Physiology and Genetics of Grain Protein Concentration and Grain Yield in Spring Wheat (*Triticum aestivum* L.)

by

Anne Leslie McKendry

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Ph.D
in
Department of Plant Science

Winnipeg, Manitoba

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PHYSIOLOGY AND GENETICS OF GRAIN PROTEIN CONCENTRATION AND GRAIN YIELD IN SPRING WHEAT (*Triticum aestivum* L.)

BY

ANNE LESLIE McKENDRY

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

DOCTOR OF PHILOSOPHY

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ABSTRACT

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In western Canada, bread wheat (Triticum aestivum L.) breeding programs generally have as their primary objective, the simultaneous improvement of grain yield (GY) and grain protein concentration (GPC). One of the major problems however, is the basis(es) on which selection should be made in the early generations of bread wheat crosses because of the well-documented negative correlation between these two parameters.

Nitrogen and dry matter accumulation, redistribution and associated characters, namely grain yield (GY), grain protein concentration (GPC), grain protein yield (GPY), total dry matter (TDM), total nitrogen at maturity (TNM), harvest index (HI), and nitrogen harvest index (NHI) were studied in eight contrasting spring wheat cultivars including, three high GPC, low GY cultivars, three low GPC, high GY cultivars and two high GPC, high GY cultivars grown at Winnipeg in 1984 and 1985. Entries were grown in eight row plots in a randomized complete block design with five replicates. Half m above-ground samples, taken from the flag leaf stage through to maturity were oven dried, separated into leaves plus culms, chaff and grain, weighed, ground and analysed for

nitrogen content using the macro-Kjeldahl technique. Inheritance of the above traits in two crosses involving three of the above eight cultivars was determined from spaced plant experiments of P_1, P_2, F_1, F_2, B_1, B_2 and F_3 generations grown at two locations in Manitoba in 1985. Parental, F_1 and F_2 generations of a third cross between the two high GPC cultivars of the inheritance study were used to determine if these cultivars were different sources of GPC.

Results from both years of the physiological study indicated that high GPC was correlated with increased TNM (r=0.35*, 0.41**) and post-anthesis nitrogen uptake (r=0.51**, 0.58**), coupled with increased remobilization efficiency (r=0.52**, 0.61**) and NHI (r=0.55**, 0.84**). High GY was correlated with TNM (r=0.67**, 0.68**), TDM (r=0.89**, 0.95**) and HI (r=0.76**, 0.71**). The two cultivars with high GPC, high GY levels achieved this through a combination of significantly higher post-anthesis nitrogen uptake, TNM and NHI coupled with high TDM and HI.

Results from the inheritance study indicated that these traits were primarily under genetic control in both crosses, with additive gene action being significant for all traits studied. Dominance gene action was detected for most traits but the direction was both trait and genotype specific. Additive x additive epistasis was significant for GY, GPY, TDM and TNM but again, was genotype specific. Broad sense heritabilities for the F_2 of grain protein related traits, ranged from 0.56 to 0.73 for TNM, from 0.39 to 0.59 for NHI, from 0.57 to 0.76 for GPC and from 0.57 to 0.76 for GPY while narrow sense heritabilities ranged from 0.27 to 0.38 for TNM, from 0.24 to 0.38 for NHI, from 0.50 to 0.75

for GPC and from 0.26 to 0.48 for GPY. Broad sense heritabilities for grain yield related traits ranged from 0.65 to 0.79 for TDM, from 0.50 to 0.67 for HI and from 0.51 to 0.70 for GY while narrow sense heritabilities ranged from 0.32 to 0.60 for TDM, from 0.53 to 0.58 for HI and from 0.27 to 0.39 for GY. It was concluded therefore, that complementary physiological strategies for nitrogen and carbon assimilation and redistribution exist and are sufficiently heritable to be used as selection criteria to maximize gains in a breeding program aimed at developing high GPC, high GY spring wheat cultivars.

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1. INTRODUCTION

Wheat is one of the most important of all cultivated plants with respect to human nutrition. World wheat production in the last 10 years has averaged 440 million tonnes, most of which has been consumed directly as flour. Wheat is also one of the more nutritious of cereals with a protein content of commercially grown wheat that ranges from 6 to 16%. If an average figure of 10% is used, it may be calculated that the total amount of protein contributed by wheat to the human diet is 44 million tonnes per year (Simmonds 1981). Wheat therefore, contributes more protein to the human diet than any crop grown.

High quality red spring wheat (Triticum aestivum L.) is the basis of the Canadian wheat industry and stringent quality standards protect this class. The success of this quality control has been demonstrated by the fact that for the past 75 years, the Canada Western Red Spring wheat class has continued to maintain at least the Marquis standard of quality. Consequently, Canada's reputation in the world market, as the most reliable producer of quality bread wheat, remains unchallenged.

Protein (both quantity and quality), is the primary quality component that most influences bread-making quality. Its importance to bread wheat quality is recognized in the marketplace and consequently, most exporting countries have some segregation of commercial grain lots on the basis of protein concentration. In bread wheat, the majority of the

variation in loaf volume can be attributed directly to protein concentration.

Maintaining this desired quality standard has been accomplished primarily by restricting the plant breeder to backcrosses to "Thatcher" as a recurrent parent in order to successfully release new cultivars. Breeding high levels of grain protein concentration has also been difficult due to the large environmental component of the variation for this trait and has generally been done at the expense of grain yield because of the well documented negative correlation between these two economically important traits.

Grain protein concentration is directly related to a number of environmental factors including temperature and moisture stress (Partridge and Shaykewich 1972). Both of these factors influence grain protein concentration primarily through their negative effect on grain yield. Interacting with these two factors, is the availability of soil nitrogen, which can increase grain protein concentration under conditions promoting low grain yields or decrease grain protein concentration when conditions promote high grain yields, primarily due to carbohydrate dilution of the grain protein. At high nitrogen levels and under conditions of adequate moisture and temperature, both grain yield and grain protein concentration can be high.

With the higher costs of nitrogenous fertilizers and concerns being voiced by environmentalists over increased fertilizer use, the interest in breeding for improved efficiency of nitrogen utilization has increased. This increase in nitrogen utilization efficiency is realized

when the protein concentration of the kernel is improved in the absence of a reduction in grain yield (Kramer 1979a). Consequently, in western Canada, bread wheat breeding programs frequently have as their primary objective, the simultaneous improvement of grain yield and grain protein concentration.

Increasing the amount of nitrogen in the grain, at constant soil nitrogen and hence, the nitrogen utilization efficiency can by accomplished through two main physiological strategies: (1) increasing the nitrogen uptake efficiency of the crop and/or (2) increasing the nitrogen remobilization efficiency of the crop. When these two complementary phyisological strategies are successfully combined, the net result must be enhanced nitrogen utilization efficiency.

Similarly, increasing carbon use efficiency through the complementary physiological strategies of enhanced carbon assimilation (total dry matter) and/or enhanced carbon partitioning to the grain (harvest index), should lead to increased grain yields at comparable levels of grain protein concentration.

Dissection of the crop into components such as total plant nitrogen at maturity, total dry matter, nitrogen harvest index and harvest index, provides an integrative measure at the community level, of a wide range of complex physiological processes. Where there is genetic variability for these traits and for the end products which they determine and where they are shown to be independent of one another as nitrogen accumulation and remobilization (Johnson et al. 1967) and total dry matter and harvest index (Donald and Hamblin 1976) have been shown to be, the breeder

should be able to manipulate them in such a way as to increase both grain yield and grain protein concentration simultaneously.

The extent of possible improvement in these traits is, however, determined by the amount of genetic variation in relation to environmental variation and by the nature and extent of their interaction. In turn, the breeding strategies are dependent on the type of action, interaction and linkage of the genes controlling these traits. The breeding strategy approaches for improvement of nitrogen and carbon utilization are therefore determined by both a thorough knowledge of the extent of genetic and environmental variation and an understanding of the properties of the genes which control phenotypic expression.

This project was designed to investigate nitrogen and carbon utilization in eight spring wheat cultivars with contrasting levels of grain protein concentration and grain yield. It had three main objectives: (1) to determine if genetic variability existed for traits related to nitrogen and carbon uptake, assimilation and redistribution, (2) to determine if these traits were correlated with increased grain protein concentration and/or grain yield and (3) to determine the inheritance of these nitrogen and carbon utilization traits as well as the end-products they determine in order to gain a better understanding of the gene action controlling these traits and their respective heritabilities. This information should enable the breeder to develop breeding strategies to enhance grain yield and grain protein concentration simultaneously, through better planned crosses and more efficient selection strategies.

2. LITERATURE REVIEW

2.1 Yield-Protein Relationships in Wheat

In the literature relating to genetic improvement in grain protein concentration in wheat, the terms grain protein, grain protein concentration, grain protein content and grain protein percentage have all been used more or less synonomously. In order to eliminate this possible source of confusion, the term grain protein concentration (GPC) has been used consistently in this literature review to refer to the concentration of protein in the grain expressed in percent.

Early investigations into the effects of alfalfa cropping on the yield and protein concentration of wheat crops (Metzger 1935) resulted in evidence that grain yield (GY) and GPC were negatively correlated, (r=-.81**). Highly significant inverse GY - GPC relationships were also found by Terman et al. (1969) in hard red winter wheats. In a study of 20 varieties over several locations in Nebraska, GPC was found to vary more widely among locations than among varieties but was consistently found to be negatively related to GY.

In the spring wheats, this negative correlation between GY and GPC persists. An investigation of eight spring wheat crosses involving one or more parents known to be high in protein showed that grain protein concentration was negatively correlated to both GY and harvest index (HI) (McNeal et al. 1972). In comparing high and low protein composites

of F_3 progeny rows, the correlation coefficient of GPC and GY was calculated to be -0.55*. Loffler and Busch (1982) evaluated progeny from three crosses of adapted hard red spring wheats and "Rageni 15", an introduction from Pakistan described as having both high GPC and high GY and again, found GY and GPC were negatively correlated (r=-0.48*). Finally, although the correlation coeffients were low, (r=-0.29*, -0.37* and -0.40*) Cox et al. (1985a) also found GPC and GY to be negatively correlated. The magnitude of the r values, however, suggested to the authors that there was potential for selecting lines with high GY and high GPC from the populations investigated. Such simultaneous improvements have been reported in the literature.

Middleton et al. (1954), in a study on protein content of 13 soft red winter wheat varieties, found large varietal differences in GPC from a series of tests over a three year period. They reported that varieties having "Frondosa" or "Fronteira" in their parentages were significantly higher in both GY and GPC than the standard varieties.

One of the most thoroughly researched genotypes possessing simultaneous improvements in GY and GPC is the soft winter wheat variety "Atlas 66" which was introduced into the Nebraska breeding program in 1953 as a source of leaf rust resistance and high GPC (Johnson et al. 1963). Later trials in Oklahoma and Texas clearly demonstrated that Atlas 66 produced grain with higher protein concentration than the hard winter wheats "Wichita" and "Comanche" when yields were comparable (Haunold et al. 1962a). Cooperative investigations (Haunold et al. 1962b, Stuber et al. 1962 and Johnson et al. 1963) have also demonstrated the feasibility of breeding productive, high GPC varieties of hard red winter wheat using Atlas 66 as the source of high GPC.

Davis et al. (1961) in studying the inheritance of GPC in four winter wheat populations varying in texture found that in three of the four populations, a negative relationship for GPC and GY, which ranged from r=-0.30* to r=-0.39*. The fourth population, resulting from an Atlas 66 cross however, showed a nonsignificant positive correlation (r=0.19) indicating selection for GPC while maintaining GY could be possible.

Johnson (1978) reporting on "Lancota" wheat, has also shown that simultaneous improvements in GY and GPC are feasible. Lancota, a hard red winter wheat released in Nebraska in 1975 was equal to the two leading varieties in GY but was 1.5% higher in GPC than either variety.

Finally, Mesdag (1979), in a study of spring wheats, found that GY and GPC were generally negatively correlated (r=-0.65**) but that genetic variability for both traits was evident. Among the seven genotypes investigated, two varieties had similar GY but differed in GPC by 1.9% while two other varieties of comparable GPC, differed in GY by 10%. The author suggested that this genetic variability could be selected for and result in simultaneous improvements in both GY and GPC.

2.1.1 Nitrogen Uptake and Assimilation

Although it is beyond the scope of this document to thoroughly review the mechanisms of nitrogen uptake, assimilation and translocation, a brief overview of the relevant points will facilitate the discussions to follow.

Nitrate is generally considered to be the predominant form of available mineralized nitrogen in fertile temperate soils and as such, uptake and reduction of nitrate and further reduction of nitrite to ammonia are essential processes in most cereals for the production of plant protein.

Nitrate uptake by cereals depends on a nitrate-inducible permease system in the roots (Jackson et al. 1972, Rao and Rains 1976a,b) and in addition, it conforms to Michaelis and Menten Kinetics. The concentration at which half-maximal uptake velocity (Km) is achieved in wheat and barley is considerably higher than the Km for maize (Neyra and Hageman 1975). This may be the result of intensive breeding of these cereals for high nitrogen response and hence low efficiency for nitrogen acquisition from the soil (Jackson et al. 1972, Rao and Rains 1976a).

