bench. At anthesis, one head from bench I was used to pollinate at random, one and only one head from bench II, and similarly, one head from bench II was used to pollinate one and only one head, at random, from bench I. In this manner, about 287 heads were successfully pollinated of which 192 produced three crossed seeds or more per head. Three seeds were taken from each of the 192 heads and composited to produce the intermated $F_{\rm 2}$ population. Since four different planting dates were used, and individual plants had produced more than one spike, it is assumed that very little if any assortive mating has taken place when synthesizing the intemated F2 population.

The F_1 of the NB 131 x Coteau cross was produced in Winnipeg during the winter of 1978, under greenhouse conditions. In the summer of the same year about sixty F_1 plants and an equal number of plants from the two parental cultivars, NB131 and Coteau, were grown in a space planted crossing block in Winnipeg. F_1 plants were crossed to

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the parental cultivars to produce the respective backcrosses, and were also selfed to produce the F_2 . To expedite the development and increase of the three base populations generated from this cross, about 500 seeds from each of the populations were grown at Ciudad Obregon, Mexico, in the winter of 1978. In each population, a minimum of 78 plants with acceptable disease resistance and maturity were harvested individually, and their seed returned to Winnipeg to be grown as single plant derived lines.

Using the parental cultivars and the base populations so generated, a series of experiments were conducted. Figure 1 presents, schematically, the advances in generations, location of experiments, facilities used, and the sequence of the experiments in chronological order. A more detailed description of each experiment follows.

3.2 Experiment 1. Comparative study of the parental cultivars

The purpose of this experiment was to evaluate the parental cultivars for various yield and quality characteristics. The four parental cultivars, 'Glenlea', 'Sinton', 'Coteau', and 'NB131' were grown during the summer seasons of 1978 and 1979 at three Manitoba locations; Winnipeg, Glenlea, and Carman. The geographic location of these sites, their soil type and pattern of rainfall are given in the table below.

Winnipeg, Fleid	Summer (1979)		Winnipeg, Field	Summer (1978)			Winter (1978) Winnipeg, Greenho	Fall (1977) Winnlpeg, Greenho
(Expt. 3)	Random Lines		Nursery (Expt.2.)	Space Planted	≪ ≪ N	Intermat		use Glenled
Experiment (Expt. 4)	Selection				≤	α Ν Ω	B.C. Sinton	Sinton
Random Lines (Expt.5)	*	Mexico Nursery	Block	Crossing	≪ ≪	BC-NB 131 F BC Coteau	NB 131 Coteau	
Winnipeg, Field	Summer (1979)	Winter (1979) Maxico Fiald		Winnipeg, Field	Summer (1978)			
Trial (Expt. 1)	1070 Multi-location		Trial (Expt. 1)	1978 Multi-Location				

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Fig. 1. Schematic presentation method of developing base population and experiments conducted.

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Experimental location	Geographi locatio	c* Soil n type	Year	May	Rai June	n fall July	(mm) Aug	TOTAL
Winnipeg	<u>_</u>	Red River Clay	1978 1979	123 120	51 58	81 20	75 16	330 214
Glenlea	20 km S	Red River Clay	1978 1979	86 130	31 52	137 37	39 85	293 304
Carman	65 km SW	Riverdale Sandy loam	1978 1979	122 111	47 58	119 20	42 16	330 205

* Distance in km and direction from Winnipeg.

The experiment was a randomized complete block design with 4 replications at each test environment. Plots were 5.44 meter long with 4 rows spaced 20 cm. apart. A seeding rate of 100 seeds per meter length of row was used at all locations. A 30 cm border was trimmed from the ends of each plot, and only the middle two rows were harvested resulting in an effective plot size of 2.916 square meters.

Data on grain yield, kernel weight, test weight, grain protein content, protein yield per plot and protein per kernel were measured. A full scale bread-making quality test was also conducted on the material harvested in 1978 from the Glenlea and Winnipeg locations. A list of the quality and agronomic parameters and the methods by which they were determined is given in Appendix 1.

All data collected in each test enviroment were analyzed

existed for the various traits.

3.3 Experiment 2. Space planted nursery of four base populations and parental cultivars generated from the Glenlea x Sinton cross

This experiment was designed to: (1) evaluate the four populations generated from the Glenlea x Sinton cross as potential sources for extracting high yielding-high protein genotypes, (2) investigate if the negative correlation between yield and protein content often reported in wheat was caused by genetic linkages, and (3) provide genetic material to be used in subsequent experiments.

The two parental cultivars, Glenlea and Sinton, and the four base populations generated from them were grown in a space planted nursery during the summer of 1978. Before field planting, seeds were pregerminated in germination boxes under laboratory conditions and transplanted individually, by hand, after both the radicle and the plumule had emerged. The experiment was planted at the University of Manitoba Research farm in Winnipeg, on an area of fertile soil planted to faba beans (Vicia faba L.) in the previous season.

A 36 replicate randomized complete block design with sub-sampling was used. Each replicate consisted of 4 plots in which each plot was a row consisting of 15 plants from the same base population. Spacing between rows was 1 meter, and plants within plots were planted 60 cm apart. No plots (rows) were specifically assigned for the parental cultivars. Instead, both parents were included alternately and systematically within each row after every 5th plant, to serve as checks. Consequently, a group of 5 plants from each base population were surrounded by four parental plants (2 Glenlea and 2 Sinton) in a rhombus grid fashion as depicted in Figure 2. The whole nursery was surrounded by guard rows to avoid edge effects.

Data, on an individual plant basis, were recorded on plant height, number of spikes per plant, grain yield per plant, number of kernels per plant, and grain protein content. Other data derived from these primary data were 1000 kernel weight, number of kernels per spike, protein per kernel and protein per plant.

On the whole, the growing season was satisfactory, but for reasons beyond experimental control, too many plants were missing from some of the plots. As result, 7 replications were discarded from the test. For the same reason, the number of plants per plot in the remaining 29 replications was reduced from 15 to 10 in order to provide a constant number of plants per plot. Reduction of the number of plants per plot was done on the basis of 'out-liers' for yield. This procedure left a total of 290 plants for each of the four base populations and 145 plants for each of the two parental cultivars to be analyzed in the experiment.

Before any analysis of variance was conducted, an effort was made to transform the data to a scale that would fulfill all the assumptions of the analysis of variance (Bartlett, 1947). To achieve this,

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Fig. 2. A rhombus grid design arrangement of the Summer, 1978 single plant nursery grown in Winnipeg.



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Bartlett's test for homogeneity of variances was used to test for stability of error (within plot) variance from population to population; Tukey's test for additivity of variances was used to test if treatment effects were additive; skewness and kurtosis were calculated to test if a variate had a normal distribution, and simple correlation between population means and variances were used to test if variances were independent of the means on the transformed scale. The variable, plant height did not require any transformation, while all other variables required transformation. The square root transformation was adequate for the characteristics, grain yield, number of spikes per plant, and number of kernels per plant, while the log transformation was appropriate for grain protein content, protein yield per plant, kernel weight, and kernels per spike. Although not totally satisfactory, the inverse transformation was the best for protein per kernel. Except where indicated otherwise, these transformations were used consistently throughout the analysis of the experiment.

Analysis of variance was conducted for each character by using a model for a randomized complete block design with subsampling. Parental and base populations were also analyzed separately using a model for a completely randomized design. This analysis enabled the removal of significant replicate variation by dividing the total variance and(or) covariance into that due to differences among plots and that due to average variation or covariation within plots. Interrelationships among pairs of characters were studied by computing

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phenotypic correlation coefficients using the within plot variances and covariances. A path coefficient analysis was applied to estimate the direct and indirect effects of the various characteristics on grain yield and grain protein content. Multiple regression, and stepwise multiple regression analyses were conducted to determine how much of the total variation in yield and (or) protein content was accounted for by various characteristics. Base populations were evaluated for their breeding potential on the basis of their means, variances, and phenotypic correlation coefficients.

For advance into the next generation, the experiment was divided into two parts. Part I consisted of replications I to 15, and part 2 consisted of replications 16 to 29. In part 1, 7 plants were chosen at random from each plot, to form 105 random lines per population to be used in Experiment 3 in the following year. In Part 2, individual plants from each of the four base populations were selected for yield or protein content by using several selection criteria, and plants so selected formed the material used in Experiment 4.

3.4 Experiment 3. Evaluation of base populations generated from the Glenlea x Sinton cross and simulated selection experiments.

A random sample of 105 single plants from each of the four base populations of Experiment 2 were self-pollinated to produce the corresponding families. During the summer of 1978 these families and the two parental cultivars, Glenlea and Sinton, were evaluated at the University of Manitoba Research Farm in Winnipeg in a modified randomized

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complete block design with 3 replications. The form of the experimental layout used was a blocks within sets within replicates design which allowed valid comparisons both within and among populations. To achieve this, the 105 families from each base population were divided into 15 sets of 7 families each. The 7 families within a set within a population formed a group and traced their origin to 7 single plants of the corresponding population grown in the same plot in the previous year (Experiment 2). A block was assigned to each population and consisted of the 7 entries from the same group plus an entry of one of the two parental cultivars to make a total of 8 entries per block. A set consisted of 4 blocks, each block assigned to one population at random and had a total of 32 entries (7 entries from each of the 4 base populations plus 2 entries from each parental cultivar). Fifteen such sets made up a replication. The entries per block and the blocks per set remained together in all replications, but were randomized to assign populations to blocks first and then entries within blocks. The entries were planted in single row 3 meter long plots with rows spaced 60 cm apart. Two hundred fifty seeds were planted in each plot (row). Each test entry was surrounded by single rows of each of the two parental cultivars on both sides to provide uniform competitional stress among entries. The material was harvested by hand after all entries had reached physiological maturity. As much as possible, care was taken to harvest all entries in the same set of the same replication on the same day.

Data on grain yield per plot, 1000 kernel weight, grain protein

content, protein yield per plot, and protein per kernel were either collected or computed. Grain harvested from some plots (approximately 6%) were found to contain soil, and weights were adjusted after the extent of the contamination was determined. Grain yield data from 13 plots, and grain protein content and kernel weight data from 8 plots were missing. Analysis of covariance (Steele and Torrie, 1960) was conducted to estimate the value of missing observations.

Before conducting an analysis of variance, Bartlett's test for homogeneity of variance was computed to test the stability of error variance. Errors were heterogeneous for all characteristics investigated and in all cases the log transformation removed the error heterogeneity.

Analysis of variance and covariance were conducted for each base population separately. Variance components were estimated by equating the observed mean squares to their expectation. The pertinent portion of the analysis of variance and covariance from which genetic variances and covariances were computed is presented in Table 16. Standard errors of genetic components of variance were calculated by using the method of Anderson and Bancroft (1952). A combined analysis of variance consisting of the four base populations was also conducted to determine whether population means were significantly different.

Interrelationship among pairs of plant characteristics were studied by computing phenotypic and genotypic correlation coefficients. Phenotypic correlations were computed after removing replications and

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set effects. Genotypic correlation coefficients were estimated from the genotypic components of variances and covariances as follows:



Where σ_{gij} = genotypic component of covariance and

 $\sigma_{gii}, \sigma_{gjj}$ are the genotypic components of variances of the two characters. Variances of genetic correlation coefficients were estimated as outlined by Mode and Robinson (1959). Genetic correlations were declared significant if their absolute values exceeded twice their standard error.

In each population heritabilities were calculated using two methods: (1) component of variance method and (2) the offspring-parent regression method. The formula used for estimating heritability using the variance component method was as follows:

$$H^{2} = \frac{\sigma_{g}^{2}}{\sigma_{p}^{2}}$$

where σg^2 and σp^2 are genotypic and phentoypic components of variance respectively. Estimates of the standard error of heritability were calculated using the method of Dickerson (1960).

In the offspring-parent regression method of estimating heritability, the performances of the offspring were regressed as dependent variables on the performances of the parents which were considered as

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independent variables. The regression values were used as estimates of heritabilities and the standard errors of the regression coefficients were considered as estimates of the standard errors of the heritabilities.

In each population, intergeneration correlations were computed to investigate if single plant characteristics observed in 1978 were correlated with 1979 grain yield and grain protein content, and also to investigate if characteristics observed in early generations persisted in later generations.

Selection was simulated using two methods of selection: (a) individual trait selection and (b) index selection. In each base population, the effects of selection were examined by comparing the mean grain yield and grain protein content of the selected lines with the mean grain yield and grain protein content of the unselected population. Correlated response to selection in grain protein content when selection was exercised for yield and vice versa were also investigated. Furthermore, an attempt was made to determine the optimum selection intensity that would retain the best progenies of a population without significant loss in either population mean or population variance.

Base populations were evaluated on the basis of their means, variances, genotypic and phenotypic correlations, heritabilities, response to selection, ability to provide desirable progenies and protein-yield regressions. Balanced composite samples of elite lines selected on the basis of individual plant performances in each of the four base populations generated from the Glenlea x Sinton cross and grown in a space planted nursery during the summer of 1978 formed the genetic material for this experiment. (The selected lines used in this experiment were grown in replications 16 to 29 inclusive of Experiment 2.).

Experiment 4 had 2 sections designated A and B. In Section A, a 10% selection intensity for yield on an individual plant basis was exercised using one of the following methods.

(i) mass selection for yield, (ii) stratified selection for yield using Gardner's (1961) method (in this method, a plot of 10 plants was used as a selection unit, and the best plant from each of the 14 plots of each of the 4 base populations was selected on the basis of its yield performance), (iii) Rhombus grid selection (in this method, the yield of each plant of the 4 base populations was expressed initially as percentage of the mean of 4 plants of the parental cultivars surrounding it. Then, mass selection was exercised within each of the 4 base populations using the adjusted yield values so obtained, and (iv) a random selection of 14 plants from each population to be used as controls.

Equal numbers of seeds (250 seeds) from each of the 14 plants selected using each of the above four methods within each of the 4 base

populations generated from the Glenlea x Sinton cross were bulked to provide a balanced composite sample. These bulked samples of the selected lines were yield tested in the summer of 1979 in Winnipeg. The field design was a factorial in a randomized complete block design with 4 replications. The parental cultivars, Glenlea and Sinton, were included in the test for the purpose of comparison, but were excluded from the statistical analysis. The experiment had a total of 18 entries. Plots consisted of 3 rows, 3 meters long, with rows spaced 15 cm apart and plots 60 cm apart. Plots were planted at a rate of 83 seeds per meter of row length. The experiment was combine harvested and data on grain yield/plot and grain protein content were recorded. Base populations and selection methods were compared in two ways: (1) by using analysis of variance to evaluate if selection methods were statistically different from random selection within each population and (2) using gain from selection as a measure of effectiveness of selection. Gain from selection was expressed as:

X_{iq} - random selection j

Where X_{ig} is the mean plot yield of a balanced composite sample selected using procedure i in base population j; and random selection j is the mean plot yield of the balanced composite of 14 plants selected at random from base population j.

Section B of Experiment 4 was essentially similar to section A in all aspects except that selection was for grain protein content and the selection criteria were grain protein content and protein per kernel.

3.6 Experiment 5. Comparison of base populations using NB131 x

Coteau Cross

This experiment was conducted with the purpose of obtaining additional information that would supplement Experiments 2 and 3. The F1 of this cross was made in the winter of 1978 under greenhouse conditions. Sixty F1 plants and an equal number of plants from the parental cultivars, Coteau and NB131, were grown in a space planted crossing block during the summer of 1978. F1 plants were crossed to the two parental cultivars to produce the respective backcrosses and were also selfed to produce the F2. The direction of the crosses are given in Table 2.

In the winter of 1979, about 500 seeds from each of these crosses were grown at Ciudad Obregon, Sonora, Mexico to produce about 500 plants from each population. From each population, seed from a minimum of 78 plants with acceptable disease resistance and maturity were harvested individually, and returned to Winnipeg to be grown as single plant derived families. Except for the following minor changes, the single plant derived families were tested in a manner similar in field design and statistical analysis to that used in Experiment 3. The changes were the following: (1) there was no intermated F_2 population included in this experiment, (2) since the single plant nursery was grown in Mexico, there was no simulated selection study undertaken, (3) the same entries within blocks within sets, within replicates design was used, but the number of entries within blocks was 8, the number of blocks within sets was 3 and the number of sets within replicates was 9. In each block, an entry of one of the two parental cultivars were included. The experiment had 3 replications. Plots were 3 meters long with 3 rows per plot spaced 15 cm apart. Adjacent plots were spaced 60 cm apart. A seeding rate of 250 seeds per row was used. At maturity, plots were combine harvested and measurements of grain yield per plot, kernel weight, grain protein content, protein yield per plot and protein per kernel were either collected or computed. The same statistical analysis as in Experiment 3 was conducted whenever possible.

- 53 -4. RESULTS

4.1 Experiment 1. Characterization of parental lines for agronomic and quality factors.

The four cultivars used in the present study namely Glenlea, NB131, Sinton and Coteau were evaluated for agronomic and quality characteristics at three Manitoba locations, Winnipeg, Glenlea, and Carman, over a test period of two years (1978 and 1979). The range of soil type sampled and the temperature and rainfall conditions encountered were representative of conditions typical to the wheat growing regions of Southern Manitoba. In general, favorable growing conditions prevailed throughout the test period with no major disease or insect problems. In all locations weeds were fully controlled by chemicals in 1978 and by hand weeding in 1979.

Six quality and agronomic characteristics: grain yield, kernel weight, test weight, grain protein content (%), protein yield per hectare, and protein per kernel were measured for each location each year. In addition, a full scale milling and baking test was conducted on the material grown at Glenlea and Winnipeg in 1978.

