EARLY GENERATION SELECTION FOR PROTEIN CONTENT IN DURUM WHEAT

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by

William Grant Legge

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ABSTRACT

Legge, William Grant. Ph.D., The University of Manitoba, October, 1987. Early Generation Selection for Protein Content in Durum Wheat. Major Professor; D. Leisle.

Three durum wheat (Triticum turgidum L. var durum) crosses were studied to determine the effectiveness of two methods of early generation selection for grain protein content (%). The first method used near infrared reflectance (NIR) data from F_3 families grown in replicated hill plots in 1984 to establish high (HP) and low (LP) protein content selection groups. The second method used a sucrose-NaCl solution (ISD) to separate bulked F_2 seed samples, previously imbibed in water for 7 days at 0 to 2°C, into low and high density fractions for HP and LP, respectively. A random (RP) selection group was also established for each method. Selection groups were evaluated in F_5 at two locations in 1985 using replicated four-row and hill plots for NIR, and hill plots for ISD.

Overall, response to selection as determined in F_5 ranged from 0 to 0.4% protein content. HP had significantly higher protein content than LP in three, one, and one of six cross locations for NIR row, NIR hill, and ISD hill plots, respectively. RP seldom differed from HP or LP. Low

response to selection was probably due to genotype x environment interactions. Heritability in standard units for protein content using F_3-F_5 correlations ranged from 20 to 57 and 11 to 37% for NIR row and hill plots, respectively. Hill plots were only 45 to 98% as efficient as row plots in selecting for protein content, and require additional replication. Early generation selection for protein content had little effect on yield, test weight, kernel weight, protein yield, protein per kernel or kernel shrivelling although HP had significantly higher protein yield than LP in NIR F_5 row plots. In general, protein content was negatively correlated with yield, kernel weight and test weight, positively correlated with kernel shrivelling, and inconsistently correlated with protein yield and protein per kernel. The highest, most consistent correlation coefficients for protein content were with kernel weight and shrivelling.

It was concluded that response to selection was too low for either method to justify the effort required to select for protein content in early generations.

1. INTRODUCTION

Durum wheat (Triticum turgidum L. var durum), a tetraploid (2n = 28) species with the AB genomes, is used to make pasta products such as spaghetti and macaroni (Feldman, 1976). It is adapted to the semi-arid regions of the world and is grown primarily in the Mediterranean basin, India, Soviet Union, Argentina, United States and Canada (Matsuo, 1982). The latter three countries are the major exporters while the other countries, Western Europe and Japan are the main importers. In Western Canada, durum wheat occupied approximately 1.74 million ha in 1985 and yielded 1.957 million metric tonnes (Statistics Canada, 1985). This represented about 13% of the total area sown to wheat and 8.6% of the total wheat production in Western Canada in 1985.

An important breeding objective in durum wheat is to maintain or increase protein content while increasing grain yield. Protein content, expressed as a percentage of the total seed weight, is a critical factor in determining the cooking quality of pasta products (Dexter and Matsuo, 1977; Grzybowski and Donnelly, 1979). Importing countries, particularly Italy, demand high protein content in the durum wheat that they purchase. As in other cereal crops,

recent high yielding cultivars tend to have lower protein content.

Selection for quantitative traits in the earliest possible generation of a breeding program is theoretically advantageous because a greater proportion of desirable genotypes would be retained (Shebeski, 1967). The variable results of many studies on early generation selection for yield in wheat suggest that response to selection is low relative to the extra labor and resources required (Knott and Kumar, 1975; Weber, 1984). Although much less studied, early generation selection for protein content in wheat appears to be more effective. For example, Guthrie et al. (1984) reported that the response to selection for protein content in F_3 of six hard red winter wheat (Triticum aestivum L.) crosses ranged from 0.5 to 1.1% when the selections were grown in F_4 yield trials. Several recurrent selection studies also indicated that progress can be made in selecting for protein content in wheat (McNeal et al., 1978; Loffler et al., 1983). Heritability estimates are generally higher for protein content than yield (Davis et al., 1961; Baker et al., 1968b; Cox et al., 1985). In durum wheat, there is a lack of information on the heritability of and early generation selection for protein content.

An important constraint to early generation selection for protein content is the time and cost of screening large numbers of experimental lines (Peterson et al., 1986). Even

near infrared reflectance spectroscopy (NIR), which is generally more rapid and easier to use than most other methods, may have inadequate capacity for this purpose (Johnson et al., 1979a). Garzon-Trula (1984) reported that protein will absorb five times more water than will starch when wheat seeds are soaked for 10 days at 0 to 3° C. Thus, imbibed seeds could be separated into high and low protein fractions on the basis of density using a suitable solution. Peterson et al. (1986) evaluated imbibed seed density (ISD) selection as a rapid, cheap, simple mass selection procedure for increasing the protein content of early generation bulk populations of wheat. They obtained increases in protein content ranging from 0.6 to 1.1% in 10 of 52 populations.

A second major constraint is the inverse relationship between protein content and yield observed in many studies (Johnson et al., 1985). Breeders are generally reluctant to select for protein content if yield is compromised. However, it has been suggested that the negative correlation between protein content and yield is not an insurmountable barrier (Johnson et al., 1979a, 1985). A better understanding of the relationship of protein content to yield and yield components is clearly needed. The effect of early generation selection for protein content on other important agronomic and economic traits has received little attention.

The overall objective of this study was to determine the effectiveness of early generation selection for protein content in durum wheat. Specific objectives were to:

(1) evaluate and compare two methods of early generation selection for their ability to identify genetic differences in protein content and to measure their response to selection in the F_5 generation
   - first method used NIR to determine protein content of F_3 families grown in replicated hill plots
   - second method used ISD in bulk seed samples from F_2 plants,

(2) compare the efficiency of hill and four-row plots in selecting for protein content,

(3) determine the heritability of protein content using intergeneration correlations,

(4) determine the effect of early generation selection for protein content on yield and other important traits, and

(5) examine the relationship of these other traits to protein content through correlation studies.

2. LITERATURE REVIEW

2.1 Factors Determining Protein Content

Protein content in wheat is controlled by both genetic and environmental factors. Johnson et al. (1985) reported that the total variation in protein content of common wheats (Triticum aestivum L.) in the USDA World Wheat Collection ranged from approximately 7 to 22%, with genetic variation accounting for 5% or about a third of the total. They indicated that the large proportion of nongenetic variation has made the genetic study and manipulation of protein content difficult. Johnson et al. (1973b) observed similar variation in protein content for durum wheats.

2.1.1 Environmental Factors

The protein content of a single wheat genotype can range from 8 to 18% depending on the environmental conditions under which it is grown (Johnson et al., 1969). In general, protein content is increased by high temperatures (Hopkins, 1968; Partridge and Shaykewich, 1972; Kolderup, 1975a, b, 1979; Campbell and Davidson, 1979; Campbell et al., 1981, 1983a), conditions of moisture stress (Hutcheon and Rennie, 1960; Hopkins, 1968; Terman et al., 1969; Kolderup, 1975b; Campbell et al., 1977, 1981, 1983a;

Campbell and Davidson, 1979; Nicolas et al., 1985), and high levels of soil fertility, particularly available nitrogen (Sosulski et al., 1966; Terman et al., 1969; Partridge and Shaykewich, 1972; Johnson et al., 1973a; Campbell et al., 1977, 1981, 1983a;). Terman et al. (1969) found that with adequate water, the main effect of nitrogen (N) was to increase yield; with a severe water deficit, N only increased protein content; and in intermediate situations, N increased both protein content and yield. They also observed that water stress may not increase protein content if soil N levels are low. Campbell et al. (1981) reported that the effect of temperature on protein content was generally independent of N and moisture. Photoperiod and the amount of light may also affect protein content (Kolderup, 1975a).

Agronomic practices which influence soil moisture or N affect protein content in wheat. Johnson et al. (1973a) and McNeal et al. (1971) found linear increases in protein content with applied N fertilizer while Nass et al. (1976) and Kramer (1979) reported that protein content was increased only at higher rates. Late applications of N fertilizer at or after flowering often increase protein content without affecting yield (Finney et al., 1957; Eilrich and Hageman, 1973; Miezan et al., 1977). However, McNeal et al. (1963) found no differences in protein content when N was applied at sowing or flowering in a dry year. In durum wheat,

Robinson et al. (1979) also observed that protein content was affected by the amount of N applied and its timing. Campbell et al. (1977) reported that irrigation decreased protein content in wheat at a given level of N fertilizer when compared to dryland conditions. In a long term study, Campbell et al. (1983b) found that the protein content of wheat grown on fallow was higher than on stubble with the exception of flax stubble. Austenson (1983) has reviewed the effects of crop rotations, herbicides and growth regulators on protein content in wheat.

Environmental conditions conducive to lodging generally increase protein content (Pinthus, 1973). In wheat, Laude and Pauli (1956) reported that lodging increased protein content by 10% overall relative to the standing crop with the greatest increase occurring 11 to 15 days after heading. Pumphrey and Rubenthaler (1983) found a 14% increase overall relative to the standing crop when lodging occurred just before or during heading, while Weibel and Pendleton (1964) observed only a 5% increase. Robinson et al. (1979) reported a positive correlation between protein content and lodging in durum wheat.

Protein content may be affected by disease and insect pests. For example, Fitzgerald and Stoner (1967) found that wheat infected by barley yellow dwarf virus had a slightly higher protein content than uninfected plants. Williams (1966) suggested that some diseases such as stem and leaf

rust reduce protein content. Ba-Angood and Stewart (1980) demonstrated that cereal aphid infestations may greatly reduce protein content in wheat.

2.1.2 Genetic Factors

Protein content in wheat is a quantitatively inherited trait (Clark, 1926; Clark and Smith, 1928; Aamodt and Torrie, 1935; Worzella, 1942; Ausemus et al., 1967). Various studies have shown that nearly all chromosomes of wheat affect protein content (Law and Payne, 1983). Most researchers agree that protein content is controlled by a few major genes and many minor ones (Haunold et al., 1962; Lofgren et al., 1968; Johnson et al., 1979a; Law and Payne, 1983). Genes having major effects on plant growth and development, such as the semi-dwarfing genes, may have important pleiotropic effects on protein content (Law and Payne, 1983; McClung et al., 1986).

Few studies have been conducted to determine the inheritance of protein content in durum wheat. Johnston (1980) found that additive genetic effects for protein content were most important, accounting for 96% of the genetic variation in a study with 2 crosses involving the parental, F_1, F_2, F_3, BC_1, and BC_2 generations in North Dakota. Bebyakin and Martynov (1983) in the Soviet Union also reported that protein content was controlled by additive genes. Diallel analyses by Zitelli et al. (1979) in Italy and Maloo and Mehrotra (1984) in India revealed a predominance of additive

gene action for protein content although non-additive effects were also significant. In Israel, Avivi et al. (1983) found weak dominance for low protein content in four crosses involving a durum wheat cultivar and four high protein lines of Triticum turgidum var dicoccoides. They suggested that several genes plus modifiers with minor effects were responsible for high protein content. Working with similar material, Millet et al. (1984) also reported weak dominance for low protein content. In addition, they concluded that protein content was determined mainly by the maternal plant.

Both additive and nonadditive gene action may influence protein content in common wheat (Johnson et al., 1985). A preponderance of additive gene action has been reported by many workers (Stuber et al., 1962b; Chapman and McNeal, 1970; Ram and Srivastava, 1975; Ketata et al., 1976; Bhullar et al., 1979; Mihaljev et al., 1979; Sampson et al., 1983), while others have reported a preponderance of dominance effects (Kraljevic-Balalic et al., 1982; Corpuz et al., 1983a). Dominance or partial dominance for low protein content has often been found (Davis et al., 1961; Lebsock et al., 1964; Chapman and McNeal, 1970; Johnson et al., 1973b; Diehl et al., 1978; Halloran, 1981; Kushnir and Halloran, 1982; Vojdani et al., 1983;). Cowley and Wells (1980) and Corpuz et al. (1983a) have reported dominance for high protein content. Hsu and Sosulski (1969) indicated that

both dominant and recessive genes contribute to high protein content, while Kaul and Sosulski (1965) found no net dominance for high or low protein content. In both studies, transgressive segregation for both high and low protein content was observed. Johnson et al. (1979b) reported similar results. Halloran (1975) and Mihaljev et al. (1979) indicated that genetic control of protein content, whether by dominant or recessive genes, may change depending on the environment. Epistasis and linkage have been reported to affect protein content in a number of studies (Kaul and Sosulski, 1965; Halloran, 1975; Ketata et al., 1976; Konzak, 1977; Diehl et al., 1978; Bhullar et al., 1979; Sampson et al., 1983).

Significant genotype x environment interactions have frequently been reported for protein content (Clark, 1926; Aamodt and Torrie, 1935; Miezan et al., 1977; Diehl et al., 1978; Jatasra and Paroda, 1982). However, Johnson et al. (1973a) found that the expression of genes for high protein content derived from Atlas 66 was very stable over a wide range of environments. In contrast, Konzak (1977) reported marked differences in the stability of protein content in durum wheat. He indicated that genotype x environment interactions are subject to genetic control.

2.2 Heritability of Protein Content

Heritability estimates indicate the relative importance of heredity in determining phenotypic values for a trait and

are useful in predicting response to selection (Falconer, 1960). Since they are specific to the population, environment, experimental procedures and method of estimation, use of heritabilities out of context is not legitimate though it is useful to consider general orders of magnitude of heritabities in a wider framework (Simmonds, 1979). Heritabilities for different traits as well as the trait of interest may be helpful in determining the relative ease of selection.

Heritability of protein content in durum wheat has been determined in only a few studies. Gill and Brar (1977), using 23 diverse strains of durum wheat in India, obtained heritabilities of 56, 41 and 87% for protein content, yield per plant and kernel weight, respectively. In Italy, Zitelli et al. (1979) calculated broad sense heritabilities of 83% for protein content and 90% for kernel weight using variance components derived from a diallel analysis. Vallega (1985), also working in Italy, reported intergeneration correlations ranging from 38 to 67% for protein content in advanced lines of a durum wheat cross. In Israel, broad sense heritabilities for protein content ranging from 65 to 74% were obtained using the F_2 and parental populations of four crosses involving a durum wheat cultivar and high protein lines of T. turgidum var dicoccoides (Avivi et al., 1983). In contrast to these studies, work in the Soviet Union indicated that heritabilities of protein content in

durum wheat were low and highly variable (Bebyakin and Piskunova, 1982).

Heritabilities for protein content in common wheat vary widely (Table 1). Overall, most heritabilities for protein content appear to fall between 30 and 70% with an average of approximately 50%. In some studies, heritabilities for protein content were not significantly different from zero (Clark, 1926; Lofgren et al., 1968).

Heritabilities for protein content are generally greater than those for yield but less than those for kernel weight in common wheat (Table 2). This suggests that selection for protein content will be more difficult than selection for kernel weight but easier than selection for yield.

TABLE 1. Summary of heritability estimates for protein content in common wheat.

Reference	Method[1]	Generation	Heritability
Aamodt and Torrie (1935)	HSU	F_3, F_4	44 - 85
Corpuz et al. (1983a)	OPR	F_3, F_4	41 - 77
	HSU	F_3, F_4	30 - 52
Halloran (1981)	OPR	F_3, F_4, F_5	48 - 71
Haunold et al. (1962)	OPR	F_2, F_3	25 - 36
	HSU	F_2, F_3	41 - 58
Hsu and Sosulski (1969)	VC, BS	P_1, P_2, F_2	42 - 80
Johnson et al. (1973b)	HSU	F_3, F_4	34 - 43
Kaul and Sosulski (1965)	VC, BS	P_1, P_2, F_1, F_2	79 - 82
	VC, NS	F_2, BC_1, BC_2	66
Lebsock et al. (1964)	OPR	F_3, F_5, F_6	37 - 70
Milczak (1979)	VC, BS	P_1, P_2, F_2	33 - 41
	HSU	F_2, F_3	38 - 39
Sampson et al. (1983)	HSU	F_4, F_6	25 - 50
Vojdani et al. (1983)	VC, NS	P_1, P_2, F_1, F_2, BC_1, BC_2	43 - 54

[1]HSU = heritability in standard units.
OPR = offspring-parent regression method.
VC = variance components method.
BS = broad sense heritability.
NS = narrow sense heritability.

TABLE 2. Comparison of heritabilities for protein content, yield and kernel weight in common wheat.

Reference	Heritability		
	Protein Content	Yield	Kernel Weight
Baker et al.(1968b)	47 - 82	28 - 74	77 - 93
Cox et al. (1985)	30 - 70	34 - 37	
Davis et al. (1961)	54 - 69	14 - 53	
Dyck and Baker (1975)	59 - 63	46 - 60	76 - 77
Guthrie et al. (1984)	39 - 61	0 - 23	
Jain et al. (1975)	17 - 22		75 - 78
Knott and Kumar (1975)	50 - 72	12 - 31	
Loffler and Busch (1982)	76 - 83	70 - 78	
Pearson et al. (1981)	19 - 43		72 - 88
Randhawa and Gill (1978)	40 - 51	6 - 40	62 - 90
Schlehuber et al. (1967)	47	41	
Sharma et al. (1973)	27 - 28		68 - 96
Sunderman et al. (1965)	24 - 26	7	
Worzella (1942)	30 - 37		47 - 65

2.3 Early Generation Selection for Protein Content

For quantitatively inherited characters, Shebeski (1967) and Sneep (1977) have shown that the frequency of plants with the most desirable gene combinations is highest in the F_2, declining rapidly in subsequent generations. To reduce the probability of losing the best genotypes, they suggested that selection should begin in the earliest possible generation. On the other hand, Lupton and Whitehouse (1957) and Allard (1960) suggested that selection for quantitative traits should be delayed until later generations when the proportion of homozygotes is greater because the phenotype of the heterzygote is not a reliable guide to the lines which might be derived from it. The magnitude of environmental variation and genotype x environment interactions may also affect the success of early generation selection since there is usually inadequate seed for replicated tests over a range of environments (Whan et al., 1982; Weber, 1984). To be of value, early generation testing must be able to predict the performance of selections in later generations (O'Brien et al., 1978; Whan et al., 1981).

2.3.1 Response to Selection

Although it is generally agreed that selection for yield among individual F_2 plants is ineffective (McGinnis and Shebeski, 1968; Knott, 1972, 1979), conflicting results have been obtained when selecting for protein content in the F_2 of wheat crosses. Haunold et al. (1962) reported that

the gain in protein content in F_3 due to selection in spaced F_2 plants was approximately 8% of the mean of the unselected sample for two winter wheat crosses. Heritability in standard units ranged from 41 to 58%. In a further study with one of the above crosses, Johnson et al. (1963) found that a number of families selected for high protein content in F_2 and high yield in F_3 were consistently more productive and had a protein content averaging 3% higher than the low protein parent over a three year period. Clark (1926) found no correlation between F_2 and F_3 protein content in spring wheat although some high protein F_3 samples were obtained as a result of selection in F_2. He observed genotype x environment interactions for protein content in F_3 families. Several researchers suggested that selection for protein content among F_2 plants and among unreplicated, spaced F_3 plants is of limited value (Sunderman et al., 1965; Bhatia and Rabson, 1976; Pearson et al., 1981; Konzak and Rubenthaler, 1984; Paccaud et al., 1985). The considerable variation in protein content found among plants of the same genotype grown in the same test supports this point of view (Clark, 1926; Levi and Anderson, 1950; Kaul and Sosulski, 1965; Diehl et al., 1978).

Guthrie et al. (1984) used grid selection in unreplicated F_3 rows of six hard red winter wheat crosses to select for high and low protein content and grew the selections in F_4 replicated yield trials. High and low protein selection

groups differed significantly with differences ranging from 0.5 to 1.1% protein content. Realized heritabilities for protein content ranged from 39 to 61%. Yields of the high protein selection groups were equal to the low protein selection groups in three crosses, less in two crosses and greater in the remaining cross. They concluded that selection in F_3 was effective in identifying lines with high protein content.

McNeal et al. (1972) selected F_3 progeny rows for high and low protein content in eight spring wheat crosses. For each cross, they composited the seed from 14 high protein F_3 progeny rows for the high protein sample and 14 low protein F_3 progeny rows for the low protein sample. The samples were grown as F_4's at three locations in Montana. In 23 of 24 comparisons, the high protein sample had a higher protein content than the low protein sample.

With a selection pressure of 10% for protein content in a hard red spring wheat cross, Lebsock et al. (1964) found that F_5 and F_6 lines derived from selected F_3 lines had 0.7% higher protein content than F_5 and F_6 lines derived from unselected F_3 lines.

Using two cycles of recurrent selection for protein content in spring wheat, McNeal et al. (1978) found significant and consistent differences between the high and low F_4 protein selections from each cycle. Differences between the high and low protein selections ranged from 1.5 to 3.3%

protein content after the first cycle and from 1.5 to 4.7% after the second cycle. Loffler et al. (1983) reported an increase in protein content ranging from 0.7 to 1% after two cycles of recurrent selection in hard red spring wheat. In a cross between spring and winter wheats, Randhawa and Gill (1978) found that one cycle of recurrent selection and pedigree selection in F_3 increased protein content by 4.3 and 3.25% of the mean of checks, respectively.

2.3.2 Improving Efficiency of Selection

The efficiency of early generation selection for protein content may be improved by minimizing environmental variation. Konzak and Rubenthaler (1984) indicated that the conditions under which plants are grown before selection for protein content may have considerable influence on the results, and proposed that cultural conditions conducive to high yield are optimal for identifying high protein selections. They recommended applying dry N fertilizer at planting and heading, and controlling diseases chemically or avoiding them if possible. Haunold et al. (1962) indicated that the correlation between F_2 plants and F_3 progenies may be improved by ample soil N and water, uniform spacing and uniformly filled grain since highly shrivelled seed may bias protein content. Bhatia and Rabson (1976) suggested that early generations should be evaluated at soil N levels higher than considered optimal for commercial production. Terman et al. (1969) indicated that differences in protein

content among cultivars are more clearly shown when applied N increases yield rather than protein content. However, Lebsock et al. (1964) reported that conditions resulting in low yield and high protein content increased the heritability of protein content, while conditions resulting in high yield and low protein content decreased it. Johnson et al. (1969) indicated that the expression of high protein content was most difficult to detect in a high yielding environment with limited soil N. Law et al. (1984) recommended the "high protein" environment of spaced plants over the "low protein" environment of solid seeded plots because the former increased the range between high and low protein lines. However, Kibite and Evans (1984) reported that different plant densities may favor different genotypes.

Several methods have been used to adjust protein content for soil heterogeneity and thus improve the efficiency of selection. Briggs et al. (1969) and Hadjichristodoulou and Della (1976) recommended the use of systematic controls at frequent intervals to adjust protein content. In a nursery where the protein content of systematic controls of Manitou wheat ranged from 10.3 to 16.5%, Briggs et al. (1969) showed that contiguous plots were more similar in protein content than those further apart. Guthrie et al. (1984) found that grid selection in six winter wheat crosses increased the efficiency of selection for protein content by 9.2% on average. Haunold et al. (1962) suggested selecting

among plants or within rows of comparable productivity as a means of improving efficiency of selection for protein content. Moving means do not appear to have been used for protein content although Townley-Smith and Hurd (1973) found them more effective than systematic controls in reducing error for yield in wheat.

Loffler and Busch (1982) found a significant correlation between the protein content of spring wheat in single unreplicated rows and adjacent four-row replicated plots at two locations in one year. In contrast, Newton and Malloch (1930) indicated that results for protein content from unreplicated plots of spring wheat were unreliable and that adequate plot replication was required. Lebsock et al. (1964) reported that genotype x environment interactions can reduce the effectiveness of early generation selection for protein content in spring wheat since widely different heritabilities were found for protein content in different years. This suggests that plot replication at several locations may be necessary if early generation selection for protein content is to be successful. O'Brien (1983) routinely utilizes two replications at three locations to determine yield, protein content and other quality traits for F_3 families grown in three-row plots. However, such a procedure requires a large amount of seed, labor and land.

The use of replicated hill plots at several locations has been proposed to increase the precision of yield

measurements and improve adaptability (Shebeski and Evans, 1973; Seitzer and Evans, 1978). A number of studies have indicated that hills are useful for early generation selection for yield because of their ability to predict performance in row plots (Jellum et al., 1963; Frey, 1965; Baker and Leisle, 1970; O'Brien et al., 1979). High genetic correlations between hill and row plot yields have been found although coefficients of variation for yield were considerably higher for hill plots indicating that more replications of hill plots were needed to estimate yield differences between cultivars (Baker and Leisle, 1970; O'Brien et al., 1979).

Protein content has been determined in hill plots for barley (Baker et al., 1968a), wheat (Ellison et al., 1985), and oats (Takeda and Frey, 1985). However, none of these studies compared protein content in hills to that in row plots of similar material. Torrie (1962) compared the performance of soybean varieties grown in hills and rows over a four year period. For protein content, five of seven correlation coefficients between hills and rows were significant ($r = 0.50$ to 0.94). Variety x plot type interactions were occasionally significant. Hills and rows appeared to measure protein content with similar precision, whereas for yield, nine replications of hill plots were required to obtain the precision equal to four replications of row

plots. Coefficients of variation were smaller for protein content than for yield.

2.3.3 Evaluation of Protein Content by Kernel Density

An important constraint to selecting for protein content in early generations has been the time and cost involved in screening large numbers of experimental lines (Peterson et al., 1986). Methods commonly used to evaluate protein content include Kjeldahl, dye binding capacity, Biuret and near infrared reflectance (NIR) spectroscopy (Pomeranz and Moore, 1975; Williams, 1975; Johnson et al., 1979a). Although NIR is more rapid and easier to use than the other methods (Rotolo, 1978; Johnson et al., 1979a), its capacity may still be limiting in breeding programs. In addition, all methods are destructive.

Hartwig and Collins (1962) used differences in the densities of oil (0.93 g/cm^3) and nonoil (1.3 - 1.4 g/cm^3) portions of soybean seed to select for protein or oil content. A glycerol-water solution with a density of approximately 1.23 g/cm^3 separated seed into high and low density fractions. Selecting for high density increased the frequency of high protein lines while selecting for low density increased the frequency of high oil lines. Later studies confirmed the effectiveness of bulk seed separations based on density as a coarse screening method for protein or oil content in soybeans (Fehr and Weber, 1968; Smith and Weber, 1968; Hiraiwa and Tanaka, 1978).

Taylor et al. (1982) reported that protein content and seed density were positively correlated in one wheat cultivar. Germination was unaffected by the hexane-chloroform solutions used in this study. In a study with four wheat cultivars, Brunori et al. (1982) found that the relationship between protein content and seed density, as determined by chloroform-methanol solutions, depended on the cultivar. The relationship was positive in two cultivars, negative in one, and not significant in another. They suggested that the inconsistencies among cultivars may depend on the internal structure of the seed since all cultivars had seed densities lower than the densities of the two major components, starch (1.6 g/cm^3) and protein (1.40 - 1.45 g/cm^3).

Garzon-Trula (1984) reported that protein will absorb approximately five times more water than starch when wheat seeds are soaked for 10 days at 0 to 3° C. Imbibition significantly increased the differential density of starch and protein, and allowed the separation of high and low protein seeds on the basis of seed density. Seed germination was unaffected by soaking the seeds at low temperatures or by the carbon tetrachloride (CCl_4)-hexane solution used for density separations. Seed could be dried and stored for planting.

Peterson et al. (1986) evaluated the technique of imbibed seed density (ISD) selection as a simple mass selection procedure for increasing the mean protein content

of early generation wheat bulk populations. Wheat seeds were passed over a screen to attain a relatively uniform kernel size and soaked in water for 9 to 10 days at 0 to 3° C. Protein content of seeds separated by CCl_4-hexane solutions ranging in density from 1.16 to 1.28 g/cm^3 was linearly related to both imbibed density and water absorption. A mixture of sodium chloride (NaCl) and sucrose in water was successfully substituted for CCl_4-hexane as a safe, inexpensive, effective solution for density separations. After screening and low temperature imbibition, seeds from 52 early generation bulk populations were separated into two density fractions using NaCl-sucrose solutions. The seeds were rinsed, dried and planted in the field along with unselected samples from the original populations. Analyses after harvest showed that selection for low imbibed seed density increased protein content by 6 to 11 g/kg relative to the unselected samples in 10 of 52 populations. Selection for low imbibed seed density had no effect on protein content of the remaining populations except for one in which protein content was actually decreased by 9 g/kg. Seed weights were unaffected by selection. They concluded that large amounts of nongenetic variation in protein content of individual seeds may limit the effectiveness of ISD selection for protein content.

2.4 Relationship of Protein Content to Other Traits

2.4.1 Yield

A major constraint to early generation selection for protein content in wheat is the negative correlation between protein content and yield reported in many studies (Malloch and Newton, 1934; Grant and McCalla, 1949; Baker et al., 1968b; McNeal et al., 1972; Loffler and Busch, 1982; and others). However, other studies have shown no correlation between protein content and yield (Clark, 1926; Schlehuber et al., 1967; Johnson et al., 1973b; Dyck and Baker, 1975; Knott and Kumar, 1975; Dubois and Fossati, 1981; Halloran, 1981; Zitelli et al., 1983; Fjell et al., 1985), while positive correlations have occasionally been reported (Shebeski, 1967; Briggs et al., 1969; Johnson et al., 1973b; Robinson et al., 1979; Puri et al., 1980). Kramer (1979) indicated that the correlation between protein content and yield within a genotype may be zero, positive or negative depending on the genotypic response to environmental conditions such as soil fertility. Among cultivars, he indicated that protein content and yield were inversely related. Donovan and Lee (1978) suggested that there was no simple relationship between protein content and yield even for a single cultivar, while Johnson et al. (1973b) reported that all cultivars may not exhibit similar relationships between protein content and yield.

The magnitude of the correlation coefficient depends on environmental conditions and the set of cultivars or populations being evaluated (Johnson et al., 1973b). Johnson et al. (1985) suggested that the correlation between protein content and yield seldom exceeds -0.60. Since an r-value of 0.6 would account for only about one third of the variation in protein content, they concluded and subsequently showed that simultaneous improvement can be made in protein content and yield. However, correlations greater than -0.60 have been reported (Grant and McCalla, 1949; Baker et al., 1968b; Pepe and Heiner, 1975; Loffler et al., 1985).

The cause of the inverse relationship between protein content and yield is not clear. Bhatia and Rabson (1976) suggested a bioenergetic constraint. They showed that increased inputs of carbon assimilates and N are necessary for increasing protein concentration while maintaining high yields in cereal grains. Their calculations were based on the assumption that biochemical pathways of microorganisms and crop plants do not differ significantly and that growing environments were favorable with the essential supplementary inputs. Johnson et al. (1979a) noted that much of the world's wheat in produced in areas where powerful environmental constraints prevent full expression of the genetic potential for yield.

Hageman et al. (1976) suggested that the primary cause of the negative correlation between protein content and

yield is the lack of available soil N just before and during the reproductive phase. This may be due to the depletion of N from the soil or lack of water which limits the availability, uptake, and assimilation of N. They indicated that late spring applications of N fertilizer may increase protein production but are not considered practical under dryland conditions. Canvin (1976) suggested that the negative correlation between protein content and yield results from compensation to the extent that, if N is limiting and more seeds are obtained, less N is available for each seed.

Kramer (1979) proposed that the negative correlation between protein content and yield among cultivars is largely a consequence of the high harvest index (HI) of high yielding cultivars. Since approximately two thirds or more of the protein in the grain at maturity is present in the plant at anthesis, any decrease in the amount of straw relative to the amount of grain would probably lower protein content of the grain. Ellison et al. (1977) found that the negative correlation between protein content and yield became nonsignificant when adjusted for HI. Negative correlations between protein content and HI have often been reported (Bhatia, 1975; Dubois and Fossati, 1981; Day et al., 1985; Loffler et al., 1985; Paccaud et al., 1985).

Law and Payne (1983) suggested that a lack of variation in the genetic systems controlling protein content in the populations studied may contribute to the inverse relation-

ship between protein content and yield. Crossing outside these populations may break down the correlation.

Takeda and Frey (1985) proposed the use of independent culling for simultaneous improvement of protein content and yield in oats. They recommended selecting 25 to 50% of the original population on the basis of protein content in hills with few replications during the first year, and selecting for yield with a fairly high intensity in large plots with more extensive replication during the second year.

A number of alternatives to direct selection for protein content have been advocated to reduce the effect of the inverse relationship between protein content and yield. McNeal et al. (1972) suggested selecting for protein yield per unit area because of favorable correlated responses with yield and yield components. They found very high positive correlations ($r = 0.93$ to 0.98) between protein yield and yield. Positive correlations of approximately 0.70 have been reported between protein yield and protein content (McNeal et al., 1971; Bhatia, 1975). McNeal et al. (1982) observed that selecting for protein yield increased both protein content and yield, while selecting directly for protein content increased protein content more than selecting for protein yield but decreased yield. However, no correlation between protein yield and protein content was found in several other studies (Hansel and Seibert, 1978; Loffler and Busch, 1982; Cox et al., 1986). Loffler et al.

(1985) reported a negative correlation ($r = -0.55$) between protein yield and protein content, but a very high positive correlation ($r = 0.95$) between protein yield and yield.