Once nitrate has been taken up by the plant, it is reduced in the root or shoot to ammonia by nitrate and nitrite reductase enzymes. Nitrate reduction will be limiting to protein synthesis and growth if nitrate is not absorbed fast enough for the requirements of the plant, if nitrate reductase is inadequate, its activity is impaired directly (by unfavorable conditions) or if it is limited by ancillary requirements such as reductants (Hewitt 1979). The reduction of nitrate to ammonia and its subsequent metabolism to glutamate requires 10 electrons, and 1 ATP with participation of NADH and ferredoxin or NADPH. Together with the production of oxoglutarate from carbohydrate and the utilization of ATP in peptide bond formation, the process of protein synthesis from nitrate involves a substantial drain on photosynthetic energy (Hewitt 1979). Cereals are among the most active species for potential photosynthesis, however, and they have large potential rates

for nitrate reduction so it is unlikely that photosynthesis is directly limiting nitrate reduction or protein synthesis (Moss and Stinson 1961, Knipmeyer et al. 1962).

In field grown cereals where soil nitrogen is limiting, it is common for the levels of soil inorganic nitrogen to be low after flowering leading to grain nitrogen accumulating as a consequence of the mobilization of nitrogen from other organs. With anthesis and the conversion from vegetative to reproductive growth, there is an increase in the activity of a broad range of peptide-hydrolase enzymes (Waters et al. 1980). With the peak in activity of these enzymes, proteins from the leaves, glumes and stems are degraded to provide nitrogen for grain filling. Accompanying protein degradation is the conversion of nitrogen to forms suitable for transport from the vegetative tissue to the developing grain and resynthesis into protein. Glutamine and glutamate appear to be the major forms of nitrogen transport in wheat (Simpson and Dalling 1981).

This partitioning of nitrogen between the grain and straw is important in crops like wheat which are extensively grown under climatic conditions where plants face receeding soil nitrogen and moisture during the grain filling period. However, where soil moisture and nitrogen are not limiting, nitrogen uptake by the plant may continue during the grain filling period (Evans and Wardlaw 1976, Austin et al. 1977a).

2.1.2 Energetics of Enhanced Grain Yield and Grain Protein Concentration

As noted, one of the major problems in combining high GY with increased GPC is the negative correlation that often exists between these two traits.

Sinclair and de Wit (1975), reviewed the carbon and nitrogen demands for seed production in 24 crop species and concluded that simultaneous increases in GPC and GY are incompatible from an energetic point of view. The processes of dry matter and nitrogen accumulation compete for carbon skeletons and for the energy derived from photosynthesis. Therefore, the synthesis of more protein and more carbohydrate in the grain requires both the availability of additional photosynthates and an increase in nitrogen to the grain (Bhatia and Rabson 1976).

Penning de Vries et al. (1974) found that in plants under aerobic conditions, 1 gram of glucose can be used to produce 0.83 grams of carbohydrates, or 0.40 grams of proteins (assuming nitrate to be the nitrogen source) or 0.33 grams of lipids. Sinclair and de Wit (1975) used these calculations and knowledge of the composition of wheat seeds to predict that 1 gram of photosynthate would produce 0.71 grams of biomass and would require 16 milligrams of nitrogen. In relation to the 24 crop species examined, the cereals had among the highest rates of biomass production per gram of photosynthate while having only moderate nitrogen requirements. The authors concluded that much of these nitrogen demands could theoretically be met from soil nitrogen. However, they also concluded that where nitrogen availability does not meet seed demands, translocation from the vegetative tissues during seed develop-

ment could render the leaf tissue physiologically inactive and therefore result in the self-destruction of the plant. Nitrogen fertilization in cereals can therefore act to minimize the effects of the self-destructive process and enhance GY by postponing senescence.

Since carbohydrates are the major constituents of the dry matter of the grain, it is assumed that an increase in GPC would result in an offsetting decrease in percent carbohydrate (Bhatia and Rabson 1976). Using the calculations of Penning de Vries et al. (1974), Bhatia and Rabson (1976) calculated the energetic costs of increasing GPC by 1 percent in a typical bread wheat variety with the following constitution: 14 percent protein, 82 percent carbohydrate, 2 percent lipid and 2 percent minerals in the grain. Assuming the weights of grain and constituents other than protein and carbohydrate remain constant, they calculated that a 1 percent increase in photosynthate would be required to increase GPC by 1 percent. From calculations based on those of Sinclair and de Wit (1975), the authors also calculated that for a 1 percent increase in GPC, an additional 6 to 11 percent increase in percent nitrogen would be required for grain protein stoichiometry alone. Bhatia and Rabson (1976) concluded that the increased photosynthate demands could be met by having a higher rate of photosynthesis or additional leaf area or by extending the period of photosynthetic activity or maximizing the mobilization of photosynthetic reserves into the grain. The increased nitrogen demands on the other hand could be met by increasing the amount or duration of nitrate uptake from the soil or by enhancing the remobilization of vegetative tissue nitrogen present before grain filling.

2.1.3 Potential for Enhanced Grain Yield and Grain Protein Concentration

As noted earlier, GY and GPC may increase together. A review of the literature indicates that nitrogen (McNeal and Davis 1955, Boatwright and Haas 1961, Hucklesby et al. 1971, Alkier et al. 1972, Spiertz 1979, Morris and Paulsen 1985), water (Terman et al. 1969, Partridge and Shaykewich 1972, Spiertz 1979), and temperature (Sosulski et al. 1966, Partridge and Shaykewich 1972), all have significant effects on GY and GPC in wheat and may result in their simultaneous increase. Frequently, both environmental and genotypic factors contribute to increased GY and GPC levels of wheat (Dubetz 1972, Johnson et al. 1973, Fowler and de la Roche 1975, Miezan et al. 1977, Terman 1979). From a plant breeding perspective, however, and from the perspective of this work, the potential for improvement of GY and GPC through genetic manipulation is of most interest and as such, will be reviewed here.

2.1.3.1 Genetic Potential for Enhanced Grain Protein Concentration.

Although the literature on the genetic bases for enhanced GPC in cereals is extensive, a sound physiological basis to account for genotypic differences in GPC at comparable yield levels is lacking. Various hypotheses have been proposed, however, that could account for these genotypic differences.

In order to genetically improve GPC while maintaining yield levels, the plant must be able to increase the amount of nitrogen accumulated in the seed. This can be accomplished through two basic physiological strategies: (1) increased nitrogen uptake and assimilation and/or (2)increased remobilization of vegetative nitrogen to the grain. Researchers have looked extensively at both of these strategies.

Nitrogen uptake and assimilation. Seth et al. (1960) studied nitrogen uptake in four wheat varieties of varying GPC under field and culture conditions in order to determine if vegetative nitrogen was correlated to GPC. No significant differences among the four varieties were detected in protein content of above ground vegetative material or roots. The authors attributed grain protein differences to differential rates of protein synthesis in the kernel.

McNeal et al. (1966) initiated a similar study to determine if spring wheats, ranging in GPC from 15% for "C.I. 13636" to 17.5% for Thatcher differed in nitrogen uptake. No significant genotypic differences were detected in N uptake among the five varieties investigated.

In a study of nitrogen accumulation in plants of selected varieties of hard red winter wheat ranging in GPC from 13.8% to 17%, plant nitrogen was not related to GPC (Johnson et al. 1967). Translocation, however, was positively correlated with GPC and therefore, the authors concluded that nitrogen uptake and nitrogen translocation function as separate physiological processes in the wheat plant.

Two recent studies also failed to link GPC with plant nitrogen at maturity. In a thorough analysis of GY and GPC relationships in 30 spring wheat genotypes, Loffler et al. (1985) found that total plant nitrogen at maturity was not correlated with GPC. Similarly, studies of populations involving the spring wheat cultivars "Anza" and "Cajemi 71" (Cox et al. 1985a,b), showed that total nitrogen accumulated in the above ground parts at maturity was not correlated with GPC.

Finally, Desai and Bhatia (1978) investigated genotypic variation in nitrogen uptake in 15 durum wheat cultivars, selected again for their range in GPC. Although plant nitrogen at maturity was not significantly correlated with GPC, they found it was positively correlated with both GY and grain protein yield.

Studies in spring wheat reveal that much of the total plant nitrogen is taken up prior to anthesis. In fertilizer experiments, Boatwright and Haas (1961) found maximum nitrogen uptake occurred by heading while Simmons and Moss (1978) and Loffler et al. (1985) found that spring wheat accumulated 90% and 93% respectively of their total reduced nitrogen before anthesis.

Researchers, however, have found cultivar differences for the duration of nitrogen uptake. Frequently, increased duration of nitrogen uptake is positively correlated with increased GPC.

Neales et al. (1963), found that prolonged leaf activity after anthesis promoted higher nitrogen uptake and resulted in enhanced GPC. Since the removal of flag leaves decreased the amount of grain nitrogen in excess of the amount of nitrogen contained in the flag leaf, it was postulated that the leaves actively transpire and photosynthesize, promoting further uptake of soil nitrogen in addition to providing a source of translocated nitrogen.

Woodruff (1972) also found that leaf area duration was correlated with nitrogen uptake. In a comparison of nitrogen uptake in four wheat cultivars, large genotypic differences were observed for nitrogen content at heading and uptake after heading. Greater duration of nitrogen uptake was positively correlated with leaf area duration (r=.87**).

In a study of 47 winter wheat cultivars, Austin et al. (1977a) found that on average, plants at anthesis contained 83% of the nitrogen present at maturity, however, cultivar variability for the duration of uptake was evident. A significant positive correlation between duration of nitrogen uptake and GPC was not reported but among the cultivars with the greatest duration of uptake was the high GPC, high GY cultivar, Atlas 66.

Kramer (1979b), also found cultivar variation for the duration of nitrogen uptake to be important for the nitrogen economy of the wheat plant. Evidence from an investigation of two cultivars differing in post-anthesis nitrogen uptake suggested however, that the duration of uptake was more critical to grain protein yield than to GPC.

Cox et al. (1985b), drew similar conclusions. Genetic variation in pre-anthesis and post-anthesis nitrogen assimilation was observed in the spring wheat cultivars Anza and Cajeme 71 and their F_5 lines but it was not correlated to GPC. Rather, nitrogen assimilation after anthesis strongly influenced GY and grain protein yield under both low nitrogen (r=.56**, .62**) and high nitrogen (r=.54**,.52**) environments.

In field experiments, factors that may affect nitrogen uptake include the degree of association between the roots and the soil, the nitrate supply, the requirement of the plant for nitrate, the efficiency of the nitrate uptake mechanism in the root and the water status of the soil (Huffaker and Rains 1978).

From solution culture studies, Smith et al. (1983) observed that under conditions of adequate nitrogen and moisture, continuous nitrogen

uptake supplied much of the nitrogen in the grain. This post-anthesis nitrogen was attributed to current root uptake. As noted earlier, (Neales et al. 1963, Woodruff 1972), leaf area duration and source-sink relationships may play an active role in prolonging root uptake of nitrogen. However, quantitative information on genotypic effects on root development remains limited.

Troughton (1968) suggested that a larger root system would result in more efficient extraction of diminishing soil nitrate supplies late in the growing season. On the other hand, plant scenescence during the grain filling period may actually starve the root system of photosynthate thereby decreasing post-anthesis nitrogen uptake (Pate 1980).

Leaf area duration is also critical for the supply of energy and carbohydrates to the developing kernel as cereals rely heavily on currently fixed photosynthates to meet these demands.

In early investigations, many authors (Barnell 1936, Archbold 1938, Archbold and Mukerjee 1942) found that soluble carbohydrates accumulate in appreciable amounts in cereal stems and other vegetative tissues shortly after anthesis. Cultivar differences with respect to the level of extractable carbohydrates have also been noted (Lopatecki et al. 1962, Stoy 1965). This accumulation of soluble carbohydrates is related to the shift from vegetative to reproductive growth, initiated by the onset of anthesis. Soluble carbohydrates accumulated in the stems of cereals are subsequently remobilized and translocated into the growing grain but are not the major source of assimilate for grain filling.

In temperate cereals grown under non-stress conditions, pre-anthesis assimilates contribute only 10-12% of the final grain weight (Lupton 1969, Austin et al. 1977b). Under severe drought however, there is an increase in the input of pre-anthesis fixed assimilates. In situ $^{14}CO_2$ labelling of the crop canopy (Bidinger et al. 1977) resulted in estimates of pre-anthesis assimilate contribution for wheat under irrigated conditions of 13% and under dry conditions of 27%. Austin et al. (1977b) similarly estimated the redistribution of pre-anthesis fixed assimilates on average at 7% of the final grain weight while Stoy (1979) estimated pre-anthesis assimilate contributions of wheat of 18%. Under conditions of severe drought or reduced photosynthesis however, remobilization of stem reserves is enhanced and therefore contributes a greater proportion of the carbohydrates required for grain fill (Rawson and Evans 1971).

Nitrate reductase activity. Two possible sources of grain nitrogen in wheat are: from nitrate reduced during grain filling or from the reassimilation of vegetative nitrogen accumulated pre-anthesis. In either case, the enzymes nitrate reductase and nitrite reductase assume important roles. Of the two, nitrate reductase has the biochemical characteristics which suggest that the reaction it controls is the rate-limiting step of the inorganic phase of nitrogen metabolism (Beevers and Hageman 1969). On this basis, Hageman advanced the hypothesis that, under conditions of non-limiting soil nitrate, plants with higher levels of nitrate reductase activity should possess a greater potential for accumulating reduced nitrogen in the grain.