The data from each location each year were analyzed separately by conventional analysis of variance for a randomized complete block design. Because of the large number of characteristics and environments involved, mean squares and F ratios from the conventional analyses of variance are not presented. However, it is noteworthy that for all characteristics studied, cultivar effects were highly significant (p<0.01). This was true regardless of location and (or) test year, and should not be surprising in view of the fact that the four culutivars tested belong to two distinct market classes of wheat.

Combined analyses of variance across locations and years were conducted with the assumption that locations and years are random (Cochran and Cox, 1966). The combined analyses were made after the necessary transformation of the data was made, and Bartlett's test for homogeneity of variances, as described by Snedecor and Cochran (1967), indicated homogeneity of error variances. The mean squares and degrees of freedom for the various characteristics studied are presented in Table 3. Since milling and baking quality data were available for only two test environments, the combined analysis of variance was not conducted on these characteristics. Therefore, they are not included in Table 3.

Significant differences among cultivars for all characteristics except protein yield per plot are indicated by the combined analysis of variance. The analysis also showed significant location and year effects for all characteristics except for grain protein content which did not show a statistically significant year effect. Significant cultivar x location, cultivar x year, and cultivar x location x year interactions indicated that for some of the characteristics studied the cultivars responded differently and (or) ranked differently relative to each other, due to changes in environments. Graphic analyses showed that in most cases, these interactions were mainly due to reversals in

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TABLE 3. Mean squares (x 10⁴) from analysis of variance of transformed agronomic and quality characteristics of 4 wheat cultivars grown at 3 locations and 2 years.

Source of variation	d.f.			Chara	cteristics		
		Yield	Kernel weight	Test weight	Grain proteín	Protein yield	Protein per grain
Location	22	50638**	2768**	201**	398**	46938**	2537**
Year	,1	15924**	3120**	1503**	23	17155**	2608**
Cultivar	ε	2140**	6859**	29**	1393**	250	2165**
Location x year	2	14468*	45**	82**	1573**	12729**	1934**
Cultivar x year	ς	581 **	52**	8**	35**	412**	25
Cultivar x location	9	189	23**	**7	16*	190	8
Cultivar x (location x year)	9	246	34**	9**	33**	261*	102**
POOLED ERROR	72	115	6	Т	9	112	12
* ** Sionificant at 5% and	1% Taval	a of probab	i] i tu noo	n o o t 4 o 1			

of probability, respectively. revers Ŷ۲ and °° ר ק Canc יייאיט ~ the performance of the cultivars, rather than to differences in degrees of relative performances.

Because of the copius amount of data collected, it would not be possible to present results of all characteristics in equal detail. Grain yield and grain protein content are more pertinent to the present study than are other characteristics studied. Therefore, data for grain yield and grain protein content are summarized by cultivar, location and year in Table 4. For all other characteristics, cultivar performances are averaged over locations and years and are presented in Table 5.

The data in Table 4 showed that the utility varieties, in general, produced significantly higher yields than the bread wheat cultivars. The higher yields of the utility cultivars as compared to the bread wheat cultivars should probably be due to their higher kernel weights and test weights (especially of NB131) as presented in Table 5. Analysis of partial correlation of yield versus kernel weight and test weight provided further evidence that differences in these two characteristics may have been the basis for the yield differences observed among wheat classes. The partial correlation coefficient between yield and kernel weight when test weight was held constant was + 0.394 (p<0.0006) and that of yield and test weight when kernel weight was held constant was + 0.262 (p<0.025). Other yield components such as number of kernels per spike, and number of spikes per unit area were not assessed, but they too may have contributed in a major way to the observed yield differences among the two market classes.

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TABLE 4. Grain yield and grain protein content of 4 wheat cultivars grown at 3 locations during the summers of 1978 and 1979.

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rene and a second back of the second			Loca	tion			Cultivar mean
	Carmé	II	Glen	lea	Winni	peg	and s.e.
	1978	1979	1978	1979	1978	1979	
Yield (kg/plot)							
Coteau	0.264	0.689	0.799	0.847	0.820	0.861	0.713 ± 0.045
Sinton	0.295	0.566	0.815	0.750	0.810	0.881	0.686 ± 0.044
Glenlea	0.356	0.594	0.925	0.798	1.033	1.094	0.800 ± 0.055
NB131	0.339	0.806	0,886	0.947	1.009	1.037	0.837 ± 0.052
Location mean	0.313 0.48	0.664 9	0.856 0.84	0.835 6	0.918 0.94	0.968 .3	
Protein content	(N × 5.7 c	on 0% mois	sture bas	is)			
Coteau	21.0	18.9	21.6	20.1	18.6	20.5	20.1±0.2
Sinton	20.3	19.6	20.7	19.6	17.4	20.1	19.6±0.2
Glenlea	18.9	18.1	19.6	17.7	15.5	19.3	18.2 ± 0.3
NB131	18.0	16.8	18.1	16.4	14.6	18.3	17.0±0.3
Location mean	19.5 18.9	18.4 19.2	20.0	18.4 18.0	16.5	19.5	
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Variety				Char	acteristics			
	Yield/plot	Kernel weight	Test wt	Grain protein	Protein yield	Protein/kernel	Flour protein	Flour yield
	(kg)	(gms/1000)	(Kg/hl)	(%)	(kg/plot)	(mg)	(%)	(%)
Coteau	0.713 ± 0.045	34.3 ± 0.5	77.8±0.6	20.1 ± 0.2	0.143 ± 0.009	6.89 ± 0.14	19.3 ± 0.2	73.3 ± 0.2
Sinton	0.686 ± 0.044	35.8±0.8	77.0±0.7	19.6±0.2	0.134 ± 0.008	7.01 ± 0.15	18.8± 0.3	72.4 ± 0.4
Glenlea	0.800 ± 0.054	44.9 ± 1.0	76.7 ± 0.9	18.2 ± 0.3	0.145 ± 0.010	8.15 ± 0.21	16.9±0.3	74.3 ± 0.5
NB131	0.837 ± 0.052	48.6 ± 1.1	78.6±0.8	17.0±0.3	0.141 ± 0.009	8.27 ± 0.23	15.6 ± 0.3	73.8±0.5
Variety				Chará	acteristics			
	Amylograph viscosity ⁺	Sedimentati value (cc)	on Remix 1 volum (cc)	caf Ble le loaf v (co	end Farino volume absorp c) (%)	graph Farind tion developn (T	ograph Mixiu nent tíme nin)	ng tolerance index [†]
Coteau	586.3 ± 16.9	61.0 ± 2.2	912 ±	14 701	± 20 66.6 ±	0.3 5.6 1	0.1 40	0.0 ± 1.3
Sinton	771.3 ± 22.2	57.6 ± 0.8	892 ±	15 664 1	<u>+</u> 10 66.2 <u>+</u>	0.2 4.6 1	F 0.2 39	.5±2.3
Glenlea	488.8 ± 31.6	54.9 ± 1.5	833 +	38 829	+ 20 64.9 +	0.8 6.1	÷ 1.3 16	.9 ± 1.3
NB131	667.1 ± 17.1	47.9 ± 1.0	845 -	30 758 -	t 22 66.8 <u>t</u>	0.7 5.4	+ 0.8 It	3.8 ± 4.0
*Value 6 loc	s given for mill ations years.	ing and bakin	g characteris	tics are only	y for 2 location	s years. All oth	ner data are avers	lged over
+ Brabe	nder units.							

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In addition to the agronomic characteristics mentioned above, several criteria relating to milling and baking characteristics were used to evaluate the cultivars. These included: grain protein content, flour protein content, flour yield, amylograph viscosity, sedimentation value, blend loaf volume, remix loaf volume and farinograraph characteristics. The importance of each of these in relation to end use can be briefly stated as follows. 'Flour yield' is an important milling characteristic because it indicates the quantity of flour milled from a sample of wheat, and shows how much of the grain is lost in the milling process. 'Flour protein content' is considered to be the primary factor in measuring the potential of the flour in relation to end-use. Many of the baking characteristics of wheat including water absorption, rheological properties and loaf volume are related to flour protein content. 'Grain protein content' is important because of its relationship with flour protein content. Usually, grain with high protein content yields flour with high protein content. In addition to high protein content, wheat suitable for bread making purposes should also have a significant amount of high quality protein to produce good quality bread from a range of baking formulae. The 'sedimentation value' gives an index of the quality of the protein. Loaf volume is probably one of the best criteria of bread-making quality of a wheat Where all other characteristics are at acceptable levels, flour. loaves having large volumes are desired by both the baker and the consumer. Two measures of loaf volume, 'remix loaf volume' and 'blend loaf volume' have been used in this study. The major difference

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between the two is that in the latter case, the flour is blended with an equal quantity of flour from wheat of lower protein content and quality. 'Farinograph absorption' is a measure of the amount of water that can be added to the flour to obtain a dough of proper consistency for baking purposes. In bread making by conventional methods, mixing the dough is generally considered a critical step that influences the overall bread making quality. The 'Farinograph dough development' time is a measure of the optimim mixing time; and the 'mixing tolerance index' measures the length of time the dough can be mixed before the rheological properties begin to break down.

The results of this experiment showed that despite sizeable differences in test weight and kernel weight observed between the two market classes, the flour extraction percentage remained essentially the same among the four cultivars. The results also showed that both grain protein content and flour protein content of the utility cultivars were significantly lower than the bread wheat cultivars. A more interesting comparison among the four cultivars is the drop in protein percentage from the grain to the flour as a result of the milling process. The protein percentage in the two bread wheat cultivars, Coteau and Sinton, dropped by only 0.8 percentage point, whereas, drops of about 1.3 and 1.4 percentage points were registered for Glenlea and NB131, respectively. A drop in protein percentage greater than 1% is not generally acceptable to the milling industry as it indicates that much of the protein is concentrated in the bran fraction, and is not useful for breadmaking purposes.

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The higher sedimentation value for the two bread wheats, Sinton and Coteau, as compared to the utility wheats attest to the fact that the bread wheats had, not only significantly higher protein quantities, but also had protein of better quality than the utility wheats. The two loaf volume measurements gave some interesting and contrasting results. The remix loaf volume of the two bread wheat cultivars were larger than those of the utility wheats. However, when flours from the four cultivars were blended with flour of low protein content from another cultivar and baked, the utility wheats and particularly Glenlea, produced larger loaves of bread.

It appears that the flour water absorption of all four cultivars were at acceptable levels as indicated by the 'Farinograph absorption' values. The data showed that there were no distinct market class differences in dough development time, although Sinton had a much lower mixing requirement while Glenlea had a much longer mixing requirement. In mixing tolerance, however, distinct market class differences were observed. The two utility cultivars appeared to tolerate longer mixing time without losing their rheological properties.

An interesting finding from the present study is the observation that, in spite of their low grain protein content, the utility wheats excelled the bread wheats in protein per kernel (Table 5). These observations suggest that although the utility wheats were expressing lower protein percentage values, they were actually absorbing higher quantities of nitrogen from the soil; and were also accumulating higher amounts of nitrogen in the developing kernels. One might conclude from these observations that the utility wheats are more efficient in their nitrogen metabolism than the bread wheats. The lower protein content of the utility wheats should be attributed to dilution of the protein in the kernel by non-protein compounds rather than to inefficient genes or biosynthetic pathways for protein synthesis in these cultivars.

The results of this experiment can be generally summarized as follows. The two bread wheat cultivars, Sinton and Coteau, are characterized by excellent milling and baking characteristics, but have relatively low yield potentials. On the other hand, the major attributes of the two utility wheat cultivars, NB131 and Glenlea, are: distinct and significant yield advantages; good milling characteristics; larger blend loaf volume; and greater mixing tolerance. The major weakness of the utility cultivars, in relation to bread making are: low grain protein content; low flour protein quality; a larger drop in protein percentage from the grain to flour and generally inferior baking characteristics.

4.2 Experiment 2. Evaluation of base populations in single

plant nursery

4.2.1. Comparison of population means

A single plant nursery consisting of the two parental cultivars, Glenlea and Sinton, and the four base populations generated from them (Table 2) was grown in Winnipeg during the summer of 1978. Average single plant performances of the parental cultivars for various characteristics are summarized in Table 6, and similar data for the base populations are given in Table 7.

The two parental lines, Glenlea and Sinton, contrasted sharply in all characteristics investigated, except number of kernels per spike. Unpaired t-tests (Steel and Torrie, 1960) showed Glenlea to be higher yielding, to have heavier kernels, and also to have a greater number of spikes per plant than Sinton. These findings were as expected because Glenlea was chosen (on the basis of its performance in several years and locations) as the high yielding parent. In addition, Glenlea also showed significantly higher grain protein content, protein yield per plant and protein per kernel. These observations, however, were not expected because Sinton was chosen as the high protein parent. No logical reason could be found to explain why the protein content of Sinton was higher in solid planted conditions and yet was lower than Glenlea under space planted conditions. Perhaps such differences could be due to genotype-environment interaction in which different planting densities favoured different genotypes.

Of interest is the comparison of the means of the four base populations for various characteristics, and particularly for grain yield and grain protein content. Significant differences for all characteristics were observed (Table 7). However, these were not large considering the genetic constitution of the populations. The two backcrosses had 75% of their genes from their respective recurrent parents, while the intermated F_2 and the F_2 populations had equal doses of genes from the parental cultivars and presumably differed from one another in genetic architecture.

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TABLE 6. Average single plant performance for 8 yield and protein characteristics of Glenlea and Sinton grown in a space planted nursery.

Characteristics	Glenlea	Sinton	differences
Yield per plant (gm)	31.8 ± 0.8	18.0 + 0.6	13.8**
Plant height (cm)	87.2 + 0.5	78.3 + 0.5	8.9**
Spikes/plant	36.4 + 0.7	25.7 ± 0.7	10.7**
Kernels/spike	27.6 - 0.4	28.7 + 0.4	1.1
1000 Kernel weight (gm)	32.0 + 0.4	24.2 + 0.2	7.8**
Grain protein (%) ¹	22.1 + 0.1	21.7 ± 0.1	0.4**
Protein/kernel (mg)	7.1 + 0.1	5.2 + 0.0	1.9**
Kernels/plant	994.8 + 23.6	735.6 ± 20.8	259.2**

**Significantly greater than zero at the 1% level of probability by unpaired t-test.

 1 Grain protein content = (N x 5.7) on 0% moisture basis.

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Population	Yield per	Plant	Spikes/	Kernels/	1000	Grain	Protein/	Kernels/
	planî	height	plant	spike	kernel	protein ¹	kernel	plant
	(gm)	(cm)			(gm)	(%)	(mg)	
F2	26.4 b*	82.6 b	34.1 b	28.9 ab	27.1 bc	21.6 b	5.83 bc	972.4 b
Intermated F_2	29.9 a	84 . 5 a	36.0 a	30 . 0 a	27.8 ab	21.7 ab	6.04 ab	1074.5 a
BC Glenlea	28.1 b	84.6 a	34.9 ab	28.6 b	28.4 a	22.0 a	6.22 а	989.4 ab
BC Sinton	22.1 c	80.0 c	28.6 c	29.8 ab	26.8 c	21.6 b	5.79 c	832.7 c
*Means in th	e same column	followed 1	by the same	letter are	not sienifi	cantlv diffe	trent at the	5% lavel

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¹Grain protein content = (N x 5.7) on 0% moisture basis.

The performance of the four base populations were compared by using the F₂ as the reference population. For all characteristics investigated, the performance of the backcross to Glenlea and the intermated F₂ population were equal to or significantly better than the F₂ population (Table 7). In contrast, the performance of the backcross to Sinton population was significantly lower or at the most equal to the F₂ population. The means of the intermated F₂ and the backcross to Glenlea populations were essentially equal except for grain yield and kernels per spike, in which case the intermated F₂ population had higher means.

On the basis of these comparisons, the backcross to Glenlea and the intermated F_2 populations are considered the most desirable base populations when simultaneous improvement of yield and protein content is the ultimate goal of a breeding program. If selection is equally effective in all four populations one would expect to find desirable progenies more frequently in these two populations than in the others.

4.2.2 Comparison of phenotypic variances

Phenotypic variances, measured as the within plot variances, of parental lines and base populations are presented in Table 8. On the basis of population genetics theories, one would expect the variances of parental lines to be relatively small, those of the backcrosses to be intermediate, and those of the F₂ populations to be large. Such clearly defined trends in variances are not

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Phenotypic variances	ations generated from
TABLE 8.	popul

Population	đf				Charact	eristics			
		Yield/ plant	Plant height	Spikes/ plant	Kernels/ spike	Kernel weight	Grain protein	Protein/ kernel	Kernels/ plant
Glenlea	115	5844	328793	4964	35	38	5.2	3.34	154842
Sinton	115	5780	349448	4864	57	21	4.8	3.94	193408
F2	261	6664	463400	5406	52	41	5.4	4.94	193322
Intermated F ₂	261	6416	432739	4419	33	33	5.5	4.96	178124
BC Glenlea	261	6643	407736	5533	43	31	6.4	4.49	187734
BC Sinton	261	6474	409908	5819	47	75	5.9	3.89	218619

See page 43 for transformations used.

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indicated by the data presented in Table 8. Test for equality of variances in the base populations was conducted in the form of F ratios where,

F = larger variance smaller variance

and the values so calculated were compared with tabulated values using the appropriate degrees of freedom. For all characteristics, the variances of the populations were not found to be significantly different from one another, nor were they found larger than those of the parental cultivars. The absence of significant differences among variances of the different populations is attributed to large genotype-environment interactions. It is likely that single plants of the more heterozygous and heterogeneous populations were individually and collectively buffered against genotype-environment interaction, while the homogeneous and homozygous parental lines lacked such individual and population buffering. The presence of such buffering mechanisms have been suggested by several workers including Lerner (1954), Sprague and Federer (1951), Shank and Adams (1960), and Eberhart et al (1964).