Jain et al. (1975) suggested that selecting for the absolute amount of protein per kernel is more reliable than selecting for protein content as a percentage. They indicated that the heritability of protein per kernel was approximately three times greater than the heritability of protein content, and that protein content was generally negatively correlated with kernel weight and yield, while protein per kernel was positively correlated with kernel weight. They concluded that selecting for protein per kernel would have less detrimental effect on yield than selecting for protein content. Brunori et al. (1982) suggested that selecting for high protein content favored poorly developed seeds while selecting for protein per kernel would avoid this problem. However, Johnson et al. (1979a) suggested that the effectiveness of selection for protein per kernel may be reduced by the negative correlations often found among yield components. Loffler and Busch (1982) found that selecting for protein per kernel increased protein content but reduced yield in two of three populations studied.

Kramer (1979) and Paccaud et al. (1985) suggested that protein content should be adjusted for HI since HI may account for considerable variation in protein content. High

protein content in some cultivars may be the result of a low HI. Such cultivars would be of limited value for improving protein content in crosses.

Loffler and Busch (1982) proposed the use of nitrogen harvest index (NHI) as a selection criterion in wheat. NHI is the proportion of total plant N in the grain at maturity. They found that NHI was positively correlated with yield but not protein content. They suggested that selection for NHI would increase yield while, at best, maintaining protein content. Similar results were reported in other studies (Dubois and Fossati, 1981; Cox et al., 1986). Dalling and Lyon (1977) recommended selecting for NHI to break the negative correlation between protein content and yield in wheat grown on limited soil N. In a later study, Loffler et al. (1985) found that NHI and protein content were negatively correlated. Desai and Bhatia (1978) found no correlation between NHI and either yield or protein content. Canvin (1976) indicated that NHI was subject to considerable variation within a cultivar and, consequently, may not be useful as a selection tool.

Selection for components of N metabolism has been advocated as a means of improving protein content and productivity (Austin and Jones, 1975; Rao et al., 1977; Edwards and van der Mey, 1978; Huffaker and Rains, 1978; Kramer, 1979; Cregan and van Berkum, 1984; Loffler et al., 1985). In a recent review, Cregan and van Berkum (1984)

indicated that components of N metabolism with potential to affect protein content and productivity include nitrate uptake, translocation and reduction; phloem loading and unloading; N remobilization from vegetative tissue to grain; and protein synthesis in developing grains. They recommended an integrated physiological/biochemical selection program in which several components of N metabolism are measured over the growing season. They noted that consideration must be given to the production environment. Austin and Jones (1975) recommended that breeders should select for higher plant weight which is highly correlated to total N accumulation, higher translocation percentage, and continued N uptake during grain filling. They suggested that N assimilation during grain filling plays an important role in contributing to grain protein content under favorable conditions. Other studies have reported similar results (Mikesell and Paulsen, 1971; Cox et al., 1985, 1986). However, several studies in common wheat (Blacklow and Incoll, 1981; Gregory et al., 1981; Kotlyar and Kumakov, 1983; Nicolas et al., 1985) and durum wheat (Desai and Bhatia, 1978; Bhatia et al., 1979) have shown that the contribution of remobilized N to grain N increases while that of N assimilated after anthesis decreases when soil water and N supplies are limited. Thus, translocation or remobilization of N from vegetative tissues to grain appears to be particularly important in determining protein content

in wheat (McNeal et al., 1966; Johnson et al., 1968). Rao et al. (1977) and Huffaker and Rains (1978) suggested that no single factor can be used to select for higher protein content and yield. Carbon assimilation, accumulation and partitioning should also be considered along with components of N metabolism (Galterio et al., 1983; Vose, 1984).

2.4.2 Yield Components

The relationship between protein content and kernel weight in common wheat varies greatly. Kaufmann et al. (1969), Jain et al. (1975, 1976), and Kibite and Evans (1984) reported negative correlations between protein content and kernel weight, while Briggs et al. (1969) and Loffler and Busch (1982) reported positive correlations between these two traits. Others have found no correlation (Worzella, 1942; Baker et al., 1968b; Randhawa and Gill, 1978; Vogel et al., 1978; Peterson et al., 1985). Fjell et al. (1985) observed a positive correlation between protein content and kernel weight at individual locations over all cultivars but a negative correlation within each cultivar over locations. The correlation between protein content and kernel weight can vary with the cross or population under study (Dyck and Baker, 1975; Shahani and Saulescu, 1984).

In durum wheat, no correlation between protein content and kernel weight has generally been found (Walther, 1978; Robinson et al., 1979; Zitelli et al., 1983). However, Porceddu et al. (1975) reported a negative correlation

between protein content and kernel weight, while Zitelli et al. (1979) found a negative correlation during a dry year.

The relationship between protein content and other yield components has seldom been studied in wheat. Croy et al. (1978) found no correlations between protein content and kernels per spike, tiller number and kernel weight. Corpuz et al. (1983b) reported that protein content was positively correlated with tillers per meter and kernel weight but negatively correlated with kernels per tiller. Law et al. (1984) also found that protein content was positively correlated with kernel weight but negatively correlated with kernels per ear. Bhatia (1975) found a negative correlation between protein content and both kernels per plant and kernel weight. In durum wheat, Gill and Brar (1977) reported a negative correlation between protein content and spikes per plant.

2.4.3 Kernel Shrivelling

It is generally agreed that kernel shrivelling increases protein content in wheat (Philips and Schlesinger, 1974). Johnson et al. (1973b) demonstrated that kernel plumpness strongly affected protein content in four winter wheat cultivars. Large, plump kernels with a closed crease had a slightly lower protein content (0.6%) than large, plump kernels with an open crease and a much lower protein content (2.3%) than large, wrinkled kernels. Open creases and wrinkling increased protein content more in small

kernels than in large ones. Shahani and Saulescu (1984) suggested that shrivelled kernels had a higher protein content that plump kernels because the incomplete development of kernels caused by unsuitable climatic conditions greatly affected starch deposition and proportionately increased protein content. Nicolas et al. (1985) suggested that the increased protein content of kernels produced under drought conditions was due to smaller kernel size. Croy et al. (1978) reported that hot, dry conditions hastened maturity, decreased yield and kernel weight but increased protein content. In durum wheat, Zitelli et al. (1979) observed that shrunken kernels produced in a dry year increased protein content. In contrast to most studies, Ghaderi et al. (1971) reported that shrivelling reduced protein content in soft winter wheat.

Although Kaufmann et al. (1969) and Corpuz et al. (1983b) have reported a negative correlation between protein content and test weight, no correlation between these two traits has been found in most studies (Worzella, 1942; Schlehuber et al., 1967; Briggs et al., 1969; Ghaderi et al., 1971). Fjell et al. (1984) suggested that high protein content was caused by low test weight and kernel weight. Ghaderi and Everson (1971) indicated that, although test weight and kernel weight are often positively correlated, this correlation was not genetic. They found that low test weight may result from environmental conditions other than

those causing kernel shrivelling. In durum wheat, Porceddu et al. (1975) reported that protein content tended to be higher in long, narrow, light-weight kernels.

2.4.4 Kernel Position

Levi and Anderson (1950) reported that the range in protein content of individual kernels within a plant of a wheat cultivar may be as high as 6%. They found that the range in protein content among heads within individual plants of the same cultivar averaged 1.7% but was as high as 4.9%. Protein content tended to be higher in shorter tillers of plants with more than three tillers. Among spikelets of the same head, they reported a range of 5.1% in protein content. Within spikelets, they observed that the protein content of the two basal kernels generally exceeded the protein content of distil kernels. Several studies have reported similar results for protein content of kernels within spikelets (McNeal and Davis, 1954; Bremner, 1972; Sofield et al., 1977; Simmons and Moss, 1978; Sclater, 1982; Herzog and Stamp, 1983).

McNeal and Davis (1966) found that, under irrigated conditions, the head of the main tiller had a higher protein content than the heads of other tillers, while the reverse was found under dryland conditions. They showed that spikelets from the top third of the head had a lower protein content than spikelets from the lower two thirds of the head. Similar results were obtained for spikelets in an

earlier study (McNeal and Davis, 1954) and by Stuber et al. (1962a) and Ali et al. (1969). However, Herzog and Stamp (1983) found that protein content was hardly affected by spikelet position.

2.4.5 Maturity

The relationship between protein content and maturity varies. Kaufmann et al. (1969) and Hansel and Seibert (1978) reported that protein content was negatively correlated with days to maturity in wheat. In durum wheat, Gill and Brar (1977) found a negative correlation between protein content and days to heading. However, Croy et al. (1978) found a positive correlation between protein content and days to heading in wheat. They suggested that hot, dry conditions late in the growing season were responsible. Corpuz et al. (1983b) reported no correlation between protein content and days to anthesis in one year and a positive correlation the next year.

3. MATERIALS AND METHODS

3.1 Evaluation of Parental Cultivars

The purpose of this experiment was to characterize the four durum wheat cultivars used as parents in the experiments that follow. The pedigrees and origin of the cultivars are given in Table 3. Results of Durum Wheat Cooperative Tests in Western Canada have indicated that DT367 is a high yielding cultivar with a relatively low protein content. Wakooma is a lower yielding cultivar but has a protein content approximately 2 to 2.5% higher than DT367. The other two parents, Medora and DT447, are intermediate in yield and protein content. DT447 is generally higher yielding than Medora but has a slightly lower protein content.

The four cultivars were grown on an Osborne heavy clay soil at the Agriculture Canada Research Station experimental site, Glenlea, and on a Riverdale clay loam at the University of Manitoba research farm, Winnipeg, in 1984 and 1985. At Glenlea, the previous crop was a fertilized cover crop of tame buckwheat worked down as green manure. The Winnipeg plots had been fallowed during the previous year. The fertility level of each site was determined by the Manitoba Provincial Soil Testing Laboratory, Winnipeg (Appendix Table 1).

TABLE 3. Pedigree and origin of four durum wheat cultivars used as parents.

Cultivar	Pedigree	Origin	Year of Release
Wakooma	Lakota*2/Pelissier	Agriculture Canada, Swift Current, Saskatchewan	1973
Medora	Ward/Macoun	Agriculture Canada, Winnipeg, Manitoba	1982
DT447	Vic/RL7095	Agriculture Canada, Winnipeg, Manitoba	Experimental line
DT367	S-017/Wascana//7168	Agriculture Canada, Swift Current, Saskatchewan	Experimental line

A randomized complete block design with six replications was used for each location and year. Plots consisted of four rows approximately 5.6 m long and 30.5 cm apart with a distance of 30.5 cm between plots. All plots were sown with a double disc plot seeder except for the Winnipeg plots in 1984 when a single disc seeder was used. Approximately 375 seeds per row were sown at a depth of 5.0 to 7.5 cm. Seeding dates were May 30 and May 31 for Glenlea and Winnipeg, respectively, in 1984, and May 23 and May 24 for Winnipeg and Glenlea, respectively, in 1985.

In 1984, HoeGrass II was applied at the recommended rate with a bicycle sprayer on June 19 to control weeds at Glenlea. The Winnipeg plots were hand-weeded and also irrigated with approximately 25 mm of water on July 27 and again on July 31. Malathion 50% EC was applied with a backpack sprayer on August 8 at a rate of 2 ml of product per 1 water to control aphids at Winnipeg.

In 1985, all plots were hand-weeded. Lorsban was applied at the recommended rate with a bicycle sprayer on June 10 to control cutworms at Glenlea.

A number of traits were measured before harvest. Days to heading were recorded as the number of days from seeding until approximately 50% of the heads in a plot had completely emerged from the boot. Days to maturity were recorded as the number of days from seeding until seeds in most heads were not easily dented by a finger nail. Days

from heading to maturity were calculated from the above data. Lodging was rated on the FAO scale with one being erect and nine completely flat. Height was recorded in cm.

The two center rows of each plot were trimmed to 5 m just before harvest, harvested by hand at maturity, allowed to dry in cloth bags, and threshed with a stationary Vogel thresher.

Plot yields were determined and converted to yield on a kg/ha basis. Test weight was determined by pouring a sample through a Cox funnel into 250 and 500 ml containers in 1984 and 1985, respectively, striking off the excess, weighing the remainder, and converting to kg/hl. Kernel weight was calculated from the number of seeds in 20 and 10 g samples of clean, sound seed in 1984 and 1985, respectively.

Protein content (%) was determined by NIR and reported at a standard moisture content of 13.5%. Grain samples from each plot were ground with a U D Cyclone Sample Mill using a 1.0 mm screen. In 1984, protein content was measured with a Dickey-John Instalab 800 NIR Product Analyzer at the Agriculture Canada Research Station, Winnipeg, using 6 to 7 g samples. In 1985, protein content was determined at the Canadian Grain Commission, Winnipeg, with a Neotec Instruments Automated Digital Analyzer using samples of approximately 20 g. Protein yield was calculated by multiplying yield by protein content. Protein per kernel was calculated by multiplying kernel weight by protein content. The

abbreviation and unit of measurement for each trait in this and all following experiments are given in Table 4.

An analysis of variance was performed for each trait in each location and year individually. Bartlett's test was used to test the homogeneity of error variances (Steel and Torrie, 1980). A pooled analysis of variance was performed for locations and years using the split-plot approach outlined by LeClerg et al. (1962). Cultivars, locations and years were considered to be fixed factors. In testing the significance of cultivars and year x cultivar, location x cultivar and year x location x cultivar interactions for traits with heterogeneous error variances, the calculated F was compared with tabulated F for 3 and 15 degrees of freedom instead of 3 and 60 degrees of freedom. This procedure was recommended by Cochran and Cox (1957). Duncan's multiple range test was used to detect differences among cultivar means.

TABLE 4. Abbreviations and units of measurement for traits.

Abbreviation	Unit of Measurement	Trait
DH	days	Days to heading
DHM	days	Days from heading to maturity
DM	days	Days to maturity
HT	cm	Height
KS	1-5	Kernel shrivelling
KW	mg	Kernel weight
LDG	1-9	Lodging
PC	%	Protein content adjusted to 13.5% moisture content
PK	mg	Protein per kernel
PY	kg/ha (g/hill)[1]	Protein yield
TW	kg/hl	Test weight
YLD	kg/ha (g/hill)	Yield

[1]Unit of measurement in brackets is for hill plots.

3.2 Early Generation Selection for Protein Content

3.2.1 Experimental Material

The breeding and protein selection scheme is outlined in Figure 1. Using the cultivars described in section 3.1, the following three crosses were made in the growth cabinet in the summer of 1983:

(1) Wakooma/DT367 (WK),

(2) DT367/Medora (MD), and

(3) DT447/DT367 (DT).

Since the low protein parent is common to all crosses, the higher protein parent will be used to designate each cross and abbreviated as shown above by the letters in brackets after each cross. The F_1 plants were grown in the growth cabinet in the fall of 1983. Approximately 350 seeds per cross from the F_1 plants were planted in the greenhouse in February, 1984. Each F_2 plant was harvested individually to produce an F_3 family. Because of the short time between harvesting and planting in the field, the seed was treated on May 18 with gibberellic acid (GA_3) to ensure uniform germination. Envelopes containing seed were soaked for 15 to 20 min in pans containing an acetone solution with 10^{-3}M GA_3. The envelopes were then removed from the pans and allowed to dry for at least 15 min in the fume hood.

The F_3 families were grown in replicated hill plots at Glenlea in 1984 adjacent to the experiment described in section 3.1. A 15 x 15 triple lattice design, consisting of

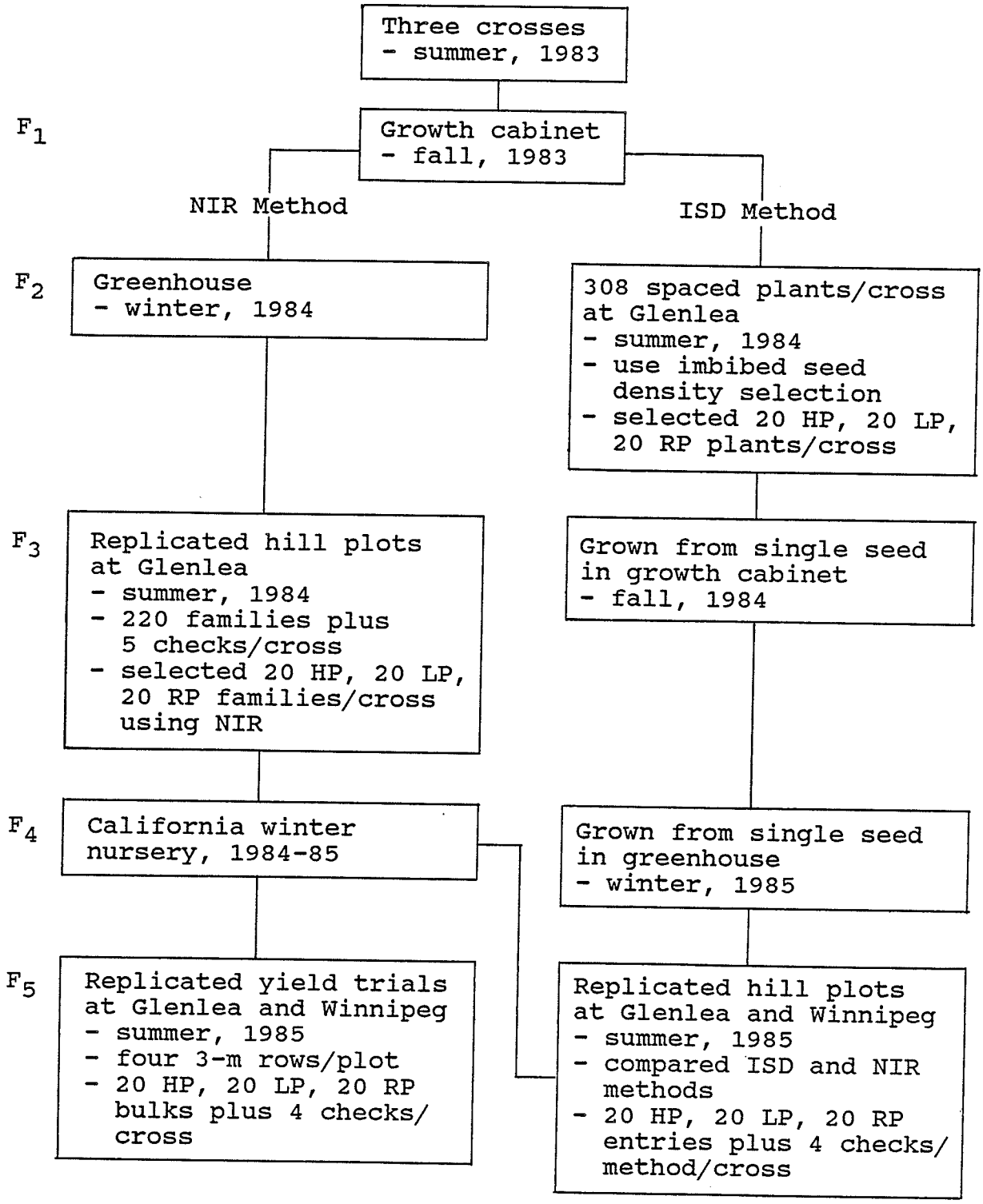

Figure 1. Outline of the breeding and protein selection scheme.

220 F_3 families and five check cultivars, was used for each cross. The checks included the four parental cultivars and Coulter. Each block consisted of three rows of five hill plots while each replication was five blocks long and three blocks wide. The three crosses were sown separately side by side, with two rows of border hill plots surrounding the entire experiment. Hill plots were planted 61 cm apart in perpendicular directions on May 23 by opening a hole in the soil approximately 5.0 to 7.5 cm deep and 15 cm in diameter with a hoe, scattering 15 seeds in the hole, covering them with soil, and lightly packing. The F_3 hill plots were used for the NIR selection method.

For each cross, 308 seeds from F_1 plants and six seeds from each parent were planted at Glenlea adjacent to the F_3 hill plots in a completely randomized design with Wakooma checks every third plot. Seeds were planted 61 cm apart in perpendicular directions on May 24 with a corn planter at a depth of 5.0 to 7.5 cm. The three crosses were planted side by side and the entire experiment surrounded by two border rows of spaced plants. The resulting F_2 spaced plants were used for the ISD selection method.

HoeGrass II was applied at the recommended rate with a bicycle sprayer on June 19 to control weeds in both experiments. Additional weeding by hand was required.

3.2.2 Selection Methods

3.2.2.1 NIR Method. Each F_3 and check hill plot was harvested individually by hand. Early maturing hill plots were threshed immediately upon harvesting with a Seedburo small bundle thresher, while the remaining hill plots were placed in cloth bags and allowed to dry before threshing.

Protein content was determined for each hill plot using NIR as described for 1984 in section 3.1. Three protein selection groups per cross were established as follows:

(1) 20 high protein F_3 families in the high protein selection group (HP),

(2) 20 low protein F_3 families in the low protein selection group (LP), and

(3) 20 randomly selected F_3 families in the random selection group (RP).

Selection intensity for each selection group was 9.1%. Each selected F_3 family was grown as an F_4 bulk population in the winter nursery at Brawley, California, in 1984-1985.

In addition to protein content, yield was determined for each hill plot and expressed in g/hill. Protein yield (g/hill) was calculated from protein content and yield. Kernel weight and protein per kernel were determined using remnant seed from the selected F_3 families and checks as described for 1985 in section 3.1. These samples were also rated visually for kernel shrivelling on a scale from one to five with one being plump, sound, well filled kernels and

five being extremely shrivelled. Visual ratings have been used by others to measure kernel shrivelling, particularly in triticale (Muntzing, 1966; Darvey, 1973; Thomas et al., 1980).

3.2.2.2 ISD Method. The number of F_2 plants used for the ISD method was reduced by poor emergence and disease, particularly aster yellows. Sterile plants and plants setting only a small quantity of highly shrivelled seed were not harvested. Each of the remaining plants was harvested at maturity and placed in a paper bag. While harvesting, a head from one of the primary tillers of each plant was marked with a piece of masking tape. This head was threshed separately using a single head thresher, while the remaining heads of the plant were threshed in bulk. Only plants with a sufficient quantity of relatively well filled, undamaged seed were retained. The number of F_2 plants actually used for the ISD method was 154, 145 and 115 for the WK, MD and DT crosses, respectively.

Two samples of ten seeds and four samples of one seed each were selected from each F_2 plant using the seed from the marked head whenever possible. For each sample, the seeds from all plants within a cross were bulked. For example, there were two samples of 1540 seeds each and four samples of 154 seeds each for the WK cross. One of the large bulked seed samples was used for selecting low density (high protein) seeds and the other for selecting high

density (low protein) seeds. The small samples were used for adjusting solution density.

The samples from each cross were imbibed in distilled water for 7 days at 0 to 2°C. For density separation, a large sample was removed from the refrigerator, drained, rinsed with tap water, and placed on several layers of paper towels in a large metal tray. The seeds were sponged gently with a paper towel and allowed to dry for 25 to 30 min to remove most of the excess surface moisture. The seeds were then placed into a 2000 ml beaker containing approximately 1500 ml of sucrose-NaCl solution similar to that used by Peterson et al. (1986). The solution was prepared from a stock solution of approximately 19.5% NaCl (lab quality), 21.2% sucrose (commercial grade), and 59.3% distilled water by weight. The stock solution had a density of approximately 1.251 g/cm^3. Prior to adding the large sample, the density of the solution was adjusted by the addition of distilled water or sucrose using two of the small samples as guides. Minor adjustments were occasionally necessary after the large sample had been added. After placing the large sample in the solution, it was stirred gently for a few seconds and allowed to stabilize for up to one min. The floating seeds were removed as quickly as possible with a small strainer and the density of the solution recorded with a hydrometer.

For separation of the high protein fraction, the desired density was that which would float approximately 200 seeds of the large sample. The floating and submerged seeds comprised the selected and unselected fractions, respectively. For separation of the low protein fraction, the density of the solution was adjusted so that approximately 200 seeds of the large sample remained submerged. In this case, the floating and submerged seeds comprised the unselected and selected fractions, respectively.

Immediately following the density separations, the various fractions were rinsed with tap water. Fifty-five to 60 seeds from each of the selected fractions of each cross were allowed to dry at room temperature for at least 5 h. The samples were then germinated on moist filter paper in Petri dishes at 22°C for 3 days. Forty-three to 50 young seedlings from each fraction were transplanted into pots of moist soil in the growth cabinet. These plants were the F_3 selections for the ISD method with the low and high density fractions being the high (HP) and low protein (LP) selection groups, respectively.

After seed samples had been taken from each F_2 plant for density separations, 20 F_2 plants were selected at random from each cross to establish the random selection group (RP) for the ISD method. Four seeds from each plant were sown in a pot in the same growth cabinet used for HP and LP.

The remaining seeds from all fractions, including the unselected fractions, were placed in a forced air oven one to two h after completing the density separations and dried overnight at 70°C. After storing at room temperature for several weeks, the seeds from each fraction were counted and weighed. All seeds from each of the HP and LP fractions, 6 g samples from the unselected fractions, and two composite samples per cross from the Wakooma checks grown with the F_2 plants were ground using a U D Cyclone Sample Mill with a 1.0 mm screen. Protein content was determined by the Kjeldahl method (AACC Method 46-12, American Association of Cereal Chemists, 1983) and adjusted to a standard moisture content of 13.5%. Moisture content was determined by drying 2 g samples at 145°C for 20 min in a forced air drying oven.

To assess the variation in protein content due to environmental effects in the plot area, 20 healthy Wakooma plants were selected at random from each cross. Protein content of these and the remnant seed of each F_2 random plant was determined by NIR as described for 1984 in section 3.1.

The F_3 selections were harvested in January, 1985. Twenty plants were selected at random from HP and LP, and one plant per pot was selected from each of the 20 RP families. Three seeds per plant were sown in the greenhouse on February 8, 1985, to constitute the F_4 generation. In

the spring, one plant from each F_4 family of three plants was selected to produce an F_5 family for the ISD method.

3.2.3 Evaluation of NIR Selection Method

3.2.3.1 Experimental Procedure. Each selection was grown as an F_5 bulk population in 1985 at Glenlea and Winnipeg adjacent to the experiments described in section 3.1. For each cross, the 20 F_5 bulks from each of the three selection groups plus the four parental cultivars were grown in an 8 x 8 lattice design with four replications. Plot size was four 3.6-m rows 30.5 cm apart with approximately 40.6 cm between plots to facilitate harvesting. Seeding dates were May 15 and May 16 for Winnipeg and Glenlea, respectively. Approximately 290 seeds were sown per row at a depth of 5.0 to 7.5 cm with a double disc plot seeder.

HoeGrass II was applied at the recommended rate with a tractor-mounted field sprayer on May 30 to control weeds at Glenlea. The Winnipeg plots were hand-weeded as were the Glenlea plots later in the growing season. The Glenlea plots were also sprayed for cutworms on June 11 with Lorsban at recommended rates using the field sprayer. Ammonium nitrate fertilizer (34-0-0) was applied by hand on July 4 to each Winnipeg plot at a rate of 40 kg actual N per ha. The flag leaf was beginning to emerge in some early plots at the time. Heading and maturity dates, height, and lodging were recorded as described in section 3.1.

Prior to maturity, the plots were trimmed to 3 m. All four rows were harvested with a Hege plot combine at maturity. Protein content, yield, test weight, kernel weight, protein yield and protein per kernel were determined for each plot as described for 1985 in section 3.1. In addition, samples from each plot were rated for kernel shrivelling as described in section 3.2.2.1

3.2.3.2 Statisical Analyses. For the initial analysis of protein content in F_3, a lattice analysis of variance was performed for each cross (Cochran and Cox, 1957). Missing plot values and least significant difference (LSD) at the 5% probability level were calculated as suggested by Cochran and Cox (1957) for lattice designs. The adjusted mean protein content of each F_3 family was used to make selections.

In following analyses, only the selected F_3 families were examined to detect differences in protein content, yield, kernel weight, protein yield, protein per kernel and kernel shrivelling among the three selection groups of each cross. A randomized complete block analysis of variance was performed with F_3 families nested within selection groups. The mean square of families within selection groups was used to test selection groups for significance. Orthogonal contrasts were used to partition the selection groups sums of squares into single degree of freedom comparisons of HP versus RP, and HP plus RP versus LP. Fischer's LSD test was

also used to detect differences among the means of the selection groups (Milliken and Johnston, 1984). Missing plot values were calculated by SAS GLM procedures (SAS Institute Inc., 1985).

The four parental cultivars grown in hill plots with the F_3 families were combined over the three crosses for each trait using a randomized complete block design analysis of variance. Each replication in each cross was used as a replication for the combined analysis; there were nine replications and four cultivars for each trait when combined. Differences among cultivar means were detected by Fischer's LSD test.

Simple correlation coefficients between all pairs of traits were calculated on the basis of F_3 family means. Means adjusted by the lattice analysis were used for protein content, while unadjusted means were used for the other traits. Since RP occasionally contained HP or LP families, the duplicated RP families were eliminated from the correlation analysis.

In the initial analysis of F_5 bulks and checks, a lattice analysis of variance was performed for all traits in each cross location. Missing plot values and LSD at the 5% probability level were calculated as for F_3 families.

The effectiveness of early generation selection for protein content was evaluated by two methods. In the first, differences among the three selection groups in F_5 were

evaluated using a randomized complete block analysis of variance with F_5 bulks nested within selection groups as described above for the F_3 families. The check cultivars were eliminated from this analysis. Each cross location was analyzed separately because variances were generally heterogeneous as determined by Bartlett's test. The observed response to selection was estimated by the difference between HP and RP, LP and RP, and HP and LP.

The second method used to evaluate the effectiveness of early generation selection for protein content was to determine the number of high protein F_5 bulks retained by each selection group when all 60 F_5 bulks in a cross were examined together. High protein F_5 bulks were taken to be bulks with a mean protein content at least one standard deviation greater than the population mean. Selection for low protein content was evaluated in a similar manner.

The four check cultivars grown in row plots with the F_5 bulks were combined over crosses at each location for all traits using a randomized complete block design analysis of variance with 12 replications and four cultivars at each location. Fischer's LSD test was used to detect differences among cultivar means.

Heritability in standard units (Frey and Horner, 1957) was estimated for protein content in each cross location by the correlation between adjusted F_3 family means and adjusted F_5 bulk means from the lattice analyses.

Heritabilities for all other traits were calculated in a similar manner using unadjusted F_3 family means and adjusted F_5 bulk means. However, unadjusted F_5 bulk means were used for kernel shrivelling.

The effect of selection for protein content on other traits was determined by evaluating differences in these traits among F_5 selection groups as described for protein content.

Simple correlation coefficients between all pairs of F_5 traits were calculated on a plot basis. In addition, intergeneration correlations between pairs of different traits were calculated.

3.2.4 Comparison of ISD and NIR Selection Methods

3.2.4.1 Experimental Procedure. The ISD and NIR selection methods were compared in F_5 hill plots grown in 1985 at Glenlea and Winnipeg adjacent to the experiments described in section 3.1. For each cross, the ISD method had 20 HP, 20 LP and 20 RP F_5 families plus the four parental cultivars, while the NIR method had a similar number of F_5 bulks in each selection group plus the four checks. The California winter nursery provided seed for the checks of both methods (section 3.2.2.1). All seed was treated on May 22 with GA_3 as described in section 3.2.1.

An 8 x 8 lattice design with four replications was used for each method. For each cross, the replications of the

two methods were randomized together in a split plot arrangement. Each block within a replication of each method consisted of two rows of four hill plots, while each replication was four blocks long and two blocks wide. Two rows of border hill plots were sown around the entire experiment. The hill plots were planted on 61 cm centers in the same manner as the F_3 hill plots (section 3.2.1) on May 23 and May 24 for Glenlea and Winnipeg, respectively.

Weeds were controlled by hand. Lorsban was applied at the recommended rate with a bicycle sprayer on June 10 to control cutworms at Glenlea. A spraying program was carried out to control leafhoppers and prevent the spread of aster yellows. Malathion 50% EC was applied with a backpack sprayer at a rate of 2 ml product per 1 water twice weekly from July 2 to August 1 at both locations. The Winnipeg hill plots were also sprayed on June 19 and June 23.

Heading and maturity dates, and height were recorded for each hill plot. Heading date was the date when approximately half of the heads in a hill plot had fully emerged from the boot. A hill plot was rated mature when at least half of the heads had firm seeds not easily dented by a finger nail.

At maturity, each hill plot was harvested by hand, placed in a cloth bag, dried and threshed with a Seedburo small bundle thresher. Protein content was determined for each hill plot as described for 1985 in section 3.1. Yield,

protein yield, kernel weight, protein per kernel and kernel shrivelling were determined as for the F_3 hill plots (section 3.2.2.1).

3.2.4.2 Statistical Analyses. Mean protein contents and standard errors were calculated for RP in F_2 and for the 20 random Wakooma checks in each cross of the ISD method. A randomized complete block analysis of variance was performed to determine if HP and LP differed significantly from each other and from the unselected fractions in protein content and kernel weight after density separation in F_2 . Crosses were used as blocks.

Statistical analyses used for the F_3 hill plots of the NIR method were described in section 3.2.3.2.

In F_5, the initial analyses, response to selection and effect of selection for protein content on other traits were calculated individually for each method in each cross location as described in section 3.2.3.2. The ISD and NIR methods were also combined for each cross location. Selection groups were nested within methods, while F_5 entries were nested within selection groups within methods for the combined analysis. The mean square of F_5 entries within selection groups within methods was used to test the significance of selection groups within methods, while the error mean square was used for testing F_5 entries within selection groups within methods and the replication x method interaction. The mean square of the replication x method inter-

action was used to test the significance of methods and replications. Selection groups within methods were compared by Fischer's LSD test.

The four check cultivars grown with the F_5 bulks and families of the NIR and ISD hill plots, respectively, were combined over methods and crosses at each location for all traits using a randomized complete block with 24 replications and four cultivars at each location. Fischer's LSD test was used to detect differences among cultivar means.