Researchers have looked at two lines of evidence in considering this proposal. Firstly, does there appear to be a significant positive correlation between nitrate reductase activity and grain protein production and secondly, is the level of the enzyme heritable?

Croy and Hageman (1970) studied two wheat varieties, "Ponca" and "Monon", in an effort to determine if nitrate reductase activity was correlated with GY, GPC or grain protein yield. They found increased nitrate reductase activity from the addition of supplemental nitrogen resulted in an associated increase in GPC and GY. Further to this study, they evaluated nitrate reductase activity, GY and grain protein yield in 32 hard and soft winter wheat varieties. Little genotypic variation was observed for nitrate reductase activity yet selection among the genotypes based on nitrate reductase activity would have resulted in 9 of 13 varieties being selected which ultimately produced the highest grain protein yield.

Results of Mikesell and Paulsen (1971) also suggested the importance of nitrate reductase activity to GPC but focussed more on the duration of enzyme activity. From defoliation studies of the high and low GPC wheat varieties, Atlas 66 and "Triumph", they concluded that a primary difference between these lines was the greater demand of Atlas 66 (with high GPC) for continued assimilation of nitrogen by the flag leaves during grain filling. Triumph, with lower GPC, relied more heavily on translocation of nitrogen from the lower leaves.

Duffield et al. (1972), also working with populations derived from Atlas 66 similarly found that, although nitrate reductase activity was

seasonably variable, it was positively correlated with GPC (r=0.40*). The substrate-inducible nature of the enzyme was also evident from this study as nitrate reductase activity was positively correlated with nitrate (r=0.53*) early in the season when nitrate levels were high and then declined later in the season with the level of nitrate.

The dependency of nitrate reductase activity on the availability of tissue nitrate was also noted in the short-strawed soft red winter wheat "Arthur" (Eilrich and Hageman 1973). Results from a nitrogen fertilizer application study indicated a good correlation between nitrate reductase activity and tissue nitrate levels and at maturity with GY and GPC. It was concluded that the maintenance of nitrate reductase activity during grain filling, particularly in varieties resistant to lodging, can increase GY without a corresponding decrease in GPC.

Since one objective of many wheat breeding programs is to reduce plant height, Deckard et al. (1977) looked at the effectiveness of selecting for nitrate reductase activity in lines segregating for plant height. From a comparison of nitrate reductase activity in tall and semi-dwarf near isogenic lines of T. aestivum and T. turgidum they found nitrate reductase activity to be significantly correlated with GY, grain protein yield and GPC. The data suggested that the effectiveness of using nitrate reductase activity as a selection criterion would not be reduced in populations segregating for plant height.

Dalling et al. (1975), examined the interrelationship between nitrate reductase activity, total plant nitrogen and total grain nitrogen in five wheat cultivars differing widely in their capacities to accumulate

grain nitrogen. Although seasonal nitrate reductase activity was closely related to total plant nitrogen at maturity, there was cultivar variability for total accumulated nitrogen for a given level of nitrate reductase activity. From a plant breeding perspective, this would limit the usefulness of nitrate reductase activity as a selection tool for selecting genotypes with potential for nitrogen productivity. On further investigation, the authors concluded that this cultivar variability was due to differences among the cultivars in translocation efficiency. It appeared from this study that a high level of grain nitrogen depends on two aspects of nitrogen metabolism: high nitrate reductase activity and high translocation efficiency.

To gain maximum effectiveness from using nitrate reductase activity as a selection criterion, the breeder should be able to carry out selection at the seedling stage so that lines worth keeping could be identified early in the program. Dalling and Loyn (1977) examined the relation between nitrate reductase activities of seedlings raised in a growth cabinet with grain nitrogen yields of field grown plants. From the 24 genotypes studied, they concluded that the potential for grain nitrogen yield could be predicted from the activity of nitrate reductase at the seedling stage. Deckard and Busch (1983) however, showed that although the midparent values for nitrate reductase activity predicted crosses that produced a higher frequency of higher yielding lines, seedling nitrate reductase activity could not differentiate among GY and GPC levels within a cross.

Nitrogen remobilization. The total level of nitrate reductase activity during vegetative and reproductive growth determines the potential for

accumulation of nitrogen in the grain. The extent of remobilization of nitrogen from the vegetative tissue to the grain, however, exerts a major influence on the actual amount of nitrogen accumulated in the grain. A growing body of evidence indicates that more efficient and complete translocation of nitrogen from foliage to the grain is the physiological basis for higher GPC of various genotypes.

Seth et al. (1960) analysed 2 high and 2 low GPC wheat varieties at various stages of growth in order to determine whether varieties with high GPC utilized a larger proportion of the nitrogenous materials of the vegetative parts of the plant to form protein in the kernel. The authors found that, although the vegetative protein content of the high and low GPC entries until heading was comparable, the high GPC cultivars (Atlas 66 and a Fronteira derivative), accumulated nitrogen in the kernels more rapidly than low GPC cultivars. They attributed this to higher nitrogen translocation rates in the genotypes with high GPC.

Boatwright and Haas (1961), found that dry matter and nitrogen increased in the kernel up to maturity when fertilizer was not applied. They concluded that nitrogen in the grain was derived primarily from the leaves, stems and chaff rather than by absorption from the soil during the period of grain filling.

McNeal co-operated with a number of researchers to investigate the relationships between grain and plant nitrogen. In the initial study, McNeal et al. (1966) examined 5 spring wheat varieties ranging in GPC, kernel colour, and height with Thatcher wheat as the high GPC check. Vegetative tissue nitrogen content varied with sampling date but not

with variety and very little difference in translocation efficiency was detected among the 5 varieties tested. A second study of 7 spring wheat varieties that possessed a wider range of protein also failed to correlate GPC differences with differences in translocation from top growth to the grain (McNeal et al. 1968), although close correlations (r=0.92**) between top growth and hence nitrogen content and grain nitrogen yield were found. A third study (McNeal et al. 1972) lead to the conclusion that GPC was related more to plant growth characteristics than to translocation. In an investigation of 8 spring wheat crosses, each of which involved one or more parents with high GPC, all genotypes absorbed and translocated equal amounts of nitrogen to the grain but genotypes with low GPC translocated more carbohydrate into the grain. These results however, may have been due to differential sink size among the varieties investigated.

Johnson et al. (1967) however, working with six varieties and five experimental high GPC Atlas 66 derived lines concluded that translocation efficiency was important in determining high GPC. The high GPC lines contained the least vegetative nitrogen among the varieties studied while maintaining relatively high nitrogen concentration in the grain throughout the grain development period. Since all varieties were equally productive, the authors concluded that the line with high GPC had the capacity to translocate nitrogen to the grain more readily than the low GPC varieties.

Rao et al. (1977) found that the difference between Anza and "UC44-111" at 3 levels of nitrate concentration in solution culture studies also corresponded to the differences in translocation of nitro-

gen to the kernel during grain filling. At maturity, UC44-111 with high GPC retained a lower proportion of straw protein than Anza. This enhanced nitrogen use efficiency was also noted in fertilizer experiments where UC44-111 responded to higher levels of nitrate with enhanced production of GY and GPC over Anza.

Further studies compared the nitrogen accumulation and growth characteristics of these two cultivars in the field (Gallagher et al. 1983). While UC44-111 retained a significantly higher GPC in the field, Anza frequently was more efficient in translocating nitrogen to the grain as measured by the grain to straw nitrogen ratio.

From a study of nitrogen translocation in 6 bread wheats under four levels of nitrogen, Halloran (1981a) concluded that translocation efficiency, both within the primary tiller and within the whole plant is important to grain nitrogen yield at maturity but not to GPC. A close correlation between translocation efficiency within the primary tiller and the whole plant ($r=0.74^{**}$) suggested that within-main-tiller translocation efficiency could be used by breeders to enhance grain nitrogen yield as it would not be confounded by variation in the number of fertile to infertile tillers common to whole plant assessments. However, because nitrogen translocation efficiency varied with soil nitrogen levels, decreasing with increasing availability of soil nitrogen, it was concluded that selection should be made at nitrogen levels appropriate to field conditions.

Canvin (1976) called the proportion of total plant nitrogen that occurs in the seeds at maturity the harvest nitrogen index. This ratio

was called nitrogen harvest index (NHI) by Austin et al. (1977a). Since nitrogen in the roots has little influence on the efficiency of nitrogen partitioning (McNeal et al. 1966), the NHI ratio refers only to nitrogen in the above ground parts of the plant.

Loffler and Busch (1982) studied the relationships of GPC, GY and nitrogen partitioning efficiency as measured by NHI in populations derived from high GPC spring wheat crosses. NHI was positively correlated with the ratio of GY over above ground biological yield (HI) (r=0.54*) but was not significantly correlated to GPC. NHI was however, significantly correlated to GY (r=0.62**) and grain protein yield (r=0.71**) and therefore it was suggested that selection for NHI may actually increase GY while maintaining GPC because it would result in a more complete depletion of the nitrogen reservoir in the straw as well as a greater amount of grain relative to straw. From selection studies on this material, the authors concluded that although the evaluation of NHI requires the expenditure of time and money, it remains the most effective method for enhancing GY while maintaining GPC.

In a further study of 30 wide-ranging spring wheat genotypes, Loffler et al. (1985) found that NHI was negatively correlated with GPC (r=-0.60*) but was again highly correlated with HI (r=0.93**), GY (r=0.85**) and grain protein yield (r=0.85**). Total nitrogen at maturity was also positively correlated with GY (r=0.72**) and grain protein yield (r=0.82**) but was not found to be significantly related to GPC. Stepwise regression analysis indicated that when taking HI into account, increases in NHI and total nitrogen at maturity could lead to increases in both GPC and grain protein yield while maintaining GY.

In field experiments with Anza, Cajeme 71 and 96 random F_5 lines Cox et al. (1986) also examined the relationship of NHI to grain yield and GPC. NHI and translocation efficiency (defined by the amount of nitrogen translocated/nitrogen assimilation prior to anthesis x 100) were marginally correlated (r=0.22*, 0.25* respectively) with GPC. Consistent with Loffler and Busch (1982) and Loffler et al. (1985) NHI and HI were both correlated, although moderately, with GY (r=0.29*, 0.58* respectively). Cox et al. (1986) attempted to exclude the influence of carbohydrate partitioning (HI) on nitrogen partitioning (NHI) through the construction of a ratio of the two terms (NHI/HI). Significant yet moderate relationships were found between this ratio and GPC (r=0.45*), which emphasized again the need to study both nitrogen and carbon partitioning when studying the genetic and physiological relationship between GY and GPC.

Studies in durum wheat have also suggested the importance of translocation efficiency in determining grain protein yield. Desai and Bhatia (1978) found NHI ranged from 57% to 83% and was correlated significantly with HI (r=0.58*) but not significantly correlated with GPC (r=0.14). In addition, they found that total plant nitrogen was highly correlated with GY (r=0.81**) and grain protein yield (r=0.92**) but not significantly correlated with GPC (r=0.36), which suggested that it may be a useful selection criterion for enhancing GY while maintaining GPC in durum wheat.

Most of the nitrogen in green plants is in the form of high molecular weight compounds which presumably must be hydrolysed to amino acids and other low molecular weight compounds by proteases before translocation.

Studies in cereals have shown that these leaf proteases are important in determining the levels of tanslocation and perhaps therefore, the efficiency of nitrogen remobilization.

Rao and Croy (1972) examined seasonal activities of both nitrate reductase and leaf proteases in four wheat genotypes, three of which had Atlas 66 in their parentage. Triumph 64 was used as the genotype with low GPC. The authors concluded that the genotypes with high GPC were more efficient at accumulating grain nitrogen because they had higher nitrate reductase activity prior to anthesis and higher leaf protease activity after anthesis than the genotype with low GPC.

The importance of acid proteinase in leaf senescence was also examined in a study of nitrogen loss from the vegetative tissue of two wheat cultivars (Dalling et al. 1976). A highly significant relationship was observed between the rate of nitrogen loss from the tissues and the rate estimated from acid proteinase activity measurements. This again suggests the importance of leaf proteases in nitrogen remobilization.

It appears, therefore, that in addition to adequate absorption of nitrogen and subsequent assimilation, higher GPC and grain protein yield are associated with a more rapid breakdown of protein in the vegetative parts during the reproductive phase. This is coupled with a more efficient translocation of vegetative nitrogen to the developing kernel and a more efficient synthesis of protein therein. Since nitrogen uptake and nitrogen translocation are independent processes which can be manipulated independently (Johnson et al. 1967), it is reasonable to conclude that, (if these processes are genetically controlled), it should theo-

retically be possible for the plant breeder to combine these complementary physiological strategies into one genotype, thereby enhancing GPC while maintaining GY.

2.1.3.2 Genetic Potential for Enhanced Grain Yield. Grain yield may be expressed as the product of biological yield and HI (Donald and Hamblin 1976). Biological yield, measured as total dry matter of the shoot, integrates the physiological processes of photosynthesis and respiration. Photosynthesis in turn is a function of leaf area duration and photosynthetic capacity (Evans and Wardlaw 1976) and HI, defined as the ratio of GY to biological yield, measures the efficiency of conversion of photosynthate into economic yield (Baker and Gebeyehou 1982). From an applied breeding context then, both biological yield and HI could be important in programs aimed primarily at yield improvement.