4.2.3 <u>Comparison of phenotypic correlations</u>

For each population, phenotypic correlation coefficients between pairs of characteristics in all possible combinations were calculated using the within plot mean squares and cross products. Other than small differences in the magnitude of the correlation coefficients, the coefficients for most pairs of characteristics were essentially similar across populations (Table 9).

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The results of the correlation analyses conducted in all six populations can be summarized as follows. (1) Grain yield per plant was positively correlated with kernel weight, number of spikes per plant and number of kernels per spike. These correlations were as expected because grain yield is a conglomerate trait the components of which are the aforementioned characteristics. (2) Relationships among yield components were often negative, but in some cases, the correlation coefficients were not statistically significant. (3) Grain protein content was negatively and significantly correlated with grain yield and yield components. However, the r values obtained between grain yield and grain protein content were low suggesting that the development of high yielding-high protein genotypes should be possible. (4) Protein per kernel was positively and significantly correlated with grain yield and grain protein This characteristic should be interesting from a plant content. breeding point of view because it is positively correlated with both grain yield and grain protein content and can be used as a single character for the simultaneous improvement of both characteristics.

Since the parental lines are composed of genetically uniform plants, any significant correlations among plant characteristics in these populations are not due to genetic linkages and therefore should be environmental or developmental (allometric) in origin. Since the correlations among plant characteristics in the base populations were not significantly different from those of the

Charac	teri	stics			Popula	ations		
			Glenlea	Sinton	F ₂	Inter	BC Glen	BC Sint
Yield	vs	Protein %	304**	165*	164**	359**	243**	168**
		Plant height	.398**	. 580**	.340**	.444**	.347**	.483**
		Spikes/plant	.615**	.777**	.695**	.717**	.709**	.725**
		Kernels/plant	.855**	.973**	.896**	. 898**	.914**	.765**
		Kernels/spike	.399**	.577**	.401**	.470**	.399**	.380**
		Kernel wt	.443**	.585**	.479**	.477**	.437**	.300**
		Protein/ kernel	.373**	.586**	.418**	.342**	.349**	.270**
Protein %	vs	Plant height	.241**	.071	.204**	.015	.154**	.199**
		Spikes/plant	.219*	079	.047	140*	.027	.010
		Kernels/plant	022	057	055	287**	134*	152**
		Kernels/spike	358**	042	130*	282**	246**	171**
		Kernel wt	580**	482**	261**	234**	279**	447**
		Protein/Kernel	.251**	.235**	.186**	.167**	.152**	.325**
Plant height	vs	Spikes/plant	.693**	.483**	.607**	.437**	. 569**	. 556**
		Kernels/plant	.585**	.568**	.429**	.435**	.436**	.481**
		Kernels/spike	129**	.304**	156**	.099	136*	.116*
		Kernel wt	289***	.333**	111	.119	106	212**
		Protein/Kernel	245**	.414**	050	.120	.048	088
Spikes/plant	vs	Kernels/plant	.771**	.806**	.740**	.799**	.786**	.642**
		Kernels/spike	300**	.003	220**	084	223**	078
		Kernel wt	192*	271**	.088	.043	.025	.229**
		Protein/ kernel	154	.275**	.110	027	036	016
Kernels/plant	vs	Kernels/spike	.370**	.576***	.486**	.528**	.422**	.701**
		Kernel wt	076	.398**	.048	.049	.040	626**
		Protein/ kernel	116	438**	.016	.059	.007	.597**
Kernels/spike	vs	Kernel wt	192*	359**	025	.011	.025	548**
		Protein/kernel	.082	.403**	091	069	.061	679**
Kernel wt	vs	Protein/Kernel	.92 9**	.886**	.920**	.914**	. 894**	.882**

TABLE 9. Phenotypic correlation coefficients among pairs of variables in parental cultivars and 4 base populations generated from Glenlea x Sinton cross.

*,** = Correlation coefficient significantly different from zero at the 5% and 1% level
of significance, respectively.

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parental cultivars, it can be assumed that the correlations among plant characteristics in the genetically segregating base populations were caused mainly by non-genetic rather than by genetic causes of variation.

Correlations between grain yield and grain protein content are considered among the most important criteria in evaluating the four base populations. In all four base populations correlation coefficients between these two characteristics were significantly different from zero. However, correlation coefficients from different populations were not found to differ significantly from one another nor from the two parents.

4.2.4. Path coefficient analyses of grain yield and grain protein content

Further information on the relationships among plant characteristics were obtained through path coefficient analysis. coefficients Correlation were partitioned into direct (unidirectional pathways) and indirect effects (through alternate pathways) of independent variables such as number of spikes per plant, kernel weight, etc. on resultant variables such as grain yield and grain protein content. The path analyses were performed in each population separately. The procedure used in developing the path model and subsequently its analyses were as follows: first, standardized multiple regression and stepwise multiple regression analyses were performed to choose independent variables which would provide the best possible prediction of grain

yield and grain protein content. Independent variables which did not contribute significantly to the total variation of a dependent variable were excluded from the test on the basis of these analyses. Then, the technique of path analysis was applied to explore the relationships among plant variables after assigning cause and effect relationships on a priori grounds.

The results of the standardized multiple regression analyses are presented in Table 10, and those of the stepwise multiple regression analyses are given in Tables 11 and 12, for grain yield and grain protein content, respectively. The standardized multiple regression analyses indicated large and significant contributions of spikes per plant, kernels per spike and kernel weight to grain other characteristics did not show regression yield. A11 significantly coefficients that were different from zero. Similarly, kernel weight and protein per grain were the only two characteristics that contributed significantly towards grain protein content. The partial regression of grain protein content on the remaining variables were not significantly different from zero.

Stepwise multiple regression analyses (Table 11) indicated the importance of spikes/plant in accounting for the total variation in grain yield. Averaged over the four base populations and the two parental cultivars, it alone accounted for about 52% of the total sum of squares for yield. Number of kernels/spike was the next important character in reducing the residual sum of squares for grain yield, and kernel weight was the third important character.

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Dependent variables	Population	3	Standardiz regression	ed partial coefficien	ts	R ²
		Spikes/ plant	Kernels/ spike	Kernel wt.	Protein/ kernel	
Yield	Glenlea	0.80**	0.51**	0.46**	0.00	0.98
	Sinton	0.75**	0.44**	0.20**	0.00	0.95
	F ₂	0.81**	0.54**	0.41**	0.00	0.94
	Inter.	0.75**	0.56**	0.41**	0.00	0.97
	BC. Glen.	0.80**	0.57**	0.38**	0.00	0.96
	BC. Sint.	0.71**	0.26**	0.51**	0.00	0.78
Protein	Glenlea	0.00	0.00	-2.52**	2.08**	0.98
	Sinton	0.00	0.00	-2.11**	1.84**	0.96
	F ₂	0.00	0.00	-2.48**	2.36**	0.98
	Inter.	0.00	0.00	-2.19**	2.18**	0.98
	BC. Glen.	0.00	0.00	-2.19**	2.18**	0.98
	BC. Sint.	0.00	0.34**	-3.06**	2.94**	0.97

TABLE 10. Multiple regression analysis of grain yield per plant and grain protein content on selected traits.

**Significant at the 1% level of probability.

Population	Variables added to equation	Par	tial regre coefficien	ssion ts
Glenlea	Spikes/plant Kernels/spike Kernel weight	0.74	0.85 1.16	0.89 1.06 1.10
	R2	0.45**	0.77**	0.98**
Sinton	Spikes/plant Kernels/spike Kernel weight	0.67	0.68 0.65	0.63 0.57 0.52
	R ²	0.65**	0.91**	0.95**
F ₂	Spikes/plant Kernels/spike Kernel weight	0.69	0.80 0.78	0.77 0.82 0.96
	R ²	0.53**	0.78**	0.94**
Inter.	Spikes/plant Kernels/spike Kernel weight	0.73	0.82 1.07	0.81 1.05 1.02
	R ²	0.46**	0.79**	0.97**
BC Glen.	Spikes/plant Kernels/spike Kernel weight	0.74	0.85 0.99	0.82 1.00 0.94
	R ²	0.52**	0.82**	0.96**
BC Sint.	Spikes/plant Kernels/spike Kernel weight	0.74	0.71 0.81	0.74 0.10 0.92
	\mathbb{R}^2	0.51**	0.71**	0.78**

TABLE 11. Stepwise multiple regression analysis (maximum R^2 improvement) of grain yield per plant of 6 wheat populations on other selected variables.¹

** Significantly different from zero at the 1% level of probability.

¹Regression analysis was conducted on transformed data. See page 43 for transformation used. In total, these three characteristics accounted for more than 94% of the variation in grain yield of all populations except the backcross to Sinton, in which they accounted for only 78% of the variation.

Stepwise multiple regression analyses for grain protein content (Table 12) also showed that three characteristics, namely kernel weight, protein per kernel and kernels/spike, accounted for more than 95% of the total variation for grain protein content. Of these three characteristics, the negative effects of kernel weight appeared to be the single most important characteristic, protein per kernel was the next, and kernels/spike was the third most important characteristic. No other characteristic contributed significantly to total variation in grain protein content except spikes/plant in the backcross to Sinton population.

A comparison of the two stepwise multiple regression analyses (Tables 11 and 12) showed that the relative importance of the variables that accounted for variations in grain protein content was the order in reverse of the relative importance of the characteristics that accounted for variations in grain yield. For example, kernel weight was the most important characteristic that affected grain protein content, but its effect on grain yield was the lowest among the three primary yield components. On the other of spikes per plant was hand, number the most important characteristic affecting grain yield, but its importance in relation to grain protein content was not significant.

Information collected from the multiple regression and stepwise

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Population	Variables added to equation	Pa	rtial regress coefficient	ion
Glenlea	Kernel weight	-0.16	-0.70	-0.08
	Protein/kernel		3.01	0.69
	Kernels/spike			2.98
	R ²	0.36**	0.78**	0.98**
Sinton	Kernel weight	-0.22	-0.09	
	Protein/kernel		4.17	
	R ²	0.25**	0.96**	
F ₂	Kernel weight	-0.10	-0.77	
	Protein/kernel		3.56	
	R ²	0.10*	0.98**	
Inter.	Kernels/spike	-0.07	-0.63	0.01
	Kernel weight		-0.08	0.08
	Protein/kernel			3.54
	R ²	0.06	0.12*	0.98**
3C Glen.	Kernels/spike	-0.07	-0.07	-0.01
	Kernel weight		-0.09	-0.76
	Protein/kernel			3.46
	R ²	0.08	0.14**	0.98**
SC Sint.	Kernels/spike	-0.02	-0.80	-0.19
	Protein/grain		3.54	0.80
	Spikes/plant			-3.62
	R ²	0.12**	0.86**	0.97**

TABLE 12. Stepwise multiple regression analysis (maximum R^2 improvement) of grain protein content of 6 wheat populations on selected variables.¹

** Significantly different from zero at the 1% level of probability.

1 Regression analysis was conducted on transformed data. See page 43 for transformation used.

multiple regression analysis laid the foundation for constructing the path model. A path diagram based partly on a priori grounds and partly on phenotypic correlation coefficients and multiple and stepwise multiple regression analysis is presented in Figure 3. Although conglomerate characteristics such as grain yield, grain protein content, protein yield per plant and number of kernels per plant were available for selection as components in the multiple regression analyses and stepwise multiple regression analyses, none of these characteristics were found important in affecting grain yield and (or) grain protein content. These variables were therefore deleted from the path model. Likewise, plant height was not found to be an important character affecting grain yield or grain protein content and therefore was not included in the model. The direct and indirect effects of the remaining independent variables on grain yield and grain protein content based on this model are presented, by population, in Table 13.

The path analysis showed that spikes per plant had highly significant direct effects on grain yield, but these large direct effects were slightly reduced due to negative indirect effects through number of kernels per spike. The path analysis also showed that the direct effects of kernels per spike were close to the total correlations because the indirect effects of this characteristic on grain yield in the various populations were not large. The correlation between grain yield and grain protein content was all attributed to the direct effects of kernel weight on grain yield.

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Fig. 3. Path relationships of grain yield, and grain protein content with selected characteristics.

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Pathway of association			Popu	lations		
	Glenlea	Sinton	F ₂	Inter.	BC Glen.	BC Sint
GRAIN YIELD			1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 - 1999 -			
- vs. <u>Kernel weight</u>						
Direct	0.448	0.581	0.438	0.437	0.413	0.492
TOTAL	0.448	0.581	0.438	0.437	0.413	0.492
- vs. <u>Kernels/spike</u>						
Direct	0.396	0.344	0.364	0.469	0.417	0.193
Indirect via Kernel wt.	0.045	0.158	-0.031	0.014	-0.015	-0.133
TOTAL	0.441	0.502	0.323	0.482	0.402	0.060
- vs. <u>Spikes/plant</u>						
Direct	0.802	0.705	0.809	0.752	0.799	0.710
Indirect via Kernel wt.	-0.050	0.112	0.035	0.002	0.025	0.028
Indirect via Kernels/spike	-0.093	-0.011	-0.115	-0.077	-0.107	-0.023
TOTAL	0.672	0.805	0.725	0.678	0.717	0.715
R ²	0.977	0.946	0.941	0.966	0.957	0.758
GRAIN PROTEIN CONTENT	<u> </u>	<u></u>				
- vs. Kernel weight						
Direct	-0.448	-0.494	-0.313	-0.242	-0.237	-0.340
TOTAL	-0.448	-0.494	-0.313	-0.242	-0.237	-0.340
- vs. Protein/Kern.						01210
Direct	0.262	0.044	0.086	0.207	0.213	0.065
TOTAL	0.262	0.044	0.086	0.207	0.213	0.065
- vs. Kernels/spike						
Direct	-0.032	-0.030	-0.016	-0.027	0.009	0.039
Indirect via Kernel wt.	-0.068	0.185	0.028	0.008	0.008	0.066
Indirect via Protein/ Kern.	-0.184	-0.212	-0.107	-0.211	-0.266	-0.247
TOTAL	-0.284	-0.057	-0.119	-0.246	-0.283	-0.352
	0.981	0.965	0.981	0.978	0.979	0.996

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Table 13. Path coefficients from path-coefficient analysis of grain yield and grain protein content of 6 wheat populations grown in space planted nursery.

As regards protein content, path analysis showed that the correlations between grain protein content and kernel weight were due entirely to the direct negative effects of kernel weight on grain protein content. Likewise, the correlations between grain protein content and protein per kernel were due entirely to direct effects. The correlations between kernels per spike and grain protein content were largely due to an indirect effect through protein per kernel. Direct effects of kernels per spike on grain protein content were not large in all populations.

Despite the presence of significant negative correlations between grain yield and grain protein content, multiple regression analyses showed that variations in grain yield did not significantly account for differences in grain protein content. Converselv. differences in grain protein content did not significantly account for variations in grain yield. As a result, a cause and effect relationship between grain protein content and grain yield has not been established in the path model depicted in Figure 3. The implication of these analyses is that the negative correlation between yield and protein content emerged because of their joint dependence on the same set of primary characteristics, among which kernels per spike and kernel weight were the most important. The interpretation to be made of these analyses is that, if the number of kernels per spike increased, yield will also be increased, but the concentration of protein per grain will be decreased to the detriment of grain protein content. Alternately, increased kernel

weight without a proportional and concomitant increase in protein per kernel results in increased grain yield but lowered grain protein content. On the basis of these analyses, and the relationships among plant characteristics established from them, the logical plant breeding strategy for improving both yield and protein content simultaneously would appear to be to increase grain yield through selection for large numbers of kernels per plant (especially through selection for a large number of spikes per plant) and to increase grain protein content by selecting for increased protein per kernel.

4.3 Experiments 3 and 5. Evaluation of 7 Base Populations

Generated from two Crosses.

Except for minor differences, Experiment 3 and Experiment 5 were similar in their field layout and statistical design. It would, therefore, be convenient to present results from these two experiments concurrently.

Experiment 3 and Experiment 5 had the following 3 main objectives:

 To compare base populations for means, phenotypic and genotypic variances, phenotypic and genotypic correlations and heritabilities;

(2) To simulate early generation selection in space planted nurseries for yield and (or) protein content by using various selection criteria;

(3) To compare the worth of base populations on the basis of response to selection and correlated response to selection; and finally,

(4) To investigate if the results obtained in Experiment 2 are reproducible under a different set of conditions.

4.3.1 Comparison of means

Parental cultivars that were used to synthesize the 7 base populations (4 from the Glenlea x Sinton cross and 3 from the NB131 X Coteau cross) were compared in pairs. Performance data of parental cultivars grown in replicated experiments (Table 14) showed that the means within pairs of parental lines differed significantly for all characteristics. Except for grain protein content, Glenlea was superior to Sinton in all characteristics studied. Similarly, NB131 was superior to Coteau in all characteristics except grain protein content.

The means of 105 progeny families in each of the four base populations generated from the Glenlea X Sinton cross together with similar data from 72 families in each of the 3 base populations generated from the NB131X Coteau cross are presented in Table 15. The 105 single plant derived progenies of each base population in the Glenlea X Sinton cross were intended to be random samples of the populations. The restriction in Experiment 3, that each plant had to produce at least 750 seeds so that 3 replicate single row plots

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TABLE 14. Comparison (by cross) of means of parental cultivars.