For the NIR method, heritability in standard units for protein content was estimated in each cross location by the correlation between adjusted F_3 family means and unadjusted F_5 bulk means. Heritabilities for all other traits were calculated in a similar manner except that unadjusted F_3 family means were used. For the ISD method, heritability in standard units for protein content was estimated in each cross location by the correlation between individual F_2 RP plants and the unadjusted means of the F_5 RP families derived from them.

Simple correlation coefficients between all pairs of F_5 traits were calculated for both methods on a plot basis. In addition, intergeneration correlations between pairs of different traits were calculated for the NIR method. Intergeneration correlations between protein content of individual F_2 RP plants and the means of other traits

studied in F_5 RP families were also calculated for the ISD method.

3.2.5 Comparison of NIR Hill and Row Plot Efficiency

To compare NIR hill and row plots, phenotypic correlations between NIR hill plots (section 3.2.4.1) and four-row plots (section 3.2.3.1) were calculated for each trait on a mean basis using all 60 F_5 bulks and four check cultivars for each cross location. The range in protein content was standardized for plot type by expressing the minimum and maximum entry means as a percentage of the overall mean protein content (Baker and Leisle, 1970). Estimates of components of variance due to genotypes, environment and replications were obtained for protein content from a randomized complete block analysis of variance for each plot type in each cross location (Comstock and Moll, 1963). Heritability of protein content for each plot type in each cross location was calculated on a single and mean plot basis as described by Sidwell et al. (1978).

Genetic correlations between hill and row plots were calculated for protein content from the following relationship outlined by Falconer (1960):

$$r_P = h_x h_y r_G + e_x e_y r_E$$

where r_P, r_G and r_E are the phenotypic, genetic and environmental correlations between hill and row plots, respectively; h_x and h_y are the square roots of the heritabilities of row and hill plots on a mean basis, respectively; and e_x

and e_y are the square roots of one minus the heritabilities of row and hill plots on a mean basis, respectively. Since environmental effects in one randomized experiment (row plots) are not likely to be correlated with those of another randomized experiment (hill plots), r_E was assumed to be zero (O'Brien, 1977).

The efficiency of selection in hill plots for protein content in row plots was calculated using the relationship between correlated and direct response to selection described by Falconer (1952):

$$ER = \frac{\text{Correlated response}}{\text{Direct response}} = \frac{h_H \, r_G}{h_R}$$

where ER is the efficiency ratio of hill to row plots, and h_H and h_R are the square roots of the heritabilities of hill and row plots on a single plot basis, respectively. The number of replicates of hill plots required to equal the efficiency of a single four-row plot was calculated for protein content at each cross location by replacing h_H with $\sqrt{\frac{\sigma_G^2}{\sigma_G^2 + \sigma_E^2/n}}$ where σ_G^2 and σ_E^2 are the genetic and environmental variances for hill plots, respectively, and n is the number of replicates of hill plots required (Frey, 1965). The formula for ER was equated to one and solved for n as follows:

$$\frac{\left(\sqrt{\frac{\sigma_G^2}{\sigma_G^2 + \sigma_E^2/n}}\right) r_G}{h_R} = 1.0$$

$$\therefore \quad n = \frac{\sigma_E^2}{\left(\frac{r_G^2 \, \sigma_G^2}{h_R^2} - \sigma_G^2\right)}$$

4. RESULTS AND DISCUSSION

4.1 Evaluation of Parental Cultivars

Highly significant ($P<0.01$) differences were found between the 1984 and 1985 growing seasons for all traits studied in the parental cultivars except kernel weight, protein yield and height (Table 5). Protein content and protein per kernel were higher, but yield, test weight and lodging score were lower in 1984 than 1985 (Table 6). Fewer days to heading, to maturity, and from heading to maturity were required in 1984 than 1985 (Table 6). The results reflect the contrasting growing conditions in 1984 and 1985 (Appendix Table 2). During the 1984 grain filling period, hot, dry conditions and diseases such as tan spot and Septoria spp. resulted in premature ripening, which was probably responsible for reducing days from heading to maturity, yield and test weight, while increasing protein content and protein per kernel. Cool, wet conditions during the 1985 grain filling period delayed maturity, increased yield and lodging, and reduced protein content.

Location had much less effect than year on the traits studied. Significant differences between the Glenlea and Winnipeg locations were found only for days to heading ($P<0.01$), days from heading to maturity ($P<0.01$) and height

TABLE 5. Analysis of variance for protein content and ten other traits combined over locations and years for parental cultivars.

Source Of Variation	DF	Trait[1] Mean Squares										
		PC	YLD	TW	KW	PY	PK	DH	DM	DHM	LDG	HT
Years (Y)	1	170.4001**	5936171**	350.75**	19.71	222	19.7200**	100.04**	7038.38**	5460.17**	322.67**	170.67
Locations (L)	1	0.1426	2091	10.73	12.98	384	0.3444	60.17**	6.00	104.17**	0.04	368.17*
Y x L	1	0.0001	173230	6.88	9.95	2731	0.2214	26.04**	280.17**	135.38**	1.50	18.38
$Error_a$	20	0.3436	85679	3.31	9.19	1232	0.1561	0.98	7.17	4.07	1.64	54.37
Cultivars (C)	3	13.5104**	3012839**	123.82**	444.43**	33731**	5.1182**	113.00**	85.49**	82.49**	29.57**	370.85**
Y x C	3	0.3368**	22385	7.74**	21.93**	1828*	0.1940**	12.93**	91.82**	44.28**	8.53**	29.19**
L x C	3	0.3120**	104967*	1.30	2.15	3185**	0.0584	1.17*	10.78**	9.06**	5.57**	18.75**
Y x L x C	3	0.5512**	127730**	6.38**	8.09**	2164*	0.0615	0.26	6.72*	8.49*	2.03*	7.24
$Error_b$[2]	60	0.0573	30251	0.91	1.40	632	0.0223+	0.32++	1.94++	1.58++	0.45++	3.72
C.V.(%)[3]		1.7	6.8	1.3	3.1	6.9	2.7	1.0	1.3	2.7	14.2	1.8

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Heterogeneous error variances significant at the 0.05(+) or 0.01(++) probability level.

[3]Coefficient of variation for $Error_b$.

TABLE 6. Means for protein content and ten other traits for years, locations and cultivars.

	Trait[1]										
Year	PC	YLD	TW	KW	PY	PK	DH	DM	DHM	LDG	HT
1984	15.7**	2315**	73.7**	38.2	361	5.98**	55.6**	94.7**	39.1**	2.9**	109
1985	13.0**	2813**	77.5**	39.1	364	5.08**	57.6**	111.8**	54.2**	6.6**	111
Location											
Glenlea	14.4	2569	75.9	39.1	365	5.59	57.4**	103.0	45.6**	4.7	108*
Winnipeg	14.3	2559	75.3	38.3	361	5.47	55.8**	103.5	47.7**	4.8	112*
Cultivar											
Wakooma	15.4a[2]	2053c	73.7b	33.9d	312c	5.21c	59.4a	103.7a	44.3c	6.1a	112b
Medora	14.4b	2658b	77.8a	37.7c	379b	5.44b	54.2d	100.5b	46.3b	3.4c	109c
DT447	14.0c	2873a	77.3a	44.3a	400a	6.21a	56.7b	104.3a	47.7a	4.8b	114a
DT367	13.6d	2672b	73.6b	38.9b	361b	5.27c	56.1c	104.6a	48.5a	4.6b	105d

*,** Means within locations or years are significantly different at the 0.05 and 0.01 probability levels, respectively, according to analysis of variance.

[1]Abbreviations for traits are defined in Table 4.

[2]Means for cultivars followed by the same letter are not significantly different at the 0.01 probability level according to Duncan's multiple range test.

($P<0.05$) (Table 5). Heading was later at Glenlea, but once it had occurred, fewer days were required to reach maturity than at Winnipeg (Table 6). Plant height was shorter at Glenlea than Winnipeg (Table 6). Few differences between Glenlea and Winnipeg were expected because the locations were planted within a day of each other in both years and were only about 20 km apart. Weather conditions were similar in both years at both locations. Significant ($P<0.01$) year x location interactions occurred only for days to heading, days to maturity and days from heading to maturity (Table 5).

The parental cultivars differed significantly ($P<0.01$) for all traits studied and interacted significantly ($P<0.05$ or $P<0.01$) with years and locations for most traits (Table 5). Exceptions were year x cultivar interactions for yield, location x cultivar interactions for test weight, kernel weight and protein per kernel, and year x location x cultivar interactions for protein per kernel, days to heading and height (Table 5). Pooling of locations and years for traits with heterogeneous error variances (i.e., protein per kernel, days to heading, days to maturity, days from heading to maturity, and lodging) appeared to be valid. Comparing the calculated F values for cultivars and related interactions with the tabulated F value for 3 and 15 degrees of freedom, as suggested by Cochron and Cox (1957), resulted in the same conclusions as using 3 and 60 degrees of freedom.

The only exception was the year x location x cultivar interaction for protein per kernel which was not significant ($P>0.05$) at 3 and 15 degrees of freedom but reached significance ($P<0.05$) at 3 and 60 degrees of freedom.

Over years and locations, Wakooma had the highest protein content at 15.4% followed by Medora at 14.4%, DT447 at 14.0% and DT367 at 13.6% (Table 6). The ranking of the cultivars was as expected but the range in protein content was only 1.8% between Wakooma and DT367. The protein content of DT367 appeared to be closer to the other cultivars than would normally be expected. When the cultivars were compared for protein content by location and year, Wakooma continued to have a higher protein content than the other cultivars, while Medora had a consistently higher protein content than DT367 (Table 7). The protein content of DT447 was equal to DT367 and less than Medora at Glenlea in 1984, but greater than DT367 and equal to Medora at Winnipeg in 1984 and Glenlea in 1985. DT447 did not differ significantly in protein content from either Medora or DT367 at Winnipeg in 1985. The variable results for DT447 probably account for the highly significant ($P<0.01$) interactions of cultivars with years and locations.

Wakooma was the lowest yielding cultivar overall (Table 6) as expected on the basis of past yield trials and the often reported negative correlation between protein content and yield (Malloch and Newton, 1934; Grant and McCalla,

TABLE 7. Mean protein content and yield of each cultivar at each location in each year.

		1984		1985	
Trait[1]	Cultivar	Glenlea	Winnipeg	Glenlea	Winnipeg
PC	Wakooma	16.9a[2]	16.4a	14.1a	14.1a
	Medora	15.9b	15.7b	13.3b	12.9b
	DT447	15.0c	15.5b	13.0b	12.6bc
	DT367	15.1c	15.1c	12.0c	12.3c
YLD	Wakooma	1732b	1901c	2334c	2247b
	Medora	2539a	2190b	2923ab	2981a
	DT447	2741a	2529a	3088a	3133a
	DT367	2438a	2454a	2754b	3042a

[1]Abbreviations for traits are defined in Table 4.

[2]Cultivar means within a location year followed by the same letter are not significantly different at the 0.01 probability level according to Duncan's multiple range test.

1949; Baker et al., 1968b; and others). DT447 was the highest yielding cultivar, exceeding Wakooma by approximately 40% (Table 6). Medora and DT367 did not differ significantly in yield, but were approximately 29 to 30% higher yielding than Wakooma and 8% lower yielding than DT447 (Table 6). DT367 yields were lower than expected relative to the other cultivars. The higher than expected protein content of DT367 probably resulted from the failure of DT367 to express its full yield potential. DT367 was bred under the relatively dry conditions that prevail at Swift Current, and consequently, may not be adapted to the wet growing conditions and disease prior to grain filling in 1984, and to cool, wet conditions with lodging during the grain filling period in 1985. Although Wakooma was bred under similar conditions, it appears to be more stable in yield and protein content than DT367. Medora and DT447 were developed in Manitoba and may be better adapted to the growing conditions experienced in this study.

When the cultivars were compared by year and location, Wakooma was consistently the lowest yielding cultivar (Table 7). No significant differences in yield were found among the other three cultivars at Glenlea in 1984 and Winnipeg in 1985. At Winnipeg in 1984, DT447 and DT367 were similar in yield and higher yielding than Medora. At Glenlea in 1985, DT447 had a higher yield than DT367, while Medora did not differ significantly from either cultivar. Cultivars

appeared to interact more with location than year since the year x cultivar interaction was not significant in contrast to other traits (Table 7).

Medora and DT447 had much higher test weights than Wakooma and DT367 overall (Table 6). DT447 had the highest kernel weight followed by DT367, Medora, and Wakooma in that order (Table 6). The cultivars showed the same ranking for protein yield as for yield, suggesting that protein yield was more dependent on yield than protein content (Table 6). McNeal et al. (1972) and Loffler et al. (1985) found very high positive correlations between protein yield and yield. DT447 had the highest protein per kernel despite a relatively low protein content (Table 6). Medora ranked second in protein per kernel followed by Wakooma and DT367.

Medora required the fewest days to head followed in order by DT367, DT447 and Wakooma (Table 6). The range in days to heading was approximately five days. Medora matured approximately three to four days earlier than the other cultivars among which no significant differences were found (Table 6). Consequently, Wakooma required the fewest days from heading to maturity (Table 6). Medora took approximately two days longer than Wakooma from heading to maturity, but approximately one day less than DT367 and DT447.

Medora was the most resistant to lodging, DT447 and DT367 were intermediate, while Wakooma was the most suscep-

tible (Table 6). Lodging did not appear to be directly related to height since DT447 was the tallest cultivar followed in order by Wakooma, Medora and DT367 (Table 6). However, the mean difference in height was less than 9 cm.

Of the traits evaluated, protein per kernel appeared to be the least affected by genotype x environment interactions since only the year x cultivar interaction was significant (Table 6). Other workers have indicated that protein per kernel is more stable than protein content (Jain et al., 1975; Brunori et al., 1984).

4.2 Effectiveness of NIR Selection Method

Highly significant ($P<0.01$) differences in protein content were found among the F_3 families and checks of each cross grown in hill plots in 1984 for the NIR selection method (Table 8). The overall mean protein contents were high and similar for the three crosses, while the overall range in protein content was from 3.6 to 4.4% depending on the cross (Table 8). Coefficients of variation were low, ranging from 3.0 to 3.3% (Table 8). Since variation in protein content existed among the F_3 families of each cross, HP, LP and RP selection groups were established. The means of the individual F_3 families in each selection group are given by cross in Appendix Table 3.

The F_3 selection groups differed significantly ($P<0.01$) in protein content for all crosses (Table 9). Orthogonal contrasts indicated that HP differed significantly ($P<0.01$)

TABLE 8. Lattice analysis of variance for protein content of F_3 families and checks in each cross for the NIR method.

Source of Variation	Cross					
	WK		MD		DT	
	DF	Mean Square	DF	Mean Square	DF	Mean Square
Replications	2	5.8050	2	2.5831	2	5.6325
Entries	224	0.5706**	224	0.7901**	224	0.5670**
Blocks	42	0.4286	42	0.3305	42	0.2303
Error	406	0.2550	404	0.2276	406	0.1991
Mean	15.5		15.7		15.2	
Range	14.0-18.3		14.1-18.5		13.9-17.5	
C.V.(%)[1]	3.3		3.1		3.0	
R.E.(%)[2]	102.5		101.3		100.2	

**Significant at the 0.01 probability level.

[1]Coefficient of variation.

[2]Relative efficiency of the lattice design compared to the randomized complete block design.

TABLE 9. Analysis of variance and orthogonal contrasts for protein content of F_3 selection groups in each cross for the NIR method.

	Cross					
	WK		MD		DT	
Source of Variation	DF	Mean Square	DF	Mean Square	DF	Mean Square
Replications	2	1.1927*	2	2.1930**	2	1.0804*
Selection Groups (G)	2	35.6792**	2	47.2940**	2	32.4957**
HP vs. RP	1	19.6021**	1	23.5853**	1	17.1763**
(HP+RP) vs. LP	1	51.7563**	1	71.0026**	1	47.8151**
Families within G	57	0.3271	57	0.3330	57	0.1848
Error	118	0.3693	117	0.2838	118	0.2877

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

from RP, and that HP and RP combined differed significantly ($P<0.01$) from LP in each cross (Table 9). HP mean protein content was 0.8% higher than RP in each cross, and ranged from 1.5 to 1.7% higher than LP over all crosses (Table 10). RP mean protein content ranged from 0.7 to 0.9% higher than LP. Using the LSD values for protein content in Table 11, it was observed that all HP families differed significantly from all LP families in each cross. The HP range appeared to be wider than the LP range (Table 10). In the WK and MD crosses, the RP range was the widest and overlapped both HP and LP ranges. However, the RP range in the DT cross was considerably smaller than in the other crosses and overlapped only the HP range. In all three crosses, the RP mean in Table 10 was similar to the overall population mean given in Table 8. The differential between the selection groups in F_3 appeared to be adequate for selecting successfully for protein content.

The four parental cultivars included as checks with the F_3 families of each cross did not perform as expected with respect to protein content (Table 11). When combined over crosses, Wakooma did not differ significantly from DT447 or even DT367; normally Wakooma has the highest while DT367 has the lowest protein content. The protein content of Medora was significantly higher than that of DT447 and Wakooma, and similar to that of DT367.

TABLE 10. Protein content of F_3 selection groups in each cross for the NIR method.

Cross		Selection Group		
		HP	RP	LP
WK	Mean	16.4a[1]	15.6b	14.8c
	Range	16.1-16.9	14.8-16.9	14.5-15.0
MD	Mean	16.6a	15.8b	14.9c
	Range	16.4-17.4	14.9-16.9	14.6-15.1
DT	Mean	16.0a	15.2b	14.5c
	Range	15.7-16.7	14.7-15.8	14.2-14.6

[1]Means within a cross followed by the same letter are not significantly different at the 0.01 probability level according to Fischer's LSD test.

TABLE 11. Mean protein contents of the four parental cultivars grown with the F_3 families in each cross for the NIR method.

	Cultivar				
Cross	Wakooma	Medora	DT447	DT367	LSD[1]
WK	15.9	16.6	15.5	15.4	0.8
MD	15.6	16.2	15.3	16.1	0.8
DT	15.5	16.2	15.1	15.5	0.7
Combined[2]	15.6b[3]	16.3a	15.3b	15.7ab	

[1]Least significant difference at the 0.05 probability level calculated from the lattice analysis of all 225 entries in each cross.

[2]Parental cultivars were combined over crosses using a randomized complete block design (Appendix Table 34).

[3]Cultivar means over crosses followed by the same letter are not significantly different at the 0.01 probability level according to Fischer's LSD test.

Comparison of parental means in each cross (Table 11) with F_3 family means (Appendix Table 3) revealed that five F_3 families in HP of the WK cross, had significantly higher protein content than the high protein parent, Wakooma. Only one F_3 family in LP had significantly lower protein content than the low protein parent, DT367. In the MD cross, two F_3 families in HP exceeded Medora in protein content, while all F_3 families in LP had lower protein content than DT367. In the DT cross, all but two F_3 families in HP had higher protein content than DT447, while all F_3 families in LP had lower protein content than DT367. These results suggest that transgressive segregation, particularly for low protein content, occurred in F_3. However, the relative performance of the check cultivars may indicate that genotype x environment interactions caused these F_3 families to exceed the parental range.

Highly significant ($P<0.01$) differences in protein content were found among the F_5 bulks and checks of each cross location grown in four-row plots in 1985 for the NIR selection method (Table 12). The overall mean protein contents were higher at Glenlea than Winnipeg, and tended to be lowest for the DT cross, particularly at Glenlea (Table 12). The coefficients of variation were low, ranging from 1.5 to 2.6% (Table 12). In contrast to the results for protein content in the 1984 hill plots (Table 8), the lattice design was more efficient for protein content in the

TABLE 12. Lattice analysis of variance for protein content of F_5 bulks and checks in each cross location for NIR row plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	0.1280	3	3.8955
	Entries	63	0.5043**	63	0.4448**
	Blocks	28	0.3398	28	0.1824
	Error	161	0.0763	159	0.0327
	Mean		13.9		13.0
	C.V.(%)[1]		2.1		1.5
	R.E.(%)[2]		136		150
MD	Replications	3	18.0305	3	0.5274
	Entries	63	1.0536**	63	0.4885**
	Blocks	28	1.2676	28	0.1094
	Error	161	0.1093	161	0.0321
	Mean		13.8		12.7
	C.V.(%)		2.6		1.5
	R.E.(%)		226		123
DT	Replications	3	12.0500	3	0.8160
	Entries	63	0.5510**	63	0.4548**
	Blocks	28	0.5545	28	0.0985
	Error	159	0.0559	161	0.0300
	Mean		12.9		12.5
	C.V.(%)		2.0		1.5
	R.E.(%)		206		121

**Significant at the 0.01 probability level.

[1]Coefficient of variation.

[2]Relative efficiency of the lattice design compared to the randomized complete block design.

1985 row plots than the randomized complete block design (Table 12).

The F_5 selection groups for the NIR row plots differed significantly in protein content for the WK cross ($P<0.05$) at both Glenlea and Winnipeg, and for the DT cross ($P<0.01$) at Glenlea (Table 13). No significant differences in protein content were detected for the MD cross at either location or for the DT cross at Winnipeg. However, the selection groups of the MD cross at Glenlea were close to significance ($0.05<P<0.1$). The orthogonal contrasts for the WK cross at both locations indicated that HP did not differ significantly ($P>0.05$) in protein content from RP, while HP and RP combined differed significantly ($P<0.05$) from LP (Table 13). Both orthogonal contrasts were highly significant ($P<0.01$) for the DT cross at Glenlea.

For the WK cross at Glenlea, the mean protein content of HP was 0.3% higher than LP, but neither HP nor LP differed significantly from RP (Table 14). For the WK cross at Winnipeg, HP and RP were identical in protein content and exceeded LP by 0.2% (Table 14). This was the only case in which LP differed significantly from RP. For the DT cross at Glenlea, the protein content of HP exceeded RP and LP by 0.4% (Table 14). This was the only case in which HP had significantly higher protein content than RP. Although significant differences were not found among the selection groups in the other three cross locations, the trend

TABLE 13. Analysis of variance and orthogonal contrasts for protein content of F_5 selection groups in each cross location for NIR row plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	0.1730	3	3.7594**
	Selection Groups (G)	2	1.8303*	2	1.2421*
	HP vs. RP	1	0.9456	1	0.2033
	(HP+RP) vs. LP	1	2.7150*	1	2.3107*
	Bulks within G	57	0.4124**	57	0.3531**
	Error	177	0.1067	175	0.0552
MD	Replications	3	17.8340**	3	0.4578**
	Selection Groups (G)	2	2.9671	2	0.4758
	HP vs. RP	1	2.8622	1	0.3706
	(HP+RP) vs. LP	1	3.0720	1	0.5810
	Bulks within G	57	0.9921**	57	0.3352**
	Error	177	0.2821	177	0.0435
DT	Replications	3	10.7860**	3	0.8023**
	Selection Groups (G)	2	3.2685**	2	0.4470
	HP vs. RP	1	3.6913**	1	0.4000
	(HP+RP) vs. LP	1	2.9239**	1	0.4941
	Bulks within G	57	0.3251**	57	0.2932**
	Error	175	0.1232	177	0.0391

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

TABLE 14. Protein content of F_5 selection groups in each cross location for NIR row plots.

Cross	Location		Selection Group HP	RP	LP
WK	Glenlea	Mean	14.0a[1]	13.9ab	13.7b
		Range	13.5-14.7	13.0-14.5	13.0-14.3
	Winnipeg	Mean	13.0a	13.0a	12.8b
		Range	12.2-13.7	12.5-13.6	12.2-13.2
MD	Glenlea	Mean	14.0a	13.7a	13.6a
		Range	13.2-15.1	12.7-14.7	13.0-14.6
	Winnipeg	Mean	12.8a	12.7a	12.6a
		Range	12.3-13.3	12.0-13.5	12.3-13.2
DT	Glenlea	Mean	13.1a	12.7b	12.7b
		Range	12.8-13.5	12.0-13.4	12.0-13.1
	Winnipeg	Mean	12.5a	12.4a	12.4a
		Range	12.3-13.0	11.7-13.1	11.8-13.2

[1]Means within a cross location followed by the same letter are not significantly different at the 0.05 probability level according to Fischer's LSD test.

appeared to be in the desired direction, particularly for the MD cross at Glenlea (Table 14).

In contrast to the F_3 generation, the range for the mean protein contents of the individual F_5 bulks in HP overlapped considerably with those of LP, while the range for RP was generally similar in magnitude to HP and LP (Table 14). The range in mean protein content for the individual F_5 bulks over all selection groups was from 1.5 to 2.4% depending on the cross location (Table 14).

The four parental cultivars included with the F_5 bulks in the NIR row plots of each cross performed more as expected than in hill plots the previous year. When combined over crosses at Glenlea, Wakooma had significantly higher protein content than the other cultivars (Table 15). Medora had higher protein content than DT447 and DT367, while DT447 and DT367 did not differ significantly. DT367 had higher protein content than expected relative to the other cultivars at Glenlea; the difference between Wakooma and DT367 was 1.1% overall. The protein content of the check cultivars was lower at Winnipeg than Glenlea (Table 15). However, the protein content of DT447 was reduced much less than that of the other cultivars. Consequently, DT447 had significantly higher protein content than DT367 at Winnipeg, and did not differ significantly from Medora. Wakooma had the highest protein content at Winnipeg, while DT367 had the lowest with a difference of 1.6% between the

TABLE 15. Mean protein contents of the four check cultivars grown with the F_5 bulks in each cross location for NIR row plots.

Location	Cross	Cultivar				LSD[1]
		Wakooma	Medora	DT447	DT367	
Glenlea	WK	14.6	14.2	13.5	13.6	0.4
	MD	14.5	14.2	13.5	13.3	0.5
	DT	14.3	13.7	13.2	13.0	0.4
	Combined[2]	14.4a[3]	13.9b	13.4c	13.3c	
Winnipeg	WK	13.8	13.1	13.2	12.4	0.3
	MD	14.0	13.3	13.4	12.5	0.3
	DT	13.8	13.3	13.1	12.2	0.3
	Combined	13.9a	13.2b	13.2b	12.3c	

[1]Least significant difference at the 0.05 probability level calculated from the lattice analysis of all 64 entries in each cross location.

[2]Check cultivars within a location were combined over crosses using a randomized complete block design (Appendix Table 35).

[3]Cultivar means over crosses within a location followed by the same letter are not significantly different at the 0.01 probability level according to Fischer's LSD test.

two cultivars overall. Although the range appeared to be greater at Winnipeg than Glenlea, it was still less than normally expected.

Comparison of parental means in each cross location (Table 15) with means of individual F_5 bulks (Appendix Table 4) indicated that, in contrast to F_3 families, very few F_5 bulks in a cross location significantly exceeded the parental range, except for the DT cross at Glenlea in which 12 F_5 bulks in LP had significantly lower protein contents than DT367. It is of interest that 18 of 20 F_5 bulks in HP of this cross location were equal to DT447 in protein content. These results are reflected in the relatively high response to selection observed for this cross location (Table 16).

Overall, the response to selection determined by differences among selection groups was low, ranging from 0 to 0.4% protein content (Table 16). In five of six cross locations, HP and LP did not differ significantly from RP, indicating that selection for high or low protein content was little better than random selection. Significant differences in protein content occurred more frequently between HP and LP, ranging from 0.2 to 0.4%. This would indicate that selection for protein content was at least in the desired direction.

Response to selection, as determined by the number of high protein F_5 bulks (one standard deviation greater than

TABLE 16. Response to selection for protein content by cross location for NIR row plots.

Cross	Location	Difference in Protein Content (%)		
		(HP - LP)	(HP - RP)	(LP - RP)
WK	Glenlea	0.3 *	0.1	-0.2
	Winnipeg	0.2 *	0.0	-0.2 *
MD	Glenlea	0.4	0.3	-0.1
	Winnipeg	0.2	0.1	-0.1
DT	Glenlea	0.4 **	0.4 **	0.0
	Winnipeg	0.1	0.1	0.0

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

the mean) retained by selection group, indicated that selection for high protein content was successful in four of the six cross locations (Table 17). HP appeared to retain at least two thirds of the high protein F_5 bulks for all crosses at Glenlea and for the WK cross at Winnipeg. Selection for low protein content appeared to be less successful as indicated by the number of low protein F_5 bulks (one standard deviation less than the mean) retained by selection group, but the trend was in the desired direction (Table 17). However, these results cannot be tested statistically for significance.

The magnitude of response to selection for protein content in this study was lower than reported in the literature. Lebsock et al. (1964) observed a response to selection of 0.7% protein content when the upper 10% of F_3 lines in a hard red spring wheat cross grown in North Dakota were retained and evaluated as F_5 and F_6 lines against F_5 and F_6 lines derived from unselected F_3 lines. In a study with eight spring wheat crosses grown at three locations in Montana, McNeal et al. (1972) reported significant differences in 23 of 24 comparisons between high and low protein F_4 bulk populations derived from compositing 14 high and 14 low protein F_3 progeny rows, respectively. The response to selection in their study ranged from 0.12 to 0.47% grain nitrogen content on a dry weight basis which is equivalent to approximately 0.6 to 2.3% protein content

TABLE 17. Number of F_5 bulks with high or low protein content retained by selection group in each cross location for NIR row plots.

Cross	Location	Number of High Protein[1] F_5 Bulks			
		HP	RP	LP	Total
WK	Glenlea	6	2	0	8
	Winnipeg	6	2	0	8
MD	Glenlea	6	2	1	9
	Winnipeg	5	4	2	11
DT	Glenlea	7	2	0	9
	Winnipeg	4	1	5	10
Total		34	13	8	55
		Number of Low Protein[2] F_5 Bulks			
WK	Glenlea	1	1	4	6
	Winnipeg	1	3	7	11
MD	Glenlea	1	4	7	12
	Winnipeg	2	5	5	12
DT	Glenlea	0	5	6	11
	Winnipeg	4	3	5	12
Total		9	21	34	64

[1]Mean protein content one standard deviation greater than the mean of all 60 F_5 bulks in a cross location.

[2]Mean protein content one standard deviation less than the mean of all 60 F_5 bulks in a cross location.

adjusted to 13.5% moisture content. They reported that the results were consistent among locations and crosses, and suggested that selection among F_3 progeny rows was effective. Randhawa and Gill (1978) also indicated that selection for protein content in F_3 was effective in contrast to the present study.

In a later study using two cycles of recurrent selection in nine crosses of spring wheat, McNeal et al. (1978) reported significant and consistent differences between high and low F_4 protein selections developed from F_3 progeny rows in each cycle of recurrent selection. When the F_4 selections from the two cycles were grown in the same year, differences ranged from 1.5 to 4.7% protein content on a dry weight basis (1.3 to 4.1% protein content at 13.5% moisture content) after the first cycle, and from 1.5 to 2.7% (1.3 to 2.3% protein content at 13.5% moisture content) after the second cycle. These responses are among the highest reported in the literature. However, they reported that, when the F_5 selections from the first cycle were grown in a year when protein content was unusually high, significant differences were found between high and low protein selections in only six of nine crosses, and ranged from 0.4 to 1.4% protein content (0.3 to 1.2% protein content at 13.5% moisture content). Thus, environmental conditions producing unusually high protein content appeared to narrow the range between high and low protein selection groups. In the

present study, protein content was unusually high in 1984 when the F_3 families were grown in hill plots, but the difference between high and low protein selection groups was much greater than in 1985 when protein content was lower. This illustrates the profound effect that environmental conditions can have on the ability to detect differences in protein content among genotypes.

Guthrie et al. (1984) indicated that response to selection, as determined by the differences between high and low protein selection groups in F_4 of six hard red winter wheat crosses grown in Oklahoma, ranged from 0.5 to 1.1% protein content. The selection groups were established using grid selection in unreplicated F_3 rows at the same location as the F_4 trials were later grown. The response to selection may be biased upwards because only one location was used and thus would not account for genotype x environment interactions.

The relatively low response to selection for protein content observed in the present study may be due to a number of factors. Firstly, genetic variation for protein content in the crosses of the present study may not be as great as in other studies. Secondly, the experimental material used here differs considerably from the other studies because, although durum wheat and common wheat are related, they are different species. Guthrie et al. (1984) used Atlas 66 as one of their high protein parents. This cultivar carries at

least one major gene for protein content on chromosome 5D and a gene or genes with a lesser effect on chromosome 5A (Morris et al., 1978). Selection for major genes would give a greater response to selection than selection for minor genes. Thirdly, environmental variation, such as soil heterogeneity throughout the experimental area, may have been a factor. However, this does not appear to be very important in the present study because the coefficients of variation were less than 4% (Tables 8, 12). An exception may be the MD cross at Glenlea which had a slightly higher coefficient of variation than the other cross locations in 1985 (Table 12). The variable appearance of plots in this cross location may account for the fact that no significant differences in protein content were found among selection groups (Table 13). Finally, the most important factor contributing to the low response to selection was probably the unfavorable and contrasting growing conditions in 1984 and 1985 during the grain filling period. Environmental conditions have a strong influence on protein content and may mask genetic differences (Johnson et al., 1969, 1985; Konzak and Rubenthaler, 1984). Lebsock et al. (1964) reported the occurrence of widely different heritabilities for protein content in different years, and suggested that such genotype x environment interactions could reduce the effectiveness of early generation selection for protein content.

As discussed previously, the check cultivars included with the F_3 families in 1984 did not perform as expected with respect to protein content (Table 11). As a result of disease and hot, dry conditions during the 1984 grain filling period, Medora and DT367 generally had more kernel shrivelling, lighter kernels, lower yield and higher protein content than expected relative to Wakooma and DT447 (Tables 11, 18). Wakooma, in contrast, had less kernel shrivelling, heavier kernels, higher yield and lower protein content than expected relative to the other cultivars. These results suggest that genotype x environment interactions were present.