Grain yield can be improved in two distinct ways: (1) an increase in the biomass production per unit area, while keeping the distribution of dry matter between grain and straw more or less constant and (2) a change in the distribution of dry matter between grain and straw (in favour of the grain), while leaving the total biomass production unaffected (Kramer 1979b).

Biological yield. Growth analysis has become one of the more widely used techniques in the search for physiological parameters that effectively predict yield. Through measurements made at intervals throughout the growing season, data on plant productivity with respect to time can be accumulated. The measurement of biological yield is the simplest

step in growth analysis and yet it provides the researcher with an integrated account of the exploitation of the environment by the genotype (Donald and Hamblin 1976).

Biological yield or total dry matter production is determined by the net assimilation rate and the leaf area index. Also critical to the final dry matter level is the duration of the leaf area, the latter being the main determinant of crop yield (Watson 1952) and, as noted earlier, also important for nitrogen accumulation. In a review of the physiological aspects of crop yield, Watson (1952) suggested that considerable progress could be made in cereal productivity if leaf area duration could be adjusted so that the period of maximum leaf area could be brought to coincide more closely with the period of greatest photosynthesis per unit area.

In a study of five wheat genotypes adapted to British conditions, Lupton et al. (1967) concluded that leaf area duration and shoot dry weight differed among the genotypes and were significantly correlated to yield.

Fischer and Kohn (1966) investigated yield physiology in the wheat variety "Heron", under various seeding and fertilizer rates. They found GY was closely correlated with leaf area duration after flowering ($r=0.97^{**}$) and with vegetative growth at anthesis ($r=0.88^{**}$).

Thorne et al. (1969) studied tall and "Norin 10" derived semi-dwarf wheat varieties for GY, HI, leaf area duration and total dry matter. Yields were found to be equivalent due to the compensating actions of decreased biological yield but increased harvest index in the semi-

dwarfs. The authors concluded that if semi-dwarfs produced as much biological yield as the tall varieties, coupled with their high HI, their GY would be considerably higher.

Yoshida (1972) reviewed the physiology of GY in wheat and rice and concluded that leaf area duration strongly influenced GY. As well, he indicated that increased biological yield resulted in increased GY up to an optimal level for the crop. Yoshida concluded, as did Bingham (1967), that both source and sink capacities were of equal importance in determining GY and that, in breeding for higher yielding varieties, genetic improvements should be sought in both characters.

Finally, Khalifa (1973), in studying the response of GY in wheat to levels of nitrogen fertilizer under irrigated conditions also noted the importance of leaf area duration in determining final GY levels. Growth analysis indicated that the variation in GY was mainly a reflection of the effect of nitrogen treatments at sowing in enhancing leaf area duration ($r=.96^{**}$).

This significant correlation of leaf area duration with biological yield and GY is reflected in studies aimed at investigating the relationship of biological yield or total dry matter with GY.

Tehlan et al. (1979), studied dry matter production in four wheat varieties, differing in height, under different planting densities and nitrogen levels. Dry matter was first initiated in the leaf tissue followed by the stem tissue and by maturity, 50% of the dry matter produced was found in the grain. Therefore,it was concluded that total dry matter production was closely related to GY.

In a study involving four spring wheat cultivars of varying heights, McVetty and Evans (1980a,b) looked at the effectivness of using physiological selection parameters on F_2 plants to predict F_4 bulk GY. They concluded that biologcial yield and peduncle length in the F_2 were the two most important criteria for predicting yield. Where biological yields were relatively similar, HI was also an important selection criterion. McVetty and Evans (1980b) concluded that HI, in a biological yield and height framework, could be useful in increasing GY in spring wheats.

Baker and Gebeyehou (1982), studied the spring wheat cultivars "Neepawa" and "Pitic 62" in comparison to Bonanza barley, and found significant genotypic effects for biological yield, GY and HI. They also concluded that biological yield was an important predictor of GY.

Significant correlations of biological yield with GY (r=0.64**), have also been found in crosses among three hard red spring wheats and an exotic high protein parent (Loffler and Busch 1982) as well as in a thorough assessment of 30 diverse spring wheat cultivars (r=0.75**) (Loffler et al. 1985). Positive correlations in these studies were also found between biological yield and grain protein yield (r=0.68**, r=0.79** respectively), although not with GPC (r=-0.10 ns, r=-0.45*)

High positive correlations between grain protein yield and biological yield have also been observed in a study of 120 diverse cultivars (Bhatia 1975). A positive correlation (r=0.70**) was detected between biological yield and grain protein yield but again its correlation with GPC was significant and negative (r=-0.44*)

Austin et al. (1977a), concluded from similar findings in a study of 47 diverse genotypes that, in breeding for enhanced GY and grain protein yield, it should be easier for breeders to select for enhanced nitrogen uptake from among heavy than from among light genotypes. The results of their study indicated that nitrogen present in the plants at anthesis and at maturity was strongly correlated to aerial biomass. A causal connection was suggested because increased plant weight and the uptake and reduction of nitrate are processes which are dependent on photosynthetic carbon fixation. The authors concluded that breeders therefore must be particularly alert when selecting short varieties or GPC may be sacrificed.

Harvest index. Harvest index or 'migration coefficient' as it was originally called (Engledow and Wadham 1924), is a measure of the plant's efficiency in converting photosynthate into economic yield. It is measured as the ratio of grain (economic) yield over biological yield (above ground). Engledow and Wadham (1924) initially considered it to be an index of the yielding power of the plant, but it was not widely adopted. Since then, many authors have found it to be strongly linked to plant yield when biomass is held constant (Fischer 1975, Austin et al. 1980) and therefore, interest in it as an index of GY has been revived.

Theoretically, GY is a function of HI when biological yield is held constant and in this case HI will be correlated with GY with a correlation of r=1.0 (Donald and Hamblin 1976).

Syme (1970), in a study of wheats of diverse geographical origin and height, found that while the biological yield ranged from 11,040 to 12,540 kg/ha, GY ranged from 2920 to 4890 kg/ha, and HI ranged from .24 to .39. The resulting correlation between GY and HI was r=0.96**. However, in most studies, biological yield tends to be much more variable.

Singh and Stoskopf (1971) evaluated HI in a number of cereals, which varied in biological yield and found a large amount of genetic variation for HI. Correlations with GY ranged from r=0.50* for oats to r=0.66** for spring wheat. The authors concluded that considerable improvement in cereal GY could be made by selecting for higher HI through high yielding, shorter plants.

Syme (1972) used greenhouse grown single plants to predict field plot mean GY performance. He found that HI, days from sowing to emergence of leaf seven and kernel weight, accounted for 78.5% of the variation of cultivar mean plot GY.

In a two year study of 22 spring wheat cultivars of diverse geographical origin (Nass 1973), HI, kernels per ear and GY per ear were all positively associated with plot GY. It was concluded that an index including these three variables would be an effective means of selecting for increased GY levels in spring wheats.

Fischer and Kertesz (1976) found that HI on spaced plants of 40 homozygous spring wheat lines was correlated with large plot GY (r=0.56*). They recommended therefore, that HI could be used, over other parameters, as an early generation selection criterion for large plot GY.

A study designed to look at the use of the HI of F_2 spaced plants as a yield potential estimator, failed to show significant correlations between these two parameters (Okolo 1977). In the four crosses of spring wheat tested, HI of F_2 spaced plants did not adequately predict either F_3 or F_4 bulk yields.

Nass (1983) also investigated the use of HI as an early generation selection criterion for GY. Forty F_2 populations from two spring wheat crosses were selected using head weight, HI and random selection and evaluated for F_4 GY performance. For GY, there appeared to be no advantage of either criterion over random selection. The author concluded that visual selection was at least as effective a selection technique in the F_2 and much less labour intensive than either head weight or HI.

Harvest index has also been positively linked by some authors to grain protein yield but negatively correlated to GPC. In a study of eight spring wheat crosses at three locations, McNeal et al. (1972), found that HI was negatively correlated with GPC (r=-0.64**, -0.71**) but positively correlated with grain protein yield (r=0.95**, 0.67**).

Bhatia (1975) reported on selection criteria for enhancing grain protein productivity from a study of 21 diverse spring wheat genotypes. Correlation studies again detected a significant positive relationship between HI and grain protein yield (r=0.59*) but a negative correlation between HI and GPC (r=-0.71**). Similar findings have been noted in spring wheat (Loffler and Busch 1982, Loffler el al. 1985).

Kramer (1979a,b) also reported a negative correlation between HI and GPC. However, from a study of GPC - HI relationships among 10

varieties he noted that much of the genetic variance for GPC resulted from 'plant type' genes rather than from 'protein' genes. With higher HI, the amount of straw and thereby the protein reservoir, was decreased and at the same time, a larger quantity of grain biomass was formed, resulting in a decrease in GPC. Once GPC was assessed on a common HI basis, the negative correlation disappeared. He concluded that when breeding strategies improve GY by improving biomass productivity (either by a higher growth rate or a longer vegetative period), rather than by increasing HI, the negative correlation between GY and GPC will diminish or disappear.

Halloran (1981a) suggested that in semi-dwarf wheat varieties, with proportionately less biomass and a higher HI, the efficiency of translocation of nitrogen from the vegetative tissues is more critical than in tall varieties. This should offset the effect of 'plant type' genes and enhance GPC.

In summary, Fischer (1975), in reporting on the future role of physiology in wheat breeding, comments that the improvement in GY potential of spring wheats, apart from the elimination of obvious genetic defects, has resulted from decreased height and increased HI. He suggested that further manipulation of the crop for enhanced GY should come from combining complementary physiological strategies to ultimately increase GY. The complementary strategies for GY would appear to be enhanced biological yield (source) coupled with equal or enhanced HI, resulting in improved yield potential and perhaps, when coupled to complementary strategies for nitrogen accumulation and redistribution to the grain, improved GPC.

2.2 Quantitative Inheritance

The majority of economically important characters in crop plants display continuous variation and are usually quantitatively inherited. Whereas the kinds of qualitative characters which Mendel studied in his classic experiments could be easily classified without ambiguity into one of two or more classes, discrete classes can not be recognized in quantitative traits and therefore, classical Mendelian methods of genetic analysis prove impractical. Also complicating the issue is the effect of the environment on these traits. The magnitude of differences between individuals with respect to qualitative characters is so great that the effects of the environment for the purpose of genetical analysis can be effectively discounted. Quantitative traits, on the other hand, are controlled by many genes, inherited in a Mendelian fashion, but subject to environmental modification, to the extent that the environment is frequently a larger source of variation than the genotype itself (Breese 1971).

2.2.1 Types of Gene Action

The first attempt to partition the genetic component of continuous variation into its component parts was made by Fisher in 1918 (Allard 1960). He recognized three major components of genetic variance (1) additive (2) dominance and (3) epistatic gene action. In additive gene action, the substitution of one allele for another at a given locus produces a plus or minus shift on the scale of measurement which is inde-

pendent of other alleles present. On the other hand, alleles which interact with each other in the same gene pair, with one allele masking the effect of the other to varying degrees, produce dominance effects. Finally, phenotypic expression can also be caused by the interaction of genes at two or more loci. These inter-allelic interactions are called epistatic effects and are divisible into additive x additive, additive x dominance and dominance x dominance variation for two or more loci (Gardner 1963). Gardner (1963) also described other components of the genetic variance which are useful to the plant breeder. These include (1) the average degree of dominance which is the ratio of dominance variance to additive genetic variance, (2) genotype x environment interactions which are divisible into both additive gene effects x environment and non-additive gene effects x environment interactions and (3) genotypic correlations among quantitative characters of importance for a particular crop.

Since Fisher's early work, many scientists have contributed over the years to the development of mating designs to allow these components to be estimated, most notably, R.E. Comstock, B.I. Hayman, K. Mather, and H.F. Robinson (Sprague 1965), but it is beyond the scope of this investigation to give a detailed review of the contributions.

2.2.2 Genetics of Grain Protein Concentration

GPC in wheat has been the subject of numerous studies, many of which have shown it to be a heritable trait (Clark 1926, Davis et al. 1961.

Haunold et al. 1962b, Lofgren et al. 1968, Chapman and McNeal 1970, Halloran 1981b). Genetic control of this trait is likely to be polygenic since its expression results from the interaction of a number of physiological processes within the plant.

The earliest work of Clark (1926), suggested that the inheritance of GPC was as complex as that of GY, with the effects of the environment adding to that complexity. A review of early investigations into the inheritance of GPC in hexaploid and tetraploid wheats (Ausemus et al. 1946), indicated that most early authors concluded that GPC was under polygenic control.

Differences in GPC between certain varieties have been reported recently, however, which suggest that GPC is controlled by one to a few major genes with many minor genes modifying protein expression (Haunold et al. 1962b, Lofgren et al. 1968, Cowley and Wells 1980 and Halloran 1981b). Cowley and Wells (1980), in a study of the high protein hard red winter line, "Hand" versus the low protein line, "Centurk" differing in protein content by 4.4%, found that these two lines differed by only one dominant gene. In crosses involving three winter wheat varieties and including Atlas 66, Haunold et al. (1962b) found GPC was conditioned by a few genes. Lofgren et al. (1968), also working with Atlas 66 crosses similarly found that the difference in GPC between parents was due to 3 to 4 genes. Finally, Halloran (1981b), working with the soft white spring wheats "Olympic" and "Kenya B" concluded that the difference in GPC was again governed by a small number of major genes.