Difference 2.0** 2.1** 168.2** 15.2** 17.0** NB131 x Coteau² 0.4 668.0 ± 11.0 0.1 0.2 133.9 ± 20.4 Coteau 34.0 + 6.8 1 + 1 20.1 0.1 0.1 0.1 4.1 836.2 ± 25.6 NB131 49.2 ± 18.1 + + 6.8 150.9 ± **Significantly different at the 1% level of probability using unpaired t-test. Cross Difference 6.0** 1.4** 0.6** 6.5** 95.6** Glenlea x Sinton¹ 6.5 63.8 ± 1.3 38.4 ± 0.2 19.6 ± 0.1 7.5 ± 0.1 Sinton 325.2 ± 44.4 ± 0.4 420.8 ± 7.9 18.2 ± 0.1 8.1 ± 0.1 76.3 ± 1.3 Glenlea Grain protein content $(\%)^3$ Kernel weight (g/1000) Protein yield (g/plot) Characteristic Grain yield (g/plot) Protein/kernel (mg)

lplot size = 3 meter long single row plots (1.8 sq m/plot).

2Plot size = 3 meter long 3 row plots (1.8 sq m/plot).

 3 Protein content (N x 5.7) on 0% moisture basis.

could be grown could have skewed the backcross to Sinton population (the population that produced the smallest number of seeds/plant) towards higher than expected yields. Problems of this nature, however, were not encountered in the NB131 X Coteau cross.

Differences among the four populations generated from the Glenlea X Sinton cross were found to be highly significant for all characteristics (Table 15). Except for grain protein content the mean performance of the backcross to Glenlea population was higher than the remaining three base populations derived from the same cross, when grown under the conditions of Experiment 3. In contrast, the backcross to Sinton population was inferior to the other three populations for all characteristics except grain protein content. For grain protein content, the backcross to Sinton population expressed the highest value among the four populations generated from the Glenlea X Sinton cross. As expected, the two populations approached more closely toward backcross their respective recurrent parent. The intermated F_2 and the F_2 populations were intermediate between the two backcross populations in all characteristics investigated.

Base populations generated from the NB131 X Coteau cross behaved very similarly to those generated from the Glenlea X Sinton cross. Except for protein content, the backcross to Coteau population was inferior to the other two populations and, except for grain protein content the backcross to NB131 population was superior. The F_2 population was intermediate between the two

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Comparison (by cross)	ited from two crosses.
TABLE 15.	genera

			Characteristi	CS	
5	Grain yield (g/plot)	Kernel wt. (g/1000)	Grain protein ^{1'} (%)	Protein/grain (mg)	Protein yield (g/plot)
			Glenlea x Sinton	cross	
F2	299 .5 b¥	42.4 b	19.2 b	8.1 b	57.3 b
Intermated F ₂	307.2 b	4 2. 0 b	19.4 a	8.2 ab	59.5 b
Backcross to Glenlea	336.9 а	43.2 a	19.1 b	8,3 а	64.4 a
Backcross to Sinton	282.7 с	41.0 c	19.4 a	8.0 c	54.8 b
8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8		9 5 5 7 7 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8			
			NBLJL X COTERU C	ross	
F2	776.9 b	41.2 b	19.5 b	8.1 b	151.2 a
Backcross to NB131	815.8 a	48.8 a	18.8 c	9.4 a	153.6 a
Backcross to Coteau	719.0 c	38.4 c	19.9 a	7.7 c	142.6 b

*Means within a cross followed by the same letter are considered not significantly different at the 5% level of significance on Duncan's multiple range test.

¹Protein content (N x 5.7) on 0% moisture basis.

backcrosses for all characteristics.

4.3.2. Comparison of Population Phenotypic Variances

For the purpose of comparing the magnitudes of phenotypic and genotypic variances in the different populations, separate analyses of variance and covariance were conducted for each population, and for all characters and pairs of characters assuming a random effect model. The format for the analysis of variance and covariance is presented in Table 16.

Phenotypic variances for various characteristics in the four parental cultivars and the 7 base populations generated from the two crosses are presented in Table 17. Variances of base populations within a cross were compared using the F ratio as a test criterion. This test showed phenotypic variances in the base population were unequal in some cases. No clear cut trend in the phenotypic variances among base populations generated from the Glenlea X Sinton cross was found. however, the F2 and the intermated F2 showed higher (but necessarily significant) populations not phenotypic variances than the two backcross populations in most cases. Except for kernel weight, phenotypic variances among the 3 base population generated from the NB131 X Coteau cross were generally similar. For all characteristics the backcross to NB131 population showed the lowest phenotypic variance.

Since parental cultivars are composed of genetically uniform plants, it follows that differences between plots within these cultivars must be entirely due to differences in non-genetic causes

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Source of variation or covariation	Degrees of freedom	Mean square expectation	Mean product expectation
Total phenotypic	RS(E-1)	σ_{ii} + R σ_{ES}_{ii} + ES $\sigma_{R_{ii}}$	$\sigma_{ij} + R\sigma ES_{ij} + ES\sigma R_{ij}$
Entry (set)	S(E-1)	σ_{ii} + r $\sigma_{ES_{ii}}$	σ_{ij} + R σ_{ES}_{ij}
Error	S(E-1)(R-1)	G. 11	$\sigma_{i,j}$
Error	S(E-1)(R-1)	$\sigma_{1,i}$	G ij

genetic variances and covariances, respectively; $\mathbf{O}R_{ii}$ and $\mathbf{O}R_{ij} = replicate variances$ and covariances, respectively; E, S, and R = number of entries within sets, number of sets and number of replicates, respectively.

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TABLE 17. Phenotypic variances (mean squares x 10⁶) for 5 characteristics in parental lines and base populations generated from 2 crosses.

Cross	Population	Yield	Protein	RWT	Prot/kernel	Prot yield
Glenlea x Sinton	Glenlea	3014	195	528	580	2971
	Sinton	3810	168	202	205	4046
	\mathbf{F}_{2}	6778	320	677	1125	6133
	Intermated F ₂	6344	305	915	1356	6121
	BC Glen.	6445	294	799	981	0697
	BC Sint.	5606	236	914	1018	4751
NB131 x Coteau	NB131	2477	236	591	470	2269
	Coteau	1373	147	371	182	1159
	F 2	4310	602	713	1555	3503
	BC NB131	3470	441	675	1291	2895
	BC Coteau	4736	456	1381	1378	3577

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* See page 46 for transformations used.

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of variation. Comparison of phenotypic variance of the various base populations with those of the appropriate parental cultivars (Table 17) show the former to be significantly (P<0.01) greater than the latter, demonstrating the presence of significant genetic variations for most of the characteristics investigated.

4.3.3. <u>Comparison of Population Genetic Variances</u>

Because it is the main source of resemblance between relatives, and also because it is the chief determinant of response of populations to selection pressure, it is actually the magnitude of the genetic variance, rather than that of the phenotypic variance that is of prime importance in plant breeding programs. Genetic components of variance for 5 characteristics measured in each of the 7 base populations generated from the two crosses, are presented in Table 18. Genetic variances for all characteristics and in all base populations were highly significant suggesting that the base populations should provide sufficient genetic variability for selection in any of the characteristics. Within a cross, the more heterogeneous and heterozygous populations, the F_2 and (or) the intermated F₂ populations, appeared to have slightly higher genetic variances than the two backcross populations. The larger genetic variances in the intermated F_2 , and the F_2 populations probably consequences are a broader of genetic base, and particularly due to contributions from the dominance component of genetic variance.

TABLE 18. Genotypic variances (mean squares x 10^{6}) and standard errors for 5 characteristics of 7 base populations generated from 2 crosses.

Cross	Population	Yield	Protein	KWT	Prot/grn	Prot yiel	Ld
Glenlea x Sinton	F_2	2610 ± 555	180 ± 30	260 ± 65	450 ± 99	2050 ± 47	78
	Intermated F ₂	2014 + 477	150 ± 30	380 ± 80	540 ± 125	1780 ± 42	28
	BC Glen.	1780 ± 378	130 ± 28	220 ± 65	180 ± 78	1560 ± 35	57
	BC Sint.	1930 ± 433	90 ± 20	360 ± 85	370 ± 85	1420 ± 35	20
							1
NB131 x Coteau	н 2	1650 ± 332	320 ± 18	570 ± 30	721 ± 14.5	++ 0	18
	BC NB131	1503 ± 341	190 ± 11	510 ± 44	800 ± 34.6	+ ı 0	Э
	BC Coteau	630 ± 243	220 ± 14	920 ± 51	790 ± 45.1	10 +	2

* See page 46 for transformations used. Comparisons of the genetic variances of the four base populations generated from the Glenlea X Sinton cross showed that, for grain yield and protein yield differences among the populations were not significant. However, genetic variance for grain protein content in the backcross to Sinton population was significantly lower than the F₂ and the intermated F₂ populations, but was not significantly different from the backcross to Glenlea population. The genetic variance for grain protein content in the backcross to Glenlea population was not found significantly different from any of the other populations. In kernel weight, the backcross to Sinton population had higher genetic variance than the backcross to Glenlea population while all other comparisons were not significant.

Although significant genetic components of variance were obtained for most characteristics in each of the 3 base populations synthesized from the NB131X Coteau cross, no clear cut trend in the distribution of the variances could be noticed. Estimates of genetic variance for protein yield per plot in all 3 base populations was found to be not significantly different from zero.

The above genetic variance comparisons suggested that genotypic variances of the backcross to Glenlea and the backcross to NB131 populations, for important characteristics such as grain yield and grain protein content were not significantly lower than those of the other base populations.

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4.3.4. Comparisons of Phenotypic and Genotypic Correlations

Phenotypic and genotypic correlations among pairs of characteristics for parental lines and base populations generated from the two crosses are listed in Table 19. Most of the 10 phenotypic correlation coefficients calculated in each of the parental lines and 7 base populations were significant at least at the 5% level of significance. In contrast, most of the genotypic correlation coefficients were not found significant, and in some cases the standard error of the estimates of the genotypic correlations were larger than the correlation coefficients An evaluation of Table 19 character by character themselves. resulted in the following appraisal of the phenotypic and genotypic correlation coefficients.

4.3.4.1. Associations of grain yield with other characteristics

a) <u>Grain yield vs grain protein content</u>. Phenotypic correlations between grain yield and grain protein content were negative and highly significant in all populations except in the cultivar Sinton, where a positive but non-significant correlation coefficient was obtained. However, variation in yield accounted for a maximum of only 30% of the variation in grain protein content of any of the 7 segregating base populations studied. In contrast, variation in grain yield determined about 25% and 32% of the variation in grain protein content in the non-segregating parental lines Glenlea and NB131, respectively. This comparison of the strength of phentoypic correlations in segregating and non-segregating populations

ch	aracter			Glenlea x	Sinton cros	ŝ			NB13	l x Coteau	cross	
ရာ တ	oclations	Glenlea	Sinton	F ₂	Inter	BC Glen	BC Sint	NB131	Coteau	F2	BC NB131	BC Cot
						ਰ	henotypic c	orrelations				
Yield	vs ^p rotein	497**	.164	328**	353**	441**	309**	568**	455*	437**	410**	550**
	KWT	.120	.067	.225**	.062	.131*	.205**	.319	.358	.071	.152*	.346**
	Prot /Kern.	.174	.028	.012	116*	122*	.045	565**	179	320**	350**	.031
	Prot Yld	.975**	.992**	.976**	.978***	.974**	.977**	.976**	.952	.928**	.935**	.954**
Protein	vs KWT	223**	278**	271**	128**	212*	142**	.218	199	183**	160**	289**
	Prot /Kern.	.367**	.301	.555**	.580**	.443**	.348**	.779***	.774**	.746**	.700**	.286**
	Prot Yld	294**	290**	116*	150**	231**	121*	368	162	070	.059	275**
KWT	vs Prot/Kern.	. 825**	.832**	.846**	.882**	.841**	.879**	.781**	.467**	.791**	.871**	.296**
	Prot Yld	.076	101	.243**	.093	.112*	.184**	302	.328	003	104	.835**
Prot /Ker	n.vs Prot Yld	098	.067	.140**	. 006	.023	.125*	.429*	.066	046	110	.138**
							Genotypic c	orrelations				
Yield	vs Protein			573	603	701	644			553	782	797
	KWT			.294	.074	.492	.705			.734	.706	.909
	Prot /Kern.			.114	240	397	.315			.443	.889	.934
	Prot Yld			.972	.941	.972	.978			.865	.983	.449
Protein	vs KWT			016	120	246	322			379	- <u>.158</u>	<u>383</u>
	Prot/Wern.			.585	.616	.556	.203			.773	.612	. 111
	Prot Yld			363	244	512	466					.183
KWT	vs Prot/ Kern.			.795	. 842	.693	.873			.880	.877	.876
	Prot Yld			.345	.199	.160	.715			0.0	0.0	.869
Prot /Ker	n.vs Prot Yld			.048	.019	279	.411					.046

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TABLE 19. Phenotypic and genotypic correlations among pairs of characteristics in 4 parental lines and 7 base populations generated from them.

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KWT= kernel weight; Prot/Kern= protein/Kernel; Prot Yld = Protein yield.

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indicated that genetic relationships are not the main factors responsible for the negative correlation between grain yield and grain protein content. This was further substantiated by the genotypic correlation analysis (Table 19), which showed that genetic correlation between grain yield and grain protein content were not significant except in the backcross to NB131 population synthesised from the NB131 X Coteau cross.

The observations, in Experiments 3 and 5, that 6 of the 7 genetic correlations between grain yield and grain protein content were not significant, and also the observation that grain yield accounted for a small fraction of the total variation in grain protein content, reinforces the hypothesis, that there is very little in terms of a genetic barrier to the simultaneous improvement of yield and protein content.

b) <u>Grain yield vs kernel weight</u>. Phenotypic correlations between grain yield and kernel weight would appear to be different in different populations. In the parental cultivars and the intermated F_2 population of the Glenlea X Sinton cross, no significant correlations between these two characteristics were obtained, while positive and highly significant (P<0.01) correlations were obtained in the F_2 and the backcross to Sinton populations and a correlation coefficient significant only at the 5% level was obtained in the backcross to Glenlea population. Similar results obtained in the NB131 X Coteau cross indicated that phenotypic correlations were not significant in the two parental lines and the F_2 population. while in the two backcrosses highly significant correlation coefficients were obtained. When the genetic correlations between grain yield and kernel weight were considered, significant associations were observed in 6 of the 7 base populations (Table 19).

c) Grain yield vs protein per kernel. In the Glenlea X Sinton cross, phenotypic correlations between grain yield and protein per kernel were not significant except in the two high yielding populations, the backcross to Glenlea and the intermated F2 populations, in which phenotypic correlation coefficients were negative and significant at the 5% level of significance. In the NB131 X Coteau cross, phenotypic correlations between these two characteristics were significant in one of the parental lines, NB131, in the F₂ population, and also in the backcross to NB131 population. A negative association was indicated in all cases in which significant phenotypic correlations between these two characteristics were obtained. Genotypic correlations between grain yield and protein per grain were generally nonsignificant with the one exception of the backcross to NB131 where a significant positive association was registered.

d) <u>Grain yield vs protein yield.</u> The results of this experiment strongly suggested the presence of highly significant phenotypic and genotypic correlations between grain yield and protein yield per plot.

4.3.4.2. Association of grain protein content with other characteristics. The results given above were pertinent to the association of grain yield with other characteristics investigated. Considering the phenotypic and genotypic correlations of grain protein content with other characteristics, the following results were obtained.

a) <u>Grain protein content vs kernel weight</u>. Genotypic as well as phenotypic correlations between grain protein content and kernel weight were found to be negative and highly significant in all populations. This suggests that the larger the kernel weight, the lower would be the grain protein content.

b) Grain protein content vs protein per kernel. Phenotypic correlations between grain protein content and protein per kernel consistently positive were and highly significant in a11 populations. This suggests that, for the expression of high grain protein content, each kernel must contain a larger quantity of protein per kernel. However, the non-significant genetic correlation coefficient for these two characteristics implies that the cause of these associations has no genetic basis.

c) <u>Grain protein content vs protein yield per plot</u>. The phenotypic correlations between grain protein content and protein yield/plot were in most cases negative and significant, but the genetic correlations between these two characteristics were not significantly different from zero.

Associations among other characteristics are not important from the point of view of this investigation, but generally the following results were obtained. Associations between kernel weight and protein per kernel were phenotypically significant and suggested that increasing the quantity of protein accumulated in each grain will result in an increased kernel weight. However, no significant genetic association among these characteristics were obtained. Kernel weight was also significantly correlated with protein yield in some populations, but no significant genetic correlations were obtained between these two characteristics. Protein per kernel was neither phenotypically nor genotypically correlated with protein yield per plot.

4.3.5. Estimates of Heritabilities

Heritabilities estimated on the basis of components of variance methods (broad sense heritability) in each of the 7 base populations generated from the two crosses and are presented in Table 20. In addition, heritabilities estimated from the offspring-parent regression, have been calculated for 4 base populations derived from the Glenlea X Sinton cross and are listed in Table 21. Since the single plant nursery of the NB131 X Coteau cross was grown in Mexico, no attempt has been made to compute heritabilities using the offspring-parent regression technique.