Several studies in wheat indicate that shrivelled, poorly filled kernels have a higher protein content than plump, well filled kernels (Johnson et al., 1973b; Philips and Schlesinger, 1974). Shahani and Saulescu (1984) suggested that incomplete development of kernels caused by unfavorable climatic conditions greatly affected starch deposition and proportionately increased protein content. As in the present study, Croy et al. (1978) observed that hot, dry conditions hastened maturity, decreased yield and kernel weight, but increased protein content in wheat. Zitelli et al. (1979) also reported that shrunken kernels produced in a dry year resulted in higher protein content in durum wheat. Thus, selection for high protein content under stress conditions may actually select the genotypes that are

TABLE 18. Mean combined over crosses for yield, protein yield, kernel weight, protein per kernel and kernel shrivelling of the four check cultivars grown with the F_3 families for the NIR method.

	Cultivar[2]			
Trait[1]	Wakooma	Medora	DT447	DT367
YLD	65.2a[3]	55.2a	68.9a	59.5a
PY	10.2a	9.0a	10.5a	9.3a
KW	36.6b	36.5b	44.4a	35.7b
PK	5.72b	5.95b	6.80a	5.58b
KS	1.9b	2.3ab	1.6b	3.1a

[1]Abbreviations for traits are defined in Table 4.

[2]Check cultivars were combined over crosses using a randomized complete block design (Appendix Table 34).

[3]Cultivar means over crosses followed by the same letter are not significantly different at the 0.01 probability level according to Fischer's LSD test.

most susceptible to these conditions rather than the genotypes with genetic potential for high protein content.

The effect of incomplete kernel development on protein content was evident in comparisons of the F_3 selection groups. HP had lower kernel weights and more kernel shrivelling than RP and LP in all crosses (Table 19). RP, in turn, had lighter kernels and more kernel shrivelling than LP, except for the DT cross in which RP and LP had the same kernel weight. The selection groups did not differ significantly in yield, except for the WK cross in which HP was lower yielding than RP and LP (Table 19). No significant differences in protein yield or protein per kernel were detected among selection groups (Table 19). Analyses of variance for detecting differences among F_3 selection groups are given in Appendix Tables 5 to 7 to support these results. The apparent relationship between protein content and incomplete kernel development, and the differential response of the check cultivars to unfavorable growing conditions in 1984 strongly suggest that genotype x environment interactions were at least partly responsible for the low response to selection for protein content observed in this study. However, it is also possible that growing the experimental material in hill rather than normal row plots may have influenced the results.

In contrast to 1984, growing conditions during the grain filling period in 1985 were cool and wet. Such

TABLE 19. Mean yield, protein yield, kernel weight, protein per kernel and kernel shrivelling of F_3 selection groups in each cross for the NIR method.

Trait[1]	Cross	Selection Group		
		HP	RP	LP
YLD	WK	60.4b[2]	68.7a	70.4a
	MD	64.4a	64.4a	69.3a
	DT	66.7a	68.7a	75.0a
PY	WK	9.8a	10.7a	10.4a
	MD	10.7a	10.1a	10.3a
	DT	10.6a	10.4a	10.9a
KW	WK	32.2c	34.3b	36.6a
	MD	32.7c	35.6b	38.3a
	DT	38.5b	40.8a	42.1a
PK	WK	5.25a	5.33a	5.43a
	MD	5.44a	5.60a	5.69a
	DT	6.12a	6.20a	6.10a
KS	WK	3.3a	2.8b	2.2c
	MD	3.3a	2.7b	2.0c
	DT	3.0a	2.4b	2.0c

[1]Abbreviations for traits are defined in Table 4.

[2]Means within a cross followed by the same letter are not significantly different at the 0.01 probability level according to Fischer's LSD test.

differences in growing conditions increase the probability of genotype x environment interactions which would, in turn, reduce the response to selection. As noted above, the check cultivars included with the F_5 bulks in 1985 were generally ranked in the expected order with respect to protein content, but the range in protein content was less than normal (Table 15). The relatively high protein content of DT367 may have resulted from its relatively low yield, particularly at Glenlea where it did not differ significantly from Wakooma when combined over crosses (Table 20). Both cultivars yielded less than DT447 and Medora. At Winnipeg, DT367 yielded more than Wakooma, but less than Medora and DT447. Thus, DT367 did not appear to express its full yield potential even at Winnipeg. For most of the remaining traits studied, DT367 was adversely affected by the Glenlea environment, resulting in greater kernel shrivelling and lower protein yield, test weight, kernel weight and protein per kernel than expected (Table 20). Since DT367 was common to all three crosses, its relatively poor performance may contribute to genotype x environment interactions among its progeny.

Severe lodging occurred during the grain filling period in 1985. Lodging can reduce yield, kernel weight and test weight, and increase kernel shrivelling and protein content (Laude and Pauli, 1956; Weibel and Pendleton, 1964; Pinthus, 1973; Pumphrey and Rubenthaler, 1983). In general,

TABLE 20. Mean combined over crosses for yield, protein yield, test weight, kernel weight, protein per kernel and kernel shrivelling of the four check cultivars grown with the F_5 bulks at each location for NIR row plots.

Trait[1]	Location	Cultivar[2]			
		Wakooma	Medora	DT447	DT367
YLD	Glenlea	2893b[3]	3481a	3789a	2720b
	Winnipeg	2898c	4200a	4385a	3759b
PY	Glenlea	417b	485a	506a	362c
	Winnipeg	403c	556a	578a	464b
TW	Glenlea	74.6c	76.7b	77.9a	72.2d
	Winnipeg	73.6c	78.6a	77.7a	75.7b
KW	Glenlea	31.6c	34.4b	40.9a	34.1b
	Winnipeg	34.7c	40.5b	45.3a	41.1b
PK	Glenlea	4.56b	4.78b	5.45a	4.53b
	Winnipeg	4.82d	5.36b	5.97a	5.07c
KS	Glenlea	2.3a	1.6b	1.0b	2.8a
	Winnipeg	2.3a	1.0c	1.0c	1.5b

[1]Abbreviations for traits are defined in Table 4.

[2]Check cultivars within a location were combined over crosses using the randomized complete block design (Appendix Table 35).

[3]Cultivar means over crosses within a location followed by the same letter are not significantly different at the 0.01 probability level according to Fischer's LSD test.

the earlier lodging occurs during the grain filling period, the greater is the effect on the above traits (Pinthus, 1973). Pumphrey and Rubenthaler (1983) reported that lodging can increase protein content in wheat by as much as 14% relative to the standing crop, depending on the stage at which it occurred. Interactions between different genotypes and lodging effects may have reduced the response to selection for protein content in the present study.

In conclusion, although significant responses to selection for protein content were observed in durum wheat using the NIR selection method, they were small in magnitude and of doubtful value in a practical breeding program. Genotype x environment interactions were probably the main cause of the relatively low response to selection.

4.3 Comparison of ISD and NIR Selection Methods

When the ISD selection method was used to establish protein selection groups in F_2, the density of the solution required for the high protein separation ranged from 1.202 to 1.212 g/cm^3, while that for the low protein separation ranged from 1.241 to 1.248 g/cm^3 (Table 21). The selection intensities for the high and low protein fractions were 14.0% in the WK cross and 15.7% in the MD cross (Table 21). In the DT cross, selection intensities were 17.3 and 18.0% for the high and low protein fractions, respectively.

The protein contents of the less dense, selected fractions for the high protein separation were 1.2, 0.8 and 0.5%

TABLE 21. Protein content and kernel weight of selected and unselected fractions, and the selection intensity and solution density used to separate the fractions by the ISD method in F_2 of each cross.

Cross	Protein Separation	Solution Density (g/cm^3)	Selected Fraction				Unselected Fraction	
			No. of Seeds	Selection Intensity (%)	PC[1]	KW[2]	PC	KW
WK	High	1.212	215	14.0	16.3	41.5	15.1	47.1
	Low	1.248	215	14.0	14.6	49.6	15.2	46.0
MD	High	1.202	228	15.7	15.9	41.5	15.1	46.9
	Low	1.241	227	15.7	14.7	48.5	15.7	46.1
DT	High	1.205	199	17.3	15.2	46.0	14.7	50.7
	Low	1.243	207	18.0	14.3	52.7	15.0	50.1
Mean[3]	High	1.206	214	15.7	15.8	43.0	15.0	48.2
	Low	1.244	216	15.9	14.5	50.3	15.3	47.4

[1]Protein content (%) adjusted to 13.5% moisture content as determined by the Kjeldahl method.

[2]Kernel weight (mg).

[3]Mean over the three crosses.

greater than the unselected, submerged fractions for the WK, MD and DT crosses, respectively (Table 21). However, when averaged over the three crosses, the mean protein content of 15.8% for the selected fractions did not differ significantly ($0.05<P<0.1$) from the mean protein content of 15.0% for the unselected fractions, although the F value was close to significance (Tables 21, 22). The mean difference of 0.8% protein content between the two fractions was similar in magnitude to that reported by Peterson et al. (1986) for the ISD method used in 52 F_3 to F_5 bulk populations of winter wheat. They observed that the protein content of the less dense, selected fractions was, on average, 1.2 g/kg (1.0% protein content adjusted to 13.5% moisture content) greater than that of the more dense fractions remaining after low density selection. They used mean selection intensities of 10.6 and 15.4% for populations grown in Nebraska and Arizona, respectively.

The protein contents of the more dense, selected fractions for the low protein separation were 0.6, 1.0 and 0.7% less than the unselected, floating fractions in the WK, MD and DT crosses, respectively (Table 21). When averaged over all three crosses, the mean protein content of 14.5% for the selected fractions was significantly ($P<0.05$) less than that of 15.3% for the unselected fractions (Tables 21, 22). As expected, the selected fractions from the high protein separation had a significantly ($P<0.05$) higher

TABLE 22. Analysis of variance for protein content and kernel weight of selected (low or high density) and unselected fractions separated by the ISD method in F_2.

Trait[1]	Source of Variation	DF	Mean Square: Low Density vs. Unselected	Mean Square: High Density vs. Unselected	Mean Square: Low Density vs. High Density
PC	Crosses	2	0.3016	0.1517	0.2716
	Fractions	1	1.0416	0.8818*	2.4067*
	Error	2	0.0616	0.0215	0.0815
	C.V.(%)[2]		1.6	1.0	1.9
KW	Crosses	2	11.2119	10.0068	11.2217
	Fractions	1	41.0811**	12.3262*	79.2061**
	Error	2	0.1118	0.2065	0.2715
	C.V.(%)		0.7	0.9	1.1

[1]PC=protein content (%) adjusted to 13.5% moisture content as determined by the Kjeldahl method.
KW=kernel weight (mg).

[2]Coefficient of variation.

protein content than the selected fractions from the low protein separation when considered over all crosses (Table 22). Differences in protein content between the selected fractions from the high and low protein separations were 1.7, 1.2 and 0.9% for the WK, MD and DT crosses, respectively (Table 22). Thus, imbibed seed density appeared to be inversely related to protein content as reported by Garzon-Trula (1984) and Peterson et al. (1986).

The mean kernel weight of the selected fractions for high protein separation was significantly ($P<0.01$) less than that of the unselected fractions, with the difference averaging 5.2 mg per kernel over the three crosses (Tables 21, 22). Peterson et al. (1986) similarly observed that kernel weight of the low density, selected fractions averaged 2 mg per kernel less than that of the more dense, residual fractions over all populations, with a range from 6 mg per kernel lower to slightly higher than the more dense, residual fractions.

The mean kernel weight of the selected fractions for low protein separation was significantly ($P<0.05$) greater than that of the unselected fractions averaged over crosses (Table 22), but the difference in this case was only 2.9 mg per kernel (Table 21). Kernels of the selected fractions for high protein separation weighed significantly ($P<0.01$) less than those of the selected fractions for low protein separation, with the difference averaging 7.3 mg per kernel

(Tables 21, 22). In this study, there appeared to be a strong, positive relationship between imbibed seed density and kernel weight. The lighter kernel weights may have been due to kernel shrivelling which would tend to increase protein content.

The ISD method was effective in establishing HP with a higher protein content than LP. HP and LP are represented by the selected fractions from the high and low protein separations, respectively. The mean protein content of F_2 plants selected at random for RP ranged from 16.1 to 16.8% depending on the cross, and appeared to be considerably greater than that for HP in the MD and DT crosses (Table 23). However, the protein content of RP is not directly comparable to HP and LP because it was determined by a different method. The range in protein content for the F_2 RP plants was 3.8, 4.6 and 4.3% for the WK, MD and DT crosses, respectively (Table 23).

The protein content of 20 randomly selected Wakooma plants included as checks for each cross averaged 17.0 to 17.3% with a range of 2.8 to 3.7%, depending on the cross (Table 23). Within a cross, the standard error for the Wakooma plants was nearly as high as that for the F_2 RP plants (Table 23). Thus, environmental variation would appear to greatly affect the protein content of spaced plants, making selection difficult.

TABLE 23. Mean protein content, standard error and range for F_2 plants in RP and random Wakooma plants grown with the F_2 plants in each cross for the ISD method.

	F_2 RP Plants			Wakooma Plants		
Cross	Mean	S.E.[1]	Range	Mean	S.E.	Range
WK	16.1	0.21	14.7-18.5	17.0	0.19	15.7-18.8
MD	16.8	0.31	15.0-19.6	17.3	0.19	15.8-19.5
DT	16.1	0.25	14.5-18.8	17.3	0.18	15.9-18.7

[1]Standard error of the mean.

The results for the F_3 families grown in hill plots for the NIR method have been discussed in section 4.2. Although results of the ISD and NIR methods at the selection stage are not directly comparable, HP and LP established in F_3 for the NIR method appeared to differ more in protein content than HP and LP established in F_2 for the ISD method (Tables 10, 21).

Highly significant ($P<0.01$) differences in protein content were found among the F_5 families and checks for the ISD hill plots (Table 24) and among the F_5 bulks and checks for the NIR hill plots (Table 25) in each cross location. The overall means and coefficients of variation were similar for both ISD and NIR hill plots within a particular cross location (Tables 24, 25). The overall means for protein content were higher at Glenlea than Winnipeg. Coefficients of variation were relatively low, ranging from 2.8% to 5.8% over all cross locations and methods. The lattice design generally resulted in only small increases in efficiency over the randomized complete block design (Tables 24, 25).

The F_5 selection groups within each method differed significantly ($P<0.05$) in protein content for only the DT cross at Glenlea (Tables 26, 27). Although no significant differences in protein content were detected among selection groups for any of the other cross locations of either method, the probability of a greater F value for selection groups for the WK cross at Glenlea was approximately 0.1 for

TABLE 24. Lattice analysis of variance for protein content of F_5 families and checks in each cross location for the ISD hill plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	6.7986	3	2.4521
	Entries	63	1.1658**	63	1.7313**
	Blocks	28	0.4664	28	0.7837
	Error	159	0.2932	156	0.5656
	Mean		14.7		14.2
	C.V.(%)[1]		3.8		5.4
	R.E.(%)[2]		103		102
MD	Replications	3	1.9638	3	4.4906
	Entries	63	1.0916**	63	1.5987**
	Blocks	28	0.2933	28	0.5097
	Error	158	0.2333	158	0.3503
	Mean		14.3		13.4
	C.V.(%)		3.4		4.5
	R.E.(%)		101		102
DT	Replications	3	0.6901	3	1.3742
	Entries	63	1.2691**	63	1.0556**
	Blocks	28	0.4733	28	0.2959
	Error	157	0.1529	158	0.1465
	Mean		13.6		12.7
	C.V.(%)		3.0		3.1
	R.E.(%)		120		107

**Significant at the 0.01 probability level.

[1]Coefficient of variation.

[2]Relative efficiency of the lattice design compared to the randomized complete block design.

TABLE 25. Lattice analysis of variance for protein content of F_5 bulks and checks in each cross location for the NIR hill plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	6.6030	3	1.6277
	Entries	63	1.0848**	63	1.7328**
	Blocks	28	0.6396	28	1.0783
	Error	158	0.2243	161	0.6081
	Mean		14.8		14.0
	C.V.(%)[1]		3.4		5.8
	R.E.(%)[2]		117		105
MD	Replications	3	1.9759	3	3.3971
	Entries	63	1.0394**	63	0.9944**
	Blocks	28	0.2697	28	0.3219
	Error	161	0.2746	159	0.3089
	Mean		14.3		13.2
	C.V.(%)		3.7		4.2
	R.E.(%)		100		100
DT	Replications	3	1.1718	3	0.2434
	Entries	63	0.6460**	63	0.7882**
	Blocks	28	0.2539	28	0.2217
	Error	158	0.1597	156	0.1180
	Mean		13.5		12.6
	C.V.(%)		3.0		2.8
	R.E.(%)		103		106

**Significant at the 0.01 probability level.

[1]Coefficient of variation.

[2]Relative efficiency of the lattice design compared to the randomized complete block design.

TABLE 26. Analysis of variance and orthogonal contrasts for protein content of F_5 selection groups in each cross location for the ISD hill plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	6.9694**	3	2.2824*
	Selection Groups (G)	2	2.4352	2	0.7170
	HP vs. RP	1	2.3544	1	0.7457
	(HP+RP) vs. LP	1	2.5628	1	0.7082
	Families within G	57	1.0274**	57	1.7424**
	Error	175	0.3102	172	0.6086
MD	Replications	3	1.5602**	3	4.9062**
	Selection Groups (G)	2	1.3210	2	0.6642
	HP vs. RP	1	0.3624	1	1.2956
	(HP+RP) vs. LP	1	2.2707	1	0.0270
	Families within G	57	1.0022**	57	1.5674**
	Error	174	0.2464	174	0.3810
DT	Replications	3	0.6030*	3	1.3166**
	Selection Groups (G)	2	2.9962*	2	0.6171
	HP vs. RP	1	1.6534	1	0.0683
	(HP+RP) vs. LP	1	4.2890*	1	1.1659
	Families within G	57	0.9314**	57	0.7496**
	Error	173	0.2002	174	0.1660

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

TABLE 27. Analysis of variance and orthogonal contrasts for protein content of F_5 selection groups in each cross location for the NIR hill plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	5.4349**	3	1.6532
	Selection Groups (G)	2	1.3257	2	1.8078
	HP vs. RP	1	2.2849	1	1.4823
	(HP+RP) vs. LP	1	0.3407	1	2.1333
	Bulks within G	57	1.0035**	57	1.5717**
	Error	174	0.2631	177	0.6936
MD	Replications	3	1.8079**	3	2.9283**
	Selection Groups (G)	2	2.3806	2	0.1242
	HP vs. RP	1	0.2176	1	0.0678
	(HP+RP) vs. LP	1	4.5435	1	0.1784
	Bulks within G	57	0.8972**	57	0.8733**
	Error	177	0.2504	175	0.3037
DT	Replications	3	1.1776**	3	0.2556
	Selection Groups (G)	2	1.3826*	2	0.7428
	HP vs. RP	1	0.2250	1	0.7204
	(HP+RP) vs. LP	1	2.5402*	1	0.7658
	Bulks within G	57	0.4110**	57	0.4953**
	Error	176	0.1689	173	0.1392

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

the ISD method (Table 26), while the selection groups for the MD cross at Glenlea approached significance ($0.05<P<0.1$) for the NIR method (Table 27). For both methods, the orthogonal contrasts for the DT cross at Glenlea indicated that HP did not differ significantly ($P>0.05$) from RP, while HP and RP combined differed significantly ($P<0.05$) from LP (Tables 26, 27). For all cross locations, highly significant ($P<0.01$) differences in protein content were found among F_5 families within selection groups for the ISD hill plots (Table 26) and among F_5 bulks within selection groups for the NIR hill plots (Table 27). The mean protein contents of the individual F_5 families for the ISD hill plots and F_5 bulks for the NIR hill plots are given in Appendix Tables 8 and 9, respectively.

The mean protein content of HP for the DT cross at Glenlea was 0.4 and 0.3% higher than LP for the ISD and NIR F_5 hill plots, respectively (Table 28). However, RP did not differ significantly from HP or LP for either method. Although significant differences in protein content were not found among the selection groups in the remaining cross locations for either method, the trend for the NIR hill plots appeared to be in the desired direction with HP greater than LP and RP intermediate (Table 28). For the ISD hill plots, RP tended to be higher than HP and LP, except for the DT cross (Table 28). The range in mean protein contents of the individual F_5 families and bulks in each

TABLE 28. Protein content of F_5 selection groups in each cross location for the NIR and ISD hill plots.

Cross	Method		Location					
			Glenlea			Winnipeg		
			HP	RP	LP	HP	RP	LP
WK	NIR	Mean	14.9a[1]	14.6a	14.7a	14.2a	14.0a	13.9a
		Range	14.3-15.8	14.1-16.6	13.5-15.7	13.1-15.6	13.1-14.9	12.7-15.2
	ISD	Mean	14.7a	14.9a	14.6a	14.2a	14.4a	14.2a
		Range	13.8-15.7	14.1-15.6	13.6-15.7	12.7-15.3	13.5-15.6	13.1-15.5
MD	NIR	Mean	14.4a	14.3a	14.0a	13.2a	13.2a	13.1a
		Range	13.6-15.0	13.3-15.9	13.2-14.5	12.5-13.9	12.2-14.3	12.2-14.1
	ISD	Mean	14.3a	14.4a	14.1a	13.3a	13.5a	13.4a
		Range	13.4-15.1	13.2-15.5	13.3-15.1	12.1-14.5	12.5-14.4	12.4-15.0
DT	NIR	Mean	13.6a	13.5ab	13.3b	12.6a	12.5a	12.4a
		Range	13.1-14.2	13.2-14.2	12.7-13.9	12.1-13.0	11.8-13.4	11.8-13.4
	ISD	Mean	13.8a	13.5ab	13.4b	12.8a	12.7a	12.6a
		Range	12.8-14.8	12.7-14.4	12.5-13.9	12.0-13.5	11.9-13.5	11.6-13.6

[1]Means within each method for each cross location followed by the same letter are not significantly different at the 0.05 probability level according to Fischer's LSD test.

selection group tended to be similar within a particular cross location for the two methods (Table 28).

Significant ($P<0.05$) differences in protein content among selection groups within methods were detected for only the DT cross at Glenlea when the F_5 hill plots for the ISD and NIR methods were combined for each cross location (Table 29). The LSD at the 0.05 probability level was 0.3% protein content for selection groups within methods for this cross location. Thus, HP, RP and LP of the ISD method did not differ significantly from their respective selection groups of the NIR method (Table 28). No significant ($P>0.05$) differences in protein content were found between methods, while highly significant ($P<0.01$) differences were found among F_5 entries within selection groups within methods for all cross locations (Table 29).

The mean protein contents of the parental cultivars included with the F_5 hill plots for ISD and NIR methods are given by cross location in Table 30. DT367 had a higher protein content than expected relative to the other cultivars; the difference in protein content between Wakooma and DT367 ranged from 0.9 to 2.4% over all cross locations and methods, averaging 1.5 and 1.7% for Glenlea and Winnipeg, respectively (Table 30). When combined over methods and crosses, Wakooma had the highest protein content followed by Medora at both locations (Table 30). DT447 and

TABLE 29. Analysis of variance for protein content of NIR and ISD F_5 hill plots combined for each cross location.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications (R)	3	11.2643**	3	2.7403**
	Methods (M)	1	0.4542	1	8.4985
	R x M	3	1.1225**	3	1.1806
	Selection Groups (G) within M	4	1.8805	4	1.2624
	Entries within G within M	114	1.0155**	114	1.6571**
	Error	349	0.2867	349	0.6517
MD	Replications (R)	3	3.1227**	3	6.9436**
	Methods (M)	1	0.3032	1	5.4124
	R x M	3	0.2486	3	0.8843
	Selection Groups (G) within M	4	1.8508	4	0.3942
	Entries within G within M	114	0.9497**	114	1.2204**
	Error	351	0.2484	349	0.3422
DT	Replications (R)	3	1.0052**	3	0.8090**
	Methods (M)	1	0.7067	1	4.0023
	R x M	3	0.7615**	3	0.7713**
	Selection Groups (G) within M	4	2.1894*	4	0.6800
	Entries within G within M	114	0.6712**	114	0.6224**
	Error	349	0.1845	347	0.1526

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

TABLE 30. Mean protein contents of the four check cultivars grown with the NIR and ISD F_5 hill plots in each cross location.

Location	Cross	Method	Cultivar				
			Wakooma	Medora	DT447	DT367	LSD[1]
Glenlea	WK	NIR	15.3	15.2	13.8	14.4	0.7
		ISD	15.2	14.3	13.6	14.0	0.8
	MD	NIR	15.6	14.6	13.6	13.9	0.7
		ISD	15.5	14.4	14.2	13.9	0.7
	DT	NIR	15.1	14.5	13.8	13.5	0.6
		ISD	15.5	14.6	13.9	14.0	0.6
	Combined[2]		15.4a[3]	14.6b	13.8c	13.9c	
Winnipeg	WK	NIR	15.3	13.4	13.1	12.9	1.1
		ISD	14.3	13.5	13.4	13.2	1.1
	MD	NIR	14.8	13.7	13.1	13.2	0.8
		ISD	14.7	13.6	13.0	13.1	0.9
	DT	NIR	14.5	13.5	12.6	12.7	0.5
		ISD	14.8	13.7	13.0	12.8	0.6
	Combined		14.7a	13.6b	13.1c	13.0c	

[1]Least significant difference at the 0.05 probability level calculated from the randomized complete block analysis of all 64 entries for each method in a cross location.

[2]Check cultivars within a location were combined over methods and crosses using a randomized complete block design (Appendix Table 36).

[3]Cultivar means over methods and crosses within a location followed by the same letter are not significantly different at the 0.01 probablility level according to Fischer's LSD test.

DT367 had the lowest protein content and did not differ significantly (Table 30).

Less than five of the F_5 families and bulks for the ISD and NIR hill plots, respectively, significantly exceeded the protein content of the high protein parent of a particular cross (Table 30, Appendix Tables 8, 9). Similarly, less than five of the F_5 families and bulks for the ISD and NIR hill plots, respectively, had significantly lower protein content that DT367 for all cross locations, except the DT cross at Glenlea and Winnipeg (Table 30, Appendix Tables 8, 9). For the DT cross, the ISD hill plots had 23 and 10 F_5 families at Glenlea and Winnipeg, respectively, with lower protein content than DT367, while the NIR hill plots had 4 and 15 F_5 bulks at Glenlea and Winnipeg, respectively, with lower protein content than DT367.

Response to selection, as determined by the number of high protein F_5 families and bulks (one standard deviation greater than the mean) retained by selection group for the ISD and NIR hill plots, respectively, suggested that selection for high protein content by either method was generally no more effective than random selection; in some instances, it was no more effective than selection for low protein content (Table 31). An exception was the DT cross at Glenlea in which HP of the NIR and particularly the ISD hill plots appeared to retain more high protein F_5 bulks and families, respectively, than RP or LP. This was expected

TABLE 31. Number of F_5 entries with high or low protein content retained by selection group in each cross location for the NIR and ISD hill plots.

		Number of High Protein[1] F_5 Entries							
		NIR				ISD			
Cross	Location	HP	RP	LP	Total	HP	RP	LP	Total
WK	Glenlea	2	1	3	6	2	4	2	8
	Winnipeg	3	2	2	7	2	6	4	12
MD	Glenlea	2	4	0	6	3	3	3	9
	Winnipeg	1	4	4	9	2	1	4	7
DT	Glenlea	4	2	2	8	9	5	0	14
	Winnipeg	3	4	2	9	3	4	2	9
Total		15	17	13	45	21	23	15	59
		Number of Low Protein[2] F_5 Entries							
WK	Glenlea	0	2	4	6	4	1	9	14
	Winnipeg	2	5	2	9	3	6	2	11
MD	Glenlea	1	4	5	10	4	1	4	9
	Winnipeg	1	4	4	9	2	3	5	10
DT	Glenlea	1	0	5	6	4	4	4	12
	Winnipeg	1	3	6	10	2	4	4	10
Total		6	18	26	50	19	19	28	66

[1]Mean protein content one standard deviation greater than the mean of all 60 F_5 entries within a method in a cross location.

[2]Mean protein content one standard deviation less than the mean of all 60 F_5 entries within a method in a cross location.

since the DT cross at Glenlea was the only cross location to have significant differences among selection groups for either method (Table 28). Selection for low protein content appeared to be somewhat more effective in retaining low protein F_5 families and bulks (one standard deviation less than the mean) than selection for high protein content was in retaining high protein F_5 families and bulks, particularly for the NIR hill plots (Table 31). However, in some cases, HP retained as many low protein F_5 families and bulks as LP for the ISD and NIR hill plots, respectively.

The magnitude of response to selection for protein content by the ISD method in this study (i.e., 0 to 0.4%) was lower than that reported by Peterson et al. (1986). They found that populations selected for low density had a significantly higher protein content than unselected control populations in 10 of 52 bulk populations evaluated in the field following density separation; increases ranged from 6 to 11 g/kg (0.5 to 1.0% protein content adjusted to 13.5% moisture content). In one bulk population, low density selection actually decreased protein content by 9 g/kg (0.8% protein content adjusted to 13.5% moisture content). Over all 52 bulk populations, they observed that low density selection increased protein content an average of 1 and 2 g/kg (0.1 and 0.2% protein content adjusted to 13.5% moisture content) over the unselected control in Nebraska and Arizona, respectively. The low density selected populations

and unselected control populations in their study are equivalent to HP and RP, respectively, in the present study. They also found a wide range in protein content and imbibed seed density within the winter wheat cultivar, Bennett. They concluded from these results that a large amount of nongenetic variation in the protein content of individual seeds appeared to limit the effectiveness of imbibed seed density selection for increasing protein content in wheat.

Nongenetic variation was probably the major factor responsible for the lack of response to selection for protein content observed in the present study using the ISD method. As noted above, the protein content of spaced Wakooma plants varied by as much as 3.7% within a cross, and standard errors were nearly as high as for the same number of random F_2 plots (Table 23). A number of studies have indicated that considerable variation in protein content exists among plants of the same genotype grown in the same test (Clark, 1926; Levi and Anderson, 1950; Kaul and Sosulski, 1965; Diehl et al., 1978). However, variation among plants is only one source of nongenetic variation; Levi and Anderson (1950) reported that the protein content of individual kernels within a plant of a wheat cultivar may be as high as 6%. They observed that protein content tended to be higher in the shorter tillers of plants with more than three tillers. Similarly, Gericke (1930) and McNeal and Davis (1966) reported differences in protein content among

tillers. In the present study, attempts were made to reduce this source of variation by using a head from one of the primary tillers of each plant. Several researchers have reported that spikelets from the top third of the head generally have a lower protein content than those from the lower two thirds of the same head (Levi and Anderson, 1950; McNeal and Davis, 1954, 1966; Stuber et al., 1962a; Ali et al., 1969). Many studies have shown that the protein content of the two basal kernels generally exceeded that of distil kernels within the same spikelet (Levi and Anderson, 1950; McNeal and Davis, 1954; Bremner, 1972; Sofield et al., 1977; Simmons and Moss, 1978; Sclater, 1982; Herzog and Stamp, 1983). Thus, floret orientation may account for a large part of the nongenetic variation in protein content.

Peterson et al. (1986) indicated that nongenetic variation in protein content may be affected by variation in seed size, which is also influenced by floret orientation. They passed seed samples used for density separations over screens to remove small and shrivelled seeds. In the present study, seed samples were not screened but only relatively well filled kernels were selected from each plant by hand. However, some shrivelling was still present. As noted previously, there appeared to be a positive relationship between imbibed kernel density and kernel weight.

Variation in seed configuration may influence density and water absorption characteristics (Leopold, 1983; Peterson et al., 1986). Hallgren and Murty (1983) suggested that air bubbles trapped in the crease of dry wheat kernels may affect the buoyancy of the kernels. Fehr et al. (1968) reported that wrinkled seed coats and cracked seeds increased the buoyancy of dry soybeans regardless of chemical composition. Cracks in imbibed kernels may also distort swelling and reduce density.

Other factors that may reduce the effectiveness of the ISD method include insufficient genetic variation in protein content relative to nongenetic variation, and the presence of dominance and epistasis for protein content in early generation populations (Peterson et al., 1986). Peterson et al. (1986) suggested that a substantial amount of genetic variation in protein content will be needed to make progress using density separation. They also recommended that the proportion of less dense seeds selected be reduced. The amount of genetic variation for protein content present in most crosses of conventional durum wheat breeding programs may be inadequate for density selection to be effective. However, introduction of exotic, unadapted germplasm with high protein content into breeding programs may increase kernel shrivelling and hence reduce the effectiveness of the ISD method.

The NIR method appeared to be more effective than the ISD method because trends in protein content among selection groups for the NIR method were in the desired direction, whereas RP tended to be higher than HP and LP for the ISD method. The results may have been influenced by the different generations at which selection was applied and by different advancement of generations for the two selection methods. Selection was applied on seed from F_2 plants for the ISD method rather than seed from F_3 plants as for the NIR method. Since the ISD method can handle large numbers of plants easily and is nondestructive, the optimal time to use such a method in a practical breeding program should be the F_2 generation where the greatest proportion of desirable genotypes occurs. Selection for the NIR method was applied in F_3 because of constraints in the amount of seed, time and labor required to perform NIR measurements on a large number of samples. The use of replication and 15 plants per F_3 hill plot would probably result in more accurate determination of protein content, and increase heritability and the response to selection for the NIR method when compared to the ISD method. Although Haunold et al. (1962) and Johnson et al. (1963) reported that selection for protein content among F_2 plants was effective, others have indicated that it is of limited value (Sunderman et al., 1965; Bhatia and Rabson, 1976; Konzak and Rubenthaler, 1984). In contrast, selection for protein content in the F_3

generation has generally been effective (Lebsock et al., 1964, McNeal et al., 1972; Guthrie et al., 1984). However, even if F_3 families in replicated hill plots had been used for the ISD method, nongenetic variation among individual seeds in F_3 hill plots may have been just as great as in F_2 plants.