Stuber et al. (1962) on the other hand, investigated the inheritance of GPC in an Atlas 66 x Wichita cross and concluded that GPC was under polygenic control. The variability in this result compared to other results involving Atlas 66 crosses may have resulted from the genetic similarity of material involved in the cross with respect to the source of GPC in the genotype. Genetically similar material will usually show fewer gene differences for GPC than genetically diverse material.

Finally, Kuspira and Unrau (1957) analysed the genetics of GPC using substitution lines of Thatcher in a "Chinese Spring" background. The authors found that GPC was under polygenic control with 5 different Thatcher chromosomes responsible for increasing the GPC of Chinese Spring and therefore at least 5 genes or groups of genes affecting this character in this set of substitution lines.

A notable feature of all inheritance studies on GPC is the continuous variation observed in the segregating generations. There is therefore, a general acceptance among workers who have studied GPC, that it is under multigenic control. The literature also suggests that the gene action governing the expression of GPC in wheat is primarily additive.

Stuber et al. (1962) concluded from the results of a greenhouse grown, six generation means analysis study of the cross Atlas 66 x Wichita, that GPC was controlled by additive gene action. There was no significant dominance component. Haunold et al. (1962b) also using Atlas 66 in 3 winter wheat crosses and Lofgren et al. (1968) using Atlas 66 in a cross with 2 hard winter wheats, similarly found GPC to be governed by additive gene action.

Ketata et al. (1976) drew similar conclusions from data collected on GPC from crosses involving 12 different winter wheat cultivars. The authors found that GPC was again primarily conditioned by additive gene action. Further analysis indicated no dominance gene action influencing the expression of genes for GPC.

Chapman and McNeal (1970), investigated gene effects for GPC in each of five wheat crosses with Fronteira as the common high protein parent. For all five crosses, a highly significant additive genetic effect was detected. In three of the crosses, no significant dominance effect was observed. In two crosses, however, a significant dominance effect in the direction of the lower parent was noted and it was concluded that GPC was primarily under additive control with some dominance for low GPC.

Other work in the area also indicated dominance gene action for GPC in wheat. Johnson et al. (1963), from a cross between Atlas 66 and Comanche and their F_2 derived families, found a large significant additive component of gene action, but also found significant dominance for low GPC. Diehl et al. (1978) also used Atlas 66 as one of three high protein cultivars in an investigation of the inheritance of GPC and lysine content in the grain of wheat. From a six generation analysis, GPC was found to be primarily under additive control with some dominance for low GPC. However, lysine expressed as a percent of protein, showed no significant dominance component.

Similar control of protein expression has been noted in the spring wheats. In a study of the segregating generations of a cross between

the soft white spring wheats Olympic and Kenya B (Halloran 1981b), GPC was determined by additive gene action with partial dominance for low GPC. Sampson et al. (1983), in their investigation of five spring wheat crosses found GPC to be under similar genetic control. The authors, however, also noted possible epistatic or interallelic effects in these crosses.

Dominance for high GPC in wheat has been noted by some researchers. From a diallel cross of the red spring wheat varieties Thatcher, "Selkirk", "Gabo" and "Prairie Pride", Hsu and Sosulski (1969), found dominant genes for high GPC. Cowley and Wells (1980) also found dominant gene action for high GPC from the analysis of multiple generations of the high protein cross Hand/NE68513 (which derived recessive high GPC genes from Atlas 66). Overdominance for high GPC was also evident from this study.

Finally, Millet et al. (1984), have suggested that where inheritance of protein is studied in genotypes greatly differing in GPC, maternal effects are important. An analysis of a cross between "Inbar" (Triticum turgidum var durum) containing 14% grain protein and a high GPC line of wild wheat, T. turgidum var dicoccoides, containing 29% GPC and their subsequent generations, resulted in the conclusion that GPC was governed by a large maternal component.

In summary, additive gene action appears to be of primary importance in the expression of GPC in wheat within the range of GPC of commercial varieties. The varying degrees of dominance or epistasis reported are conditioned by the nature of the parental material used as the compo-

nents of gene action are dependent on the dispersion of genes in the parental genotypes and on the analytical technique used to estimate gene action.

2.2.3 Genetics of Nitrogen Metabolism

Literature on the nature of genetic control of the expression of genes regulating the components of nitrogen metabolism is limited. Evidence presented earlier indicated that there is significant genetic variability in the cereals for such components as nitrate uptake and accumulation, the amount of nitrate reductase and nitrate reductase activity and nitrogen remobilization but research into the nature of the genetic control of these traits has been limited to nitrate reductase activity and nitrogen remobilization.

The inheritance of nitrate reductase activity was studied in populations derived from crosses among experimental lines arising from an Atlas 66 x Comanche cross (Duffield et al. 1972). From an analysis of parental, F_1 and F_2 lines the author concluded that nitrate reductase activity was under polygenic control.

Edwards (1973) presented frequency distributions from nitrate reductase activity of random F_6 lines and single F_2 plants from greenhouse and field studies of hexaploid spring wheat Although this type of analysis was confounded by environmental effects, Edwards concluded that nitrate reductase activity was controlled by several genes.

Because bread wheat is an allo-hexaploid, genetic analysis of a trait as complex as nitrate reductase activity is difficult. One means of

overcoming this difficulty is through the use of intervarietal chromosome substitution lines. In this way, it is possible to determine which chromosomes are important in influencing the activity of this enzyme.

Sherrard et al. (1976), using the disomic substitution lines of "Hope" in Chinese Spring, determined that chromosomes 4D and 7D contained major genes and chromosomes 3D and 5A contained minor genes for nitrate reductase activity. Deckard et al. (1982) confirmed the multigenic nature of nitrate reductase activity through the use of ditelosomic and nullisomic lines of Chinese Spring. Genes for nitrate reductase activity were found on the long arm of chromosomes 1B, 5A and 5D and the short arm of chromosomes 6A, 6B and 6D.

Finally, frequency distributions for nitrate reductase activity were determined for the parents, F_1, F_2, B_1, and B_2 and randomly derived F_6 lines of a cross between the spring wheats Anza and UC44-111, known to differ for nitrate reductase activity (Gallagher et al. 1980). The authors concluded that although several genes may control nitrate reductase activity in wheat, the cultivars Anza and UC44-111 differ by only a single locus and a single dominant gene.

The nature of genetic control of nitrogen remobilization is not known, due in part, to difficulty in its measurement which requires serial nitrogen determinations during the growing season to estimate maximum and final vegetative nitrogen. As indicated earlier, proteases have been shown to be associated with the ability of the genotype to remobilize nitrogen (Rao and Croy 1972). There is limited literature on the genetic control of acid proteinases in the wheat leaf but Sherrard

et al. (1976) have shown, again through the use of Hope substitution lines, that substitution of chromosomes 1D, 4D, 2B and 4A, resulted in decreased acid proteinase activity in Chinese Spring.

Nitrogen harvest index (NHI) integrates the effects of the genetically controlled aspects of nitrogen remobilization and apart from heritability estimates discussed later, no information on the nature of the genetic control of NHI was found in the literature.

2.2.4 Genetics of Grain Yield and Related Traits

The genetic control of GY is likely polygenic since it is an expression of the interaction of a number of physiological process of the plant and therefore, must necessarily be genetically complex (Halloran 1981b). Because of the economic importance of GY, many studies have attempted to examine the nature of the gene effects governing it in order to maximize the efficiency with which available germplasm is used in plant breeding programs.

A large proportion of the phenotypic variability in GY is due to the environment but many studies have found a significant genetic component to the observed variability. In a review of the early literature, Ausemus et al. (1946) indicated that the majority of the authors found GY to be under polygenic control. Kuspira and Unrau (1957), analysed the genetics of GY using Thatcher, Hope and "Timstein" in a Chinese Spring background. On the basis of their results, GY is apparently controlled by major and minor genes on at least 14 chromosomes.

Halloran (1981b) examined the parents and segregating F_2 to F_5 generations for gene effects for GY in a soft white spring wheat cross. Segregation for GY in the F_4 and F_5 generations was continuous with partial dominance for low GY.

Stuber et al. (1962) reported from a greenhouse grown, six generation means analysis of the winter wheat cross Atlas 66 x Wichita, that GY was primarily under additive genetic control with dominance for high yield. Heterosis in the F_1 and segregating generations however, may have confounded the results.

Walton (1971), investigated gene action for GY using a diallel analysis of the Canadian wheat cultivar "Manitou" and 6 cultivars of Mexican origin. Again, a significant additive component was detected as well as partial dominance for high GY. Overdominance for GY was also evident in one cross. The authors concluded therefore, that selection for GY was best delayed until the advanced generations of a cross.

Chapman and McNeal (1971), using a six generation means analysis of the cross "Henry" x "Lemhi 53", found significant additive and dominance components of the gene action for GY. Dominance was for high GY and had a large effect relative to the additive component. The authors also detected significant additive x additive and dominance x dominance non-allelic interactions and concluded that breeders must be aware of this source of variation as it will influence predicted gains from selection.

From an analysis of crosses among 12 winter wheat cultivars, Ketata et al. (1978) also concluded that epistasis was important in the inheritance of GY. They concluded that only the additive x additive epistatic

component was significant and felt that it would not hinder breeding for yield as it can be fixed using standard breeding methods.

Singh and Singh (1978) studied gene action in three locally adapted Indian wheat genotypes, again, using a six generation means analysis. They also found GY to be governed by both additive and dominance genes but the relative magnitude of additive to dominance genes was small. They similarly found both additive x additive and dominance x dominance gene effects to be significant. In a later experiment, Singh (1981), using a triple test cross method with 30 varieties, again found significant epistasis for GY.

Singh et al. (1986), using 11 generations for genetic analysis found that in addition to additive gene action, both additive x additive and additive x dominance epistasis significantly affected GY in wheat. Dominance effects however were nonsignificant, indicating dominance genes were probably dispersed between the parents and therefore, may have been cancelled in the analysis.

In addition to additive and dominance effects, GY in the majority of the studies reported appeared to be governed by epistatic effects. There is limited information however, on the nature of gene action controlling HI and biological yield, the two physiological components of GY.

Bhatt (1976) studied the inheritance of HI in the parents, F_1 and F_2 generations of eight wheat crosses and their reciprocals. He found no reciprocal F_1 differences and concluded that HI was controlled by nuclear genes. Gene action was found to be primarily additive with sig-

nificant dominance for high HI. The minimum number of gene differences for HI was determined to be one to three in the genotypes investigated.

Nanda et al. (1982) used a triple test cross genetic analysis of 24 genotypes for HI. They also found HI was controlled by genes dominant for high HI. Epistasis was not significant.

Finally, Singh et al. (1986), using six generation means analysis also found the additive - dominance model adequately explained the gene action controlling HI in wheat. Again epistasis was nonsignificant.

Reports on gene action conditioning biological yield, other than what can be inferred from the heritability estimates discussed in the following section, were not found in the literature.

2.3 Heritability

Heritability is defined as "the portion of observed variability which is due to heredity, the remainder being due to environmental causes" (Allard 1960) and has value primarily as a method of quantifying the question of whether progress from selection for a plant character is relatively easy or difficult to make in a plant breeding program. It is used in both a broad and narrow sense. For the broad sense, the genotype is considered as a unit in relation to the environment and broad sense heritability is therefore defined as the "total genetic variability in relation to the phenotypic variability" (Hanson 1963). Heritability in the narrow sense expresses only the fraction of the phe-

notypic difference between parents which one expects to recover in the offspring. Hanson (1963) defines narrow sense heritability then, as "the additive portion of the genetic variability in relation to the phenotypic variability".

Among the simplest methods for estimating broad sense heritability is the replication of genotypes in a single micro-environment (Breese 1971). An analysis of variance then allows the total phenotypic variation to be partitioned into the genotypic component and the error component which is due to uncontrollable micro-environment fluctuations.

Narrow sense heritabilities are of more use to the plant breeder as they represent that proportion of the phenotypic variation that is fixable through selection. Because of this, a great deal of ingenuity has gone into developing mating plans which permit comprehensive breakdown of the genetic variance into component parts that allow the estimation of narrow sense heritability. These mating designs include analysis of variances from generations derived from the cross of two inbred lines, diallels, and North Carolina designs to name only a few (Mather and Jinks 1977). In a suitably designed experiment then, it is possible to extract estimates of genetic variance and its components, environmental variance and genetic x environmental interactions.

Estimation of genetic variance and its components however suffers from statisical weaknesses. Simmonds (1979), in reviewing these weaknesses, suggested that variances may be unreliably estimated as they are particularly sensitive to deviations from normality. He also indicated that variances tend to be less reliable than means as the variance of the mean is less than the variance of the variance.

An alternative approach to estimating narrow sense heritability is parent-offspring regression where close parent progeny similarity suggests a large genetic effect and a small environmental effect. The regression coefficient directly estimates narrow sense heritability empirically, without depending on genetic assumptions (Simmonds 1979). Although parent-offspring regressions are free of the troubles associated with the partition of variance, they may overestimate narrow sense heritability when selfed progeny are regressed on their parents. This is because small amounts of dominance variance and dominance types of epistasis are usually contained in the heritabillity estimate (Casler 1982). In addition, if the parents and offspring are grown in the same environment, nonzero genotype x environment interaction and error covariances between parents and progeny may result in biased heritability estimates. However, when grown in separate environments, differential environmental expression on parents and progeny can also have an effect on the magnitude of heritability estimates (Frey and Horner 1957). Heritability estimates are therefore very much a function of the procedure used and the nature of the parental material studied. Each is unique and a property of a specific population in a specific experiment and therefore should be interpreted only in terms of general orders of magnitude.