Broad-sense heritabilities obtained in the two crosses were similar for grain yield and grain protein content. However, striking differences between the two crosses for the remaining three characteristics are apparent from a study of Table 20. Estimates of broad sense heritability for kernel weight and protein per kernel

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TABL	

Glenlea x Sinton R_2 0.39 \pm 0.16 0.46 \pm 0.19 0.30 \pm 0.13 0 Intermated F_2 0.27 \pm 0.12 0.42 \pm 0.20 0.37 \pm 0.18 0 BG Glen. 0.37 \pm 0.16 0.38 \pm 0.10 0.26 \pm 0.16 0 BC Glen. 0.34 \pm 0.13 0.36 \pm 0.16 0 NB131 x Coteau F_2 0.34 \pm 0.09 0.51 \pm 0.13 0.72 \pm 0.23 0 NB131 x Coteau F_2 0.33 \pm 0.11 0.42 \pm 0.16 0.71 \pm 0.31 0 BC NB131 0.34 \pm 0.09 0.51 \pm 0.15 0.72 \pm 0.23 0	Cross	Population	Yield	Protein	Kernel weight	Protein/ kernel	Protein yield
Internated F_2 0.27 \pm 0.12 0.42 \pm 0.20 0.37 \pm 0.18 0 BC Glen. 0.37 \pm 0.16 0.38 \pm 0.10 0.26 \pm 0.16 0 BC Sint. 0.34 \pm 0.13 0.32 \pm 0.17 0.36 \pm 0.19 0 BC Sint. 0.34 \pm 0.09 0.51 \pm 0.13 0.72 \pm 0.23 0 NB131 x Coteau F_2 0.33 \pm 0.11 0.42 \pm 0.16 0.71 \pm 0.31 0	Glenlea x Sinton	F2	0.39 ± 0.16	0.46 ± 0.19	0.30 ± 0.13	0.36 ± 0.12	0.34 ± 0.06
BC Glen. 0.37 ± 0.16 0.38 ± 0.10 0.26 ± 0.16 0 BC Sint. 0.34 ± 0.13 0.32 ± 0.17 0.36 ± 0.19 0 NB131 x Coteau F_2 0.34 ± 0.09 0.51 ± 0.13 0.72 ± 0.23 0 BC NB131 0.33 ± 0.11 0.42 ± 0.16 0.71 ± 0.31 0		Intermated F_2	0.27 ± 0.12	0.42 ± 0.20	0.37 ± 0.18	0.37 ± 0.14	0.20 ± 0.14
BC Sint. 0.34 ± 0.13 0.32 ± 0.17 0.36 ± 0.19 0 NB131 x Coteau \mathbb{P}_2 0.34 ± 0.09 0.51 ± 0.13 0.72 ± 0.23 0 BC NB131 0.33 \pm 0.11 0.42 \pm 0.16 0.71 \pm 0.31 0		BC Glen.	0.37 ± 0.16	0.38 ± 0.10	0.26 ± 0.16	0.16 ± 0.16	0.32 ± 0.15
NB131 x Coteau F ₂ 0.34 ± 0.09 0.51 ± 0.13 0.72 ± 0.23 0 BC NB131 0.33 ± 0.11 0.42 ± 0.16 0.71 ± 0.31 0		BC Sint.	0.34 ± 0.13	0.32 ± 0.17	0.36 ± 0.19	0.34 ± 0.17	0.30 ± 0.07
BC NB131 0.33 $\frac{1}{2}$ 0.11 0.42 $\frac{1}{2}$ 0.16 0.71 $\frac{1}{2}$ 0.31 0	NB131 x Coteau	\mathbb{F}_2	0.34 ± 0.09	0.51 ± 0.13	0.72 ± 0.23	0.73 ± 0.28	0.07 ± 0.18
		BC NB131	0.33 ± 0.11	0.42 ± 0.16	0.71 ± 0.31	0.60 ± 0.24	0.08 ± 0.05
BC Coteau 0.50 2 0.17 0.46 2 0.19 0.62 I 0.22 0		BC Coteau	0.50 ± 0.17	0.46 ± 0.19	0.62 ± 0.22	0.54 ± 0.19	0.16 ± 0.09

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TABLE 21. Narrow sense heritability estimated by the offspring-parent regression method for 5 characteristics in 4 base populations generated from Glenlea x Sinton cross.

Population			Characteristi	cs	
	Yield	Protein	Kernel weight	Protein/ kernel	Protein yield
F 2	0.35 ± 0.09	0.19 ± 0.11	0.39 ± 0.10	0.52 ± 0.11	0.42 ± 0.10
Intermated F_2	0.22 ± 0.10	0.24 ± 0.13	0.52 ± 0.09	0.66 ± 0.08	0.27 ± 0.12
BC Glen.	0.30 ± 0.09	0.03 ± 0.09	0.26 ± 0.08	0.14 ± 0.06	0.33 ± 0.10
BC Sint.	0.29 ± 0.09	0.16 ± 0.09	0.37 ± 0.09	0.32 ± 0.08	0.27 ± 0.09

were almost twice as large in the NB131 X Coteau cross as in the Glenlea X Sinton cross. With respect to protein yield per plot, broad sense heritability in the Glenlea X Sinton cross was several times larger than in the NB131 X Coteau cross. Most of the heritability estimates were significant except for protein yield per plot in the NB131 X Coteau cross. Heritability estimates among populations within a cross were not significantly different from one another for the two most important characteristics in this study, namely grain yield and grain protein content.

Heritability estimates obtained using the two methods gave similar results in the Glenlea X Sinton cross except for the striking exception that the offspring-parent regression method indicated the absence of significant heritability for grain protein content. These discrepancies are attributable to differences in the reference population to which the heritability estimates apply. In the offspring - parent regression method, the reference populations are the populations of single plants grown in the 1978 Nursery, whereas in the components of variance method the reference populations are the 1979 progeny lines derived from the 1978 single plant nursery. Additionally, the offspring-parent regression technique measures mostly the additive portion of genetic variance and therefore would be expected to be lower than estimates obtained using the components of variance method which includes all types of gene action present in the population. The larger coefficients of heritabilities obtained by the components of variance method may also be attributed to the greater and significant reductions of

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genotype X environment interactions through the use of replication. In contrast, the low heritability coefficients obtained when the offspring-parent regression method was used could be attributed partly to differences in performance of genotypes under different planting conditions, or to differences in environmental conditions in the two test years. Furthermore, large genotype X environment effects in the spaced single plant nursery, and losses of dominance and epistatic gene actions due to inbreeding could have lowered the heritabilities obtained using this method.

The value of heritability estimates is to give a quantitative measurement of the relative importance of heredity and environment in determining the expression of characteristics, and also to give an indication as to how easy or difficult it is to improve a particular characteristic. Significant heritability estimates are good indicators of the likely performance of the progenies in succeeding generations. Results presented in Tables 20 and 21 indicate that in general, it would be easy to improve kernel weight and protein per kernel, but relatively difficult to improve grain yield, and very difficult to increase grain protein content and protein yield/plot.

4.3.6 Further Comparisons of Base Populations

In addition to the comparison of base populations on the basis of their means, variances and correlation coefficients as discussed previously, additional comparative information could be obtained

from a determination of the frequency of desirable and undesirable genotypes contained in each base population. In the present study, genotypes from each base population were subjectively classified into four categories as follows: Class I genotypes are defined as those that inherited both the high grain yield of the utility wheat parent, and the high protein content of the bread wheat parent. From a plant breeding point of view, these represent the ideal genotypes that would result from a cross between a high yielding utility wheat, and a high grain protein bread wheat cultivar. Class II genotypes are designated as those that maintained the grain protein content of the bread wheat parent, but gave yields higher than the bread wheat cultivar. Some derivatives from this class may be expected to have the potential of higher yielding bread wheat Class III genotypes are designated as genotypes that cultivars. gave greater yield than the utility parent but maintained the protein content of the utility parent. Lines in this class may have the potential of being released as high yielding utility wheat cultivars. Class IV genotypes included all other genotypes that show little potential in the breeding program. This method of classification simplified the description of the genotypes as well as the analysis and interpretation of the data. The results are presented in Table 22.

A quick perusal of Table 22 indicates that there were some dramatic differences in the frequency of the different classes of

genotypes in different base populations particularly in the NB131 X Couteau cross. It can be seen that in each base population the frequency of the different categories depended on the gene dose the base population received from the parental cultivars. No Class I type genotypes were found in any of the four base populations from the Glenlea X Sinton cross, but from the NB131 X Coteau cross 3 such genotypes (2 from the F_2 and 1 from the backcross to NB131 populations) were identified. In view of the small number of genotypes falling into this class catagory, it is not clearly known whether these 3 genotypes were chance deviates or whether they were representing genuine superior genotypes. Class II type genotypes were observed in all 7 base populations generated from the two crosses, but their frequencies varied from population to population. In the Glenlea X Sinton cross, Class II types were observed more frequently in the intermated F₂ and the back cross to Glenlea populations, but in the remaining two populations the frequency of occurence of such genotypes was relatively small. Results obtained from the NB131 x Coteau cross indicated that the frequency of Class II types was relatively large in the backcross to Coteau population and was lower in the F2 population and the backcross to NB131 population. In the Glenlea by Sinton cross only 1 genotype could be identified which gave yield higher than Glenlea (Class III type). In the NB131 X Coteau cross all 3 base populations contained some Class III genotypes (genotypes which gave yields higher than NB131) but the largest frequency occurred in the backcross to NB131

	Population		Number	of lines	
		Class I	Class II	Class III	Class IV
Glenlea x Sinton	F ₂	-	3	-	102
	Inter	-	10	-	95
	BC Glen	-	11	1	93
	BC Sint	-	2	-	103
NB131 x Coteau	F ₂	2	16	17	37
	BC NB131	1	15	30	26
	BC Coteau	-	29	5	38

TABLE 22. Frequency of 4 different classes of genotypes present in each of the 7 base populations generated from 2 crosses.¹

1 Class I = Genotypes that combined the grain yield level of the utility parent and the grain protein content of the bread wheat parent.

Class II = Genotypes that maintained the grain protein content but showed grain yield higher than the bread wheat parent.

Class III = Genotypes that gave greater yield than the utility parent but maintained the protein content of the utility parent.

Class IV = All others.

population.

Further evaluation of the base population, would be possible from a comparison of the amount of grain protein content in each population at a given value of grain yield. That is, with equal yield level, a population which expresses consistently higher protein content should give the most desirable genotypes. In an effort to achieve this comparison, the regressions of grain protein content on grain yield were computed for all base populations, and the results are depicted graphically in Figures 4 and 5 for base populations generated from the Glenlea X Sinton cross, and NB131 X Coteau cross, respectively. To equalize the residual (error) variance in the regression model, and to maintain linearity of regression of grain protein content on grain yield a logarithmic transformation was used.

The regression analyses indicated the presence of some significant differences in the values of the intercepts as well as the regression coefficients for base populations generated from the same cross. However, from Figure 4, it can be seen that, for the majority of values of grain yield, more grain protein would be expected from the backcross to Glenlea population than from any of the other 3 populations generated from the Glenlea X Sinton cross. Similarly from Figure 5, more protein would be expected to be present in the backcross to NB131 population than from the other two populations generated from the NB131 X Coteau cross.

Both the analysis of the class frequency breakdown and the re-



Fig.4. >Regression of log grain protein content on log-grain yield of 4 base populations generated from the Glenlea x Sinton cross.

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gression of grain protein content on grain yield, as presented above, indicated that it should be easier or at least as easy to extract high yielding-high protein genotypes from populations generated by backcrossing to the utility parent than from any other population considered in this study.

4.3.7 Intergeneration Correlations

Intergeneration correlations indicate whether association among plant characteristics observed in one generation are persistent in later generations. Intergeneration correlations of 1979 grain yield and grain protein content with 1978 single plant characteristics in the various base populations synthesized from the Glenlea x Sinton cross were computed (Table 23).

Despite distinct gene frequency differences, intergeneration correlations of 1979 grain yield with 1978 plant characteristics were generally consistent across populations, and were pronounced for most characteristics. There were positive and highly significant inter-generation correlations between 1979 grain yield and the following 1978 single plant characteristics: (a) grain yield per plant, (b) kernel weight, (c) protein per kernel, and (d) protein yield per plant. The strength of the intergeneration correlation coefficients obtained in the different base populations were not found to differ significantly from one another when coefficients were tested for equality. More interesting among the TABLE 23. Intergeneration correlation coefficients of 1979 grain yield and grain protein content with 1978 single plant characteristics for each of the 4 base populations generated from Glenlea x Sinton cross.

Sint. -0.09 0.18 0.08 0.02 -0.04 -0.07 -0.09 -0.07 BC 1979 Grain protein content with Glen. -0.21*-0.20* -0.06 0.04 -0.05 0.15 0.00 0.06 BC \star , $\star\star$ Correlation coefficients significant at the 5% and 1% level of significance, respectively 0.43** **67.0 0.22* -0.00 -0.06 0.09 0.14 -0.12 Inter. -0.01 0.16 0.18 0.04 0.12 0.02 0.12 -0.04 Populations \mathbf{F}_2 Sint. 0.32** 0.47** 0.39** 0.29** -0.24* 0.10 0.11 0.12 BC 1979 Grain yield with Glen. 0.28** 0.42** 0.27** 0.45** -0.13 0.00 0.05 0.01 BC 0.20** 0.20* 0.22* -0.21*Inter. -0.11 0.16 -0.07 -0.07 0.36** 0.38** 0.31** 0.33** 0.22* -0.18 0.10 0.10 \mathbf{F}_2 1978 Grain protein content Character association 1978 No of seeds/plant 1978 Protein/kernel 1978 Kernel weight 1978 Protein yield 1978 Spikes/plant 1978 Plant height 1978 Grain yield

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intergeneration correlation coefficients is the observation that correlations between 1979 grain yield per plot and 1978 kernel weight were higher than between 1979 grain yield per plot and 1978 grain yield per plant. The higher intergeneration correlation between 1978 kernel weight and 1979 grain yield per plot coupled with the generally high heritability of kernel weight and highly significant genetic correlations between grain yield and kernel weight would suggest that it would be easier to select for grain yield in space planted nurseries by selecting for kernel weight than by selecting for grain yield/plant per se. Plant height, number of spikes per plant, number of kernels per spike measured in 1978 were not correlated with 1979 grain yield per plot and therefore may not have any grain yield predictive values.

Fewer significant intergeneration correlations between 1979 grain protein content and 1978 single plant characteristics were obtained, and most of those significant intergeneration correlations were observed in the intermated F_2 population. In fact, except in the intermated F_2 population, correlations between 1979 grain protein content and 1978 single plant characteristics were generally absent. No logical explanation for the contrasting and abnormal behaviors of the intermated F_2 population was identified, but it is anticipated that the larger deviations from linear regression observed for most characteristics in this population may have some contribution to this. Lack of intergeneration correlation is indicative of a number of factors including high genotype x

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environment interaction, absence of significant genetic variance, low heritability of one or both characteristics, and also the extent of the genetic correlations between the two characteristics (Falconer, 1960). The absence of significant intergeneration correlation for grain protein content in 3 of the 4 base populations is consistent with the findings that the genetic correlation of protein content with other characteristics was negligible (Table 19); that grain protein content was sensitive to genotype x environment interactions (Table 6); and that the heritabilities of grain protein content was generally low (Table 21).

4.3.8 Response to Selection

One of the main purposes of this experiment was to test the reliability of single plant characteristics as predictors of grain yield and grain protein content in advanced generations.

Effectiveness of selection for grain yield and (or) grain protein content by using single plant characteristics grown under space planted conditions in the preceeding year were evaluated by using 4 groups of selection methods as follows:

- (1) direct selection for grain yield or grain protein content;
- (2) indirect selection for grain yield and (or) grain protein content using single plant characteristics;
- (3) indirect selection using multiplicative (product) traits;
- (4) index selection.

A more detailed listing of the selection methods used is given

in Table 24. In this experiment, the index selection method proposed by Smith (1936) and Hazel (1943) could not be practised because of problems in assigning the appropriate economic importance of grain yield and grain protein content, and also because of problems of obtaining reliable estimates of phenotypic and genotypic variances and covariances from the single plant nursery grown in 1978. The problem is further complicated because heritabilities of grain protein content and its genetic correlations with the various traits were found to be close to zero. As a substitute, use was made of a multiple linear regression model which was constructed using the 1979 grain yield and grain protein content as dependent variables, and 1978 individual plant characteristics as independent variables. The independent variables were selected using a stepwise multiple regression analysis with maximum R^2 improvement. Data from all 4 base populations were pooled to construct the selection indices. The best discriminant function constructed using this method was:

I = -5.33 + 0.17 plant height + 0.27 kernels/spike + 0.34 kernel weight; for grain yield, and

I = 0.15 - 0.21 plant height - 0.48 spikes/plant - 0.24 kernel
weight;

for grain protein content. An apparent problem of this selection method as compared to that proposed by Smith (1936) is that, while it may improve only one characteristics at a time, it does not produce simultaneous improvement for two traits, especially when the traits are negatively correlated. Despite this problem, index selection using this technique was persued with the hope of comparing this selection method with results from single traits and multiplicative trait selection.

Using each selection method, superior plants in each of the 4 base populations grown under space planted conditions in the 1978 nursery were hypothetically selected as parental stocks to propagate the 1979 progeny lines. To determine the efficiency of selection the mean performance of the selected 1979 progeny lines were compared with the mean performance of the unselected population of the 1979 progenies. This comparison of means provided information on shifts of means due to selection. As a means of an exploratory step, a selection intensity of 10% was applied consistently for each of the 12 selection methods tested. For each selection method, taking grain yield as an example of a character to be improved by selection, mean grain yield, correlated response to selection in grain protein content, the selection efficiency, the number of high yielding lines and the number of high protein lines included in the selected fraction, the sample size required to retain the top 10 high yielding lines in the selected fraction were calculated. A similar analysis was also made for grain protein content.