The F3 families selected by NIR were advanced by bulking each generation, while the seeds selected by ISD from F_2 plants were advanced by a single seed descent procedure. A single seed descent procedure was used for the ISD method because of limitations in greenhouse space and the desirability of evaluating the selections of both methods together in the same generation. Thus, F_3-derived F_5 bulks and F_4-derived F_5 families were used for the NIR and ISD methods, respectively. The single seed descent procedure used for the ISD method may have resulted in the irretrievable loss of desirable alleles for protein content because of genetic drift (Sneep, 1977). This may have reduced the response to selection for protein content for the ISD method when compared to the NIR method since bulk populations used for the NIR method would probably retain more of the desirable alleles for protein content than single seed descent procedures. However, genetic segregation would result in at least some undesirable genotypes in bulk populations. Overall, procedures used for

the ISD method may have reduced response to selection more than those used for the NIR method.

In conclusion, early generation selection for protein content in durum wheat was generally ineffective for both ISD and NIR methods when selections were evaluated in F_5 hill plots. The NIR method appeared to be more effective than the ISD method but the ISD method had the advantage of requiring less time, labor and expense. However, the relatively low response to selection ranging from 0 to 0.4% suggests that early generation selection for protein content by either method is not practical in a durum wheat breeding program.

4.4 Comparison of NIR Hill and Row Plot Efficiency

When the F_5 bulks of the NIR method were evaluated in hill rather than in four-row plots, fewer differences in protein content were found among selection groups and fewer high protein F_5 bulks were retained by HP relative to the other selection groups. This would suggest that hill plots are less efficient than row plots in selecting for protein content.

The overall mean protein content of the NIR F_5 hill plots ranged from 0.1 to 1.0% higher than that of the NIR row plots over all cross locations in 1985 (Table 32). The coefficients of variation were also higher for hill plots, particularly at Winnipeg (Table 32). Thus, hill plots were associated with increased error variation although the coef-

TABLE 32. Summary statistics for protein content in NIR F_5 hill and row plots for each cross location in 1985.

Statistic	Glenlea			Winnipeg		
	WK	MD	DT	WK	MD	DT
Row Plots:						
Mean	13.9	13.8	12.9	13.0	12.7	12.5
C.V.(%)[1]	2.1	2.6	2.0	1.5	1.5	1.5
Range (% Mean)						
Minimum	94	92	93	94	94	94
Maximum	106	109	109	107	111	110
Heritability[2]	0.46	0.41	0.45	0.64	0.72	0.72
Hill Plots:						
Mean	14.8	14.3	13.5	14.0	13.2	12.6
C.V.(%)	3.4	3.7	3.0	5.8	4.2	2.8
Range (% Mean)						
Minimum	91	92	94	91	92	94
Maximum	112	111	112	111	112	115
Heritability	0.41	0.41	0.39	0.47	0.35	0.55
Row Plots - Hill Plots:						
Phenotypic correlation	0.58**	0.72**	0.62**	0.44**	0.62**	0.44**
Genetic correlation	0.77	0.98	0.84	0.60	0.79	0.51
Efficiency ratio	0.73	0.98	0.78	0.51	0.55	0.45
Replicates of hill plots required to give equivalent information of one row plot	5.0	1.1	2.8	+	+	+

**Significant at the 0.01 probability level.

+Cannot be calculated because the genetic correlation is less than the square root of heritability for row plots.

[1]Coefficient of variation.

[2]Heritability calculated on a single plot basis using a randomized complete block analysis of variance including all 64 entries in a cross location for each plot type.

ficients of variation were relatively small in magnitude. Torrie (1962) indicated that differences in coefficients of variation between soybean hill and row plots were small, and showed no definite pattern for protein content. For yield, a number of studies have indicated that hill plots had greater error variation and coefficients of variation than row plots. (Ross and Miller, 1955; Torrie, 1962; Frey, 1965; Baker and Leisle, 1970; O'Brien et al., 1979).

The hill plots had a slightly greater range in the mean protein contents of individual entries than did the row plots (Table 32). The maximum protein content expressed as a percentage of the overall mean was higher in hill plots and generally accounted for the increased range. Baker and Leisle (1970) and O'Brien et al. (1979) reported a greater range of yield expression in hill plots than in row plots, whereas Frey (1965) found no trend for hills to give a greater or lesser range of yield expression than that given by rod rows. Although a greater range in mean performance of cultivars would be associated with a larger genetic variance (Baker and Leisle, 1970), the increase in the range of protein content observed in hill plots of the present study was probably too small to overcome the increased error variance.

Heritabilities for protein content on a single plot basis at Winnipeg were considerably higher for row than for hill plots, ranging from 64 to 72 and 35 to 55%,

respectively (Table 32). These results suggest that hill plots are less efficient than row plots and would give a lower response to selection for protein content. However, the heritabilities for protein content at Glenlea were similar in magnitude for both plot types (Table 32). The heritabilities for protein content in hill plots were generally similar over the two locations, while heritabilities in row plots were higher at Winnipeg than Glenlea.

Phenotypic correlations between entry means in hill and row plots were highly significant ($P<0.01$) for protein content in all cross locations, with coefficients ranging from 0.44 to 0.72 (Table 32). The correlations between hill and row plots for protein content were higher at Glenlea than Winnipeg, and also higher for the MD cross than the other crosses at both locations. Variation in hill plots explained only 19 to 52% of the variation in the protein content of row plots. In soybeans, Torrie (1962) reported that five of seven correlation coefficients between hill and one-row plots over a four year period were significant for protein content and ranged from 0.50 to 0.94. However, Frey (1965) indicated that phenotypic correlations are misleading since the plant breeder is interested in genotypic expression.

Genetic correlations between hill and row plots for protein content were higher than phenotypic correlations and ranged from 0.51 to 0.98 (Table 32). As for phenotypic

correlations, genetic correlations were higher at Glenlea than Winnipeg, and also higher for the MD cross at both locations. Thus, the degree of resemblance between entries in hill and row plots was moderately high at Glenlea and for the MD cross at Winnipeg. Genetic correlations for protein content between hill and row plots have not been reported in the literature. Frey (1965) reported genetic correlations of 0.98 between hill and row plots for yield in oats. Baker and Leisle (1970) indicated that genetic correlations between hill and row plots for yield in durum and common wheat cultivars ranged from 0.81 to 0.99, while O'Brien et al. (1979) reported values ranging from 0.77 to 0.91 in F_3 of four wheat crosses. The genetic correlations for protein content obtained in the present study tended to be lower than those reported for yield. These results were unexpected since the heritability of protein content is generally higher than for yield (Davis et al., 1961; Baker et al., 1968b).

Selecting in hill plots for protein content in row plots was less efficient than selecting directly for protein content in row plots (Table 32). Hill plots at Glenlea were 73 to 98% as efficient as row plots, while hill plots at Winnipeg were only 45 to 55% as efficient as row plots. The number of replicates of hill plots required to give equivalent information to one four-row plot ranged from approximately one to five at Glenlea (Table 32). At

Winnipeg, the genetic correlation between the two plot types was less than the square root of the heritability of row plot protein content for each cross, indicating that it was not possible for any number of hill plots to be as efficient as one four-row plot. Torrie (1962) reported that soybean hill plots were essentially similar in precision to row plots for protein content, while for yield, nine replicates of hill plots were equivalent to four replicates of row plots.

Several studies appear to be at variance in the methods used to calculate the efficiency of selection in hill plots for performance in row plots. Baker and Leisle (1970) used the heritabilities of yield in hill and row plots of durum and common wheat cultivars to calculate efficiency ratios rather than the square root of heritabilities as described by Falconer (1952) and outlined in section 3.2.5. They reported that hill plots were approximately 56 to 172% as efficient as row plots, and that one to eight hill plot replicates were equivalent to one row plot. In one case, it was not possible to calculate the number of hill plots required. For yield in oats, Frey (1965) used the formula $(h_1/h_2)r_g$, where h_1 and h_2 were the square roots of the heritabilites in row and hill plots, respectively, and r_g was the genetic correlation between hill and row plots. By solving the equation:

$$\frac{h_1 \, r_g}{\sqrt{\frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2/n}}} = 1.0$$

where o_g^2 and o_e^2 were the genetic and environmental variances for hill plots, respectively, and n was the number of hill replicates required, he determined that five replicates of hill plots gave selection efficiency equivalent to three replicates of row plots. In the present study, the equation was derived from the formula $(h_2/h_1)r_g$ of Falconer (1952) as outlined in section 3.2.5, rather than $(h_1/h_2)r_g$. O'Brien et al. (1979) calculated the efficiency ratio as in the present study, and obtained values ranging from 0.52 to 0.76 for yield in F_3 lines of wheat. However, they appeared to use the same equation as Frey (1965) for calculating the number of hill plot replicates equivalent to one three-row plot. They reported that two to four hill plots were as efficient as a single three-row plot for yield testing F_3 lines. The calculations of Frey (1965) and O'Brien et al. (1979) would result in lower estimates of the number of hill plot replicates required to give the information equivalent to one row plot than would the calculations used in the present study. Consequently, hill plots may be less efficient in selecting for quantitative traits than generally indicated in the literature.

The efficiency of selection in hill plots for yield in row plots was not determined in this study because phenotypic correlations between hill and row plots were not significant ($P>0.05$) for yield except in the DT cross (Table 33). In fact, no significant ($P>0.05$) differences in yield were found among F_5 bulks and checks of the WK and MD crosses grown in NIR hill plots at Glenlea (Appendix Tables 16, 17). Similar results were obtained for protein yield (Table 33, Appendix Tables 16, 17). In contrast, highly significant ($P<0.01$) phenotypic correlations were found between hill and row plots for kernel weight, protein per kernel, and kernel shrivelling at all cross locations (Table 33).

The low efficiency of selection in hill plots for protein content in row plots observed in this study may be due in part to different seeding dates. Since the hill plots were sown approximately one week later than the row plots, the grain filling period was even less favorable for hill plots than it was for row plots. Lodging in hill plots occurred at an earlier stage of development in the grain filling period than in row plots, particularly at Winnipeg. Normal ripening of hill plots at both locations was greatly hampered by the cool, wet conditions. Thus, genotype x environment interactions may have reduced selection efficiency.

TABLE 33. Correlation between NIR hill and row plots for yield, protein yield, kernel weight, protein per kernel and kernel shrivelling in each cross location in 1985.

Cross	Location	Trait[1] YLD	PY	KW	PK	KS
WK	Glenlea	0.24[2]	0.22	0.52**	0.56**	0.45**
	Winnipeg	0.11	0.09	0.74**	0.73**	0.51**
MD	Glenlea	-0.02	0.00	0.73**	0.65**	0.55**
	Winnipeg	0.11	0.10	0.82**	0.72**	0.40**
DT	Glenlea	0.26*	0.31*	0.60**	0.51**	0.49**
	Winnipeg	0.45**	0.40**	0.81**	0.70**	0.62**

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Correlation coefficients calculated on a mean basis using all 64 entries in each cross location.

Genotype x plot type interactions may exist for protein content and other traits. Torrie (1962) found that genotype x plot type interactions were occasionally significant for protein content in soybean hill and row plots. Kibite and Evans (1984) reported that different plant densities may favor different wheat genotypes. In the present study, the check cultivars tended to perform differently in hill than in row plots. As noted previously, fewer differences in protein content were observed among the check cultivars in hill plots (Tables 15, 30). For example, DT367 did not differ significantly from DT447 at either location in hill plots, but in row plots, DT367 had a lower protein content than DT447 at Winnipeg and the same protein content at Glenlea. Fewer differences in yield were also observed among the check cultivars in hill than in row plots (Tables 20, 34). DT367 tended to have higher yields in hill than in row plots relative to the other cultivars. The kernel weight of Wakooma in hill plots decreased from Glenlea to Winnipeg, while that of the other cultivars increased (Table 34). This probably resulted from the high degree of kernel shrivelling observed in Wakooma hill plots at Winnipeg (Table 34). In row plots, the kernel weight of all check cultivars increased from Glenlea to Winnipeg (Table 20). Such differences in the performance of the check cultivars in hill and row plots indicate the presence of genotype x

TABLE 34. Mean combined over methods and crosses for yield, kernel weight, protein yield, protein per kernel and kernel shrivelling of the four check cultivars grown with the NIR and ISD F_5 hill plots at each location.

Trait[1]	Location	Cultivar[2]			
		Wakooma	Medora	DT447	DT367
YLD	Glenlea	63.9a[3]	68.4a	74.5a	71.2a
	Winnipeg	82.3b	102.1a	95.9a	106.3a
KW	Glenlea	36.7c	37.1c	44.9a	40.7b
	Winnipeg	33.2d	40.6c	49.2a	44.7b
PY	Glenlea	9.8a	10.0a	10.3a	9.9a
	Winnipeg	12.0b	13.8a	12.5ab	13.8a
PK	Glenlea	5.62b	5.41b	6.20a	5.65b
	Winnipeg	4.87d	5.50c	6.43a	5.80b
KS	Glenlea	2.2ab	1.8b	1.1c	2.5a
	Winnipeg	3.1a	1.2c	1.0c	2.0b

[1]Abbreviations for traits are defined in Table 4.

[2]Check cultivars within a location were combined over methods and crosses using a randomized complete block design (Appendix Table 36).

[3]Cultivar means over methods and crosses within a location followed by the same letter are not significantly different at the 0.05 probability level according to Fischer's LSD test.

plot type interactions which may reduce the efficiency of selection for protein content in hill plots.

4.5 Heritability of Protein Content and Other Traits

Heritability estimates in standard units for protein content determined from the F_3 hill and F_5 row plots for the NIR method ranged from 43 to 57 and 20 to 38% at Glenlea and Winnipeg, respectively, and were significant ($P<0.05$ or $P<0.01$) for all cross locations except the DT cross at Winnipeg (Table 35). The highest heritability was obtained for the DT cross at Glenlea which also had the highest response to selection for protein content. Heritability estimates in standard units for protein content determined from the F_3 and F_5 hill plots for the NIR method were lower than those determined from the F_3 hill and F_5 row plots (Table 35). They ranged from 11 to 37% and were significant ($P<0.05$ or $P<0.01$) only at Glenlea. The lower heritability of protein content in hill plots probably resulted in the detection of fewer differences in protein content among F_5 selection groups of the NIR method when evaluated in hill rather than in row plots (section 4.3). However, it is not clear whether this difference is due to genotype x plot type interactions or to other environmental effects. Heritability estimates in standard units for protein content determined from the F_2 RP plants and RP in F_5 hill plots for the ISD method were not significant (section 4.7, Table 47).

TABLE 35. Heritability in standard units for protein content and other traits for the NIR method in each cross location.

Cross	Location	PC[1]	YLD	PY	KW	PK	KS
		F_3 Hill vs. F_5 Row Plots					
WK	Glenlea	0.47**	-0.08	-0.00	0.29*	0.56**	0.19
	Winnipeg	0.38**	0.09	0.13	0.38**	0.62**	0.43**
MD	Glenlea	0.43**	-0.07	0.11	0.55**	0.64**	0.30*
	Winnipeg	0.28*	-0.18	-0.14	0.48**	0.64**	0.35**
DT	Glenlea	0.57**	0.31*	0.33**	0.33**	0.59**	0.36**
	Winnipeg	0.20	0.31*	0.32*	0.51**	0.72**	0.39**
		F_3 vs. F_5 Hill Plots					
WK	Glenlea	0.28*	0.21	0.06	0.41**	0.56**	0.33**
	Winnipeg	0.11	0.09	0.01	0.27*	0.51**	0.11
MD	Glenlea	0.37**	0.23	0.18	0.60**	0.62**	0.52**
	Winnieg	0.12	0.30*	0.33**	0.52**	0.63**	0.21
DT	Glenlea	0.32*	0.27*	0.28*	0.54**	0.54**	0.48**
	Winnipeg	0.20	0.28*	0.30*	0.52**	0.61**	0.46**

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

Heritabilities for protein content in the present study were generally lower than those reported in the literature for durum wheat. Vallega (1985), also using intergeneration correlations, reported heritabilities ranging from 38% to 67% for protein content in advanced lines of a durum wheat cross grown in Italy. Gill and Brar (1977) obtained a heritability of 56% for protein content in India, while Avivi et al. (1983) reported heritabilities ranging from 65 to 74% in Israel. Higher heritabilities would be expected from these two studies because of greater genetic variation for protein content than in the present study. This was particularly true for the Avivi et al. (1983) study in which T. turgidum var dicoccoides lines with protein contents ranging from 23.7 to 27.5% were crossed to the durum wheat cultivar, Inbar, with 13.4% protein content. The highest heritability estimate for protein content in durum wheat was reported in Italy by Zitelli et al. (1979) who calculated a broad sense heritability of 83% using variance components derived from a diallel analysis. However, estimation of variance components from a diallel analysis is unreliable, because the genetic interpretation of diallel statistics is extremely sensitive to failure of the assumptions that genes are independently distributed among the parents and there is no epistasis (Baker, 1978). These assumptions are difficult to accept in practice (Baker, 1978). In contrast to the above studies, Bebyakin and Piskunova (1982) in the Soviet

Union reported that heritabilities for protein content in durum wheat were low and highly variable, although actual figures were not given.

Because of the specificity of heritability estimates and the limited number of studies in which heritability has been determined for protein content in durum wheat, it is difficult to meaningfully compare heritabilities in the present study to those in the literature. Further insight may be gained by examining the heritabilities for protein content in common wheat summarized in Tables 1 and 2. Heritabilities for protein content in durum wheat obtained in the present study would fall into the lower to intermediate range of values reported for common wheat. Corpuz et al. (1983a) and Sampson et al. (1983) obtained ranges for heritabilities in standard units for protein content similar to the range obtained when NIR F_5 row plots were used in the present study. Several studies have reported relatively low heritabilities for protein content (Sunderman et al., 1965; Sharma et al., 1973; Jain et al., 1975; Pearson et al., 1981), while in others, heritabilities were not significantly different from zero (Clark, 1926; Lofgren et al., 1968).

Heritabilities in standard units for yield estimated from F_3 and both F_5 plot types were not significant in most cases, and were generally lower than those for protein content (Table 35). Significant heritabilities for yield

were obtained for the DT cross at both locations in both F_5 plot types and for the MD cross at Winnipeg in F_5 hill plots, and reached a maximum of 31% (Table 35). Similar results were obtained for protein yield (Table 35). Gill and Brar (1977) reported heritabilities of 56 and 41% for protein content and yield, respectively, using 23 diverse strains of durum wheat in India. In studies with common wheat, heritabilities for yield were generally lower in magnitude than those for protein content (Table 2). Particularly large differences in heritability between these two traits were observed by Knott and Kumar (1975) and Guthrie et al. (1984).

Heritabilities in standard units for kernel weight were significant ($P<0.05$ or $P<0.01$) in all cross locations, ranging from 29 to 55 and 27 to 60% when using F_5 row and hill plots, respectively (Table 35). Heritabilities for kernel weight appeared to be greater than those for protein content in all cross locations for F_5 hill plots, while for F_5 row plots, they exceeded those for protein content in only half of the cross locations (Table 35). In durum wheat, Gill and Brar reported heritabilities of 56 and 87% for protein content and kernel weight, respectively, while Zitelli et al. (1979) calculated broad sense heritabilities of 83 and 90% for protein content and kernel weight, respectively. Studies in common wheat indicated that heritabilities for kernel weight were considerably higher

than those for protein content in most cases (Table 2). In general, heritabilities for kernel weight summarized in Table 2 were higher in magnitude than those observed in the present study. This may be a further indication of the effect of the unfavorable and contrasting growing conditions on kernel development during the grain filling period in 1984 and 1985.

Heritabilities in standard units for protein per kernel were highly significant ($P<0.01$) in all cross locations whether the F_5 was grown in hill or row plots, and ranged from 56 to 72 and 51 to 63% for F_5 row and hill plots, respectively (Table 35). They appeared to be relatively stable and higher than heritabilities for protein content and kernel weight even though protein per kernel is the product of the other two traits. Few heritability estimates for protein per kernel have been reported in the literature for either durum or common wheat. Jain et al. (1975) reported that heritabilities in standard units based on intergeneration correlations between F_2 and F_3 progenies in a common wheat cross were 17, 75, and 64% for protein content, kernel weight, and protein per kernel, respectively. In the present study, heritabilities for protein per kernel were of similar magnitude but heritabilities for protein content tended to be higher than reported by Jain et al. (1975). Consequently, differences in heritability between protein content and protein per

kernel were generally not as large in the present study. Loffler and Busch (1982) obtained higher heritabilities for protein per kernel and protein content, ranging from 81 to 87 and 76 to 83%, respectively, in three hard red spring wheat crosses.

Heritabilities in standard units for kernel shrivelling were significant ($P<0.05$ or $P<0.01$) except in the WK cross at Glenlea for F_5 row plots and the WK and MD crosses at Winnipeg for F_5 hill plots (Table 35). They ranged from 11 to 48% over both F_5 plot types and were similar in magnitude to those for protein content overall, although not necessarily within the same cross location. The results suggest that kernel shrivelling is at least partially controlled by genetic factors. However, it is not clear whether kernel shrivelling is due to poor adaptation or is an intrinsic characteristic of certain genotypes in this study.

Since heritabililties for protein content were generally higher than for yield but lower than for kernel weight, it was concluded that response to selection for protein content would be greater than for yield but less than for kernel weight.

4.6 Effect of Selection for Protein Content on Other Traits

The F_3 protein selection groups were characterized for yield, protein yield, kernel weight, protein per kernel and kernel shrivelling previously (section 4.2, Table 19).

Consequently, these results will be briefly mentioned only where relevant in the following discussion of the effect of selection for protein content in F_2 or F_3 on other traits in F_5.

Few differences among the protein selection groups were found for any of the traits in F_5 whether grown in NIR row plots (Table 36), NIR hill plots (Table 37) or ISD hill plots (Table 38). The lattice analyses of variance for detecting differences among entries are given in Appendix Tables 10 - 21, while analyses of variance for detecting differences among F_5 selection groups are given in Appendix Tables 22 - 33, as support for the results in Tables 36 - 38.

Selection for high protein content in F_2 and F_3 did not reduce yield in F_5 (Tables 36 - 38). In fact, HP was significantly higher yielding than LP for the MD cross at Glenlea in NIR row plots (Table 36). Yields of HP were not significantly higher than LP for other cross locations although there was a trend in that direction. No significant differences in yield were found between RP and either HP or LP, except for the MD cross where RP was higher yielding than LP at both locations (Table 36). Selection groups did not differ significantly in yield for any cross location in NIR and ISD hill plots, and there were no obvious trends (Tables 37, 38). In contrast to the F_5 generation, HP tended to be lower yielding than LP in F_3,

TABLE 36. Mean yield, test weight, kernel weight, protein yield, protein per kernel and kernel shrivelling of F_5 selection groups in each cross location for NIR row plots.

		Location					
		Glenlea			Winnipeg		
Trait[1]	Cross	HP	RP	LP	HP	RP	LP
YLD	WK	3040a[2]	2896a	2889a	3829a	3740a	3564a
	MD	2907a	2819a	2511b	3960ab	4022a	3792b
	DT	3537a	3536a	3399a	4440a	4355a	4194a
PY	WK	426a	402a	397a	498a	484ab	456b
	MD	405a	386a	340b	506a	510a	478b
	DT	461a	451ab	430b	556a	541ab	519b
TW	WK	72.7a	71.6a	72.4a	75.2a	74.1b	75.1a
	MD	72.7a	73.0a	73.1a	75.9a	76.1a	76.0a
	DT	75.7a	76.2a	76.2a	76.5a	76.9a	77.0a
KW	WK	32.2a	31.9a	32.2a	37.4a	36.8a	38.0a
	MD	32.3a	33.1a	33.6a	38.5a	39.1a	38.9a
	DT	40.4a	40.1a	39.3a	44.4a	44.1a	44.5a
PK	WK	4.52a	4.42a	4.41a	4.87a	4.77a	4.85a
	MD	4.50a	4.52a	4.56a	4.92a	4.96a	4.91a
	DT	5.26a	5.10ab	4.97b	5.57a	5.47a	5.51a
KS	WK	2.4a	2.7a	2.5a	1.8b	2.1a	1.7b
	MD	2.7a	2.4a	2.5a	1.5a	1.2b	1.4a
	DT	1.6a	1.4a	1.4a	1.4a	1.3a	1.2a

[1]Abbreviations for traits are defined in Table 4.

[2]Means within a cross location followed by the same letter are not significantly different at the 0.05 probability level according to Fischer's LSD test.

TABLE 37. Mean yield, kernel weight, protein yield, protein per kernel and kernel shrivelling of F_5 selection groups in each cross location for NIR hill plots.

		Location					
		Glenlea			Winnipeg		
Trait[1]	Cross	HP	RP	LP	HP	RP	LP
YLD	WK	66.5a[2]	69.7a	67.9a	90.5a	93.1a	93.0a
	MD	65.5a	63.6a	67.1a	102.9a	104.5a	100.7a
	DT	65.7a	70.6a	62.8a	102.2a	104.8a	99.0a
KW	WK	36.5a	36.7a	37.1a	37.4a	37.9a	37.9a
	MD	36.3b	36.7b	38.8a	39.9a	40.9a	41.8a
	DT	43.0a	44.6a	44.0a	47.7a	47.9a	47.6a
PY	WK	9.9a	10.1a	9.9a	12.7a	12.9a	12.8a
	MD	9.4a	9.1a	9.4a	13.6a	13.7a	13.1a
	DT	8.9a	9.5a	8.4a	12.9a	13.0a	12.2a
PK	WK	5.43a	5.35a	5.44a	5.25a	5.27a	5.22a
	MD	5.22a	5.23a	5.44a	5.27a	5.36a	5.46a
	DT	5.84a	6.01a	5.87a	6.01a	5.96a	5.90a
KS	WK	2.8a	2.8a	2.8a	2.4a	2.6a	2.4a
	MD	2.5a	2.6a	2.1b	2.0a	2.0a	1.9a
	DT	2.3a	1.8b	2.0b	1.8a	1.6a	1.7a

[1]Abbreviations for traits are defined in Table 4.

[2]Means within a cross location followed by the same letter are not significantly different at the 0.05 probability level according to Fischer's LSD test.

TABLE 38. Mean yield, kernel weight, protein yield, protein per kernel and kernel shrivelling of F_5 selection groups in each cross location for ISD hill plots.

		Location					
		Glenlea			Winnipeg		
Trait[1]	Cross	HP	RP	LP	HP	RP	LP
YLD	WK	71.7a[2]	64.0a	68.5a	86.7a	87.8a	89.2a
	MD	69.4a	65.2a	62.8a	102.8a	98.5a	98.7a
	DT	63.9a	61.6a	66.7a	102.0a	99.3a	99.2a
KW	WK	36.1a	36.1a	37.1a	35.5a	36.1a	36.2a
	MD	37.8a	37.5a	38.1a	40.3a	39.3a	40.4a
	DT	44.2a	43.3a	44.5a	47.6a	47.2a	46.9a
PY	WK	10.5a	9.5a	9.9a	12.3a	12.5a	12.5a
	MD	9.9a	9.4a	8.9a	13.6a	13.2a	13.1a
	DT	8.8a	8.4a	9.0a	13.0a	12.6a	12.4a
PK	WK	5.28a	5.35a	5.39a	5.02a	5.16a	5.11a
	MD	5.41a	5.39a	5.37a	5.35a	5.26a	5.38a
	DT	6.08a	5.86a	5.95a	6.06a	6.00a	5.89a
KS	WK	2.7a	3.0a	2.7a	2.8a	2.8a	2.6a
	MD	2.4a	2.4a	2.1a	2.1a	2.3a	2.0a
	DT	2.0a	1.9a	1.6a	1.6a	1.5a	1.5a

[1]Abbreviations for traits are defined in Table 4.

[2]Means within a cross location followed by the same letter are not significantly different at the 0.05 probability level according to Fischer's LSD test.

although differences were significant only in the WK cross (Table 19).

Most studies in the literature suggest that selection for protein content in early generations will reduce yield because of the negative correlation between protein content and yield (Grant and McCalla, 1949; Baker et al., 1968b; Bhatia, 1975; Bhatia and Rabson, 1976; Loffler and Busch, 1982; O'Brien and Ronalds, 1984). McNeal et al. (1972, 1978) reported that selection for high protein content in early generations of spring wheat crosses frequently resulted in lower yields in following generations when compared to selection for low protein content carried out at the same time. Although Loffler et al. (1983) also found that two cycles of recurrent selection for high protein content in hard red spring wheat resulted in a negative shift in yield, they observed that a few lines with high protein content and high yield were obtained. In a study with six winter wheat crosses selected for high and low protein content in F_3, Guthrie et al. (1984) reported that in F_4 yield trials, the high protein selection group had a significantly lower yield than the low protein selection group in two crosses, similar yield in three crosses, and a higher yield in one cross. They were able to identify some lines with higher protein content and acceptable yield, although an inverse relationship between protein content and yield was observed. Their results and the present study

indicate that selection for high protein content does not always decrease yield in later generations. Halloran (1981) suggested that it should be possible to select lines with high protein content and yield equal to the standard protein parent, while Johnson et al. (1985) indicated that simultaneous improvement in protein content and yield can be made. In a study with six spring wheat crosses, Ellison et al. (1977) concluded that improvement in protein content and the subsequent effect on yield depend to a degree on the parental genotypes. Although difficult, it appears possible to select for high protein content without reducing yield.

The neutral to positive effects of selection for protein content in F_2 or F_3 on yield in F_5 were not surprising in view of the low response to selection for protein content observed in the present study. Since selection for high protein content was generally little better than random selection, other traits would not likely be affected. However, the trend towards higher yields in HP than LP for NIR row plots may be due to genotype x environment interactions. Disease and hot, dry conditions during the grain filling period in 1984 may have affected kernel development in potentially high yielding F_3 families more than in those with lower yield potential, resulting in greatly reduced yields and higher protein content. Consequently, some of these potentially high yielding F_3 families may have been selected in HP. As noted previously,

HP had lighter, more shrivelled kernels than LP in F_3 (Table 19). More favorable growing conditions in 1985 may have allowed these potentially high yielding selections in HP to express more of their yield potential, thus increasing yield and reducing protein content of HP more than RP and LP in F_5.

Protein yield of F_5 selection groups in NIR row plots was affected more than any other trait by selection for protein content in F_3 (Table 36). Protein yields for HP were higher than those for LP in all cross locations, except in the WK cross at Glenlea where no significant differences were found among selection groups (Table 36). Protein yields for RP were similar to HP in all cross locations and LP in four cross locations (Table 36). The trend towards higher protein content and yield in HP probably resulted in the significant differences in protein yield observed between HP and LP. For NIR and ISD hill plots, no significant differences in protein yield were found among the F_5 selection groups in any cross location (Tables 37, 38). In contrast to the present study, McNeal et al. (1972) indicated that when high and low protein composites selected in F_3 from eight spring wheat crosses were evaluated in F_4, the high protein composites had lower protein yield than the low protein composites. However, in a later study, McNeal et al. (1978) observed few differences in protein yield between high and low protein progeny after two cycles of

recurrent selection in nine spring wheat crosses. Since correlations between protein content and protein yield may be positive (McNeal et al., 1971; Bhatia, 1975), negative (Loffler et al., 1975) or not significant (McNeal et al., 1972; Cox et al., 1986), the effect of selection for protein content on protein yield in subsequent generations may depend on the population (Loffler and Busch, 1982).

Selection for protein content in F_3 occasionally affected kernel shrivelling in F_5 (Tables 36, 37). For NIR row plots at Winnipeg, RP of the WK cross had significantly more kernel shrivelling than HP and LP, while RP of the MD cross had less kernel shrivelling than HP and LP (Table 36). For NIR hill plots at Glenlea, HP and RP of the MD cross had more kernel shrivelling than LP, while HP of the DT cross had more kernel shrivelling than RP and LP (Table 37). Significant differences in kernel shrivelling were not found among F_5 selection groups in ISD hill plots (Table 38). The variable and generally nonsignificant differences in kernel shrivelling among F_5 selection groups contrast with F_3 results in which HP had the greatest kernel shrivelling followed in order by RP and LP (Table 19).

Only minor differences in test weight, kernel weight and protein per kernel were detected among F_5 selection groups (Tables 36 - 38). As noted previously, no significant differences in protein per kernel were found among F_3 selection groups, while HP had lighter kernels than

LP with RP intermediate (Table 19). The effect of selection for protein content in early generations on kernel weight, protein per kernel, kernel shrivelling and test weight in later generations has received little attention in the literature. However, Brunori et al. (1982) suggested that selecting for high protein content favored poorly developed kernels.

In conclusion, the minor effect of selection for protein content in F_2 or F_3 on most traits studied in F_5 may be due to the low response to selection for protein content, the populations studied, and environmental effects, rather than to the lack of relationship between protein content and other traits.