2.3.1 Heritability of Grain Protein Concentration

Heritability estimates for GPC in winter wheats have been frequently reported in the literature. Haunold et al. (1962b), using variance data

from parental, F_1 and F_2 generations, found broad sense heritability ranged from 0.56 to 0.65 for Atlas 66 crosses. Stuber et al. (1962) using six generations of an Atlas 66 x Wichita cross, grown under greenhouse conditions estimated broad sense heritability for GPC at 0.83. Finally, Duffield et al. (1972) again using selections resulting from a cross with Atlas 66 found broad sense heritabilities for GPC ranged from 0.30 to 0.76.

Haunold et al. (1962b) used both parent-offspring regression and standard unit heritabiltiy estimates to predict narrow sense heritability for GPC in crosses with Atlas 66. Standard unit heritability estimates were obtained from the regression of generation data coded in terms of the phenotypic standard deviation (Frey and Horner 1957). The regression coefficient obtained, equal to the narrow sense heritability, is identical to the correlation coefficient on the original data. Estimates ranged from 0.25 to 0.36 and 0.41 to 0.58 for the parent-offspring and standard unit techniques respectively. Stuber et al. (1962) using similar genetic material, but the six generation components of variance approach, estimated narrow sense heritability at 0.82. Lofgren et al. (1968), using genetic material from four crosses with Atlas 66 estimated narrow sense heritability from $F_3 - F_4$ and $F_4 - F_5$ parent-offspring regression and standard unit heritability techniques. Narrow sense heritabilities for GPC ranged from 0.31 to 0.69 and 0.25 to 0.51 for the $F_3 - F_4$ and $F_4 - F_5$ regression techniques and from 0.42 to 0.73 and 0.16 to 0.66 for the standard unit heritaiblity technique. Finally, Guthrie et al. (1984), working with six winter wheat crosses reported heritability estimates ranging from 0 to 0.23 from $F_3 - F_4$ parent-offspring regressions.

In the spring wheats, estimates of broad sense heritabilities for GPC have also frequently been reported in the literature. From the components of variance for seven generations of the spring wheat cross, Selkirk x Gabo, Kaul and Sosulski (1965) found a broad sense heritability for flour protein concentration of 0.82. Baker et al. (1968, 1971), using the analysis of variance technique in spring wheats, detected broad sense heritability estimates ranging from 0.61 to 0.89. Hsu and Sosulski (1969) again looking at Canadian spring wheats, found broad sense heritabilities calculated from parental, F_1 and F_2 variances ranged from 0.42 to 0.71. More recently, Loffler and Busch (1982) studying three crosses of adapted spring wheats estimated broad sense heritability from an analysis of the components of variance. Estimates ranged from 0.76 to 0.83 for the populations studied. Finally, Wells and Kofoid (1986) found a broad sense heritability of 0.85 for GPC from an analysis of the genetic variance of 200 S_1 families.

Narrow sense heritability estimates for GPC in spring wheats have been reported less frequently in the literature. Kaul and Sosulski (1965) reported a narrow sense heritability of 0.66 for flour protein concentration from their seven generation variance analysis. Halloran (1981b), using F_3 - F_4 parent-offspring regression on soft white spring wheat found narrow sense heritability for GPC was 0.48 while Sampson et al. (1983) using the standard unit F_2 - F_3 parent-offspring approach found narrow sense heritabilities in Canadian spring wheats to range from 0.25 to 0.50.

Narrow sense heritability estimates for GPC vary with the genetic material and methodology used but for the most part are reasonably high, indicating the potential for genetic improvement with selection.

2.3.2 Heritability of Components of Nitrogen Metabolism

Estimates of heritability from the literature for the components of nitrogen metabolism discussed earlier are limited but were found for nitrate reductase activity, total nitrogen at maturity and nitrogen remobilization efficiency.

Duffield et al. (1972) used parental, F_1 and F_2 variances in an Atlas 66 cross to estimate broad sense heritability for nitrate reductase activity. Estimates ranged from 0 to 0.72 and varied with sampling date.

Broad sense heritability for total plant nitrogen at maturity was reported by Austin et al. (1977a). From a study of the genotypic and phenotypic variances of 47 winter wheat genotypes, they found the broad sense heritability for this trait to be 0.36.

Duffield et al. (1972), from the above analysis, estimated broad sense heritability for straw protein (%) at maturity to be 0.28. They considered this value a measure of the translocation efficiency of the plant. Broad sense heritability estimates for NHI, a second measure of remobilization efficiency, were reported for spring wheats by Loffler and Busch (1982). Estimates ranged from 0.59 to 0.65.

Loffler and Busch (1982) also reported broad sense heritabilty estimates for grain protein yield (kg/ha) which ranged from 0.51 to 0.63. Finally, Cox et al. (1985a) calculated broad sense heritability estimates in a spring wheat cross from genotypic and phenotypic variance components for grain protein yield under low and high nitrogen regimes. Broad sense heritability estimates ranged from 0.21 to 0.27.

2.3.3 Heritability of Grain Yield and Related Traits

Heritability estimates for GY are equally variable as those for GPC and tend to be lower due to the large environmental component of the phenotypic variance.

Stuber et al. (1962), reported from a greenhouse grown six generation analysis of GY in an Atlas 66 x Wichita cross, a broad sense heritability for GY of 0.53. Teich (1984), studying the heritability of GY in southwestern Ontario adapted winter wheats, reported a broad sense heritability estimate of 0.30. The large standard error reported for this estimate (0.32), clearly illustrates the variability that is present in heritability estimates, particularly those for GY.

Narrow sense heritability estimates for GY in winter wheat are equally variable. Stuber et al. (1962) reported an estimate of 0.53 from their components of variance analysis while Sunderman et al. (1965) using F_2 - F_3 parent-offspring regression found a narrow sense heritability of 0.07 for GY. More recently, Guthrie et al. (1984) using F_3 - F_4 parent-offspring regression reported an intermediate narrow sense estimate for GY of 0.23.

In the spring wheats, broad sense heritability estimates for GY predominate in the literature. Loffler and Busch (1982), found broad sense heritabilities ranging from 0.70 to 0.78 for GY. Wells and Kofoid (1986), from their analysis of genetic variance in 200 S_1 families, reported a broad sense heritability for GY of 0.69 while Singh et al. (1986) using the six generation components of variance approach, found broad sense heritability for GY was 0.88.

Reports of narrow sense heritability estimates for GY are meagre but Singh et al. (1986) have reported a value of 0.62 for a bread wheat cross they analysed.

Heritability estimates for both HI and biological yield have also been reported in the literature for both winter and spring wheats. Austin et al. (1977a) studied 47 genotypes of winter wheat and calculated a broad sense heritability estimate of 0.60 for HI from an analysis of the genetic and phenotypic variance. Bhatt (1976), studied HI in the parental, F_1 and F_2 generations of eight spring wheat crosses and their reciprocals. From the variances of these generations, he reported broad sense heritability estimates for HI ranging from 0.48 to 0.88. Loffler and Busch (1982) also reported broad sense heritabilities for HI in a similar range (0.60 to 0.80). Singh et al. (1986), in their multi-generation approach were able to calculate both a broad sense estimate (0.39) and a narrow sense estimate (0.28) for the heritability of HI in wheat.

Finally, Austin et al. (1977a), from their study of 47 winter wheat genotypes, reported a broad sense heritability estimate for biological yield of 0.40, while two studies reported on the broad sense heritability of biological yield in spring wheat. Loffler and Busch (1982) estimated that broad sense heritabilities for biological yield ranged from 0.59 to 0.64, while Cox et al. (1985a), from their spring wheat cross grown, under high and low nitrogen regimes, estimated that broad sense heritabilities for biological yield ranged from 0.32 to 0.34.

In summary, the heritability estimates for GY, HI and biological yield are clearly variable but are high enough (particularly the narrow sense HI and biological yield estimates), that progress can be made in these traits with selection.

3. MATERIALS AND METHODS

3.1 Description of Cultivars

Eight spring wheat (Triticum aestivum L.) genotypes, UM632, UM684, Benito, Sinton, BW90, Glenlea, HY521 and UM841 were selected for this study. The origins and pedigrees of these genotypes, hereafter referred to as "cultivars" for simplicity, are given in Table 1.

UM632 and UM684 are tall, awned, hard red spring experimental lines developed at the University of Manitoba and selected because of their unique combination of high grain protein concentration and high grain yield.

Benito and Sinton are tall, hard red spring bread wheats of the low grain yield, high grain protein concentration Thatcher type. Benito is an awnless cultivar and Sinton is awned. Both Benito and Sinton were selected as standard adapted Canadian bread wheat varieties. BW90 is a tall, awnless, Thatcher quality experimental bread wheat genotype. This genotype was selected because of its reported high grain protein concentration combined with grain yield, higher than that of the Thatcher type wheats.

Glenlea is a tall, awnless, hard red spring bread wheat of the utility class in Canada, characterized by lower grain protein concentration and higher grain yield than other Canadian varieties.

TABLE 1. Pedigree and origin of cultivars.

Cultivar	Origin	Pedigree [1]
UM632	U. Manitoba Winnipeg, Canada	HPIC. [2] /Glenlea
UM684	U. Manitoba Winnipeg, Canada	HPIC. [2] /Glenlea
BW90	Agric. Canada Winnipeg, Canada	RL4302/RL4356//RL4359/RL4535
Benito	Agric. Canada Winnipeg, Canada	Neepawa/3/RL4255*4//Manitou/C17090
Sinton	Agric. Canada Swift Current, Canada	Manitou/3/Thatcher*6/Kenya Farmer// Lee*6/Kenya Farmer
Glenlea	U. Manitoba Winnipeg, Canada	Pembina*2/Bage//CB100
HY521	U. Saskatchewan Saskatoon, Canada	Cajeme/Norquay
UM841	U. Manitoba Winnipeg, Canada	Junco/HGL

[1] Pedigree according to Purdy et al. (1968).
[2] High protein intercross composite derived from a second cycle recurrent selection program for high protein.

HY521 is a tall, experimental spring wheat genotype developed at the University of Saskatchewan and characterized by low grain protein concentration and high grain yield.

Finally, UM841 is a tall semi-dwarf, experimental, large white seeded spring wheat developed at the University of Manitoba. It was selected for its very high yields and biomass production comparable to the levels of Glenlea and HY521.

Cultivars selected for this study had relatively comparable maturity, height (with the exception of UM841) and dry matter production but expressed the full range of grain yield and grain protein concentrations. Relative grain yield and grain protein concentrations of the eight cultivars are presented in Table 2.

3.2 Physiology Study

3.2.1 Field and Laboratory Methods

Eight contrasting spring wheat cultivars, described in section 3.1 were grown on the University of Manitoba's experimental land at Winnipeg (the point), during the summers of 1984 and 1985. Soil tests showed 100 kg/ha and 120 kg/ha of available nitrogen in 1984 and 1985 respectively. As soil nitrogen was determined to be non-limiting, no additional fertilizer N was added.

TABLE 2. Characterization of the experimental cultivars for predicted levels of grain yield and grain protein concentration.

Cultivar	Grain protein concentration	Grain yield
UM632	high	high
UM684	high	high
BW90	high	moderate
Benito	high	low
Sinton	high	low
Glenlea	low - moderate	high
HY521	low	high
UM841	low	high

Cultivars were grown in 8 row plots with rows 5 m long and 30 cm apart at a planting density of 2600 seeds per plot. Each cultivar was replicated 5 times in a randomized complete block design.

Half m above ground samples were taken from the inner 6 rows of each plot at intervals through the growing season from flag leaf through to physiological maturity, where physiological maturity was defined as the point of maximum dry matter accumulation in the grain and was determined, in a preliminary year, to fall at approximately 30% kernel moisture. Seven and eight samples were taken in 1984 and 1985 respectively in accordance with sampling periods described in Table 3. Flag leaf samples were taken when the leaf blade had fully emerged and the collar was just visible. Anthesis samples were taken at first anthesis. An additional sample was taken in 1985 at anthesis plus 12 days in order to more accurately establish the point of maximum vegetative nitrogen. Kernel moisture was continually monitored for each cultivar throughout grain fill in order that samples could be taken at 50%, 40% and 30% moisture as it was felt that samples taken at specific kernel moistures could more easily be repeated in subsequent years than samples taken at the more subjective grain filling stages of published wheat growth scales.

Samples were cut at ground level and senesced leaves were collected where possible. Each sample was then tagged, bagged and oven dried at 75^{0}C for 48 h. Samples were weighed and separated into vegetative (leaves, stems and peduncles) and reproductive (spike) components. As soon as was possible, the spike was further separated into grain plus nongrain components. Individual components were weighed, ground with a

TABLE 3. Samples harvested relative to stage of plant development for the physiology study.