The mean performance of the top 10 lines selected from each population for grain yield on the basis of single plant

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characteristics (10% selection intensity) are given in Table 24. The efficiencies of the different selection methods were different in different populations with some selection methods giving negative responses. In general, however, indirect selection for grain yield by selecting for high kernel weight in the space planted nursery resulted in better selection efficiency than any of the other methods including direct selection for grain yield per plant and the index selection. Not only was the mean performance of the selected population higher, but also more of the top 10 1979 high yielding progenies were retained when kernel weight was used as a criterion of selection. Multiplicative traits such as number of seeds per plant, protein yield per plant and protein per kernel were found the least efficient methods of indirect selection for grain yield, except in the intermated F2 population where they proved to have some value.

The lines selected for grain yield on the basis of 3 selection methods viz: grain yield per plant, kernel weight and selection index, were more or less similar except differences in relative positions of the selected lines. However, the regression model gave inferior results as compared to the direct selection for grain yield/plant or the indirect selection via kernel weight. Depending on the population, the regression model was 96-101% as efficient as the direct selection for grain yield and 90-101% as efficient as the direct selection for grain yield via kernel weight. .

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TABLE 24. Characteristics of samples selected using various single plant characteristics and 10% selection intensity in 4 base populations of wheat.

<u></u>				<u> </u>		
Criteria of selection	Population	Average yield of selected lines (gm/plot)	Average protein content of the selected lines (%)	Selection efficiency	No. of high yielding lines selected	No. of high protein lines selected
	BC Glen	361.0 + 10.9	19.0 <u>+</u> 0.2	7.2	2	0
yielc lant	BC Sint	296.9 ± 12.6	19.3 + 0.2	5.0	3	0
igh er p	F ₂	322.2 ± 8.0	19.3 ± 0.2	7.6	1	1
нd	Inter	307.2 + 16.2	19.8 - 0.2	0.0	1	1.
	BC Glen	382.0 + 9.2	18.5 ± 0.2	13.4	4	0
sh wt	BC Sint	312.3 + 7.9	19.5 + 0.2	10.5	3	2
H1, kerne	F2	321.1 ± 14.9	19.3 ± 0.2	7.2	4	1
-	Inter	384.8 + 21.2	20.4 + 0.2	1.3	2	4
u	BC Glen	352.5 + 13.2	18.9 + 0.2	4.6	0	3
rotej tent	BC Sint	290.2 + 9.1	19.4 ± 0.2	2.6	1	2
ow pr cont	F ₂	307.5 + 10.4	19.0 ± 0.2	2.7	1	1
Ľ	Inter	323.5 + 8.3	19.4 + 0.2	5.3	0	3
/u	BC Glen	345.8 + 11.5	19.1 + 0.1	2.6	1	0
ote li e l	BC Sint	383.6 + 10.8	19.3 ± 0.2	0.0	2	0
h pr kern	F2	326.2 + 8.5	19.3 ± 0.2	8.9	2	1
111 g	Inter	298.6 + 9.7	19.5 + 0.2	2.8	0	0
	BC Glen	355.7 ± 13.2	19.1 + 0.3	5.6	2	2
tion *	BC Sint	304.4 - 9.5	19.6 ± 0.2	7.6	2	2
elec inde	F ₂	308.3 - 14.1	19.4 + 0.3	2.9	3	1
03	Inter	286.9 + 21.4	20.3 ± 0.3	0.0	2	4
يد	BC Glen	336.8 + 12.6	19.2 + 0.1	0.0	1	0
'plan	BC Sint	296.2 + 11.7	19.4 ± 0.2	4.8	2	1
ikes/	F ₂	312.9 + 9.5	19.2 <u>†</u> 0.3	4.5	1	1
Sp	Inter	304.4 + 9.1	19.4 + 0.2	0.9	0	0
f nt	BC Glen	329.5 ± 14.7	19.3 ± 0.2	0.2	0	1
no o /pla	BC Sint	305.5 + 10.8	19.3 + 0.2	8.1	3	1
rge eeds	F ₂	311.4 + 4.1	19.4 ± 0.1	4.0	1	0
La s	Inter	286.3 ± 14.2	19.7 ± 0.2	0.6	0	1
	BC Glen	327.5 + 12.2	19.0 + 0.1	2.3	1	0
ant ight	BC Sint	271.4 - 8.2	19.6 - 0.2	3.9	0	0
P1 he	F ₂	311.2 + 11.3	18.8 - 0.3	3.9	2	0
	Inter	331.4 <u>†</u> 19.2	19.2 ± 0.3	7.9	2	0
2	BC Glen	350.8 + 10.8	19.1 + 0.1	4.1	1	0
/ield ut	BC Sint	297.9 ± 11.5	19.4 + 0.2	5.4	2	1
rot) plar	F ₂	222.2 + 7.9	19.3 + 0.2	7.6	1	1
Γı	Inter	307.0 + 16.0	19.7 ± 0.2	0.0	1	1

A similar simulated selection study for grain protein content on the basis of single plant characteristics did not result in very encouraging results. The mean performance of lines selected for grain protein content using various single plant characteristics as criteria of selection are given in Table 25. The full range of the selection methods was not simulated because heritability estimates for grain protein content, using the offspring parent regression method were close to zero, and the intergeneration correlation of the 1978 single plant characteristics with grain protein content of the 1979 progenies were not significant. Therefore, only those characteristics which showed significant intergeneration correlation with protein content were simulated, and as a means of control the direct selection for grain protein content was included.

As indicated in Table 25, direct selection using grain protein content was ineffective in all populations. This can be attributed to the low heritability of protein content and to genotype x environment interactions in the space planted nursery, the extent of which was so high that even the relative performance of the two parental cultivars in the 1978 space planted nursery were reversed (see Table 6). Despite their strong association with grain protein content, and higher heritabilities, indirect selection for grain protein content by selecting for high protein per grain or low kernel weight were found less efficient than the direct selection of grain protein content, nor the indirect selection through high

Criteria of selection	Population	Averageyield of selected lines (gm/plot)	Average protein content of the selected lines (%)	Selection efficiency	No of high yielding lines selected	No of high protein lines selected
ŗ	BC Glen	320.5 + 4.4	19.4 - 0.1	1.6	0	2
rotei	BC Sint	260.6 ± 8.7	19.9 ± 0.1	2.6	0	2
td hg	F ₂	273.9 + 6.1	19.4 - 0.2	1.0	0	1
Hig	Inter	285.8 + 9.4	19.9 + 0.2	2.6	0	3
rnel	BC Glen	316.3 ± 4.8	19.2 ± 0.1	0.5	0	2
n/ke:	BC Sint	258.2 + 5.8	19.5 + 0.1	0.5	0	1
oteiı	F ₂	269.0 ± 3.7	19.3 ± 0.1	0.5	0	0
Pro	Inter	278.5 ± 5.4	19.4 ± 0.1	0.0	0	0
wt	BC Glen	307.9 + 4.5	19.2 ± 0.1	0.5	0	1
inel	BC Sint	245.8 + 5.7	19.4 - 0.1	0.0	0	0
v ken	F ₂	269.7 - 9.2	19.2 - 0.1	0.0	0	1
Lov	Inter	297.7 ± 6.1	19.1 ± 0.1	1.5	0	0

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TABLE 25. Characteristics of samples selected using various single plant characteristics and 10% selection intensity in 4 base populations of wheat.

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protein per kernel or low kernel weight allowed the inclusion of any of the top 10 high yield progenies in the selected fraction.

In view of the failure of single plant performance as indicators of high performing progenies, an attempt was made to investigate if single plant characteristics can be used to discard undesirable genotypes in early generations, and as such help to minimize the number of lines advanced into the next generation. The amount of space, labor and time required to evaluate and select, at later generations, individual genotypes from among a large number of entries in replicated trials is of such a magnitude that a reliable method to evaluate the progeny in early stages would be beneficial. Toward this goal, an attempt was made to determine: (1) what fraction of the population of single plants could be discarded without reducing important population parameters such as the population means, the population variances, and the number of desirable genotypes retained for advance into the next generation; (2) what effects severe selection for grain yield or grain protein content would have on response to selection, correlated response to selection, phenotypic and genotypic variances and phenotypic and genotypic correlations; (3) what region of the normal distribution (the high tail, the median, or the low tail) would give better selection results; and (4) what characteristic or selection criteria would give simple, reliable, and consistent results.

For this purpose, the 3 most important, and most interrelated characteristics, namely grain yield, grain protein content, and

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kernel weight were selected. These characeristics have been shown to have high intergeneration correlations with grain yield and grain protein content as presented in Table 23. To facilitate and simplify the investigation 3 different breeding objectives namely (1) improving grain yield only, (2) improving grain protein content only, and (3) simultaneous improvement of both grain yield and grain protein content were considered. To meet these three breeding objectives, the following hypotheses were postulated on a priori knowledge derived from phenotypic and genotypic correlations (Table 19), intergeneration correlations (Table 23), path relationships (Table 13), and retrospective selection (a simulated selection in which the best individuals are selected, and then attempt was made to describe the genotypes from which the best lines were derived).

(1) Grain yield can be increased through selection for:

- a) high grain yield per plant;
- b) heavy kernel weight;
- c) low grain protein content.

(2) Grain protein content can be increased by selecting for:

- a) high grain protein content;
- b) low kernel weight;
- c) low grain yield per plant.
- (3) Grain yield and grain protein content can be improved simultaneously by selecting for:
 - a) intermediate grain yield per plant;
 - b) intermediate kernel weight;

c) intermediate grain protein content.

To determine an acceptable selection intensity, the following procedures were undertaken. First, for each selection intensity and selection criteria, the absolute difference between the sample variance (S^2), and the population variance (σ^2) were calculated as

$$\Delta s^2 = \frac{1}{\sigma^2} \frac{s^2 - \sigma^2}{\sigma^2} \times 100$$

and \triangle s² was used as a measure of how close the difference between the variance of the unselected population, and the variance of the selected fraction approached zero. Two methods were used to determine the critical value of Δs^2 beyond which the difference between the two variances were considered significant. An empirical critical value of 20 was used as the value of Δs^2 beyond which the selection intensity would be considered unacceptable. This means, if the variance of the selected fraction was less than 80% of the variance of the unselected fraction, then that selection intensity was considered to have caused significant reduction in genetic vari-Secondly, based on the assumption that (S^2/σ^2-1) is ance. normally distributed, the theoretically expected ΔS^2 , and its standard deviation were approximated for the unselected population using the formulae 112.8/ $\sqrt{n-1}$ and 85.2 / $\sqrt{n-1}$, respectively (Kendall, 1952). Then Chi-square tests for goodness of fit between the observed $\Delta\,{
m s}^2$ of the selected fraction and the expected $\Delta\,{
m s}^2$

of the unselected population were conducted using the method of Wu et al. (1977). A significant Chi square value indicated an unacceptable selection intensity.

Although there was a good agreement between results obtained using the two methods, the second approach was considered more precise than the first approach. Since a lower selection intensity was required for estimating the variance of grain yield, than for estimating the variance of grain protein content, and also since the variance of grain protein content was much lower than the variance for grain yield, grain yield was considered as the critical characteristic for making decisions regarding selection intensities. The results of this investigation averaged over the four populations generated from the Glenlea X Sinton cross are presented in Tables 26, 27 and 28 for breeding objectives of improving grain yield, grain protein content, and for simultaneous improvement of both grain yield and grain protein content, respectively.

Tables 26, 27 and 28 indicated the following effects of selection intensity on various attributes of a population. (1) A high selection intensity resulted in higher response to selection than a lower selection intensity, and also caused the largest negative correlated response to selection. (2) Intense selection for grain yield in early generations may reduce the variability for grain protein content implying that subsequent selection for grain protein content may be ineffective. The converse was also true. (3) High selection pressure results in greater loss of desirable genotypes that may not be retrieved in later generations.

With relaxation of the intensity of selection, the efficiency of selection, response to selection, correlated response to selection were all reduced, but the number of desirable genotypes still remaining in the selected fraction, as well as the phenotypic and genotypic variances were increased. The intensity of selection did not appear to affect the phenotypic nor the genotypic correlations between grain yield and grain protein content, and therefore, these statistics were not included in Tables 26, 27 and 28.

A subjective judgement of each table resulted in the following interpretation. Table 26 presents data on the effect of selection when grain yield per se, heavy kernel weight or low protein content were used as criteria of selection to improve grain yield. The table shows that at any selection intensity, larger response to selection, and greater selection efficiency for grain yield would be obtained when heavy kernel weight was used for discriminating among genotypes, than when high grain yield or low grain protein content were used. Reduction in genetic variance for grain yield approached a non-significant level at a selection intensity of 0.4 for kernel weight, whereas at that selection intensity still significant reductions in genetic variances were observed for the remaining two

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	criteria	to selec	tion	effic	stency	genetic '	variance	Avera{ desirable	ge nu ur : genotypes	Genocypic va of phenotypi	iriance as 7 c variance
:		Yield (g/plot)	Protein (%)	Yield	Protein	Yield	Protein	Yield	Protein	Yield	Protein
H	igh yield	15.1	0.1	.05	.01	79.23**	9.4	2	1	7.2	43.9
0.1 Hi	igh KWT	17.9	0.2	.06	.01	42.13**	93.5	4	2	28.5	54.8
Lt	ow protein	11.7	-0.1	.04	01	59.86**	45.7	2	1	17.6	28.4
Hi	igh yield	5.3	0	.02	0	41.38**	37.0	4	2	22.2	45.8
0.2 Hi	gh KWT	10.9	0.1	.04	.01	64.93	47.8	5	£	27.0	50.1
Lc	w protein	10.2	-0.1	.03	01	23.10	42.0	4	2	37.3	45.0
H	igh yield	15.3	0	.05	0	48.09**	13.8	ŝ	1	23.2	45.6
0.3 Hi	igh KWT	11.1	0.1	.04	.01	4.07**	37.0	7	'n	30.8	39.0
Lc	w protein	7.9	-0.1	.03	01	4.72**	5.1	5	2	38.7	39.0
Hi	gh yield	10.8	0	.04	0	4.12**	25.4	6	2	33.8	49.7
0.4 Hi	gh KWT	11.2	0	.04	0	7.39	1.4	7	ŝ	31.2	40.5
Lc	w protein	4.8	-0.1	.02	01	13.91*	2.2	5	ε	32.8	37.3
Hi	.gh yield	8.7	0	.03	0	44.76**	16.7	7	'n	18.3	34.8
0.5 Hi	gh KWT	6.2	0	.04	0	6.4	1.4	8	Ω	31.7	41.9
Lc	w protein	1 1	0	1	I I	8	1	ł	ı	:	1 1
Ηİ	.gh yield	7.5	0	.02	0	10.33**	8.7	œ	4	31.3	44.1
0.6 HI	.gh KWT	9.5	0	.03	0	22.11	7.2	8	5	30.1	43.3
Lc	w protein	:	0	1	!	;	1	ı	ı	1	!

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probability, respectively.

¹ Values given are averages of 4 base populations. KWT = kernel weight.

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selection criteria. However, at a selection intensity of 0.4 an average of only 7 out of 10 high yielding lines and 3 out of 10 high protein lines were retained in the selected fraction. When the

selection intensity for heavy kernel weight was further relaxed to a level of 0.6, an average of 8 out of the top 10 high yielding lines and 5 out of the top 10 high protein lines were retained in the selected fraction. In addition, the mean yields of the populations were increased by 9.5 g/plot (3%) without causing any depression in the mean grain protein content of the populations. The remaining 40% of the population could be discarded without any irretrievable loss of desirable genotypes or population parameters.

Results obtained when selection for grain protein content, and simultaneous selection for both grain yield and grain protein content were simulated (Tables 27 and 28 respectively) were in general similar to those obtained when selection for grain yield was simulated (Table 26). For all selection criteria considered, in genetic variances for grain yield approached reductions non-significant levels only after the selection intensity was relaxed to levels lower than 0.5 - 0.6. At such relaxed selection intensities, undersirable shifts in population means were also minimized. A comparison of Tables 26, 27 and 28 show that, irrespective of the objectives of the plant breeding program (Viz. selection for grain yield, selection for grain protein content or selection for both grain yield and grain protein content) more favourable results in terms of preserving important population

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Selection intensity	Selection criteria	Average 1 to sele	response action	Sele effic	ction iency	Average genetic	change in variance	Average desirable	no of genotypes	Genotypic varia of phenotypic va	nce as % ariance
		Yield (g/plot)	Protein (%)	Yield	Protein	Yield	Protein	Yield	Protein	Yield	Protein
	Hígh proteín	-21.5	0.4	-0.07	0.02	42.2**	85.5	0	2	16.1	3.6
0.1	Low yield	-26.2	0.1	-0.09	0.01	* ≁0.96	34.1	0	Ч	6.8	21.4
	Low KWT	-26.4	-0.1	-0.09	-0.1	29.7**	55.8	0	1	15.4	20.5
	Hígh protein	- 9.7	0.1	-0.03	0.01	4.5**	2.9	1	٣	19.6	33.3
0.2	Low yield	-20.0	0	-0.07	0	47.1**	34.1	0	1	17.1	27.7
	Low KWT	-19.1	-0.1	-0.06	-0.1	23.6**	31.2	1	2	27.2	38.9
	High protein	- 9.9	0.2	-0.03	0.01	72.1**	23.9	2	4	37.9	40.6
0.3	Low yield	-17.0	0	-0.06	0	10.0**	34.8	1	2	29.8	26.7
	Low KWT	-15.6	0	-0.05	0	20.7**	11.6	2	e	27.4	40.3
	High protein	- 6.6	0.1	-0.02	0.01	75.5**	19.6	4	4	43.5	42.7
0.4	Low yield	-11.7	0	-0.04	0	3.7**	2.2	2	e.	32.4	37.0
	Low KWT	-13.9	0	-0.05	0	20.5	7.2	2	£	31.6	40.2
	High protein	- 5.1	0.1	-0.02	0.01	9.5**	10.9	4	4	27.0	37.0
0.5	Low yield	- 9.1	0	-0.03	0	1.2	1.4	Э	4	30.5	37.8
	Low KWT	-11.1	0	-0.04	0	8.1	2.2	2	3	31.9	39.6
	High protein	- 4.4	0.1	-0.01	0.01	13.2 * *	10.9	5	5	32.7	36.4
0.6	Low yield	1	1	:	E i	1	1	ı	ı	:	1
	Low KWT	- 7.6	0	-0.02	0	1.5	29.0	ę	4	30.9	35.8
/ ** ±	Toot of colocti	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0				•					

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Effect of selection on the genetic variance of yield was significant at the 5% and 1% level of probability, respectively. ŝ

lvalues given are averages of 4 base populations. KWT = kernel weight.