4.7 Relationship between Protein Content and Other Traits

The traits most highly and consistently correlated with protein content over all experiments were kernel weight (negatively) and kernel shrivelling (positively) (Tables 39 - 42). This was particularly true for the selected F_3 families of the NIR method; correlations were highly significant ($P<0.01$), ranging from -0.58 to -0.74 between protein content and kernel weight, and from 0.74 to 0.81 between protein content and kernel shrivelling (Table 39). Approximately one third to one half of the variation in protein content of the selected F_3 families could be explained by kernel weight, while over one half to nearly

TABLE 39. Correlations among traits of the selected F_3 families in each cross for the NIR method.

		Trait[1]				
Trait	Cross	YLD	PY	KW	PK	KS
PC	WK	-0.40**[2]	-0.14	-0.69**	-0.21	0.74**
	MD	-0.32*	0.10	-0.74**	-0.28*	0.81**
	DT	-0.25*	0.02	-0.58**	-0.07	0.79**
YLD	WK		0.96**	0.43**	0.28*	-0.40**
	MD		0.92**	0.27*	0.14	-0.27**
	DT		0.97**	0.03	-0.11	-0.14
PY	WK			0.25	0.23	-0.21
	MD			-0.00	0.08	0.03
	DT			-0.15	-0.16	0.06
KW	WK				0.84**	-0.81**
	MD				0.85**	-0.84**
	DT				0.85**	-0.73**
PK	WK					-0.57**
	MD					-0.57**
	DT					-0.38**

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Correlation coefficients calculated on a mean basis with WK = 57, MD = 57 and DT = 59 F_3 families.

TABLE 40. Correlations among traits of the F_5 bulks in each cross at Glenlea (above diagonal) and Winnipeg (below diagonal) for NIR row plots.

		Trait[1]						
Trait	Cross	PC	YLD	PY	TW	KW	PK	KS
PC	WK		-0.07[2]	0.11	-0.36**	-0.31**	0.11	0.33**
	MD		-0.15*	0.12	-0.71**	-0.64**	-0.02	0.66**
	DT		-0.09	0.24**	-0.66**	-0.48**	0.11	0.52**
YLD	WK	-0.33**		0.98**	0.11	-0.07	-0.10	-0.01
	MD	-0.29**		0.96**	0.15*	0.04	-0.07	-0.13
	DT	-0.18**		0.95**	0.05	0.04	-0.01	-0.01
PY	WK	-0.09	0.97**		0.05	-0.12	-0.07	0.05
	MD	-0.03	0.96**		-0.05	-0.14*	-0.08	0.06
	DT	0.08	0.97**		-0.17**	-0.12	0.02	0.18**
TW	WK	-0.37**	0.18**	0.09		0.70**	0.58**	-0.79**
	MD	-0.21**	0.29**	0.25**		0.89**	0.58**	-0.86**
	DT	-0.10	0.09	0.07		0.75**	0.43**	-0.77**
KW	WK	-0.26**	-0.02	0.08	0.67**		0.91**	-0.68**
	MD	-0.18**	0.20**	0.16*	0.70**		0.78**	-0.81**
	DT	0.04	0.08	0.09	0.59**		0.82**	-0.58**
PK	WK	0.24**	-0.18**	-0.13*	0.49**	0.88*		-0.57**
	MD	0.29**	0.06	0.15*	0.58**	0.89**		-0.52**
	DT	0.43**	-0.00	0.11	0.50**	0.92**		-0.33**
KS	WK	0.31**	-0.09	-0.01	-0.77**	-0.63**	-0.48**	
	MD	0.08	-0.15*	-0.13*	-0.62**	-0.51**	-0.46**	
	DT	0.05	0.01	0.03	-0.63**	-0.41**	-0.36**	

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Correlation coefficients calculated on a plot basis with WK = 238, MD = 239 and DT = 238 plots at Glenlea, and WK = 238, MD = 240 and DT = 240 plots at Winnipeg.

TABLE 41. Correlations among traits of the F_5 bulks in each cross at Glenlea (above diagonal) and Winnipeg (below diagonal) for NIR hill plots.

Trait	Cross	Trait[1] PC	YLD	PY	KW	PK	KS
PC	WK		-0.37**[2]	-0.21**	-0.53**	-0.16*	0.54**
	MD		-0.18**	-0.04	-0.39**	-0.03	0.46**
	DT		-0.07	0.06	-0.30**	0.07	0.30**
YLD	WK	-0.57**		0.98**	0.62**	0.55**	-0.57**
	MD	-0.47**		0.99**	0.66**	0.65**	-0.57**
	DT	-0.34**		0.99**	0.46**	0.46**	-0.46**
PY	WK	-0.34**	0.96**		0.55**	0.55**	-0.51**
	MD	-0.22**	0.96**		0.61**	0.65**	-0.51**
	DT	-0.18**	0.98**		0.42**	0.47**	-0.42**
KW	WK	-0.74**	0.60**	0.46**		0.92**	-0.75**
	MD	-0.60**	0.40**	0.27**		0.93**	-0.75**
	DT	-0.36**	0.14*	0.09		0.93**	-0.71**
PK	WK	-0.41**	0.48**	0.43**	0.91**		-0.63**
	MD	-0.16*	0.22**	0.21**	0.88**		-0.64**
	DT	0.09	-0.01	0.02	0.90**		-0.62**
KS	WK	0.70**	-0.59**	-0.45**	-0.83**	-0.69**	
	MD	0.63**	-0.42**	-0.28**	-0.78**	-0.61**	
	DT	0.43**	-0.17**	-0.10	-0.58**	-0.43**	

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Correlation coefficients calculated on a plot basis with WK = 237, MD = 240 and DT = 239 plots at Glenlea, and WK = 240, MD = 238 and DT = 236 plots at Winnipeg.

TABLE 42. Correlations among traits of the F_5 families in each cross at Glenlea (above diagonal) and Winnipeg (below diagonal) for ISD hill plots.

Trait	Cross	Trait[1] PC	YLD	PY	KW	PK	KS
PC	WK		-0.33**[2]	-0.16*	-0.43**	-0.01	0.46**
	MD		-0.15*	-0.00	-0.34**	-0.04	0.41**
	DT		0.14*	0.26**	-0.15*	0.27**	0.39**
YLD	WK	-0.52**		0.98**	0.58**	0.49**	-0.57**
	MD	-0.47**		0.99**	0.64**	0.61**	-0.46**
	DT	-0.24**		0.99**	0.50**	0.54**	-0.35**
PY	WK	-0.31**	0.97**		0.53**	0.51**	-0.51**
	MD	-0.24**	0.97**		0.59**	0.63**	-0.40**
	DT	-0.06	0.98**		0.47**	0.57**	-0.30**
KW	WK	-0.74**	0.66**	0.54**		0.90**	-0.73**
	MD	-0.62**	0.38**	0.26**		0.93**	-0.75**
	DT	-0.33**	0.02	-0.03		0.91**	-0.63**
PK	WK	-0.33**	0.57**	0.55**	0.88**		-0.59**
	MD	-0.19**	0.20**	0.19**	0.89**		-0.63**
	DT	0.12	-0.09	-0.06	0.89**		-0.45**
KS	WK	0.69**	-0.57**	-0.45**	-0.79**	-0.63**	
	MD	0.66**	-0.36**	-0.23**	-0.81**	-0.63**	
	DT	0.38**	-0.03	-0.04	-0.53**	-0.39**	

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Correlation coefficients calculated on a plot basis with WK = 238, MD = 237 and DT = 236 plots at Glenlea, and WK = 235, MD = 237 and DT = 237 plots at Winnipeg.

two thirds of the variation was attributable to kernel shrivelling. These results confirm the apparent relationship of protein content to kernel weight and kernel shrivelling observed previously in Table 19. They suggest that disease and hot, dry conditions during the grain filling period in 1984 reduced kernel weight and increased kernel shrivelling, which consequently increased the protein content of some F_3 families.

Correlations for protein content with both kernel weight and kernel shrivelling were significant ($P<0.05$ or $P<0.01$) for most tests in 1985 (Tables 40 - 42). The only exceptions were for the NIR row plots at Winnipeg where significant correlations were not found between protein content and kernel weight in the DT cross, and between protein content and kernel shrivelling in the MD and DT crosses (Table 40). The magnitude of the correlation coefficients for protein content with kernel weight and kernel shrivelling was smaller in 1985 than 1984; significant correlation coefficients for protein content with kernel weight and kernel shrivelling over all three experiments in 1985 ranged from -0.15 to -0.74 and 0.30 to 0.70, respectively (Tables 40 - 42). The relationship between protein content and the two traits in 1985 may have been due in part to lodging effects. Pinthus (1973) indicated that lodging can reduce kernel weight while increasing both kernel shrivelling and protein content.

In durum wheat, Walther (1978), Robinson et al. (1979) and Zitelli et al. (1983) reported no correlation between protein content and kernel weight, while Porceddu et al. (1975) found a negative correlation of -0.49 between the two traits. Zitelli et al. (1979) found no correlation between protein content and kernel weight in a year with adequate precipitation, and a negative correlation of -0.62 in a dry year, illustrating the effect of environmental conditions on the relationship between protein content and kernel weight. The results of Porceddu et al. (1975) and Zitelli et al. (1979) agree well with the correlations between protein content and kernel weight obtained in the present study.

In common wheat, the correlation between protein content and kernel weight varies considerably from study to study, including negative (Kaufmann et al., 1969; Bhatia, 1975; Jain et al., 1975, 1976; Kibite and Evans, 1984), not significant (Worzella, 1942; Baker et al., 1968b; Randhawa and Gill, 1978; Vogel et al., 1978; Peterson et al., 1985), and positive values (Briggs et al., 1969; Loffler and Busch, 1982; Law et al., 1984), depending on the cross or population under study (Dyck and Baker, 1975). Most negative correlation coefficients for common wheat fall in the lower to intermediate range of values obtained in the present study. Fjell et al. (1985) reported among the highest negative correlations between protein content and kernel weight in common wheat, with coefficients ranging

from -0.48 to -0.74 within individual cultivars over locations. However, they reported positive correlations at individual locations over cultivars.

Although correlation coefficients between protein content and kernel shrivelling have not been reported in the literature, a number of studies with common wheat indicate that kernel shrivelling increases protein content as found in the present study (Johnson et al., 1973b; Philips and Schlesinger, 1974; Shahani and Saulescu, 1984). Zitelli et al. (1979) observed that shrunken kernels produced in a dry year increased protein content in durum wheat. Similar results were obtained in the present study during the hot, dry grain filing period of 1984.

Highly significant ($P<0.01$) negative correlations ranging from -0.21 to -0.71 were found between protein content and test weight in NIR row plots for all cross locations, except the DT cross at Winnipeg where no significant correlation was observed (Table 40). Although no correlation has generally been found between protein content and test weight in most studies with common wheat (Worzella, 1942; Schlehuber et al., 1967; Briggs et al., 1969; Ghaderi et al., 1971), Kaufmann et al. (1969) reported a negative correlation of -0.26 between the two traits, while Corpuz et al. (1983b) reported a much higher negative correlation of -0.79. Most of the correlation coefficients obtained in the present study fall between these two values.

In agreement with the present study, Fjell et al. (1984) suggested that low test weight and kernel weight increase protein content.

Since test weight is partly a function of kernel weight and gives an indication of kernel shrivelling, the moderately high positive correlations between test weight and kernel weight, and negative correlations between test weight and kernel shrivelling were expected (Table 40). However, Ghaderi and Everson (1971) reported that low test weight may result from environmental conditions other than those causing kernel shrivelling. Kernel shrivelling accounted for a considerable amount of the variation in kernel weight since moderate to high negative correlations were found between these two traits in all experiments (Tables 39 - 42).

Correlations between protein content and yield were generally negative and low to moderate in magnitude (Tables 39 - 42). In F_3 families, correlations between the two traits were significant and negative, ranging from -0.25 to -0.40 (Table 39). For the NIR F_5 row plots, only the correlation coefficient for the MD cross ($r = -0.15$) was significant at Glenlea, while correlation coefficients were significant for all crosses at Winnipeg, ranging from -0.18 to -0.33 (Table 40). Correlation coefficients between protein content and yield also tended to be lower at Glenlea than Winnipeg for NIR and ISD F_5 hill plots (Tables 41, 42).

For the DT cross at Glenlea, the correlation between the two traits was not significant in NIR F_5 hill plots, while in ISD F_5 hill plots, it was significant and positive with a value of 0.14 (Tables 41, 42). For all other cross locations, the correlations between protein content and yield were significant and negative, ranging from -0.18 to -0.57 and -0.15 to -0.52 for NIR and ISD F_5 hill plots, respectively (Tables 41, 42).

Most of the correlation coefficients between protein content and yield in the present study were negative, as generally reported in the literature (Malloch and Newton, 1934; Grant and McCalla, 1949; Sunderman et al., 1965; Baker et al., 1968b; Hsu and Sosulski, 1969; McNeal et al., 1972; Jain et al., 1976; Croy et al., 1978; Loffler and Busch, 1982; Guthrie et al., 1984; Cox et al., 1985; and others). However, as in the present study, correlations between the two traits were sometimes not significant (Clark, 1926; Clark and Smith, 1928; Schlehuber et al., 1967; Johnson et al., 1973b; Dyck and Baker, 1975; Knott and Kumar, 1975; Zitelli et al., 1979, 1983; Dubois and Fossati, 1981) or positive (Shebeski, 1967; Briggs et al., 1969; Johnson et al., 1973b; Robinson et al., 1979; Puri et al., 1980). Johnson et al. (1973b) indicated that the relationship between protein content and yield is complex, depending on environmental conditions and the set of genotypes or populations being evaluated.

The correlation coefficients between protein content and yield in the present study were less than -0.60 in magnitude. Johnson et al. (1985) suggested that correlation coefficients between the two traits seldom exceed this value although examples of higher correlation coefficients can be readily found (Grant and McCalla, 1949; Baker et al., 1968b; Pepe and Heiner, 1975; Loffler et al., 1985). Under the conditions of the present study, the negative correlations between protein content and yield do not appear to present an insurmountable barrier to increasing protein content and yield since variation in yield accounts for less than one third of the total variation in protein content. However, progress would be slow and difficult.

Although protein yield is directly related to protein content mathematically, significant positive correlations between the two traits were not found except for the DT cross at Glenlea in NIR row (r = 0.24) and ISD hill (r = 0.26) plots (Tables 39 - 42). In F_3, correlations between protein content and protein yield were not significant (Table 39). In F_5 hill plots, all crosses at Winnipeg for NIR, WK and MD crosses at Winnipeg for ISD, and the WK cross at Glenlea for both NIR and ISD had significant negative correlations between the two traits, ranging from -0.16 to -0.34 (Tables 41 - 42). Significant correlations between the two traits were not found in the remaining F_5 cross locations, including those for NIR row plots (Tables 40 -

42). The results of the present study differ greatly from the positive correlations of approximately 0.70 observed between protein content and protein yield in common wheat by McNeal et al. (1971) and Bhatia (1975). However, several studies have reported no correlation between these two traits (Hansel and Seibert, 1978; Loffler and Busch, 1982; Cox et al., 1986), while Loffler et al. (1985) found a negative correlation of -0.55. The correlations between protein content and protein yield in the present study were negative or not significant because of the very high correlations between protein yield and yield, ranging from 0.92 to 0.99 over all experiments (Tables 39 - 42). McNeal et al. (1972) and Loffler et al. (1985) also reported very high correlations (r = 0.93 to 0.98) between protein yield and yield. As noted previously, protein content and yield were negatively correlated in most cases in the present study. Since protein yield was influenced mainly by yield rather than protein content, correlations between protein content and protein yield were generally negative or not significant.

Correlations between protein content and protein per kernel ranged from -0.41 to 0.43 over all experiments, although most correlations between the two traits were either negative or not significant. (Tables 39 - 42). Significant positive correlations between the two traits were found for the three crosses at Winnipeg in NIR row

plots (Table 40) and for the DT cross at Glenlea in ISD hill plots (Table 42). In common wheat, Bhatia et al. (1975) and Jain et al. (1975) reported that protein content and protein per kernel were not significantly correlated, while Loffler and Busch (1982) reported a significant positive correlation ($r = 0.58$) between the two traits. In durum wheat, Zitelli et al. (1979) found a positive correlation ($r = 0.57$) between protein content and protein per kernel in a year with adequate precipitation, but no correlation between the two traits in a dry year. As with other traits, this would suggest that the relationship between protein content and protein per kernel is strongly influenced by environmental conditions. There appear to be no reports in the literature of significant negative correlations between protein content and protein per kernel as found in the present study.

Correlations between protein per kernel and kernel weight were significant, positive and high for all experiments, ranging from 0.78 to 0.93 (Tables 39 - 42). Most values found in the literature are similar, ranging from 0.81 to 0.98 (Jain et al., 1975, 1976; Walther, 1978; Zitelli et al., 1979; Loffler and Busch, 1982; Shahani and Saulescu, 1984) although values as low as 0.51 have been reported (Bhatia, 1975). Since correlations between protein per kernel and kernel weight were generally higher than those between protein per kernel and protein content, the negative correlations between protein content and kernel

weight would explain the variable and often negative correlations between protein content and protein per kernel in the present study.

In general, correlations with yield were positive for kernel weight and negative for kernel shrivelling in hill plots (Tables 39, 41 - 42). This suggests that kernel shrivelling and reduced kernel weight impaired the expression of yield potential in hill plots which would, in turn, affect protein content. In contrast, there was little correlation with yield for either kernel weight or kernel shrivelling in NIR row plots (Table 40). These differences may account, at least in part, for the lower efficiency of hill plots in detecting differences in protein content.

Protein content in F_3 hill plots was not consistently correlated to other traits in F_5 row plots except for protein yield and, to a lesser extent, yield (Tables 43 - 44). Highly significant ($P<0.01$), positive correlations ranging from 0.33 to 0.45 were obtained between protein content in F_3 and protein yield in F_5 row plots (Tables 43 - 44). As indicated in section 4.6, selection for low protein content in F_3 decreased protein yield in F_5 row plots when compared to selection for high or random protein content in F_3. Correlations between protein content in F_3 and yield in F_5 row plots were positive but significant in only half of the cross locations (Tables 43 - 44). These results agree with trends for HP to yield more than LP in F_5 row plots

TABLE 43. Correlations between F_3 traits and F_5 traits in NIR row plots for each cross at Glenlea.

		F_5 Trait[1]						
F_3 Trait[1]	Cross	PC	YLD	PY	KW	PK	KS	TW
PC	WK		0.24	0.34**	0.05	0.24	-0.14	0.05
	MD		0.37**	0.45**	-0.26*	-0.04	0.17	-0.14
	DT		0.21	0.35**	0.27*	0.46**	0.18	-0.26*
YLD	WK	-0.14		-0.11	-0.07	-0.12	0.18	-0.22
	MD	-0.06		-0.08	0.19	0.19	-0.12	0.10
	DT	-0.04		0.27*	-0.20	-0.18	0.03	-0.02
PY	WK	0.00	0.00		-0.05	-0.05	0.14	-0.19
	MD	0.16	0.08		0.15	0.27*	-0.11	0.12
	DT	0.08	0.34**		-0.14	-0.08	0.06	-0.05
KW	WK	-0.02	-0.20	-0.20		0.26*	-0.10	0.15
	MD	-0.27*	-0.18	-0.22		0.47**	-0.38**	0.43**
	DT	-0.13	-0.22	-0.24		0.23	-0.33*	0.54**
PK	WK	0.33**	-0.07	0.01	0.45**		-0.27*	0.27*
	MD	-0.03	0.06	0.06	0.56**		-0.41**	0.49**
	DT	0.22	-0.12	-0.06	0.59**		-0.29*	0.50**
KS	WK	0.14	0.27*	0.30*	-0.13	-0.06		-0.31*
	MD	0.30*	0.42**	0.45**	-0.36**	-0.24		-0.36**
	DT	0.30*	0.28*	0.34**	0.14	0.24		-0.44**

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for F_3 and F_5 traits are defined in Table 4.

TABLE 44. Correlations between F_3 traits and F_5 traits in NIR row plots for each cross at Winnipeg.

F_3 Trait[1]	Cross	F_5 Trait[1] PC	YLD	PY	KW	PK	KS	TW
PC	WK		0.27*	0.36**	-0.02	0.13	0.10	0.02
	MD		0.22	0.33**	-0.10	0.06	0.20	-0.02
	DT		0.36**	0.43**	-0.01	0.06	0.31*	0.27*
YLD	WK	-0.30*		0.02	-0.02	-0.12	0.12	-0.14
	MD	0.02		-0.18	-0.03	-0.01	0.07	-0.16
	DT	-0.28*		0.25*	-0.18	-0.25*	0.02	-0.04
PY	WK	-0.17	0.16		-0.02	-0.08	0.14	-0.13
	MD	0.16	-0.19		-0.05	0.04	0.18	-0.12
	DT	-0.23	0.37**		-0.19	-0.25*	0.09	-0.09
KW	WK	0.02	-0.16	-0.16		0.37**	-0.34**	0.15
	MD	-0.02	-0.21	-0.14		0.42**	-0.25*	0.29*
	DT	0.24	-0.30*	-0.24		0.54**	-0.40**	0.40**
PK	WK	0.32*	-0.01	0.06	0.53**		-0.40**	0.25*
	MD	0.20	-0.11	-0.22	0.59**		-0.22	0.40**
	DT	0.42**	-0.13	-0.01	0.64**		-0.31**	0.33**
KS	WK	-0.00	0.28*	0.29*	-0.18	-0.18		-0.28*
	MD	0.07	0.29*	-0.04	-0.24	-0.18		-0.31*
	DT	-0.11	0.34**	0.32*	-0.08	-0.13		-0.35**

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for F_3 and F_5 traits are defined in Table 4.

(section 4.6). Correlations between kernel shrivelling in F_3 and yield in F_5 row plots were significant and positive, although relatively small in magnitude ranging from 0.27 to 0.42 (Tables 43 - 44). This supports the argument that growing conditions in 1984 resulted in kernel shrivelling which reduced the kernel weights and yields of some F_3 families with high yield potential. As a consequence, protein content of these F_3 families was increased. In 1985, F_5 bulks derived from these F_3 families probably expressed their yield potential more fully.

Jain et al. (1975) suggested that selection for protein per kernel was more useful than selection for protein content as a percentage because the heritability of protein per kernel was approximately three times greater than that of protein content. They also indicated that selecting for protein per kernel had less detrimental effect on yield because protein content was generally negatively correlated with kernel weight and yield, while protein per kernel was positively correlated with kernel weight. Brunori et al. (1982) also advocated selecting for protein per kernel rather than protein content. In the present study, protein per kernel did have a higher heritability than protein content (Table 35). However, intergeneration correlations between protein per kernel in F_3 and protein content in F_5 row plots were significant and positive in only half of the cross locations, ranging from -0.03 to 0.42 (Tables 43 -

44). The magnitude of the correlation coefficients between the two traits is probably too low to be of practical interest in breeding programs attempting to increase protein content. In addition, correlations between protein per kernel and protein content within generations were usually not significant, and in some cases, they were even negative (Tables 39 - 40). There was little correlation between protein per kernel and yield either between or within generations, although intergeneration and within generation correlations between protein per kernel and kernel weight were significant, positive and high (Tables 39 - 40, 43 - 44). Under the conditions of the present study, indirect selection for protein content using protein per kernel in F_3 would appear to be of limited value.

Although McNeal et al. (1972, 1982) indicated that selecting for protein yield increased both protein content and yield, the present study suggests that selecting for protein yield is similar to selecting for yield and may actually reduce protein content. Protein yield in F_3 was not significantly correlated with protein content in F_5 row plots (Tables 43 - 44). As indicated previously, very high, positive correlations were observed between protein yield and yield within generations, while no correlations were generally found between protein yield and protein content (Tables 39 - 40). Since negative correlations were observed between protein content and yield (Tables 39 - 40), it is

possible that selection for protein yield may reduce protein content. Reductions in protein content would be highly undesirable in crops such as durum wheat where protein content per se is an important economic trait.

Few significant correlations were found between the remaining F_3 traits and protein content in F_5 row plots, indicating that yield, kernel weight and kernel shrivelling in F_3 would not be useful in selecting indirectly for protein content in F_5 row plots (Tables 43 - 44). However, in some cases, direct selection for high yield, high kernel weight or low kernel shrivelling in F_3 may reduce protein content in F_5 row plots (Tables 43 - 44).

Intergeneration correlations between protein content in F_3 and other traits in F_5 for NIR hill plots were generally not significant (Tables 45 - 46). Exceptions were positive correlations between protein content in F_3 and kernel shrivelling in NIR F_5 hill plots for half of the cross locations, and a negative correlation between protein content in F_3 and kernel weight in NIR F_5 hill plots for the MD cross at both locations (Tables 45 - 46). These results support the conclusions in section 4.6 that selection for protein content in F_3 families had little effect on F_5 traits in NIR hill plots.

Few significant correlations were found between protein content in NIR F_5 hill plots and any of the F_3 traits (excluding protein content), suggesting that none of the F_3

TABLE 45. Correlations between F_3 and F_5 traits in NIR hill plots for each cross at Glenlea.

F_3 Trait[1]	Cross	F_5 Trait[1] PC	YLD	PY	KW	PK	KS
PC	WK		-0.15	-0.09	-0.17	-0.05	0.09
	MD		-0.13	-0.04	-0.39**	-0.24	0.44**
	DT		0.12	0.16	-0.19	-0.08	0.31*
YLD	WK	-0.21		0.14	0.06	-0.04	-0.04
	MD	-0.10		0.21	0.34**	0.34**	-0.38**
	DT	0.07		0.28*	-0.16	-0.14	0.09
PY	WK	-0.15	0.12		0.01	-0.07	-0.03
	MD	0.05	0.16		0.21	0.27*	-0.24
	DT	0.12	0.27*		-0.21	-0.18	0.18
KW	WK	-0.04	0.16	0.16		0.42**	-0.19
	MD	-0.17	0.17	0.12		0.57**	-0.44**
	DT	-0.23	-0.10	-0.13		0.48**	-0.43**
PK	WK	0.18	0.11	0.16	0.46**		-0.21
	MD	0.04	0.15	0.15	0.55**		-0.31*
	DT	-0.07	-0.02	-0.04	0.55**		-0.33**
KS	WK	0.12	-0.13	-0.11	-0.35**	-0.32*	
	MD	0.28*	-0.17	-0.10	-0.48**	-0.39**	
	DT	0.25	0.13	0.16	-0.27*	-0.20	

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for F_3 and F_5 traits are defined in Table 4.

TABLE 46. Correlations between F_3 and F_5 traits in NIR hill plots for each cross at Winnipeg.

		F_5 Trait[1]					
F_3 Trait[1]	Cross	PC	YLD	PY	KW	PK	KS
PC	WK		-0.07	-0.05	-0.00	0.08	0.01
	MD		0.06	0.13	-0.26*	-0.20	0.12
	DT		0.07	0.12	-0.05	0.03	0.26*
YLD	WK	-0.19		0.04	0.01	-0.11	0.09
	MD	-0.05		0.31*	0.20	0.19	-0.06
	DT	-0.07		0.28*	-0.29*	-0.32*	0.27*
PY	WK	-0.16	0.06		0.02	-0.08	0.10
	MD	-0.03	0.30*		0.11	0.11	-0.01
	DT	-0.04	0.29*		-0.31*	-0.33**	0.35**
KW	WK	-0.07	0.08	0.10		0.31*	-0.13
	MD	-0.03	-0.09	-0.12		0.56**	-0.32*
	DT	-0.10	-0.17	-0.21		0.48**	-0.39**
PK	WK	-0.01	0.09	0.13	0.39**		-0.20
	MD	0.05	-0.06	-0.04	0.53**		-0.37**
	DT	0.01	-0.16	-0.17	0.61**		-0.33**
KS	WK	-0.00	0.07	0.07	-0.07	-0.10	
	MD	0.05	0.12	0.16	-0.21	-0.19	
	DT	0.11	0.17	0.20	-0.21	-0.17	

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for F_3 and F_5 traits are defined in Table 4.

traits would be satisfactory for indirect selection for protein content (Tables 45 - 46). In the NIR F_5 hill plots, protein yield and protein per kernel were both negatively correlated to protein content in over half of the cross locations, indicating further their limited value as indirect selection criteria for protein content (Table 41). As for NIR row plots, protein per kernel in F_3 was positively correlated with kernel weight in NIR F_5 hill plots but not significantly correlated with yield (Tables 45 - 46). Since none of the F_3 traits excluding protein content were consistently correlated with protein content in F_5 hill or row plots, direct selection for protein content in F_3 would be more effective in increasing protein content in F_5 than indirect selection using other F_3 traits.

Intergeneration correlations between protein content of F_2 RP plants and F_5 traits of RP in ISD hill plots were not significant, except for a negative correlation with kernel weight in the WK cross at Winnipeg (Table 47). The lack of significant correlations may be due to the relatively small sample size and environmental effects, particularly on F_2 plants.

The results of the correlation studies reported here indicate that environmental conditions have a profound effect on the relationships among traits. The strong relationship of kernel weight, test weight and kernel

TABLE 47. Correlations between protein content of F_2 RP plants and F_5 traits of RP in ISD hill plots for each cross location.

Cross	Location	F_5 Trait[1]					
		PC	YLD	PY	KW	PK	KS
WK	Glenlea	0.09	-0.23	-0.22	-0.12	-0.10	-0.15
	Winnipeg	0.41	-0.41	-0.37	-0.48*	-0.42	0.37
MD	Glenlea	0.08	0.16	0.20	0.33	0.43	-0.33
	Winnipeg	0.00	-0.16	-0.18	0.22	0.30	-0.27
DT	Glenlea	0.21	-0.24	-0.20	-0.09	0.02	-0.15
	Winnipeg	0.26	-0.11	-0.07	-0.16	-0.02	-0.08

*Significant at the 0.05 probability level.

[1]Abbreviations for traits are defined in Table 4.

shrivelling to protein content was probably due to incomplete kernel development resulting from unfavorable environmental conditions during the grain filling period.

5. GENERAL DISCUSSION

Although selection in F_2 and F_3 of durum wheat crosses appeared to identify genotypes differing in protein content, these differences did not persist in F_5 to any great extent. When significant responses to selection were obtained, they did not exceed 0.4% protein content and were lower than those reported in the literature for common wheat (Lebsock et al., 1964; McNeal et al., 1972, 1978; Guthrie et al., 1984). Heritabilities in standard units for protein content based on intergeneration correlation were low to moderate in magnitude, reaching a maximum of 57%. Knott and Kumar (1975) suggested that intergeneration correlations greater than 0.60 were required to justify the large amount of work involved in early generation testing for yield in common wheat. Since at least as much work is required for protein content, early generation selection for protein content in durum wheat under the conditions of the present study is of doubtful value.

The effectiveness of early generation selection is influenced by the amount of genetic, environmental and genotype x environment variation (O'Brien et al., 1978). It is possible that the amount of genetic variation may have been too small in the populations of the present study to compen-

sate for environmental variation and its effect on different genotypes. The highest response to selection was obtained in the DT cross at Glenlea for both NIR and ISD selection methods. This was not expected because the two parents of the cross differed the least in protein content, suggesting that transgressive segregation may have occurred. However, high protein bulks and families obtained from the DT cross were still considerably lower in protein content than those obtained from the other two crosses particularly at Glenlea. Consequently, the DT cross would be of less interest in a breeding program aimed at improving protein content.

Using parents that differ more in protein content than those of the present study would be one method of increasing genetic variation and hence response to selection in early generations. Since Wakooma is close to the upper range of protein content in adapted durum wheat material and the use of parents with a lower protein content than DT367 is undesirable, high protein lines from wild relatives such as T. turgidum var dicoccoides could be used as parents. In addition to high protein content, some accessions of T. turgidum var dicoccoides produce large grains and are highly fertile (Law and Payne, 1983). Crosses between T. turgidum var dicoccoides and T. turgidum var durum are also easy to make. Avivi et al. (1983) crossed four lines of T. turgidum var dicoccoides having 23.7 to 27.5% protein content and a mean kernel weight of 50 mg with the durum wheat cultivar, Inbar, which had 13.4% protein content. They obtained rela-

tively high heritability estimates for protein content (64 - 74%), indicating significant potential for rapid progress in selection for high protein content. Although T. turgidum var dicoccoides offers great potential as a source of high protein content, crosses with durum wheat may produce many poorly adapted offspring with shrivelled kernels which would confound selection for protein content, since shrivelled kernels tend to have higher protein content than plump kernels (Johnson et al., 1973b). A backcrossing program using adapted durum wheat cultivars as the recurrent parent accompanied by selection for plump kernels and high protein content would probably be necessary.

Although coefficients of variation for protein content in the present study were relatively low, environmental variation may still have been too high to allow the detection of small genetic differences in some cases, such as the MD cross at Glenlea in NIR row plots. In this study, a lattice design was used to minimize the effects of soil heterogeneity. It appeared to be effective in the NIR row plots where relative efficiencies were as high as 226%, but little advantage over the randomized complete block design was observed in any of the experiments involving hill plots. Frey (1965) also reported that lattice designs did not increase efficiency in hill plots of oats, while Ross and Miller (1955) indicated that the randomized complete block design was satisfactory for hill plots of oats and barley. Other methods of reducing environmental variation in early genera-

tions include the use of systematic controls at frequent intervals (Briggs et al., 1969; Hadjichristodoulou and Della, 1976), grid selection (Guthrie et al., 1984), and moving mean selection (Townley-Smith and Hurd, 1973). Discussion of the advantages and disadvantages of each method is beyond the scope of this study.