Samples harvested		
1984	1985	Stage of plant development
1	1	Flag leaf
2	2	Anthesis
3	3	Anthesis + 4 days
4	4	Anthesis + 8 days
-	5	Anthesis + 12 days
5	6	Grain fill (50 % moisture)
6	7	Grain fill (40 % moisture)
7	8	Physiological maturity (30 % moisture)

Wiley mill through a 2mm screen, and analysed for percent nitrogen using the boric acid modification of the standard macro-Kjeldahl technique with titanium dioxide as a catalyst (American Association of Cereal Chemists method 39-10). A conversion factor of 5.7 (Tkachuk 1969) was used to convert grain nitrogen concentration to grain protein concentration.

Dry matter and nitrogen concentration data were collected for the vegetative, nongrain and grain components of each sample. Accumulated nitrogen for each component of all samples was calculated from the component dry matter and nitrogen concentration. Characteristics measured at maturity (and their abbreviations) for each half m sample, expressed on a zero percent moisture basis, were as follows:

(1) Grain yield (GY) = weight of grain (g/m^2).

(2) Grain protein concentration (GPC) = concentration of protein in the grain, expressed as a percent.

(3) Grain protein yield (GPY) = GY x GPC, expressed in g/m^2.

(4) Total dry matter (TDM) = total above ground dry matter at maturity, expressed in g/m^2.

(5) Total plant nitrogen at maturity (TNM) = TDM x total plant nitrogen percentage at maturity, expressed in g/m^2.

(6) Harvest index (HI) = GY/TDM, expressed as a percent.

(7) Nitrogen harvest index (NHI) = total grain nitrogen/TNM, expressed as a percent.

(8) Total vegetative nitrogen at maturity = total vegetative dry matter at maturity x total vegetative nitrogen percentage, expressed in g/m^2, where vegetative dry matter included leaves, stems, peduncles and nongrain spike parts.

Characteristics used for calculation of post-anthesis accumulation values (and their abbreviations), expressed on a zero percent moisture basis, were as follows:

(1) Total dry matter at anthesis (DMA) = total above ground dry matter at anthesis, expressed in g/m^2.

(2) Total nitrogen at anthesis (TNA) = DMA x total plant nitrogen percentage at anthesis, expressed in g/m^2.

(3) Maximum vegetative nitrogen = total vegetative dry matter x total vegetative nitrogen percentage, expressed in g/m^2. The date of maximum vegetative nitrogen was taken as the sample date where this calculation was maximized.

(4) Post-anthesis accumulated nitrogen (PAN) = TNM-TNA, expressed in g/m^2.

(5) Post-anthesis accumulated dry matter (PADM) = TDM-DMA, expressed in g/m^2.

(6) Remobilization efficiency = (maximum vegetative nitrogen-vegetative nitrogen at maturity)/maximum vegetative nitrogen X 100, expressed as a percentage.

3.2.2 Statistical Methods

Data sets for each sample date were analysed as a randomized complete block design using an analysis of variance (ANOVA) procedure. Cultivar means were compared using Duncan's Multiple Range test at $p=0.05$ for those traits where the ANOVA gave significant F values. Data for the

two experimental years was combined using a split-plot ANOVA with years as the main plot. Phenotypic correlation coefficients for measured traits were determined between pairs of traits using raw data values from the 1984 and 1985 field experiments. All statistical analyses were performed using the Statistical Analysis System (Helwig and Council 1982) on the University of Manitoba AMDAHL 580 mainframe computer.

3.3 Inheritance Study

3.3.1 Crosses

Cultivars used for the inheritance study were selected primarily on the basis of grain protein concentration (GPC) such that the difference between "high" and "low" cultivars was maximized. In addition, all cultivars were tall and awned in order to minimize the confounding effects of differing agronomic traits apart from those being specifically investigated.

Two crosses were made between the low GPC cultivar, HY521, and two high GPC cultivars, UM684 and Sinton, with HY521 being the common female parent for both crosses in order to minimize the effect of seed size differences among the three parents on the expression of traits investigated. Seven generations of each of the crosses HY521/UM684 and HY521/Sinton, were produced and included P_1, P_2, F_1, F_2, B_1, B_2 and F_3. Reciprocal F_1 crosses were also made in order to determine the effect of maternal or cytoplasmic genes on the expression of traits measured.

Experimental material was generated for field study in the summer of 1984 but severe Cochliobolus sativus (Ito and Kurib.) Drechsler ex Dastur (common root rot) in the spaced plants resulted in no data being collected from the 1984 experimental year. Material for two locations was therefore generated for the inheritance study in 1985.

F_1 and reciprocal F_1 material was generated in the greenhouse in the fall of 1984. F_1 crosses attempted generated 200 seeds, 40 of which were grown out in the greenhouse in the winter of 1985 while 160 seeds were retained for summer field planting. F_1 plants grown in the greenhouse were selfed to produce F_2 seed and simultaneously used as a pollen source for backcrosses to the paternal and maternal parents to produce the backcross progeny (B_1 and B_2 respectively). Eighty F_2 seeds per cross, generated from preliminary field experiments, were selfed to produce 40 F_3 families per cross, per location. Each family consisted of 10 plants.

A third cross, UM684/Sinton was made in order to establish genetic differences between the two parents with high GPC. P_1, P_2, F_1 and F_2 generations were produced. Two hundred F_1 seeds were generated in the greenhouse in the fall of 1984, 40 of which were selfed in the greenhouse in the winter of 1985 to generate F_2 seed for the 1985 field experiments.

3.3.2 Field and Laboratory Methods

Seven generations of each of the two crosses HY521/UM684 and HY521/Sinton and four generations of the cross UM684/Sinton were planted on the University of Manitoba's experimental land at Winnipeg (the point) and at Portage la Prairie, hereafter referred to as Portage, during the summer of 1985.

Within each cross, for both experimental locations, plants were completely randomized in order to equalize environmental variance due to soil heterogeneity. Seeds were hand planted on 60 cm centres to eliminate the effects of interplant competition on the expression of genetic traits and therefore on the estimation of genetic parameters (Hamblin and Rosielle 1978).

Plants harvested were fewer than those planted by approximately 30% due to persistent root rot at the Winnipeg location and brome grass mosaic virus, identified by Dr. Steve Haber of Agriculture Canada, Winnipeg, at the Portage location. Diseased plants were easily identified and discarded and therefore only plants deemed healthy were harvested for subsequent analyses. Table 4 lists generations and numbers of plants per generation analysed for all traits investigated in the high GPC, low GPC crosses in this study. For the high GPC, high GPC cross, UM684/Sinton, 35 parental and F_1 plants and 250 F_2 plants were analysed from each location for GPC.

At maturity, plants were tagged, cut at ground level, individually bagged and dried to a constant weight (4 to 5% moisture). All data from the inheritance study are therefore reported at this constant moisture. Each plant was handled separately for all subsequent analyses.

TABLE 4. Generations and numbers of plants analysed per generation for the inheritance study.

Generation	Winnipeg		Portage	
	HY521/UM684	HY521/Sinton	HY521/UM684	HY521/Sinton
P_1	35	35	30	35
P_2	41	36	30	36
F_1	34	34	30	37
F_2	314	255	231	208
B_1	218	220	163	150
B_2	220	185	170	150
F_3	150 (1)	150 (1)	125 (2)	125 (2)

(1) 30 families with 5 plants per family
(2) 25 families with 5 plants per family

Plants were weighed and separated into spike plus vegetative components, the latter consisting of leaves, stems and peduncles. Spikes were threshed and separated into grain and nongrain components. The nongrain component then became part of the total vegetative component. Grain was weighed and subtracted from total dry matter to obtain an estimate of total vegetative dry matter.

A 40 g subsample of the grain was ground at a constant feed rate through a Udy Cyclone Sample Mill fitted with a 0.5 mm diameter screen and analysed for grain protein concentration by near infrared reflectance spectroscopy using a DICKEY-john Instalab 800 NIR Product Analyzer. Vegetative material was ground through a 2 mm screen using a Wiley mill and subsequently analysed for nitrogen concentration using the macro-Kjeldahl technique.

Data collected on a per plant basis from each generation included only those traits measured at maturity in the physiological study that were found to be important in determining grain yield and grain protein concentration. These traits included grain yield (g/plant), grain protein concentration (%), grain protein yield (g/plant), total plant nitrogen at maturity (g/plant), total dry matter (g/plant), nitrogen harvest index (%) and harvest index (%). All traits were calculated on a per plant basis in a manner similar to the per sample basis reported in section 3.2.1.

3.3.3 Statistical Methods

Data for each generation of each trait were tested against a normal distribution, with the mean and variance equal to the generation mean and variance, using the Kolmogorov-Smirnov D statistic. The mean, standard error of the mean, variance and coefficient of variation for each generation of each trait were calculated. Variances of the means (standard error squared) for each generation were tested for homogeneity using a Bartlett's test. Analyses of variance for parental means for each cross at each location, were performed to ensure significant cultivar differences for each trait investigated. A split-plot ANOVA was used to detect cultivar x location interactions.

Generation means were used to estimate the magnitude of gene effects and the conformity of the genetic system governing each trait to a simple additive-dominance model. The methodology used was the joint scaling test proposed by Cavalli (1952) and outlined by Mather and Jinks (1977). It involved a simple weighted least squares analysis where the weights used were the reciprocals of the standard errors of the generation means. A chi-squared analysis of observed and expected generation means was used to test the fit of the genetic model to the data and a lack of fit implied the existence of non-additive (epistatic) gene effects other than dominance. The epistatic variation was then separated from additive and dominance variation in the means of the seven generations, by increasing the complexity of the simple additive-dominance model (m, d and h) to include additive x additive, additive x dominance and dominance x dominance interactions (i, j and l respectively) as outlined by Hayman (1958). The coefficients used for the components of means analyses are given in Appendix Table 1.

An analysis using second degree statistics was performed on the variances of the seven generations. The variation observed in the parental and F_1 generations was used to estimate the non-heritable variation while the overall variance in the F_2, F_3, B_1 and B_2 generations was partitioned into additive (D), dominance (H) and environmental (E) components as outlined by Mather and Jinks (1977). The F_3 generation was further partitioned into between family variation (V_1F_3) and within family variation (V_2F_3) in order to provide an additional equation for the estimation of D, H and E. The model was estimated using an unweighted least squares approach. For each trait, nonsignificant parameters were dropped and the analysis was re-run to give a better estimate of the significant components. The coefficients used for the components of variance analyses are given in Appendix Table 2.

It has been demonstrated from a symbolical analysis of variance (Mather and Jinks 1977) that the genetic variance of an F_2 population is equal to 1/2D + 1/4H, where D represents that portion of the variance attributable to the additive gene effects and H represents that portion due to deviations from additivity or the dominance gene effects in the F_2. Heritabilities for the F_2 generation were calculated from these theoretical proportions and the values for each component estimated in the analysis of variance. Broad sense heritability was calculated as the total genetic variance in the F_2 (1/2D + 1/4H) divided by phenotypic variance in the F_2 (1/2D + 1/4H + E), while narrow sense heritability was calculated as the additive variance in the F_2 (1/2D) divided by the phenotypic variance in the F_2.

4. RESULTS AND DISCUSSION

4.1 Parental Characterization

Means of the eight spring wheat cultivars for grain protein concentration (GPC), grain yield (GY) and grain protein yield (GPY) on a per unit area basis for the 1984 and 1985 field experiments are given in Tables 5 and 6.

UM632 and UM684 were selected for the physiology and inheritance studies because of their unique combination of high GPC, GY and GPY. Although significant year effects were detected for these three traits, UM632 and UM684 performed as expected, ranking highest for both GPC and GY over both experimental years. These two cultivars also performed as expected with respect to GY, not differing significantly from the high GY cultivars, Glenlea, HY521 and UM841 in 1984 and ranking comparably in 1985. Grain yield for all cultivars was high due to growth conditions where soil N was not limiting. Genotype x year interaction was evident for GY in 1985 as GY for UM684 did not differ significantly from HY521 or Glenlea but was significantly higher than GY for UM632.

Benito and Sinton exemplified the Canada Western Red Spring bread wheat class, possessing high GPC but low GY. BW90, an experimental bread wheat line was selected because of its high GPC and intermediate

TABLE 5. Comparison of cultivar means for grain protein concentration, grain yield and grain protein yield (1984).

Cultivar	Grain protein concentration (%)	Cultivar	Grain yield (g/m^2)	Cultivar	Grain protein yield (g/m^2)
UM684	17.3 a	UM841	596 a	UM684	96.3 a
UM632	17.1 a	HY521	570 a	UM632	95.0 a
BW90	16.9 a	Glenlea	567 a	Glenlea	84.1 b
Benito	16.6 a	UM684	556 a	UM841	81.0 b
Sinton	16.5 a	UM632	556 a	Sinton	77.0 b
Glenlea	14.8 b	Sinton	468 b	Benito	76.0 b
UM841	13.6 c	Benito	459 b	BW90	75.1 b
HY521	13.0 c	BW90	457 b	HY521	74.0 b

TABLE 6. Comparison of cultivar means for grain protein concentration, grain yield and grain protein yield (1985).