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erage effects of selection intensity and selection criteria when the objective of selection is	e both grain yield and grain protein content simultaneously. $^{f 1}$
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TABLE 28	to f

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Selection intensity	Selection criteria	Average r to selec	esponse tion	Sele effic	iency	Average (genetic v	change in variance	Avera desirabl	ge no of e genotypes	Genotypic va of phenotypi	iriance as c variance
		Yield (g/plot)	Protein (%)	Yield	Protein	Yield	Protein	Yield	Protein	Yield	Protet
	Med KWT	8.1	0.2	.03	.01	43.6**	1.4	1	1	18.9	26.1
0.1	Med yield	-1.2	0.1	0	.01	31.4**	4.3	1	1	11.1	30.2
	Med protein	-3.2	-0.1	01	01	100.0**	56.5	1	0	0	17.7
	Med KWT	7.9	0.1	.03	0	23.1**	0.7	1	1	31.2	29.2
0.2	Med yield	4.3	0	.01	0	46.8**	4.3	2	2	16.5	36.7
	Med protein	-0.4	0.1	0	.01	67.3**	55.1	1	1	13.3	22.0
	Med KWT	6.3	0.1	.02	0	51.8**	24.6	2	2	21.6	30.0
0.3	Med yield	1.3	0	0	0	21.0^{**}	5.1	С	£	32.5	37.0
	Med protein	0.4	0	0	0	44.6**	9.4	2	1	21.0	41.0
	Med KWT	4.1	0	.01	0	17.0**	24.6	2	2	29.7	33.9
0.4	Med yield	0.8	0	0	0	13.3**	19.6	4	4	35.0	42.2
	Med protein	0.1	-0.1	0	01	47.9**	25.4	ς	2	21.3	34.5
	Med KWT	2.9	0	.01	0	28.2**	21.7	ß	£	29.0	33.7
0.5	Med yield	2.7	C	.01	0	4.5*	15.9	5	4	34.9	43.7
	Med protein	0.2	0	0	0	46.5**	21.7	ς	2	21.7	37.0
	Med KWT	1.0	0	0	0	32.4**	27.5	5	ę	28.0	33.4
0.6	Med yield	1.9	0	.01	0	17.9**	14.5	9	5	40.3	43.1
	Med protein	1.3	0	С	0	27.1 **	23.9	5	£	27.4	35.3

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¹Values given are averages of 4 hase populations. KWT = kernel weight. characteristics, such as, means, variances and number of desirable progenies would be obtained if a 0.6 selection pressure for heavy kernel weight is applied than if the same selection intensity is exerted using any other selection criteria.

4.4 Experiment 4. An Evaluation of Effects of Individual Plant Selection Methods and Base Populations on the Improvement of Grain Yield and Grain Protein Content

The three main objectives of this experiment were the following:

- To investigate if stratification of environments by using different techniques would increase the efficiency of early generation selection for grain yield or grain protein content on a single plant performance basis;
- (2) To compare the performance of base populations on the basis of their means and response to selection;
- (3) To identify the best possible combination of base populations and method of stratifying environments that would facilitate selection for yield and (or) protein content.

Effectiveness of selection for grain yield on a space planted single plant performance basis was evaluated using 3 selection methods: (1) rhombus grid design, (2) Gardner's (1961) method; and (3) simple mass selection scheme. A description of these three selection methods has been given in the materials and methods section. A random sample of plants from each population was

included in the test to determine the response to selection and selection efficiency in each population.

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Mean grain yield per plot, actual gains from selection, and selection efficiency for grain yield using the 3 methods of selection in 4 different base populations is given in Table 29. Since the number of random plants selected from each population and included in the test was the same as the number of plants selected using the different selection methods, and also since these randomly selected plants were handled in exactly the same manner as the selected plants, it is anticipated that the results were not affected by differences in sample size or inbreeding depression. The data in Table 29 showed that stratification of environments can improve the efficiency of early generation selection as indicated by the significant response to selection and selection efficiencies. The effectiveness of the 3 selection methods in the four populations tested were reasonably comparable, with the rhombus grid design as the most effective and the mass selection as the least effective selection procedures. Both Gardner's (1961) method and the rhombus grid method gave significant response to selection for grain yield in all populations while mass selection gave significant responses in the two backcrosses only. These results indicated responses to individiual plant selection decreased as environmental variances due to soil heterogeneity increased, and illustrated the need for refinement of field techniques that would reduce the environmental variance to a level that would permit individual plant selection to

TABLE 29. Comparison of 4 methods of selection at 10% selection intensity with respect to grain yield per plot and gain from selection in 4 base populations generated from the Glenlea x Sinton cross.

	Selection method	Grain yield/plot (gms)	Gain from selection (g/plot)
F ₂	Random selection	779.8	0.0
	Mass selection	789.5	9.7
	Gardner's method	796.0	16.2*
	Rhombus grid	847.2	67.4**
Intermated F ₂	Random selection	793.5	0.0
	Mass selection	815.5	22.0*
	Gardner's method	837.8	44.3*
	Rhombus grid	828.8	35.3*
BC Glenlea	Random selection	779.5	0.0
	Mass selection	801.8	22.3*
	Gardner's method	802.5	23.0*
	Rhombus grid	903.8	124.3**
BC Sinton	Random selection	760.8	0.0
	Mass selection	802.0	41.2**
	Gardner's method	815.8	55.0**
	Rhombus grid	829.2	68.4**

S. E. = $\frac{+}{-}$ 9.2

*,** Differences (selection method - random selection)
 significantly greater than zero at the 5% and 1% level of
 significance, respectively.
be effective.

The degree of heterozygosity and heterogeniety of the individuals that make up the base populations appeared to have some influence on the efficiency of selection for grain yield. Selection was more effective in the more homozygous populations, the backcross to Glenlea and the backcross to Sinton populations, than in the F_2 or the intermated F_2 populations as indicated by the data presented in Table 29.

Greater and more spectacular efficiency of selection for grain yield was obtained when a combination of the backcross to Glenlea population and the rhombus grid method of selection were used.

In addition to selection for grain yield, selection for grain protein content was also exercised in the 4 base populations using the following 4 methods: (1) rhombus grid selection, (2) selection for grain protein content using Gardner's method (1961), (3) mass selection for grain protein content, and (4) mass selection for protein per kernel. A random sample of each of the 4 base populations was also included as a check. The results are given in Table 30. The findings obtained were inconsistent, and the level of selection efficiency obtained in most cases were too low to warrant any further discussion of the results. The cause of the failure of selection for grain protein content on an individual plant basis can be attributed to the high sensitivity of this characteristic to genotype X environment interactions, and the associated low heritabilities and intergeneration correlations of grain protein

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	Selection method	Grain protein content %	Gain from selection ¹
F ₂	Random selection	19.9	0.0
	Mass selection	19.8	-0.1
	Gardner's method	20.5	-0.6
	Rhombus grid	19.9	0.0
	Protein/kernel ²	20.9	0.1
Intermated F ₂	Random selection	20.1	0.0
	Mass selection	20.6	0.5
	Gardner's method	20.7	0.6
	Rhombus grid	20.6	0.5
	Protein/kernel	20.3	0.2
BC Glenlea	Random selection	19.8	0.0
	Mass selection	20.0	0.2
	Gardner's method	20.0	0.2
	Rhombus grid	19.7	-0.1
	Protein/kernel	19.9	0.1
BC Sinton	Random selection	19.9	0.0
	Mass selection	20.2	0.3
	Gardner's method	20.2	0.3
	Rhombus grid	20.1	0.2
	Protein/kernel	20.0	0.1

TABLE 30. Comparison of 5 methods of selection for grain protein content at 10% selection intensity.

S. E. = $\frac{+}{-}$ 0.4

1 Differences (selection method - random selection) were not significant.

²Mass selection for protein/kernel.

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content as suggested in previous sections.

The differences in efficiencies of the 3 selection methods for grain yield is mainly due to differences in experimental techniques unique to each of the 3 mothods. These differences in selection efficiencies indicated that the 3 methods had different capabilities of increasing the heritability of an otherwise less heritable character. In the case of the mass selection procedure, the heritability for grain yield can be represented by the formula

$$H^{2} = \frac{Sg^{2}}{(S_{q}^{2} + S_{e}^{2})}$$

where H^2 is the heritability of grain yield, and S^2g and S_e^2 are estimates of the genetic and environmental variances, respectively. If S_e^2 is large relative to S_g^2 then heritability would be low, and therefore, the response to selection and the efficiency of selection are reduced as shown by the results of the present study.

The method of Gardner (1961) is a more powerful method than the simple mass selection procedure in the sense that the estimate of the environmental component of variance is further sub-divided into two sub-components, one sub-component giving an estimate of the within stratum environmental variance, and the other giving an estimate of the between strata component of variance as indicated by the formula:

> $S_{e}^{2} = S_{b}^{2} + S_{w}^{2}$ S_b2 and S_w2 were the between and within stratum

component of variance respectively. Since selection is exercised within a stratum, the greater efficiency of Gardner's (1961) method over the mass selection method is attributable to reduced environmental variance, and therefore, increased heritability which can be mathematically expressed as follows:

$$H^{2} = \frac{S_{g}^{2}}{(S_{g}^{2} + S_{w}^{2})}$$

The Rhombus grid design is a further refinement over Gardner's (1961) method and capitalizes on 3 points: (1) adjusts the performance of each individual plant according to the microenvironment in which it is grown; (2) reduces the environmental variance into between and within grid variance in a manner similar to Gardner's (1961) method, but since the area of a grid in the rhombus design is smaller than the area of a stratum in Gardner's method the within grid variance is expected to be smaller in the rhombus grid design; and (3) selection is not restricted to strata as is the case with Gardner's (1961) method. As such, the rhombus grid design capitalizes on the underlying principles of both simple mass selection and the method of Gardner (1961). - 134 -

5. DISCUSSION

The primary objectives of this project were:

- To investigate the effectiveness of selection for grain yield and grain protein content on an individual plant performance basis;
- (2) To evaluate base populations of known differences in gene frequencies for their breeding values with special emphasis on the simultaneous improvement of yield and protein content;
- (3) To study more closely the nature and basis of the negative correlation between yield and protein content often reported in wheat.

In perspective of these objectives the discussion on the results of this investigation is presented under three sub-headings. These are: (1) Effectiveness of early generation selection; (2) Comparison of base populations for their breeding value; and (3) The nature and basis of the negative correlation between yield and protein content.

5.1 Effectiveness of Early Generation Selection

Development of a wheat cultivar acceptable for breadmaking purposes necessitates the assemblage into one genotype of a set of grain yield, agronomic and disease resistance characteristics along with another set of milling and baking characteristics. The

identification of this combination of simply and complexly inherited characteristics requires the plant breeder to screen a large number of experimental lines to obtain potential varieties.

Plant breeders are not in agreement as to how early selection for quantitatively inherited characteristics should be started. Two theories have evolved over many years concerning the generation in which selection for quantitatively inherited characteristics should begin. One theory is that, selection should be started in the earliest possible generation and preferably in the F₂. The proponents of this theory (McKenzie and Lambert, 1961; Shebeski, 1967; Shebeski and Evans, 1973; Sneep, 1977) argue that since a genotype possessing all the desirable genes in either the homozygous or heterozygous condition occur most frequently in the F₂, selection if at all possible, should start in that generation. Since each individual F₂ plant is genetically unique, F₂ plants cannot be replicated in space or time; and in lieu of this, visual F₂ selection is commonly practiced. Some beneficial responses have been obtained using visual selection, but the plant breeder's experience, knowledge and intuition have been shown to affect the efficiency of selection (Briggs and Shebeski, 1970; Townley-Smith et al., 1973; Stuthman and Steidl, 1976; Salmon and Larter, 1978).

Proponents of the second theory (Allard, 1960; Leffel and Hanson, 1961; Brim and Cockerham, 1961; Lupton and Whitehouse, 1957) argue that selection for metrical traits in the F₂ is ineffective,

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and therefore, should be deferred until the segregating lines have reached a fair degree of homozygousity (F4 or later generations) and the additive genetic variance is fixed. Plant breeders who chose to use this method were frequently forced to produce and test a large number of lines at an advanced stage only to find a great percentage to be undesirable.

A compromise procedure requires the plant breeder to assess the progenies of the F2 plants on a line basis in the F3 generation in which the principles of randomization and replication would enable him to remove the confounding effects of genotype X environment interactions, and thereby increase his selection efficiency (Baker et al., 1968; Shebeski and Evans, 1973; O'Brien et al., 1977, 1978). The widely used procedure is to select for highly heritable characteristics such as disease resistance, plant height, straw strength etc. that would permit the full expression of yield in the F2, and individual plants visually judged 'good performers' on the basis of these characteristics are advanced into the next generation, whereas 'poor performers' are discarded. Since most plant breeding programs geared towards the improvement of quantitative characteristics start with several thousand F_2 plants, the number of plants advanced for testing in the F3 generation using this procedure would be very large. For example, a plant breeding method proposed by Shebeski (1967) requires the yield testing of as many as 1000 F3 lines. When so many lines are to be included in a replicated yield test, one should be cautioned that the

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effectiveness of selection can be doubtful because experimental designs which can accommodate such a large number of entries without losing efficiency and precision are not available. Basically then, selection for quantitative characters can be justified in either early or late generations, but it appears that both systems have some serious disadvantages. This investigation was initiated with the premise that, to be efficient in the development of high yielding-high protein cultivars, a plant breeder must be able to identify desirable recombinants in the earliest possible segregating generation.

In the present study intense selection on a single plant basis did little to improve yield and was found to cause some undersirable effects. A selection intensity of 0.1 for any of the 9 characteristics investigated, resulted in loss of otherwise very desirable progenies. It also caused undesirable shifts in the means of negatively correlated characteristics and substantial reductions in genetic variances of important characteristics like grain yield and grain protein content. These observations agree with the findings of some investigators (Allard, 1960; Bell, 1963) but are at variance with the findings of other workers who reported some beneficial results (Knott, 1972; McNeal et al., 1978).

Several factors could have caused the ineffectiveness of early

generation selection on a single plant basis. Upward biases due to dominance and epistatic gene actions may have resulted in misclassification of some genotypes as desirable when in actual fact they may not have been. The omission of some of the elite lines and the inclusion of inferior genotypes in the selected fraction when a high selection intensity was used (Tables 24 to 28) attest to this Furthermore, the pattern in which the single plants were fact. grown did not correspond to the manner in which their progenies were tested, and as a result genotype X environment interactions may have not favored some desirable genotypes. Recent reports by Khalifa and Qualset (1975), and Nass (1978) present similar views, and emphasize the need to select individual F2 plants at higher population densities similar to those at which their progenies are to be Selection in the F_2 could have also become ineffective evaluated. due to inadequate nursery design in which little effort is put to minimize or correct for environmental effects. The use of stratification of environments in the present study, and especially the use of the 'rhombus grid design', tested for the first time in this project, have been shown to effectively reduce the masking effects of genotype X environment interactions and result in better selection efficiency. The rhombus grid design was more effective than Gardner's (1961) method in achieving this objective. However, because of difficulties involved in field planting and book-keeping, the use of the rhombus grid design would be recommended over other methods of individual plant selection only when environmental vari-

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ances are expected to be extremely large, or in plant breeding programs where individual plant selection is to be followed by intermating in an attempt to break undesirable linkage blocks.

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In space planted nurseries in which some form of stratifying the selection environment could not be provided, the use of a relaxed selection (selection intensity of 0.4 - 0.6) for heavy kernel weight appeared to be beneficial in terms of reducing the number of lines advanced for testing in subsequent generations. This procedure was also found not to cause the undesirable effects associated with intense early generation selection. In addition, the choice of kernel weight as a criterion of selection on a single plant basis in the earliest possible generation can be justified from genetic, plant breeding and physiological points of view.

Physiologically, kernel weight affects grain yield in many ways. Many plant characteristics including seedling vigour, date of emergence, date of flowering, date of ripening and grain yield have been shown to be positively related to seed size (Kauffman and McFadden, 1963). Large seeds with their greater endosperm are also able to grow from a greater depth before requiring photosynthesis to provide the food energy requirements for growth and development. It is also known that coleoptile length and kernel size are positively related, and therefore, larger seeds can be expected to emerge from deeper planting depths than smaller seeds, and thus help in good crop establishment (Brown, 1973). Genetically, kernel weight is controlled by a few genes, and is therefore, readily fixed in early generations. It is more stable to genotype X environment interactions, and therefore, can be more accurately predicted than grain yield or any other grain yield related single plant characteristic. It has high heritability and a stronger inter-generation correlation with grain yield; and being a morphological component of grain yield it is both phenotypically and genotypically correlated with yield.