Providing uniform conditions conducive to the expression of genetic differences in protein content would minimize environmental variation and maximize response to selection. However, the conditions considered optimal for detecting genetic differences in protein content vary greatly in the literature (Lebsock et al., 1964; Johnson et al., 1969; Terman et al., 1969; Konzak and Rubenthaler, 1984), suggesting that optimal conditions depend on the particular environment in which the genotypes are to be grown and the genotypes themselves. Chemical control of diseases, as suggested by Konzak and Rubenthaler (1984), may have been helpful in the present study in 1984.

Genotype x environment interactions may mask persistent genetic differences and reduce the effectiveness of early generation selection, particularly in crosses with a relatively small amount of genetic variation (O'Brien et al., 1978). Genotype x environment interactions for protein content were found in the present study and have been reported in the literature (Clark, 1926; Aamodt and Torrie, 1935; Lebsock et al., 1964; Konzak, 1977; Miezan et al., 1977; Diehl et al., 1978; Jatasra and Paroda, 1982). Konzak

(1977) reported marked differences in the stability of protein content in durum wheat genotypes and indicated that genotype x environment interactions are subject to genetic control. Halloran (1975) and Mihaljev et al. (1979) also indicated that genetic control of protein content may change depending on the environment. The differences in protein content observed among entries in F_2 and F_3 tests of the present study may be due in part to genetic differences expressed only under the hot, dry growing conditions with disease during the grain filling period in 1984. Similar differences in protein content were probably not observed in 1985 because the F_5 responded differently to the cool, wet conditions during the grain filling period which resulted in severe lodging. However, normal grain filling and kernel development were hampered in both years, with the extent of impairment depending on the particular genotype and year. The results of the present study strongly suggest that genotype x environment interactions were mainly responsible for the relatively low response to selection for protein content in early generations.

The presence of genotype x environment interactions indicates the need to select for protein content in early generations over a range of environments (Whan et al., 1982; Weber, 1984). The use of replicated hill plots in several locations has been advocated for yield testing in early generations because hill plots require considerably less seed and land than row plots, and are able to predict performance

in row plots (Jellum et al., 1963; Frey, 1965; Baker and Leisle, 1970; Shebeski and Evans, 1973; Seitzer and Evans, 1978; O'Brien et al., 1979). However, under the conditions of the present study, hill plots were less efficient than row plots in evaluating the protein content of F_5 bulks for the NIR method, requiring more replication to give information equivalent to one four-row plot. Estimates in the literature of the number of hill plots required to give yield information equivalent to a row plot appear too low in some cases for reasons discussed previously (section 4.4). The need for more replicates of hill plots would increase the cost and land requirements. In addition, hill plots require more labor since they must be planted and harvested by hand. Genotype x plot type interactions may also occur, reducing the ability of hill plots to predict performance of genotypes in row plots (Torrie, 1962). Although the results of the present study may have been influenced by differences in seeding dates between the two plot types, the use of hill plots for early generation selection for protein content does not appear to be practical.

The imbibed seed density selection method, utilized by Peterson et al. (1986) as a rapid, cheap, simple technique of screening large numbers of experimental lines for protein content in early generations, resulted in little response to selection for protein content under the conditions of the present study. Although differences in protein content between the high and low protein fractions separated by ISD

were observed in F_2, they persisted in only one of six cross locations in F_5. Peterson et al. (1986) reported that imbibed seed density selection gave a significant response to selection in only 10 of 52 bulk populations, and suggested that large amounts of nongenetic variation in the protein content of individual seeds were responsible for their results. Such results are not surprising since considerable variation in protein content has been reported among plants of the same genotype (Clarke, 1926; Levi and Anderson, 1950; Kaul and Sosulski, 1965; Diehl et al., 1978), among tillers of the same plant (Levi and Anderson, 1950; McNeal and Davis, 1966), among spikelets of the same head (Levi and Anderson, 1950; McNeal and Davis, 1954, 1966; Stuber et al., 1962a; Ali et al., 1969), and among kernels within the same spikelet (Levi and Anderson, 1950; McNeal and Davis, 1954; Bremner, 1972; Sofield et al., 1977; Simmons and Moss, 1978; Sclater, 1982; Herzog and Stamp, 1983). Levi and Anderson (1950) indicated that the range in protein content of individual kernels within a wheat plant may be as high as 6%. Although it may be possible to improve the effectiveness of imbibed seed density selection by increasing genetic variation or reducing the proportion of seeds selected (Peterson et al., 1986), such large amounts of nongenetic variation will limit the usefulness of imbibed seed density selection as a method of mass selection for protein content in early generations. Hence, the time and cost of screening large numbers of experimental lines for protein content will

remain an important constraint to early generation selection.

Another major constraint to early generation selection for protein content is the concern that yield will be reduced because of the often reported negative correlation between protein content and yield (Johnson et al., 1985). In the present study, selection for protein content did not adversely affect yield. In fact, selection for high protein content in F_3 tended to increase yield in F_5 row plots for the NIR method. However, a higher response to selection for protein content would probably have reduced yield because, in general, there was a negative correlation between protein content and yield among entries in a cross. The correlation coefficients between the two traits were less than -0.60 in magnitude, indicating that improvement of one trait while maintaining the other at acceptable levels, or even simultaneous improvement of both traits, should be possible (Johnson et al., 1979a, 1985). The inverse relationship between protein content and yield may, however, have been stronger under more favorable conditions, as indicated by results from the NIR row plots at Winnipeg where yields and correlations between protein content and yield were higher than at Glenlea. Consequently, under conditions conducive to high yield, the negative relationship between protein content and yield may present a more formidable barrier to improvement of the two traits.

In general, protein content was negatively correlated with kernel weight and test weight, and positively correlated with kernel shrivelling. Correlation coefficients for protein content with these traits were more consistent and higher than those between protein content and yield. The negative correlations for protein content with both kernel weight and test weight were generally higher than reported in the literature for durum and common wheat. Zitelli et al. (1979) found a negative correlation (-0.62) between protein content and kernel weight in durum wheat in a dry year, but no correlation in a year with adequate precipitation. These results suggest that the strong correlations for protein content with kernel weight, test weight and kernel shrivelling were mainly the result of environmental factors that hampered normal grain filling. It has been reported that the accumulation of starch in grain depends mainly on post-anthesis carbon assimilation (Austin and Jones, 1975), while the accumulation of protein in the grain depends more on the remobilization and translocation of N from vegetative tissues (Gregory et al., 1981; Kotlyar and Kumakov, 1983; Nicolas et al., 1985). Consequently, growing conditions that reduce carbon assimilation during grain filling would reduce starch accumulation and increase the proportion of protein, resulting in light, shrivelled kernels with high protein content (Shahani and Saulescu, 1984). It is possible that high protein selections identified in 1984 may have

accumulated less starch rather than more protein as a result of genetic factors for poor kernel development or a greater susceptibility to unfavorable growing conditions. Such selections are undesirable in protein improvement programs because they probably do not have the genetic ability to accumulate high protein levels in normal, well filled kernels.

The relationship of kernel weight and kernel shrivelling to protein content has important practical implications in selecting for protein content. Prior to protein analysis, the samples should be evaluated for kernel shrivelling. Only samples with relatively well filled kernels should be retained for further analysis. In a year such as 1984 when kernel shrivelling is severe, it may be more practical for the breeder to relax selection pressure or not select for protein content at all.

None of the F_3 traits, including protein yield and protein per kernel, appeared to be useful as indirect selection methods for protein content in breeding programs where protein content *per se* is an important economic trait. Within generation correlations between protein yield and yield were extremely high. Consequently, negative correlations between protein content and yield occasionally resulted in a negative correlation between protein yield and protein content, despite the positive mathematical relationship between the two traits. Loffler *et al*. (1985) also reported a negative correlation between protein yield and protein content.

Thus, selection for protein yield could actually reduce protein content, although McNeal et al. (1972, 1982) indicated that selecting for protein yield increased both protein content and yield. The use of protein per kernel for protein improvement rather than protein content, as advocated by Jain et al. (1975) and Brunori et al. (1982), appeared to be of limited value for similar reasons. However, under more favorable conditions resulting in well filled kernels, the negative correlation between protein content and protein per kernel frequently observed in the present study may be reduced or eliminated, allowing protein per kernel to be a useful selection criterion.

Cregan and van Berkum (1984) recommended an integrated physiological/biochemical selection program in which several components of N metabolism are measured over the growing season as a means of improving protein content and productivity. Other workers have suggested using nitrogen harvest index as a selection criterion (Dalling and Lyon, 1977; Loffler and Busch, 1982). However, in view of the results of the present study, selection criteria requiring multiple N determinations at several times during the growing season would not be practical for early generation testing. The time and labor involved in screening a large number of lines would be greatly increased, and the existence of genotype x environment interactions would reduce their effectiveness and make interpretation difficult. Although such criteria could provide useful information to the breeder, their use

should be restricted to evaluating and selecting parents for crosses.

Protein content is a complex trait under the control of many genes, and is strongly influenced by the environment (Johnson et al., 1985). The results of the present study and reports in the literature indicate that genotype x environment interactions occur for protein content. A further complexity is that the relationship between protein content and other traits also varies, depending on the environment (Zitelli et al., 1979). Significant responses to early generation selection for protein content in durum wheat were found in the present study, but they were low relative to the extra labor and resources required. Although higher responses in the literature suggest that early generation selection for protein content is feasible, the present study indicates that the breeder can not be confident of consistently attaining an adequate response to selection, particularly when only one environment is used. Testing a large amount of early generation material for protein content at more than one location is very expensive and requires large amounts of seed, land and labor. Hill plots reduce the seed and land requirement, but as noted previously, they are not practical for early generation selection for protein content. Since most breeders operate on fixed resources and must select for many traits in addition to protein content, it is recommended that selection for protein content be delayed until later generations when

there is ample seed to test the lines in row plots over a range of environments and when the number of lines has been reduced to a manageable level by selection for simply inherited traits.

6. SUMMARY AND CONCLUSION

When the four parental cultivars were evaluated at two locations over two years, significant differences were found among cultivars for protein content, yield, test weight, kernel weight, protein yield, protein per kernel, days to heading, days to maturity, days from heading to maturity, lodging and height. As expected, Wakooma had the highest protein content followed in order by Medora, DT447 and DT367, with a range in protein content of 1.8% between Wakooma and DT367. DT367 had a lower yield than expected relative to the other cultivars. The cultivars interacted significantly with years and locations for most traits including protein content.

The F_3 selection groups established for the NIR selection method in 1984 differed significantly in protein content, with HP having the highest protein content followed in order by RP and LP. However, HP also had lighter, more shrivelled kernels than LP, while RP was intermediate in kernel weight and shrivelling. No significant differences were found among selection groups for yield (except in the WK cross), protein yield, or protein per kernel.

Response to selection, as determined by differences among F_5 selection groups for the NIR row plots in 1985, was

low and ranged from 0 to 0.4% protein content. HP had significantly higher protein content than LP in three of six cross locations, while HP and LP differed significantly from RP in only one cross location each. Although selection for protein content in F_3 by the NIR selection method was little better than random, it was in the desired direction.

Response to selection, as determined by the number of high protein F_5 bulks retained by selection group, indicated that selection for high protein content was effective in four of six cross locations where HP retained at least two thirds of the high protein F_5 bulks. Selection for low protein content did not appear as effective although the trend was in the desired direction.

The ISD selection method separated high and low protein fractions from bulk samples of F_2 seed. The mean kernel weight of the high protein fraction was less than that of the low protein fraction. Protein content of 20 randomly selected Wakooma plants, included as checks, averaged 17.0 to 17.3% with a range of 2.8 to 3.5% depending on the cross. The standard error for the Wakooma plants within a cross was nearly as high as for the same number of F_2 RP plants, indicating large environmental effects.

Highly significant differences in protein content were found among the F_5 entries and checks in each cross location for both the ISD and NIR hill plots. However, significant differences were not detected among the F_5 selection groups of either method, except for the DT cross at Glenlea where

HP exceeded LP by 0.3 and 0.4% for the NIR and ISD hill plots, respectively. For both methods, random selection was as effective as selection for high or low protein content since RP did not differ significantly from either HP or LP. The NIR method was slightly more effective than the ISD method; trends for the NIR method were in the desired direction, while for the ISD method, RP tended to have the highest protein content. Response to selection, as determined by the number of high or low protein F_5 entries retained by selection group, also indicated that selection for high or low protein content by either method was generally no more effective than random selection.

The NIR hill plots were less effective in detecting differences in protein content among F_5 bulks than the NIR row plots. Phenotypic correlations for protein content between NIR hill and row plots ranged from 0.44 to 0.72, while genetic correlations ranged from 0.51 to 0.98. Depending on the cross location, hill plots were 45 to 98% as efficient as row plots in selecting for protein content. One to five replicates of hill plots were required at Glenlea to give information equivalent to one four-row plot, while at Winnipeg it was not possible for any number of hill plots to be as efficient as one four-row plot.

Heritability estimates in standard units determined from the F_3 hill and F_5 row plots of the NIR method ranged from 20 to 57% for protein content, and were significant for all cross locations except the DT cross at Winnipeg. Heri-

tabilities for protein content determined in a similar manner from F_3 and F_5 hill plots of the NIR method were lower (11 to 37%) and significant only at Glenlea. Regardless of plot type, heritabilities for protein content were generally greater in magnitude than those for yield and protein yield, less than those for kernel weight and protein per kernel, and similar to those for kernel shrivelling. Heritabilities for protein per kernel were the highest and appeared to be relatively stable.

Selection for protein content in F_2 and F_3 had little effect on any of the traits studied in F_5 except for protein yield in NIR row plots, where selection for high protein content resulted in higher protein yield than selection for low protein content. Selection for high protein content also tended to increase yield in NIR row plots, but differences among selection groups were generally not significant.

Protein content was negatively correlated with kernel weight and test weight, and positively correlated with kernel shrivelling in nearly all cases within the F_3 and F_5 generations. The coefficients of these correlations were generally intermediate to high in magnitude. The relationship of protein content to kernel weight, test weight and kernel shrivelling was probably due to incomplete kernel development as a result of unfavorable environmental conditions during grain filling. In general, protein content was negatively correlated with yield but not to the same degree as kernel weight. Although difficult, it should be possible

to maintain or even increase protein content while increasing yield in a breeding program. Correlations for protein content with both protein yield and protein per kernel were inconsistent over experiments.

Except for positive correlations with protein yield in NIR row plots, protein content in F_3 was not consistently correlated with any traits in F_5. None of the F_3 traits, including protein yield and protein per kernel, were consistently correlated with protein content in F_5, indicating that indirect selection for protein content in F_3 using these traits would not be effective.

It was concluded that:

(1) Although significant responses to early generation selection for protein content in durum wheat were found in the present study, they were too low to justify the extra labor and resources required.

(2) Unfavorable environmental conditions and their effects on different genotypes reduced the effectiveness of early generation selection for protein content.

(3) The ISD selection method was ineffective as a method of mass selection for protein content in early generations under the conditions of this study, and appeared to be limited by large amounts of nongenetic variation in the protein content of individual seeds.

(4) Since hill plots were not as efficient as row plots and require more replication, the use of hill plots to

select for protein content at several locations in early generations is not practical.

It is recommended that:

(1) Selection for protein content be delayed until later generations when there is ample seed to test the lines in row plots over a range of environments and when the number of lines has been reduced to a manageable number by selection for simply inherited traits.

(2) Before selecting for protein content at any stage of a breeding program, the material should be examined for kernel shrivelling since kernel shrivelling can confound protein content and reduce the response to selection.

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8. APPENDICES

APPENDIX TABLE 1. Available soil nitrogen, phosphorus, potassium and sulfur at each location in each year.[1]

Year	Location	Sampling Date	Amount Available (kg/ha)[2] Nitrogen	Phosphorus	Potassium	Sulfur
1984	Glenlea	June 1	170.8	42.6	946.3	>141.8
	Winnipeg	June 2	90.8	44.3	785.3	45.8
1985	Glenlea	May 30	131.0	47.4	937.4	>76.3
	Winnipeg	May 28	74.0	76.9	1035.0	44.5

[1]Determined by the Manitoba Provincial Soil Testing Laboratory, Winnipeg.
[2]Amount available in the top 15 cm of soil for phosphorus and potassium, and in the top 60 cm for nitrogen and sulphur.

APPENDIX TABLE 2. Monthly mean temperatures and precipitation for the 1984 and 1985 growing seasons.[1]

	Mean Temperature (°C)			Precipitation (mm)		
Month	1984	1985	Normal	1984	1985	Normal
May	10.1	13.1	11.3	29.8	64.0	65.7
June	17.0	14.0	16.8	227.9	67.4	80.1
July	19.6	18.8	19.6	38.3	34.0	75.9
August	21.0	16.3	18.3	21.6	218.0	75.2
September	10.6	10.0	12.4	62.0	28.5	53.3
Mean	15.7	14.4	15.7			
Total				379.6	411.9	350.2

[1]From the Annual Meteorological Summary for Winnipeg International Airport, Environment Canada.

APPENDIX TABLE 3. Adjusted means for protein content of F_3 families in each selection group of each cross for NIR method.

	HP				LP				RP		
Entry	WK	MD	DT	Entry	WK	MD	DT	Entry	WK	MD	DT
1	16.9	17.4	16.7	21	14.5	14.6	14.5	41	15.5	16.1	15.1
2	16.9	17.0	16.1	22	14.7	14.7	14.5	42	15.5	15.5	15.7
3	16.9	16.9	15.8	23	14.7	14.7	14.4	43	15.7	14.9	14.9
4	16.8	16.8	15.9	24	14.7	14.7	14.6	44	16.9	16.2	15.2
5	16.7	16.7	15.8	25	14.7	14.8	14.2	45	14.8	16.3	14.9
6	16.6	16.7	16.2	26	14.7	14.8	14.5	46	16.0	15.6	15.6
7	16.4	16.7	15.8	27	14.8	14.8	14.6	47	15.7	15.2	15.2
8	16.4	16.7	15.8	28	14.8	14.8	14.6	48	15.2	15.3	14.7
9	16.3	16.6	16.2	29	14.8	14.8	14.6	49	15.3	15.9	15.5
10	16.3	16.6	15.8	30	14.8	14.9	14.4	50	14.9	16.0	15.6
11	16.3	16.6	15.8	31	14.8	14.9	14.5	51	15.9	15.5	15.0
12	16.3	16.6	15.8	32	14.9	14.9	14.5	52	15.4	16.9	15.8
13	16.3	16.5	16.0	33	14.9	14.9	14.5	53	15.1	15.6	15.5
14	16.2	16.5	15.7	34	14.9	14.9	14.5	54	15.6	15.4	15.5
15	16.1	16.5	15.8	35	14.9	14.9	14.5	55	15.9	15.2	14.7
16	16.1	16.4	16.1	36	14.9	14.9	14.4	56	15.0	15.5	15.2
17	16.1	16.4	16.1	37	15.0	15.0	14.4	57	15.8	15.9	15.1
18	16.1	16.4	16.2	38	15.0	15.0	14.5	58	15.6	15.8	15.3
19	16.1	16.4	15.9	39	15.0	15.1	14.4	59	16.0	16.6	14.8
20	16.2	16.4	15.7	40	15.0	15.0	14.5	60	16.0	15.7	15.0

APPENDIX TABLE 4. Adjusted means for protein content of F_5 bulks in each selection group of each cross location for NIR row plots.

Glenlea

	HP				LP				RP		
Entry	WK	MD	DT	Entry	WK	MD	DT	Entry	WK	MD	DT
1	14.2	13.7	13.2	21	13.7	13.1	12.8	41	13.8	14.2	12.8
2	13.7	13.4	13.3	22	13.5	13.8	12.9	42	14.4	14.4	12.6
3	14.4	14.5	13.0	23	13.8	13.5	12.6	43	13.6	14.2	13.1
4	14.6	13.7	12.9	24	13.7	13.4	12.9	44	14.4	13.8	13.0
5	13.8	14.3	13.0	25	13.7	13.1	12.5	45	13.6	13.2	13.0
6	14.3	13.9	13.0	26	14.2	13.1	12.6	46	14.1	13.2	13.4
7	14.5	14.4	13.5	27	14.1	13.2	12.6	47	13.6	13.8	12.5
8	14.3	13.9	13.0	28	13.7	13.0	12.6	48	13.8	13.5	12.2
9	13.7	14.4	13.1	29	13.4	13.5	12.6	49	14.1	14.1	12.2
10	14.4	14.6	12.9	30	13.6	13.2	12.8	50	14.0	14.1	12.9
11	13.8	14.2	13.4	31	13.7	13.9	12.0	51	13.9	13.4	12.4
12	13.7	13.9	13.1	32	14.1	13.9	12.9	52	14.0	13.9	13.0
13	14.2	13.5	13.0	33	13.7	13.7	12.6	53	13.0	13.7	12.7
14	13.4	13.5	13.0	34	13.9	14.4	12.5	54	14.1	13.2	12.8
15	14.2	14.9	12.7	35	13.8	13.4	12.4	55	13.8	13.7	12.5
16	14.2	14.2	12.7	36	13.0	13.8	13.0	56	14.0	13.8	12.9
17	13.7	13.9	12.9	37	13.8	13.4	12.6	57	13.8	14.1	12.9
18	14.1	13.1	13.1	38	13.6	13.1	12.8	58	13.6	12.8	12.8
19	13.6	13.6	13.0	39	14.0	13.6	12.3	59	14.2	14.5	13.0
20	13.6	14.0	12.9	40	13.5	14.0	12.5	60	14.5	13.8	12.8

Winnipeg

1	13.2	12.6	12.4	21	12.6	12.3	12.4	41	13.1	13.3	12.2
2	12.8	12.3	12.6	22	12.7	12.7	12.3	42	12.9	13.1	12.4
3	13.0	12.8	12.5	23	12.9	12.7	12.4	43	13.0	12.6	12.6
4	13.3	12.8	12.3	24	13.2	12.4	12.5	44	13.0	12.9	12.9
5	13.0	13.1	12.6	25	12.8	12.6	11.8	45	12.7	12.6	12.2
6	13.2	12.8	12.5	26	12.8	12.4	12.4	46	13.2	12.7	13.0
7	13.1	12.7	13.0	27	12.9	12.5	12.3	47	12.6	12.5	12.1
8	13.1	12.9	12.6	28	12.9	12.3	12.3	48	12.9	12.4	12.4
9	12.9	12.9	12.8	29	12.3	12.8	12.3	49	13.1	13.1	11.7
10	13.5	13.3	12.4	30	12.6	12.3	12.6	50	12.9	12.4	12.3
11	12.9	13.0	12.7	31	12.9	13.0	11.7	51	12.8	12.6	12.4
12	13.5	12.6	12.5	32	13.1	12.9	12.6	52	12.9	12.8	12.7
13	13.3	12.4	12.5	33	12.6	12.7	13.2	53	12.5	12.6	12.3
14	12.2	12.6	12.3	34	13.0	12.7	12.4	54	13.1	12.3	12.5
15	13.5	13.2	12.4	35	13.2	12.8	12.3	55	12.9	12.7	12.4
16	13.4	12.8	12.3	36	12.6	13.3	12.9	56	13.2	12.6	12.7
17	12.8	13.0	12.5	37	13.0	12.6	12.3	57	12.9	12.4	12.4
18	12.8	12.5	12.4	38	12.6	12.6	12.4	58	12.6	11.9	12.2
19	12.7	12.5	12.6	39	12.9	12.5	12.3	59	13.5	13.5	12.8
20	12.7	12.8	12.7	40	12.3	12.5	12.3	60	13.4	12.6	12.3

APPENDIX TABLE 5. Analysis of variance and orthogonal contrasts for yield, protein yield, kernel weight, protein per kernel and kernel shrivelling of F_3 selection groups in the WK cross for the NIR method.

Source of Variation	DF	Trait[1] Mean Square				
		YLD	PY	KW	PK	KS
Replications	2	1034**	18.303*	94.45**	1.3715**	2.106*
Selection Groups (G)	2	1736**	11.464	300.09**	0.4922	16.106**
HP vs. RP	1	2094**	21.362	138.46**	0.1872	6.075**
(HP + RP) vs. LP	1	1378*	1.567	461.72**	0.7971	26.136**
Families within G	57	243	5.933	12.27*	0.2608**	0.680
Error	118	212	4.569	7.82	0.0937	0.563
C.V.(%)[2]		21.9	20.7	8.1	5.7	27.1

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

APPENDIX TABLE 6. Analysis of variance and orthogonal contrasts for yield, protein yield, kernel weight, protein per kernel and kernel shrivelling of F_3 selection groups in the MD cross for the NIR method.

Source of Variation	DF	Trait[1] Mean Square				
		YLD	PY	KW	PK	KS
Replications	2	1727**	49.076**	12.28	0.4260*	2.165**
Selection Groups (G)	2	490	5.141	457.45**	0.9464	24.555**
HP vs. RP	1	0	9.856	252.01**	0.8135	10.208**
(HP + RP) vs. LP	1	980	0.425	662.89**	1.0794	38.901**
Families within G	57	207	4.910	16.16*	0.3700	0.658
Error	117	217	4.899	6.96	0.1131	0.412
C.V.(%)[2]		22.3	21.4	7.4	6.0	24.1

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

APPENDIX TABLE 7. Analysis of variance and orthogonal contrasts for yield, protein yield, kernel weight, protein per kernel and kernel shrivelling of F_3 selection groups in the DT cross for the NIR method.

		Trait[1] Mean Square				
Source of Variation	DF	YLD	PY	KW	PK	KS
Replications	2	3187**	75.542**	56.96**	0.7617**	1.106
Selection Groups (G)	2	1135	2.744	209.63**	0.1581	15.356**
HP vs. RP	1	123	0.692	172.08**	0.1952	12.033**
(HP + RP) vs. LP	1	2146	4.796	247.17**	0.1210	18.678**
Families within G	57	426**	10.076**	23.29**	0.4685**	0.520
Error	118	218	4.426	10.32	0.1275	0.405
C.V.(%)[2]		21.1	19.8	7.9	5.8	26.1

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

APPENDIX TABLE 8. Unadjusted means for protein content of F_5 families in each selection group of each cross location for ISD hill plots.

Glenlea

	HP				LP				RP		
Entry	WK	MD	DT	Entry	WK	MD	DT	Entry	WK	MD	DT
1	15.4	15.0	14.2	21	15.7	14.1	13.8	41	15.1	14.6	13.7
2	14.0	15.1	14.2	22	14.5	14.8	13.0	42	14.8	14.4	13.2
3	15.7	14.1	13.8	23	14.1	13.9	13.3	43	14.8	14.6	13.7
4	14.4	14.7	13.5	24	15.2	13.3	12.9	44	15.4	14.6	13.5
5	14.4	15.0	14.4	25	13.6	13.5	13.7	45	15.3	14.6	14.1
6	14.2	14.4	12.8	26	14.7	14.2	13.4	46	14.1	14.1	13.1
7	15.2	14.2	13.7	27	13.9	14.9	13.0	47	14.9	14.3	14.0
8	15.1	14.7	14.1	28	15.6	14.1	13.1	48	14.4	14.5	13.5
9	14.3	13.7	13.8	29	14.9	14.0	13.3	49	14.9	13.2	12.9
10	14.5	13.8	12.8	30	14.6	14.3	12.5	50	15.0	14.0	14.4
11	15.1	13.7	14.8	31	14.2	14.2	13.6	51	15.4	14.5	13.7
12	14.9	14.7	14.1	32	15.1	13.9	13.6	52	14.9	13.9	14.2
13	14.6	14.4	13.9	33	14.2	13.9	13.3	53	14.8	15.0	12.7
14	14.9	14.3	13.0	34	15.0	13.7	13.6	54	14.6	15.5	14.2
15	14.0	14.7	14.1	35	14.1	15.0	13.4	55	15.2	14.0	12.7
16	14.4	14.1	13.7	36	14.1	14.2	13.8	56	15.6	14.5	13.3
17	13.8	14.4	12.9	37	14.0	14.7	13.5	57	15.1	14.2	14.0
18	14.9	13.4	13.6	38	14.9	13.9	13.9	58	14.4	14.0	14.2
19	15.1	13.7	14.2	39	15.2	13.4	13.5	59	15.0	14.6	12.9
20	14.8	14.4	14.1	40	13.9	15.1	13.3	60	14.6	15.2	13.3

Winnipeg

1	14.0	14.2	12.9	21	15.0	13.5	13.1	41	14.0	13.7	13.3
2	13.7	14.5	12.7	22	14.6	13.6	11.9	42	15.0	13.8	12.6
3	14.6	13.0	13.0	23	13.2	13.2	12.5	43	15.3	14.4	12.5
4	13.8	13.7	12.4	24	14.4	12.4	13.6	44	15.6	14.0	12.2
5	14.3	13.6	13.5	25	14.3	12.5	12.7	45	15.4	13.8	12.9
6	13.6	13.5	12.4	26	13.9	13.3	12.5	46	13.5	13.9	11.9
7	14.8	13.4	12.6	27	14.0	14.6	12.7	47	13.8	13.8	13.2
8	14.2	13.5	13.2	28	15.5	13.4	12.5	48	13.9	13.4	12.8
9	14.3	13.0	12.2	29	14.3	13.2	12.6	49	14.9	12.6	12.0
10	14.4	13.7	12.7	30	13.9	13.2	12.6	50	13.8	12.5	12.9
11	14.6	12.8	13.1	31	14.3	13.5	12.8	51	13.6	13.7	12.6
12	15.3	13.3	12.9	32	14.3	13.0	12.6	52	14.5	13.0	13.3
13	15.0	13.2	13.0	33	13.1	14.9	12.2	53	14.0	14.0	12.9
14	13.7	13.0	12.4	34	14.1	12.6	11.9	54	15.0	13.7	13.5
15	12.7	13.6	13.0	35	14.0	14.1	12.7	55	14.2	13.7	12.1
16	14.6	13.2	12.5	36	13.3	13.3	13.3	56	14.3	14.0	12.5
17	14.8	13.4	12.0	37	13.6	13.8	11.6	57	13.6	12.5	13.0
18	14.5	12.3	12.8	38	15.4	12.5	13.0	58	13.8	12.8	13.1
19	14.5	12.1	13.2	39	15.3	12.6	12.4	59	14.4	13.2	12.4
20	13.5	13.4	12.9	40	13.4	15.0	12.6	60	15.2	13.7	12.9

APPENDIX TABLE 9. Unadjusted means for protein content of F_5 bulks in each selection group of each cross location for NIR hill plots.

Glenlea

	HP				LP				RP		
Entry	WK	MD	DT	Entry	WK	MD	DT	Entry	WK	MD	DT
1	15.0	14.4	14.2	21	14.0	13.8	13.3	41	14.9	15.9	13.3
2	14.4	14.1	13.4	22	14.5	14.5	13.4	42	14.7	14.3	13.3
3	15.8	14.9	14.1	23	15.3	14.2	13.9	43	14.4	14.5	13.7
4	15.3	14.6	13.8	24	15.0	13.6	13.9	44	16.6	14.4	13.2
5	14.5	14.6	13.5	25	14.6	14.1	13.6	45	14.5	13.8	13.6
6	14.7	14.0	13.1	26	14.7	13.7	12.8	46	14.7	13.7	13.6
7	15.5	14.5	13.6	27	14.8	14.1	13.7	47	14.4	14.1	14.2
8	15.0	14.7	14.1	28	14.7	14.1	13.1	48	14.4	14.0	13.4
9	15.1	14.6	13.6	29	14.4	14.3	13.4	49	14.4	15.5	13.2
10	15.1	15.0	13.7	30	15.3	13.2	13.6	50	14.8	15.0	13.6
11	15.1	14.6	13.4	31	15.3	14.5	12.9	51	14.7	13.3	13.3
12	15.1	14.2	13.3	32	15.4	14.4	13.7	52	15.0	14.4	13.7
13	14.9	14.1	13.3	33	15.1	14.3	12.9	53	14.4	14.1	13.5
14	14.4	14.4	13.4	34	15.4	14.4	13.5	54	14.8	13.6	13.4
15	14.9	14.7	13.3	35	15.7	14.1	13.3	55	14.2	14.0	13.2
16	15.3	14.1	13.6	36	13.6	14.5	13.7	56	14.7	14.3	13.3
17	14.9	14.4	13.5	37	15.1	14.1	13.2	57	14.4	14.4	13.8
18	14.8	13.6	14.0	38	13.5	13.6	13.3	58	14.1	13.7	14.2
19	14.6	13.8	13.8	39	14.3	14.0	12.7	59	14.6	15.1	13.6
20	14.3	14.4	13.4	40	13.8	13.7	13.3	60	14.9	14.1	13.6

Winnipeg

1	14.2	13.2	12.9	21	13.8	12.9	12.1	41	14.4	14.3	12.3
2	13.8	13.1	12.1	22	13.9	14.1	11.9	42	13.6	13.4	12.4
3	14.2	13.5	13.0	23	13.7	13.1	12.5	43	13.2	13.8	12.2
4	14.1	13.2	12.8	24	14.5	13.4	12.8	44	14.5	13.4	12.2
5	14.1	13.5	12.9	25	13.4	13.7	12.5	45	14.9	13.5	12.9
6	13.2	13.1	12.7	26	14.4	13.0	12.1	46	14.0	12.9	12.9
7	15.5	13.9	12.6	27	13.7	12.8	13.0	47	13.2	13.4	13.2
8	15.6	13.3	12.5	28	13.3	13.1	12.0	48	14.4	13.2	12.4
9	14.5	13.5	12.5	29	13.7	13.5	12.3	49	14.6	14.1	11.8
10	14.3	13.4	12.4	30	13.6	12.2	12.8	50	14.5	13.0	12.4
11	14.3	13.3	12.7	31	13.5	13.2	12.2	51	13.2	12.5	12.1
12	14.0	13.1	12.6	32	14.9	13.3	12.4	52	14.4	13.3	12.4
13	13.7	13.3	12.8	33	13.8	12.6	12.3	53	13.5	13.4	12.2
14	13.1	12.9	12.5	34	15.2	13.9	13.4	54	14.0	12.3	12.6
15	13.9	12.9	12.6	35	14.4	13.0	11.8	55	13.3	12.5	12.5
16	14.0	13.2	12.2	36	13.4	13.9	12.6	56	14.3	13.1	12.1
17	14.1	13.2	12.4	37	14.2	13.6	12.2	57	13.1	12.8	12.5
18	15.6	12.5	12.6	38	13.7	12.3	12.6	58	13.4	12.2	13.4
19	13.8	13.1	12.7	39	13.9	12.7	12.8	59	14.1	13.9	12.7
20	13.4	13.4	12.8	40	12.7	13.0	12.0	60	14.8	12.9	12.6

APPENDIX TABLE 10. Lattice analysis of variance for yield of F_5 bulks and checks in each cross location for NIR row plots.

Cross	Source of Variation	Location: Glenlea DF	Glenlea Mean Square	Location: Winnipeg DF	Winnipeg Mean Square
WK	Replications	3	2233056	3	1340493
	Entries	63	442859*	63	713660**
	Blocks	28	296301	28	164361
	Error	159	174490	161	81460
	Mean		2969		3717
	C.V.(%)[1]		14.5		8.0
	R.E.(%)[2]		104		107
MD	Replications	3	920791	3	1189498
	Entries	63	716085**	63	383853**
	Blocks	28	409209	28	198505
	Error	160	170666	161	90921
	Mean		2764		3911
	C.V.(%)		15.6		8.0
	R.E.(%)		111		109
DT	Replications	3	1621501	3	1914967
	Entries	63	440759**	63	599495**
	Blocks	28	320733	28	124674
	Error	159	117287	161	49960
	Mean		3475		4304
	C.V.(%)		10.3		5.4
	R.E.(%)		115		112

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Coefficient of variation.

[2]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 11. Lattice analysis of variance for test weight of F_5 bulks and checks in each cross location for NIR row plots.

Cross	Source of Variation	Location: Glenlea DF	Glenlea Mean Square	Location: Winnipeg DF	Winnipeg Mean Square
WK	Replications	3	11.4924	3	36.9449
	Entries	63	12.1710**	63	8.4461**
	Blocks	28	3.2169	28	2.4856
	Error	161	1.1139	161	0.4431
	Mean		72.4		74.9
	C.V.(%)[1]		1.5		0.9
	R.E.(%)[2]		117		150
MD	Replications	3	189.7197	3	48.6842
	Entries	63	11.8811**	63	4.2126**
	Blocks	28	6.9769	28	1.5885
	Error	161	1.3535	161	0.4060
	Mean		73.1		76.0
	C.V.(%)		1.7		0.9
	R.E.(%)		144		129
DT	Replications	3	88.8042	3	6.5772
	Entries	63	4.9367**	63	4.1234**
	Blocks	28	3.6887	28	0.9493
	Error	159	0.6081	161	0.3248
	Mean		76.1		76.8
	C.V.(%)		1.1		0.8
	R.E.(%)		157		117

**Significant at the 0.01 probability level.

[1]Coefficient of variation.

[2]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 12. Lattice analysis of variance for kernel weight of F_5 bulks and checks in each cross location for NIR row plots.

Cross	Source of Variation	Location: Glenlea DF	Glenlea Mean Square	Location: Winnipeg DF	Winnipeg Mean Square
WK	Replications	3	32.6044	3	98.8292
	Entries	63	17.4967**	63	19.4466**
	Blocks	28	7.4867	28	5.0008
	Error	161	2.2202	161	1.2344
	Mean		32.3		37.5
	C.V.(%)[1]		4.9		3.1
	R.E.(%)[2]		122		131
MD	Replications	3	223.0378	3	109.6186
	Entries	63	21.2211**	63	12.1366**
	Blocks	28	8.8869	28	6.8468
	Error	161	2.7062	161	1.0398
	Mean		33.1		38.9
	C.V.(%)		5.2		2.8
	R.E.(%)		121		162
DT	Replications	3	196.3030	3	36.5614
	Entries	63	24.2672**	63	27.0445**
	Blocks	28	12.8406	28	5.0824
	Error	159	1.9329	161	1.4793
	Mean		39.1		44.1
	C.V.(%)		3.7		2.9
	R.E.(%)		164		123

**Significant at the 0.01 probability level.

[1]Coefficient of variation.

[2]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 13. Lattice analysis of variance for protein yield of F_5 bulks and checks in each cross location for NIR row plots.

Cross	Source of Variation	Location: Glenlea DF	Glenlea Mean Square	Location: Winnipeg DF	Winnipeg Mean Square
WK	Replications	3	42200	3	6749
	Entries	63	8403**	63	11450**
	Blocks	28	5117	28	2465
	Error	159	3440	159	1347
	Mean		412		481
	C.V.(%)[1]		14.6		7.9
	R.E.(%)[2]		102		105
MD	Replications	3	1517	3	12950
	Entries	63	14504**	63	5699**
	Blocks	28	7298	28	2983
	Error	160	3279	161	1453
	Mean		380		497
	C.V.(%)		15.7		8.0
	R.E.(%)		109		107
DT	Replications	3	32365	3	39413
	Entries	63	7751**	63	8364**
	Blocks	28	4877	28	2081
	Error	159	1930	161	837
	Mean		446		537
	C.V.(%)		10.3		5.6
	R.E.(%)		113		112

**Significant at the 0.01 probability level.

[1]Coefficient of variation.

[2]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 14 Lattice analysis of variance for protein per kernel of F_5 bulks and checks in each cross location for NIR row plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	0.4731	3	1.1733
	Entries	63	0.3429**	63	0.3522**
	Blocks	28	0.0655	28	0.0507
	Error	161	0.0284	159	0.0188
	Mean		4.47		4.85
	C.V.(%)[1]		3.9		3.0
	R.E.(%)[2]		110		115
MD	Replications	3	0.6454	3	1.2232
	Entries	63	0.3168**	63	0.2728**
	Blocks	28	0.0877	28	0.0876
	Error	161	0.0410	161	0.0176
	Mean		4.54		4.95
	C.V.(%)		4.6		2.8
	R.E.(%)		108		142
DT	Replications	3	0.4970	3	0.6029
	Entries	63	0.3881**	63	0.4694**
	Blocks	28	0.0932	28	0.0708
	Error	159	0.0311	161	0.0259
	Mean		5.09		5.51
	C.V.(%)		3.6		3.1
	R.E.(%)		118		115

**Significant at the 0.01 probability level.

[1]Coefficient of variation.

[2]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 15. Lattice analysis of variance for kernel shrivelling of F_5 bulks and checks in each cross location for NIR row plots.

Cross	Source of Variation	Location: Glenlea DF	Glenlea Mean Square	Location: Winnipeg DF	Winnipeg Mean Square
WK	Replications	3	1.3854	3	5.7643
	Entries	63	1.1895**	63	0.8556**
	Blocks	28	0.7217	28	0.3670
	Error	161	0.2897	161	0.1750
	Mean		2.5		1.9
	C.V.(%)[1]		22.6		23.4
	R.E.(%)[2]		112		108
MD	Replications	3	12.8893	3	4.6042
	Entries	63	1.2579**	63	0.4206**
	Blocks	28	0.8402	28	0.3601
	Error	161	0.2395	161	0.1218
	Mean		2.5		1.4
	C.V.(%)		20.6		26.6
	R.E.(%)		124		118
DT	Replications	3	7.4466	3	0.7227
	Entries	63	0.5781**	63	0.4265**
	Blocks	28	0.5669	28	0.2100
	Error	159	0.1962	161	0.1472
	Mean		1.5		1.3
	C.V.(%)		31.1		30.0
	R.E.(%)		117		102

**Significant at the 0.01 probability level.

[1]Coefficient of variation.

[2]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 16. Lattice analysis of variance for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 bulks and checks in the WK cross at Glenlea and Winnipeg for NIR hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square				
			YLD	PY	KW	PK	KS
Glenlea	Replications	3	5942.22	97.2709	606.6762	7.6693	14.5700
	Entries	63	274.64	5.3765	33.8000**	0.6164**	1.6350**
	Blocks	28	385.52	7.9997	15.0626	0.1767	0.7214
	Error	158	215.76	4.3684	6.1704	0.1021	0.4958
	Mean		68.1	10.0	36.8	5.41	2.8
	C.V.(%)[2]		22.3	21.6	7.0	6.1	25.9
	R.E.(%)[3]		105	105	112	104	102
Winnipeg	Replications	3	596.30	14.7410	165.1872	1.8873	3.3477
	Entries	63	611.67**	8.1157**	52.8571**	0.5830**	1.7792**
	Blocks	28	389.22	5.7226	29.1107	0.2602	1.0463
	Error	161	273.11	4.2044	16.2585	0.1545	0.6454
	Mean		92.3	12.8	38.0	5.27	2.5
	C.V.(%)		18.3	16.3	11.0	7.7	33.7
	R.E.(%)		102	101	105	104	103

**Significant at the 0.01 probability level.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

[3]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 17. Lattice analysis of variance for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 bulks and checks in the MD cross at Glenlea and Winnipeg for NIR hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square				
			YLD	PY	KW	PK	KS
Glenlea	Replications	3	4441.27	87.6756	445.2309	7.9239	7.1393
	Entries	63	343.11	6.8991	35.5609**	0.5626**	1.2985**
	Blocks	28	232.11	4.6656	15.1487	0.2720	0.6058
	Error	161	273.67	5.3964	8.5551	0.1506	0.5085
	Mean		65.3	9.3	37.4	5.32	2.4
	C.V.(%)[2]		25.0	24.7	8.1	7.5	30.7
	R.E.(%)[3]		100	100	105	105	100
Winnipeg	Replications	3	343.41	14.7446	107.4994	0.5564	5.1901
	Entries	63	608.67**	8.2860**	38.6591**	0.5140**	1.1544**
	Blocks	28	287.84	4.2160	16.5698	0.2273	0.7494
	Error	159	260.99	3.7102	10.2721	0.1054	0.6293
	Mean		102.7	13.5	41.0	5.39	2.0
	C.V.(%)		15.8	14.4	8.0	6.3	40.9
	R.E.(%)		100	100	103	109	100

**Significant at the 0.01 probability level.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

[3]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 18. Lattice analysis of variance for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 bulks and checks in the DT cross at Glenlea and Winnipeg for NIR hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square YLD	PY	KW	PK	KS
Glenlea	Replications	3	47.51	0.2949	28.0035	1.3536	1.8000
	Entries	63	525.13**	9.9330**	40.9037**	0.6545**	1.5078**
	Blocks	28	193.02	3.7756	11.4400	0.2161	0.7066
	Error	158	205.16	3.7121	9.5647	0.1437	0.5173
	Mean		66.8	9.0	43.8	5.91	2.0
	C.V.(%)[2]		21.4	21.4	7.2	6.6	36.8
	R.E.(%)[3]		100	100	101	103	101
Winnipeg	Replications	3	889.16	17.9330	67.9795	0.6626	1.0002
	Entries	63	807.17**	10.3484**	52.0940**	0.6637**	1.3531**
	Blocks	28	283.04	4.0356	13.5338	0.1290	0.4504
	Error	156	382.31	5.8537	6.5260	0.0792	0.3648
	Mean		101.9	12.7	47.5	5.94	1.7
	C.V.(%)		18.7	18.4	5.6	4.9	36.1
	R.E.(%)		101	102	108	104	101

**Significant at the 0.01 probability level.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

[3]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 19. Lattice analysis of variance for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 families and checks in the WK cross at Glenlea and Winnipeg for ISD hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square YLD	PY	KW	PK	KS
Glenlea	Replications	3	5003.59	77.9335	499.5657	5.6769	7.2411
	Entries	63	476.34**	9.9855**	30.6704**	0.6869**	1.6291**
	Blocks	28	309.73	6.1044	12.0096	0.2058	0.5838
	Error	159	259.46	5.2788	6.5866	0.1033	0.3802
	Mean		68.1	10.0	36.6	5.35	2.8
	C.V.(%)[2]		23.9	23.3	7.3	6.2	23.0
	R.E.(%)[3]		100	100	105	107	103
Winnipeg	Replications	3	796.42	7.8725	31.9251	0.0646	5.5077
	Entries	63	1002.05**	16.9588**	53.2497**	0.6619**	1.7293**
	Blocks	28	274.65	5.1254	10.0663	0.1278	0.5408
	Error	156	301.15	4.5795	15.5473	0.1443	0.8410
	Mean		88.3	12.5	36.3	5.13	2.6
	C.V.(%)		19.5	17.3	10.4	7.3	33.3
	R.E.(%)		100	100	103	100	103

**Significant at the 0.01 probability level.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

[3]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 20. Lattice analysis of variance for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 families and checks in the MD cross at Glenlea and Winnipeg for ISD hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square YLD	PY	KW	PK	KS
Glenlea	Replications	3	3057.62	65.1818	382.9915	8.1192	2.9728
	Entries	63	520.13**	9.8279**	39.7021**	0.6918**	1.9349**
	Blocks	28	278.51	6.2145	17.4855	0.3115	0.6986
	Error	158	258.40	5.3416	7.6025	0.1390	0.4771
	Mean		66.1	9.4	37.9	5.42	2.3
	C.V.(%)[2]		24.4	24.7	7.6	7.2	31.4
	R.E.(%)[3]		100	100	110	110	102
Winnipeg	Replications	3	261.05	4.4354	220.9412	2.1319	4.8209
	Entries	63	1021.21**	13.8234**	54.2218**	0.6804**	1.8633**
	Blocks	28	389.94	6.4081	18.2196	0.2053	0.7964
	Error	158	307.49	4.8431	10.4204	0.1229	0.6091
	Mean		100.0	13.3	40.2	5.36	2.1
	C.V.(%)		17.8	16.8	8.3	6.7	37.9
	R.E.(%)		101	101	105	104	101

**Significant at the 0.01 probability level.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

[3]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 21. Lattice analysis of variance for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 families and checks in the DT cross at Glenlea and Winnipeg for ISD hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square				
			YLD	PY	KW	PK	KS
Glenlea	Replications	3	244.44	3.0204	32.5034	1.1417	0.3873
	Entries	63	940.35**	18.7109**	64.1521**	1.2428**	1.3037**
	Blocks	28	350.38	7.1995	19.5042	0.4233	1.1416
	Error	157	170.36	3.1035	7.8376	0.1288	0.4811
	Mean		64.1	8.8	43.7	5.94	1.8
	C.V.(%)[2]		21.1	21.0	6.7	6.4	39.4
	R.E.(%)[3]		108	111	113	122	111
Winnipeg	Replications	3	1078.59	26.1437	259.2686	2.9224	5.4385
	Entries	63	1933.18**	28.2444**	67.3469**	0.9619**	0.9725**
	Blocks	28	222.13	3.1403	9.1993	0.0941	0.2316
	Error	158	242.88	3.7523	5.9055	0.0761	0.4250
	Mean		99.6	12.7	46.9	5.97	1.6
	C.V.(%)		15.5	15.1	5.3	4.7	39.1
	R.E.(%)		100	100	103	101	106

**Significant at the 0.01 probability level.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

[3]Relative efficiency of the lattice design compared to the randomized complete block design.

APPENDIX TABLE 22. Analysis of variance and orthogonal contrasts for yield of F_5 selection groups in each cross location for NIR row plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	2234398**	3	1352039**
	Selection Groups (G)	2	575592	2	1458488
	HP vs. RP	1	823484	1	317649
	(HP+RP) vs. LP	1	335233	1	2599328
	Bulks within G	57	353379**	57	647867**
	Error	175	196710	177	90000
MD	Replications	3	1006149**	3	1075174**
	Selection Groups (G)	2	3447440**	2	1133500*
	HP vs. RP	1	310287	1	153640
	(HP+RP) vs. LP	1	6619551**	1	2113360**
	Bulks within G	57	595785**	57	282853**
	Error	176	203497	177	103048
DT	Replications	3	1454968**	3	1753537**
	Selection Groups (G)	2	499580	2	1251572
	HP vs. RP	1	1599	1	288046
	(HP+RP) vs. LP	1	1004758	1	2215098
	Bulks within G	57	366526**	57	460537**
	Error	175	150461	177	61363

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

APPENDIX TABLE 23. Analysis of variance and orthogonal contrasts for test weight of F_5 selection groups in each cross location for NIR row plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	13.0392**	3	36.4415**
	Selection Groups (G)	2	25.0307	2	32.6265**
	HP vs. RP	1	47.0022	1	49.7513**
	(HP+RP) vs. LP	1	3.0592	1	15.5016
	Bulks within G	57	9.0841**	57	6.4083**
	Error	177	1.3627	177	0.7696
MD	Replications	3	188.9597**	3	45.0771**
	Selection Groups (G)	2	4.4014	2	1.6457
	HP vs. RP	1	4.3560	1	3.1081
	(HP+RP) vs. LP	1	4.4467	1	0.1833
	Bulks within G	57	10.3225**	57	3.4847**
	Error	177	2.2179	177	0.5816
DT	Replications	3	76.2151**	3	6.8569**
	Selection Groups (G)	2	7.2930	2	6.1624
	HP vs. RP	1	11.3898	1	6.3840
	(HP+RP) vs. LP	1	3.4061	1	5.9408
	Bulks within G	57	4.0967**	57	3.1980**
	Error	175	1.0453	177	0.4257

**Significant at the 0.01 probability level.

APPENDIX TABLE 24. Analysis of variance and orthogonal contrasts for kernel weight of F_5 selection groups in each cross location for NIR row plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	31.6837**	3	96.7033**
	Selection Groups (G)	2	3.2220	2	27.3787
	HP vs. RP	1	5.8906	1	13.9240
	(HP+RP) vs. LP	1	0.5535	1	40.8333
	Bulks within G	57	13.6170**	57	14.7971**
	Error	177	2.7462	177	1.8105
MD	Replications	3	214.7545**	3	105.2612**
	Selection Groups (G)	2	36.5630	2	7.6902
	HP vs. RP	1	27.3076	1	15.0063
	(HP+RP) vs. LP	1	45.8185	1	0.3741
	Bulks within G	57	17.7911**	57	9.2225**
	Error	177	3.5891	177	1.9170
DT	Replications	3	170.2228**	3	36.2576**
	Selection Groups (G)	2	23.7449	2	4.3945
	HP vs. RP	1	4.0851	1	5.4391
	(HP+RP) vs. LP	1	43.7173	1	3.3500
	Bulks within G	57	18.6405**	57	22.8113**
	Error	175	3.5513	177	2.0759

**Significant at the 0.01 probability level.

APPENDIX TABLE 25. Analysis of variance and orthogonal contrasts for protein yield of F_5 selection groups in each cross location for NIR row plots.

Cross	Source of Variation	Location			
		Glenlea		Winnipeg	
		DF	Mean Square	DF	Mean Square
WK	Replications	3	41712**	3	6667**
	Selection Groups (G)	2	19338	2	37611*
	HP vs. RP	1	22896	1	7909
	(HP+RP) vs. LP	1	16142	1	68281**
	Bulks within G	57	6508**	57	9858**
	Error	177	3755	175	1418
MD	Replications	3	4937	3	11503**
	Selection Groups (G)	2	89982**	2	23539**
	HP vs. RP	1	14619	1	685
	(HP+RP) vs. LP	1	166410**	1	46394**
	Bulks within G	57	11467**	57	3994**
	Error	176	3750	177	1628
DT	Replications	3	28860**	3	35024**
	Selection Groups (G)	2	20642*	2	28910*
	HP vs. RP	1	4573	1	9318
	(HP+RP) vs. LP	1	36994*	1	48501**
	Bulks within G	57	6293**	57	6354**
	Error	175	2407	177	1019

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

APPENDIX TABLE 26. Analysis of variance and orthogonal contrasts for protein per kernel of F_5 selection groups in each cross location for NIR row plots.

		Location			
		Glenlea		Winnipeg	
Cross	Source of Variation	DF	Mean Square	DF	Mean Square
WK	Replications	3	0.4388**	3	1.1787**
	Selection Groups (G)	2	0.2890	2	0.2403
	HP vs. RP	1	0.3990	1	0.4079
	(HP+RP) vs. LP	1	0.1790	1	0.0765
	Bulks within G	57	0.2873**	57	0.2928**
	Error	177	0.0327	175	0.0234
MD	Replications	3	0.6404**	3	1.1996**
	Selection Groups (G)	2	0.0754	2	0.0570
	HP vs. RP	1	0.0221	1	0.0640
	(HP+RP) vs. LP	1	0.1287	1	0.0500
	Bulks within G	57	0.2832**	57	0.2021**
	Error	177	0.0474	177	0.0287
DT	Replications	3	0.3997**	3	0.5972**
	Selection Groups (G)	2	1.7534**	2	0.1710
	HP vs. RP	1	1.0869	1	0.3367
	(HP+RP) vs. LP	1	2.4518**	1	0.0052
	Bulks within G	57	0.3083**	57	0.4557**
	Error	175	0.0384	177	0.0337

**Significant at the 0.01 probability level.

APPENDIX TABLE 27. Analysis of variance and orthogonal contrasts for kernel shrivelling of F_5 selection groups in each cross location for NIR row plots.

Cross	Source of Variation	Location: Glenlea DF	Glenlea Mean Square	Location: Winnipeg DF	Winnipeg Mean Square
WK	Replications	3	1.5611*	3	5.4778**
	Selection Groups (G)	2	2.8500	2	2.6542*
	HP vs. RP	1	5.6250	1	2.7563
	(HP+RP) vs. LP	1	0.0750	1	2.5521
	Bulks within G	57	0.9237**	57	0.7268**
	Error	177	0.3549	175	0.2009
MD	Replications	3	12.9111**	3	4.0931**
	Selection Groups (G)	2	1.7167	2	1.4292*
	HP vs. RP	1	3.0250	1	2.7563**
	(HP+RP) vs. LP	1	0.4083	1	0.1021
	Bulks within G	57	1.1193**	57	0.3401**
	Error	177	0.3264	177	0.1552
DT	Replications	3	6.4446**	3	0.8222**
	Selection Groups (G)	2	0.6796	2	1.0500
	HP vs. RP	1	1.1622	1	0.9000
	(HP+RP) vs. LP	1	0.2178	1	1.2000
	Bulks within G	57	0.4704**	57	0.3561**
	Error	175	0.2371	177	0.1556

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

APPENDIX TABLE 28. Analysis of variance and orthogonal contrasts for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 selection groups in the WK cross at Glenlea and Winnipeg for NIR hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square				
			YLD	PY	KW	PK	KS
Glenlea	Replications	3	5173.66**	84.5857**	544.1342**	6.9745**	12.7857**
	Selection Groups (G)	2	144.67	0.8173	7.7795	0.2153	0.2684
	HP vs. RP	1	288.67	1.5979	0.0415	0.3053	0.2959
	(HP+RP) vs. LP	1	0.33	0.0439	15.4914	0.1308	0.2485
	Bulks within G	57	261.82	5.3788	28.5452**	0.5762**	1.4970**
	Error	174	247.70	5.0919	6.9935	0.1089	0.5123
Winnipeg	Replications	3	422.92	10.9826	156.5460**	1.9025**	2.8056*
	Selection Groups (G)	2	177.13	1.1341	6.4193	0.0365	1.0792
	HP vs. RP	1	276.41	2.1762	9.7023	0.0063	1.4063
	(HP+RP) vs. LP	1	77.84	0.0919	3.1363	0.0667	0.7521
	Bulks within G	57	613.49**	8.2705**	42.0899**	0.5048**	1.5671**
	Error	177	299.32	4.6000	18.8360	0.1740	0.7349

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

APPENDIX TABLE 29. Analysis of variance and orthogonal contrasts for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 selection groups in the MD cross at Glenlea and Winnipeg for NIR hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square				
			YLD	PY	KW	PK	KS
Glenlea	Replications	3	4504.44**	88.9057**	398.8803**	7.1977**	6.5819**
	Selection Groups (G)	2	254.98	3.3866	145.9088**	1.2969	6.9875**
	HP vs. RP	1	146.12	5.1804	5.2201	0.0065	0.3063
	(HP+RP) vs. LP	1	363.83	1.5928	286.5975**	2.5872	13.6688**
	Bulks within G	57	358.50	7.3578*	29.2337**	0.5227**	1.0305**
	Error	177	257.95	5.1637	9.5455	0.1734	0.5226
Winnipeg	Replications	3	229.59	10.9244*	111.7916**	0.6306**	5.0201**
	Selection Groups (G)	2	298.70	7.6263	68.5236	0.7745	0.2022
	HP vs. RP	1	114.09	0.9285	37.6343	0.4042	0.1375
	(HP+RP) vs. LP	1	487.80	14.3929	98.2300	1.1316	0.2631
	Bulks within G	57	635.53**	8.5959**	29.8013**	0.3995**	1.0767**
	Error	175	248.19	3.5462	11.2388	0.1252	0.6558

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

APPENDIX TABLE 30. Analysis of variance and orthogonal contrasts for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 selection groups in the DT cross at Glenlea and Winnipeg for NIR hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square				
			YLD	PY	KW	PK	KS
Glenlea	Replications	3	47.05	0.7816	27.5867*	1.4075**	2.2173**
	Selection Groups (G)	2	1209.23	25.0890	46.6138	0.6687	7.0858**
	HP vs. RP	1	956.48	14.7137	90.9023	1.1391	13.8063**
	(HP+RP) vs. LP	1	1461.97	35.4643	2.3253	0.1982	0.3653
	Bulks within G	57	486.39**	8.8630**	38.7568**	0.6701**	1.2905**
	Error	176	205.06	3.7214	9.9976	0.1531	0.5503
Winnipeg	Replications	3	805.72	16.5396*	73.9163**	0.7108**	1.3035*
	Selection Groups (G)	2	650.27	13.1251	2.6632	0.2740	1.5864
	HP vs. RP	1	263.10	0.9529	1.2677	0.0879	3.1347
	(HP+RP) vs. LP	1	1036.98	25.2929	4.0568	0.4603	0.0383
	Bulks within G	57	824.46**	10.5447**	38.2083**	0.6026**	1.0310**
	Error	173	356.38	5.3545	7.5266	0.0852	0.3864

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

APPENDIX TABLE 31. Analysis of variance and orthogonal contrasts for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 selection groups in the WK cross at Glenlea and Winnipeg for ISD hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square				
			YLD	PY	KW	PK	KS
Glenlea	Replications	3	4906.41**	76.3226**	507.7276**	5.7646**	7.7113**
	Selection Groups (G)	2	1296.62	20.7838	33.5298	0.2633	2.8649
	HP vs. RP	1	2564.65	41.4798	0.8013	0.1490	3.2483
	(HP+RP) vs. LP	1	34.03	0.0549	66.3925	0.3729	2.5362
	Families within G	57	454.48**	9.9948**	29.7531**	0.7180**	1.3733**
	Error	175	268.45	5.4983	7.0397	0.1197	0.4016
Winnipeg	Replications	3	669.55	6.5638	25.9788	0.0402	4.7856**
	Selection Groups (G)	2	145.72	1.9355	13.8908	0.3934	0.9041
	HP vs. RP	1	26.84	1.6995	18.6929	0.7730	0.2004
	(HP+RP) vs. LP	1	262.20	2.1181	8.7288	0.0110	1.5918
	Families within G	57	1056.77**	18.2499**	38.0167**	0.4665**	1.4385**
	Error	172	293.32	4.5712	15.1607	0.1439	0.8245

**Significant at the 0.01 probability level.

[1]Abbreviations for traits are defined in Table 4.

APPENDIX TABLE 32. Analysis of variance and orthogonal contrasts for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 selection groups in the MD cross at Glenlea and Winnipeg for ISD hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square				
			YLD	PY	KW	PK	KS
Glenlea	Replications	3	2697.51**	57.3417**	360.4739**	7.5701**	3.1164**
	Selection Groups (G)	2	938.27	22.4837	3.7291	0.0412	1.6819
	HP vs. RP	1	764.41	13.1763	3.6059	0.0063	0.0972
	(HP+RP) vs. LP	1	1121.19	31.9920	3.8156	0.0763	3.2609
	Families within G	57	527.97**	9.6188**	39.6695**	0.6838**	1.7911**
	Error	174	274.12	5.7359	9.5005	0.1692	0.5277
Winnipeg	Replications	3	253.14	1.8754	212.0895**	1.8036**	4.9590**
	Selection Groups (G)	2	416.45	5.1501	35.5800	0.3270	1.4330
	HP vs. RP	1	664.56	6.1600	52.5669	0.4328	1.2267
	(HP+RP) vs. LP	1	178.44	4.2914	17.6672	0.2119	1.5969
	Families within G	57	1073.19**	14.6182**	51.5557**	0.6613**	1.8222**
	Error	174	317.06	4.9838	11.9804	0.1386	0.6362

**Significant at the 0.01 probability level.

[1]Abbreviations for traits are defined in Table 4.

APPENDIX TABLE 33. Analysis of variance and orthogonal contrasts for yield, protein yield, kernel weight, protein per kernel, and kernel shrivelling of F_5 selection groups in the DT cross at Glenlea and Winnipeg for ISD hill plots.

Location	Source of Variation	DF	Trait[1] Mean Square				
			YLD	PY	KW	PK	KS
Glenlea	Replications	3	295.67	3.8144	28.9486*	0.9673**	0.5847
	Selection Groups (G)	2	477.95	7.2859	33.3821	1.1729	3.1712
	HP vs. RP	1	266.84	8.7016	45.8344	2.2726	0.0734
	(HP+RP) vs. LP	1	696.99	6.0033	21.5078	0.0657	6.2558
	Families within G	57	963.07**	19.1649**	58.4974**	1.2210**	1.1157**
	Error	173	202.48	3.8075	9.7433	0.1731	0.5799
Winnipeg	Replications	3	1061.80**	26.3370**	243.9622**	2.6845**	5.6313**
	Selection Groups (G)	2	201.95	1.5076	7.5559	0.5328	0.3886
	HP vs. RP	1	310.02	4.9828	4.1557	0.1603	0.2213
	(HP+RP) vs. LP	1	93.88	8.0323	10.9559	0.9053	0.5559
	Families within G	57	2073.92**	30.6236**	53.2211**	0.8779**	0.7279**
	Error	174	237.78	3.6290	6.3116	0.0763	0.3842

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

APPENDIX TABLE 34. Analysis of variance combined over crosses for protein content, yield, protein yield, kernel weight, protein per kernel and kernel shrivelling of the four parental cultivars grown with the F_3 families for the NIR method.

Source of Variation	DF	Trait[1] Mean Square					
		PC	YLD	PY	KW	PK	KS
Replications	8	0.2282	275.81	6.4900	14.044	0.2251	0.1528
Cultivars	3	1.4996**	333.44	4.7493	148.797**	2.6875**	4.0741**
Error	24	0.2450	172.11	4.0709	7.557	0.1294	0.3657
C.V.(%)[2]		3.1	21.1	20.7	7.2	6.0	27.2

**Significant at the 0.01 probability level.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

APPENDIX TABLE 35. Analysis of variance combined over crosses for protein content, yield, test weight, kernel weight, protein yield, protein per kernel and kernel shrivelling of the four check cultivars grown with the F_5 bulks at each location for NIR row plots.

Location	Source of Variation	DF	Trait[1] Mean Square						
			PC	YLD	TW	KW	PY	PK	KS
Glenlea	Replications	11	0.8165**	299211*	7.4767**	13.783**	7224**	0.0589	0.6572*
	Cultivars	3	3.4706**	2992990**	75.4858**	188.185**	52207**	2.1997**	7.0208**
	Error	33	0.1910	117600	1.0866	4.304	2306	0.0587	0.3087
	C.V.(%)[2]		3.2	10.6	1.4	5.9	10.9	5.0	29.3
Winnipeg	Replications	11	0.1432**	177473	1.8098*	5.115**	3263	0.0507*	0.3239
	Cultivars	3	4.8985**	5269865**	57.2608**	227.968**	80168**	2.9234**	4.1875**
	Error	33	0.0452	131935	0.6797	1.459	2173	0.0197	0.1723
	C.V.(%)		1.6	9.5	1.1	3.0	9.3	2.6	28.9

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.

APPENDIX TABLE 36. Analysis of variance combined over methods and crosses for protein content, yield, protein yield, kernel weight, protein per kernel and kernel shrivelling of the four check cultivars grown with the NIR and ISD F_5 hill plots at each location.

Location	Source of Variation	DF	Trait[1] Mean Square					
			PC	YLD	PY	KW	PK	KS
Glenlea	Replications	23	0.4851	238.11	4.7799	24.692**	0.4398**	0.8259
	Cultivars	3	12.4092**	480.42	1.1312	333.422**	2.4940**	8.8801**
	Error	67	0.3525	228.56	4.1470	9.625	0.1434	0.5290
	C.V.(%)[2]		4.1	21.7	20.4	7.8	6.6	38.4
Winnipeg	Replications	23	0.3336	381.21	6.7133	5.964	0.0690	0.4423
	Cultivars	3	15.3352**	2636.36**	19.4288*	1082.833**	9.8005**	21.3913**
	Error	68	0.2526	312.60	5.0066	8.458	0.1207	0.3970
	C.V.(%)		3.7	18.3	17.2	6.9	6.2	34.6

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

[1]Abbreviations for traits are defined in Table 4.

[2]Coefficient of variation.