From a plant breeding point of view, kernel weight can be determined after harvest, and is fast and inexpensive because equipment is available that can accurately and rapidly count and weigh the kernels. The number of seed required for kernel weight determination is sufficiently small that single plants can be evaluated. The standard error of determination of kernel weight is so low that replication would not be required. It is also the most correctly determined characteristic as the sources of error for determination of kernel weight are almost nonexistent. By way of comparison, determination of yield on a single plant basis is affected by several factors such as pre-harvest loss to birds. shattering, lodging and stem breakage; losses during transportation due to spillage; losses during treshing and cleaning; losses to rodents and pests during storage; etc. For these reasons grain yield on a single plant basis can never be as accurately determined.

The only anticipated disadvantage of using kernel weight is

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that it is negatively correlated with grain protein content. However, at a relaxed selection intensity of 0.4 - 0.6 adverse effects such as depression in mean grain protein content; reduction of genetic variance; or significant losses of high protein progenies have not been observed.

5.2 <u>Comparison of Base Populations for Their Breeding Values</u>

The value of wheat is related to both grain yield and grain protein content; therefore, it would be desirable to increase both, or at least increase one characteristic without reducing the other. Breeding systems designed to increase these two characteristics have utilized crosses between high yieldings utility wheat cultivars and high protein bread wheat cultivars. In general, the pedigree method of selection has been used most frequently. Selection for desirable recombinants starts in the F_2 population followed by progeny row and more single plant selection in subsequent generations. Progress achieved using this method has been slow in developing strains with both the grain yield and agronomic characteristics of the utility cultivars, and the high protein content of the bread wheat cultivars. The exact cause of this problem is not known, but may be due to the negative relationship between grain yield and grain protein content, or simply due to the increased difficulty of selecting individuals with favorable combinations of genes that affect grain yield and grain protein content. If these problems are responsible for the lack of plant breeding progress, then some

modification of the conventional breeding and selection systems seems necessary. One modification possible, is changing the genetic architecture of the initial base population in which selection is started.

Alternative approaches are available which can be advantageously used to induce genetic shifts and (or) increase the frequency of desirable genotypes, and thereby improve the breeding value of base populations. One such method is the use of a random intermating population (Hanson, 1959). This method would produce the most recombinants when linkage is involved, but its disadvantage is that no genetic advance can be made during the intermating generations.

Another method which plant breeders can use advantageously is the use of backcross base populations. The objective here is not to produce near-isogenic lines, but to establish a breeding population from which desirable recombinants can be selected. The backcross method is advantageous in that it will increase the probability of reconstituting the best parental variety by further selection. In this way, it will enable the plant breeder to capitalize on both introgression and upgrading simultaneously. Additional advantages of a backcross base population is that it enables the plant breeder to select for one characteristic while holding the other characteristic at some desirable level. A problem anticipated with a backcross base population is that some favorable genes from the nonrecurrent parent might be lost or their frequency in the base population reduced significantly. Also, backcrossing may depress the population mean of a characteristic that was initially present in the non-recurrent parent to such a level that the delay in reaching the level of the non-recurrent parent may be such as to make use of the population undesirable.

The majority of the wheat breeding programs engaged in the simultaneous improvement of grain yield and grain protein content have concentrated on the F_2 and subsequent generations in the selfing series, with the result that the potentialities of the back-cross and the intermated F_2 populations have never been explored. Assuming that superior base populations are of fundamental importance to efficient improvement of grain yield and grain protein content simultaneously, an attempt has been made in this study to compare the breeding value of the backcross and intermated F_2 populations.

The seven base populations generated from two crosses were evaluated for several parameters including means, phenotypic and genotypic variances, phenotypic and genotypic correlations, heritabilities, responses to selection, correlated responses to selection, and frequency of desirable and undesirable genotypes. The rationale behind choosing these parameters were as follows. When the improvement of only one characteristic is the breeding objective, both the mean and the variance are important parameters of the population; the former gives a reflection of the superiority of individual genotypes that comprise the population, while the

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latter gives an indication of how diverse these individual genotypes are in their genetic constitution. Thus, both the population mean and the population variance are important ingredients of any breeding program. Since not all populations possess both high mean and high variance, the question of whether an increase in the variance of the population, or an increase in the mean of the population is more important, is an intriguing question. Usually, the population mean is considered to be more important than the population variance because, in order for the population mean to be high, the performance of the constituent genotypes must be high (Dyck and Baker, 1975).

When the breeding objective is the simultaneous improvement of two or more metrical traits, the selection of the base population to use in a breeding program becomes even more difficult. In this instance, not only has one to consider the two parameters mentioned above, but also the genetic and phenotypic correlations among pairs of characteristics in the different populations. Correlations among traits are of interest because they indicate the correlated response that may occur when single trait selection or index selection is Genetic correlations also give an indication of the practised. extent of linkage and (or) pleiotropism in the population. The heritability estimates give quantitative measurements of the extent to which genetic characteristics are affected by environment and the degree of progress to be expected from selection. The remaining parameters are self-explanatory and do not require further

explanations.

Comparisons of the various base populations for the above parameters showed the unique advantages of populations synthesized by backcrossing to the utility cultivars. They indicated that higher performing genotypes were most often, and more easily obtained in populations in which mean grain yield was higher. An apparent problem with populations derived by backcrossing to the utility cultivars was that mean grain protein content of the populations are reduced; yet this appears to be a small price to pay for both an increase in the frequency of the more desirable genotypes, and the opportunity to reconstitute the characteristics of the better parent. It seems that the residual variability for grain protein content would still provide the plant breeder with ample opportunity to select for genotypes that combine both high yield and high protein content. No special advantages for an intermated F₂ population were obtained, and therefore, its use is not recommended in selection programs where the ultimate objective is to increase both grain yield and grain protein content. Similarly, F2 populations and populations derived by backcrossing to bread wheat cultivars are not desirable source populations for extracting genotypes that combine high yield with high protein content.

The literature indicates that some plant breeders have used a limited backcross program and obtained favourable results. The Canadian wheat cultivar 'Selkirk' was developed from a breeding program in which a limited amount of backcrossing was followed by selection (Peterson, 1958). Grafius et al (1976) in barley and Meredith (1977) in cotton, have reported beneficial results from a limited backcross base population. These authors attributed their success to the backcross which tended to preserve the integrity of an already proven system while adding factors from another system. Their findings give firm and full support to the conclusion drawn from the present study.

5.3 The Nature and Basis of the Negative Correlation between Grain Yield and Grain Protein Content

It has been almost an article of faith from the earliest days of plant breeding, that it would be very difficult to improve both grain yield and grain protein content simultaneously. Implicit in the findings of most of the studies devoted to the improvement of these characteristics is that the cause of this negative association is genetic in origin, and in many of the studies, linkage and (or) pleiotropy have been implicated as the culprits. Not much can be done with pleiotropy, but if grain yield and grain protein content are conditioned by linkage, then the barriers to progress in improvement of both characteristics can be minimized through the use of a random mating population.

One method of determining if linkage is involved would be to compare an intermated F_2 population with a conventional F_2 population for various population parameters among which variances,

covariances and correlations are the most important (Miller and Rawlings, 1967; Meredith and Bridge, 1971; Scholl and Miller, 1976). For a single characteristic, the variance of an intermated F_2 population will either increase or decrease in magnitude with reference to an F2 population depending on whether the type of linkage involved is a coupling phase linkage or a repulsion phase When repulsion phase linkages are predominant, the linkage. variance of the intermated F₂ population would be greater than the variance of the F2 population. On the other hand, if coupling phase linkages are predominant, the intermated F_2 population would be expected to have less variance than the F₂. Where two characteristics are involved, as is in the present study, the argument would be essentially the same except that covariances are used instead of variances. If intermating is effective in breaking linkage blocks, then a reduction in the strength of the correlation coefficient would also be expected in the intermated F2 population. While significant changes in variances, covariances and correlations between two characteristics are sure indicators of the presence of breakable linkage blocks, the absence of statistically significant differences for these parameters between the F_2 and the intermated F₂ populations may not signify the absence of linkage blocks.

Comparisons between the F_2 and intermated F_2 populations were possible from data collected in the two test years. However, since the space planted material grown in 1978 appeared to have been

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affected to a considerable degree by genotype X environment interactions, only the 1979 material was used for testing if grain yield and grain protein content are genetically linked characteristics.

Genes for grain yield and grain protein content in the Glenlea X Sinton cross were contributed by two different parents. Therefore, the predominant type of linkage to be expected in the F₂ would be repulsion phase linkage; and on the basis of the aforementioned arguments, intermating would be expected to increase the absolute magnitude of the covariances and decrease the correlations between grain yield and grain protein content. Phenotypic covariances and correlations between the two characteristics were found negative and highly significant in both the F₂ and the intermated F₂ populations. However, the phenotypic covariance (mean cross product x 10^6) of the intermated F_2 population (-455) was found to be smaller (ingnoring sign) than the phenotypic covariance of the F2 population (-675). 0n the other hand, phenotypic correlations between grain yield and grain protein content in the intermated F_2 population (-0.353) was found to be slightly larger than the phenotypic correlations between grain yield and grain protein content in the F2 population(-0.328). At the genotypic level, genotypic covariance between grain yield and grain protein content was again smaller in the intermated F_2 population (-987) than in the F_2 population (-1192), while the genetic correlation coefficient obtained in the

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intermated F₂ population (-0.603) was larger than that obtained in the F_2 population (-0.573). These observations are not compatible with the genetic expectations and suggest that factors other than genetic linkage may be the cause of the negative correlation between the two characteristics.

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Probably the strongest and most direct evidence suggesting that the negative correlation between grain yield and grain protein content is not caused by linkages was obtained from analysis of genetic correlations. In 6 of the 7 populations tested, genetic correlations between grain yield and grain protein content were nonsignificant. This finding is in agreement with the findings of Dyck and Baker (1975) who also observed that there was no significant genetic correlation between the two characteristics. Further evidence supporting this could be obtained from a comparison of the strength of the negative correlation coefficient obtained in parental populations, and the various base populations. Since parental lines are genetically uniform, any significant correlation between grain yield and grain protein content would not be due to genetic linkage or pleiotropy. In this experiment it was found that the magnitude of the negative correlation in the parental cultivar Glenlea was larger than coefficients obtained in base populations generated by using it as one of the parents. Similarly, NB131 showed more negative correlation than any of the 3 base populations synthesized using it as a parent.

Although negative correlations between grain yield and grain

protein content were frequently observed in the present study, multiple regression analyses showed that variation in grain yield accounted for only a small fraction of the variation in grain protein content. Standardized partial regression analysis indicated that when effects of other factors such as morphological yield components and protein per grain are removed, the correlation between the two characteristics is not different from zero. A path anaylsis of the data suggested that negative correlations between the two characteristics emerged not because of the direct relationships, but because of indirect relationships through joint dependence of both characteristics on the same set of primary characteristics among which kernel weight and kernels per spike were the most important. Data obtained from a comparison of utility wheat cultivars and bread wheat cultivars showed that the low grain protein content of the high yielding lines could have resulted from a limited amount of protein diluted in a larger mass of dry matter.

Extensive studies have been conducted to localize the genes that control grain yield and grain protein content in wheat. Lelley (1976) based on an extensive literature review reported that 19 chromosomes influence grain protein content, and at least 16 chromosomes govern grain yield. With such a large number of genes and chromosomes involved, it would be very unlikely that restricted genetic recombination would be the obstacle in the simultaneous improvement of grain yield and grain protein content.

According to results obtained in the present study, kernel

weight seems to be the fulcrum about which the yield-protein lever oscillates. High kernel weight increases yield but reduces protein content, and conversely, low kernel weight increases grain protein content and reduces yield. The relationships of kernel weight with high grain protein content was also noticed by Pomeranz and Betchel (1978) who attributed the negative correlation between the two characteristics to the surface to volume ratio of the seed. According to these authors, much of the protein in the wheat grain is concentrated in the aleurone and sub-aleurone layers, and as kernel size decreases, the surface to volume ratio increases resulting in increased grain protein content.

The conclusion drawn from this study is that the reported negative correlation between grain yield and grain protein content is phenotypically real, but is not genetic in origin. The development through plant breeding, of high yielding, high protein cultivars such as Atlas 66 (Johnson et al., 1968) attest to the fact that simultaneous improvement of both characteristics is possible but difficult to accomplish.

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6. CONCLUSIONS

1. The bread wheat cultivars used in this study were found to be excellent in milling and baking characteristics, but relatively low yield potential. The major attributes of the utility wheat cultivars were a distinct and significant yield advantage over the bread wheat cultivars; good milling characteristics; larger blend loaf volumes and longer mixing tolerance. Their major weaknesses were low grain protein content; inferior flour protein quality, a larger drop in protein percentage from the grain to flour; and generally inferior baking qualities.

2. Negative correlations between grain yield and grain protein content occured, but the r values obtained were small suggesting that optimizing both characteristics would be hindered but not precluded by the negative association.

3. The underlying factor responsible for the negative relationships between grain yield and grain protein content appeared to be non-genetic in origin. Evidence has been obtained that: (a) environmental effects; (b) dilution of protein by non-protein compounds; and (c) source-sink relationships may cause negative associations between the two characteristics. More significant was the observation that the negative correlation between grain yield and grain protein content may have emerge from the opposite but joint

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dependence of both characteristics on the same set of primary characteristics like kernel weight and number of kernels/spike.

4. Significant inter-generation correlations between highly heritable single plant characteristics, and grain yield and grain protein content were found, but the r values obtained were not sufficiently large to warrant intense early generation selection (0.1 selection intensity) selection for grain yield or grain protein content by indirectly selecting for these characteristics.

5. Intense early generation selection (selection intensity of 0.1) was found not only to be ineffective in improving grain yield or grain protein content, but also to cause some adverse effects including significant reduction in genetic variances; undesirable shifts in the means of the characteristics for which selection has not been practised; and a considerable loss of desirable progenies. A relaxed selection pressure of between 0.4 and 0.6 for kernel weight was shown to cause no such adverse effects, and was beneficial in minimizing the number of elite lines advanced for testing in subsequent generations.

6. Stratification of environments improves the efficieny of early generation selection. A rhombus grid design, proposed for the first time in this study, was more effective than either Gardner's (1961) method or simple mass (individual plant) selection in reducing

environmental effects, and in improving selection for grain yield on a single plant performance basis.

7. Base populations, though generated from the same set of parents may provide different chances of success in trying to improve both yield and protein content in wheat. A bace population synthesized from a limited backcross to the utility wheat parent was more desirable in this respect than an F_2 or an intramated F_2 population. On the other hand, a base population synthesized by backrossing to the bread wheat parent is of little use in a program aimed at the simultaneous improvement of both yield and protein content.

8. For a breeding objective of developing a high yielding high protein cultivar, a breeding strategy was formulated on the basis of the above information. The most logical approach would be: (i) a relaxed selection intensity of 0.4 to 0.6 for kernel weight in the earliest possible generation should be used to minimize the number of undesirable lines advanced into the next generation; (ii) in later generations to improve grain yield through selection for yield components other than kernel wieght and to improve grain protein content through selection for protein per grain; (iii) the selection scheme should include appropriate means of stratifying environments so that genetic effects would not be masked by large environmental effect. When individual plant selection under space planted conditions is practised use of a rhombus grid design would be more beneficial than the conventional individual plant selection method or the method of Gardner (1961); (iv) the base population in which to start selection should be one in which the F_1 has been backcrossed to the high yielding utility parent so that large sacrifices in yield would not have to be made in an attempt to improve protein content, as would be the case if the F_2 is used as a source population.

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AACC* method 56-60.	2. Sedimentation value	12.
Same as 7 above.	1. Flour protein content (%)	
AACC* method 26-20 14% moisture basis.	0. Flour yield (%)	10
1000 kernel weight X % grain protein.	9. Protein/kernel ¹ (mg)	9
Grain yield/plant or plot X 0% grain protein.	 Protein yield¹ (g/plant or kg/plot) 	œ
By using Kjehdahl method, % N x 5.7 on 0% moisture basis.	<pre>7. Grain protein content (%)</pre>	7
Count out 250 or 1000 unbroken kernels and weigh. Multiply weight by 4 if 250 kernels used.	<pre>6. Kernel weight (g)</pre>	6
Pour grain into 250 cc container, strike-off and weight. Multiply weight by 400.	5. Test weight (kg/hl)	ហ
By dividing total number of kernels/plant by number of spikes/plant.	4. Kernels/spike	4
Number of fertile spikes on the plant measured about a week before harvest.	3. Spikes/plant	ω
Measured from ground level to the top of the main culm at physiological maturity (one week before harvest).	2. Plant height (cm)	N
Total grain dry weight measured on materials dried at 30°C for a minimum of 4 days and equillibrated for a minimum of 7 days.	<pre>1. Grain yield (g/plant or plot)</pre>	щ
Method	Parameter	1
omic and quality parameters and methods by	APPENDIX TABLE 1. List of agron- which they were determined.	1

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13.	Remix loaf volume (cc)	Following the procedure of Irvine and McMullan, 1960.**
14.	Blend loaf volume (cc)	Same as 13 except that the sample being tested is blended with an equal weight of soft white wheat flour.
15.	Farinograph absorption (%)	AACC method 54-21.
16.	Dough development time (min)	AACC method 54-21.
17.	Mixing tolerance index (Brabender units)	AACC method 54-21.

*American Association of Cereal Chemists, 1962. Cereal laboratory methods (7th ed.), St. Paul, Minnesota.

** Irvine, G.N., and M.M. McMullan, 1960. The remix baking test. Cereal Chem. 37: 603.

 $^{\mathrm{I}}$ Values were not compensated for moisture content.

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