Cultivar	Grain protein concentration (%)	Cultivar	Grain yield (g/m^2)	Cultivar	Grain protein yield (g/m^2)
UM632	20.1 a	HY521	698 a	UM684	129.3 a
UM684	19.0 b	UM684	682 ab	UM632	123.6 a
BW90	18.7 b	Glenlea	662 ab	BW90	107.7 b
Benito	17.9 c	UM841	656 ab	Genlea	103.4 bc
Sinton	16.8 d	UM632	614 bc	HY521	98.0 cd
Glenlea	15.6 e	BW90	577 cd	Benito	94.0 de
UM841	14.3 f	Sinton	532 de	UM841	93.6 de
HY521	14.0 f	Benito	525 e	Sinton	88.2 e

GY. Benito and Sinton performed as expected in 1984, not differing significantly from UM632 and UM684 for GPC while having the least GY of the range of cultivars investigated. In 1985, Benito and Sinton exhibited the low GY expected but, although still high with respect to the low GPC cultivars, ranked significantly lower in GPC than UM632, UM684 and BW90. BW90 on the other hand, performed as expected with respect to GPC but exhibited considerable genotype x environment variability for GY and hence GPY, ranking last for GY in 1984 but third last in 1985.

Finally, Glenlea, HY521 and UM841 were selected as cultivars which exhibited low GPC and high GY. These three cultivars ranked significantly lower than all other cultivars for GPC in both experimental years while at the same time, ranked highest for GY. Glenlea ranked highest among these three cultivars for GPY, although differences were nonsignificant in 1984. This reflected the significantly higher GPC of Glenlea relative to HY521 and UM841.

In summary, the eight cultivars investigated in the physiology study performed very nearly as expected when grown in significantly different years at Winnipeg.

4.2 Physiology Study

Environmental conditions varied greatly between the 1984 and 1985 experimental years and resulted in a significant year effect for many of the traits measured in the physiology study. In 1984, temperatures were

below normal with below normal rainfall for the early seedling stages and near normal with above normal precipitation for the remainder of the vegetative period. During grain fill, the weather was generally warm and dry, shortening the grain filling period and resulting in physiological maturity dates for the 8 cultivars ranging from 90 to 95 days after planting. In 1985, the vegetative phase was extended due to a prolonged period of below normal temperatures and precipitation in June and early July. The grain filling period was also extended by below normal temperatures in late July and August coupled with very much above normal precipitation in August and at harvest. Maturity dates for the 8 cultivars studied consequently ranged from 105 to 110 days after planting. The longer vegetative and grain filling periods in 1985 resulted in significantly greater GY and GPY for the cultivars studied.

Although significant year effects were detected for most traits analysed, the high GPC, high GY cultivars (UM632, UM684) and the low GPC, high GY cultivars (Glenlea, HY521), ranked relatively consistently over years and therefore environments. Significant genotype x year interactions were, however, detected for many of the traits measured and consequently, results were not combined over years. Within environments, analyses of variance indicated significant genotypic differences for all traits reported. The length of these analyses of variance precluded their inclusion in this thesis but the data are available upon request from the author.

4.2.1 Nitrogen Uptake and Assimilation

A comparison of the seasonal patterns of total nitrogen uptake and assimilation per half m sample for the high GPC, high GY cultivars, UM632 and UM684 and low GPC, high GY cultivars Glenlea and HY521 for the 1984 and 1985 experimental years are presented in Figures 1 and 2, respectively.

Cultivars reached anthesis 56 to 61 days after planting in 1984 (Figure 1) and 62 to 66 days after planting in 1985 (Figure 2). UM632 and UM684 were consistently the earliest cultivars, reaching physiological maturity in 90 and 91 days respectively in 1984 and 105 and 106 days respectively in 1985 while Glenlea and HY521 were consistently the latest cultivars, maturing in 95 days in 1984 and 110 days in 1985.

During the early stages of plant development for both experimental years, these 4 cultivars showed very similar patterns of nitrogen (N) accumulation. During grain fill however, UM632 and UM684 continued to accumulate plant N at a relatively constant rate whereas the rate of N accumulation in Glenlea and HY521 decreased. These differences became significant at mid grain fill or 50% kernel moisture. At physiological maturity, the high GPC, high GY cultivars UM632 and UM684 had accumulated significantly more N than HY521 in 1984 and significantly more N than both Glenlea and HY521 in 1985. Although Glenlea ranked lower than UM632 and UM684 in 1984, the difference in total nitrogen at maturity (TNM) was nonsignificant.

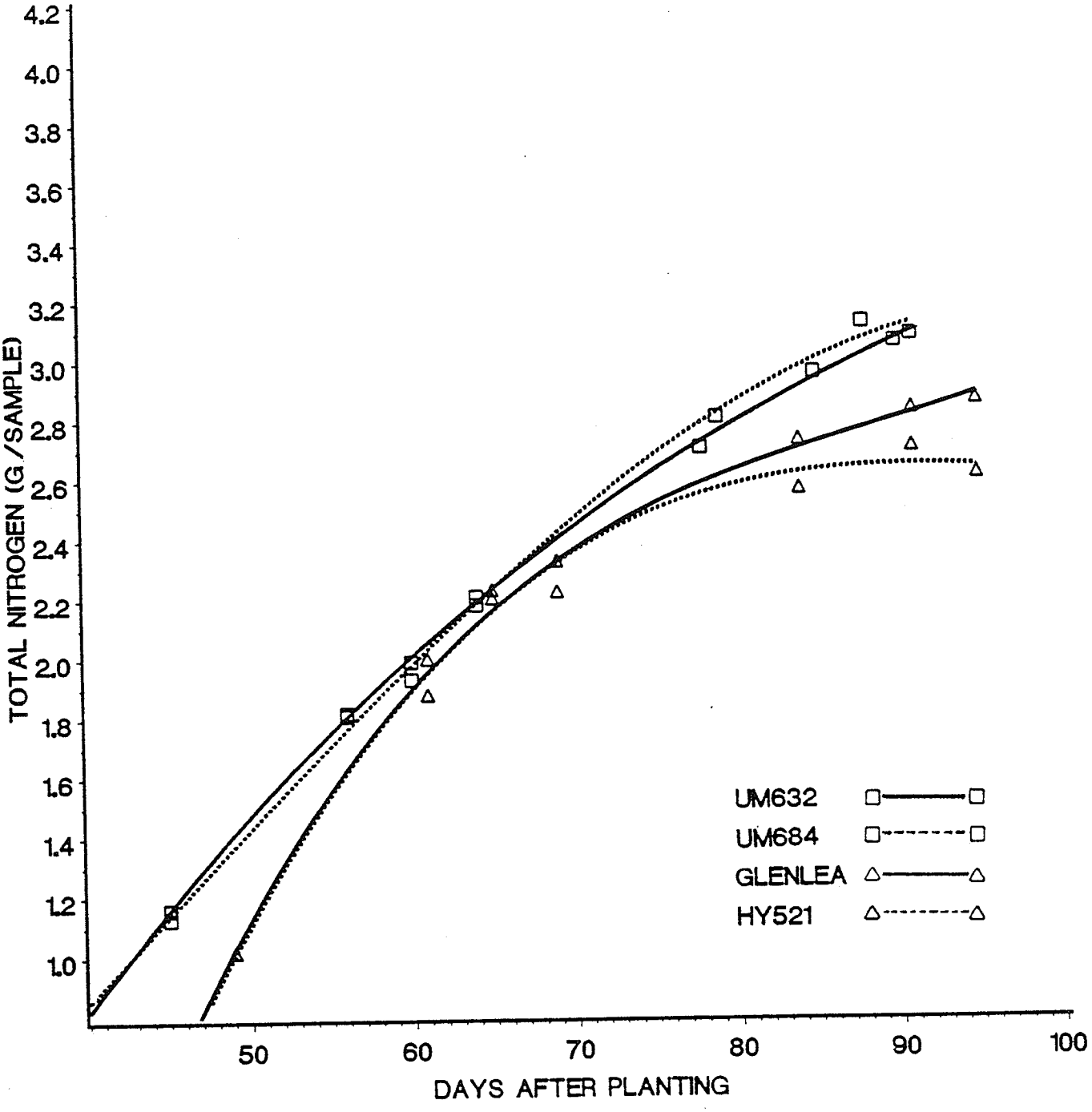

Figure 1. Total accumulated nitrogen in high grain protein concentration, high grain yield versus low grain protein concentration, high grain yield cultivars (1984).

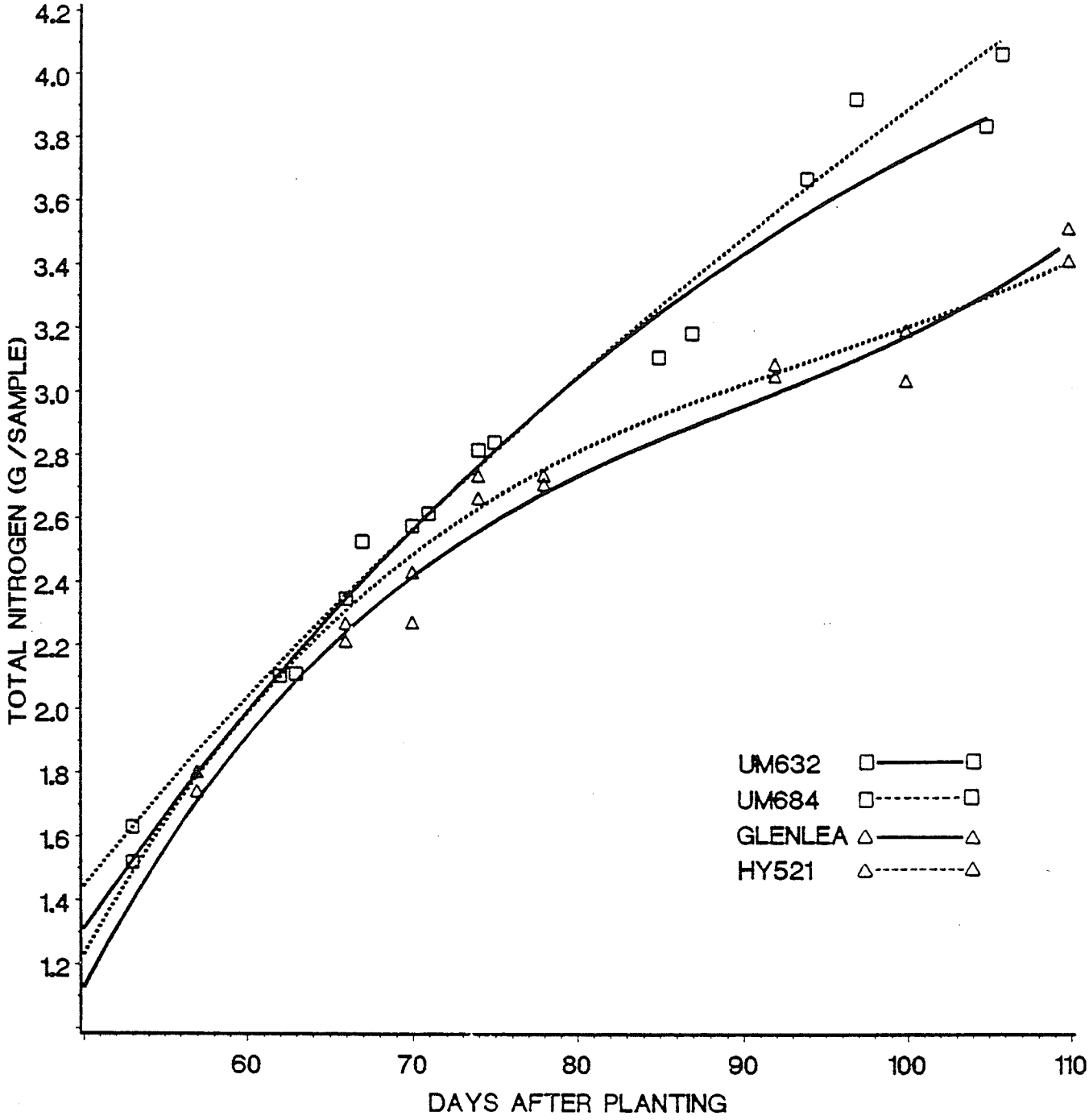

Figure 2. Total accumulated nitrogen in high grain protein concentration, high grain yield versus low grain protein concentration, high grain yield cultivars (1985).

Seasonal patterns of N uptake and assimilation for UM632 and UM684 were compared to those of the bread wheat cultivars Benito and Sinton for the two experimental years (Figures 3 and 4). Benito and Sinton were later than both UM632 and UM684, reaching anthesis 63 and 64 days respectively after planting in 1984 and 64 and 65 days after planting in 1985. and were were slightly later in maturity than UM632 and UM684, reaching physiological maturity in 91 and 93 days respectively in 1984 and 106 days after planting in 1985.

From flag leaf through to anthesis, the patterns of nitrogen accumulated in the 4 cultivars compared are very similar. Again however, during grain fill, UM632 and UM684 continued to accumulate plant N at a greater rate than either Benito or Sinton. Total N per sample of Benito or Sinton was significantly lower than that for UM632 and UM684 by mid grain fill or 50% kernel moisture in 1984 (Figure 3) and by one week post anthesis in 1985 (Figure 4). By physiological maturity, the high GPC, high GY cultivars had consistently accumulated significantly more plant N than either of the high GPC, low GY cultivars.

Cultivar comparisons for traits related to N uptake and assimilation on a unit area basis for the 1984 and 1985 growing seasons, are presented in Tables 7 and 8. An examination of cultivar means for total N uptake at anthesis (TNA) indicated that although there were significant genotypic differences, a clear association between TNA and GY, GPC or GPY levels could not be established over years. This was due partly to the small range of genotypic means detected for this trait.

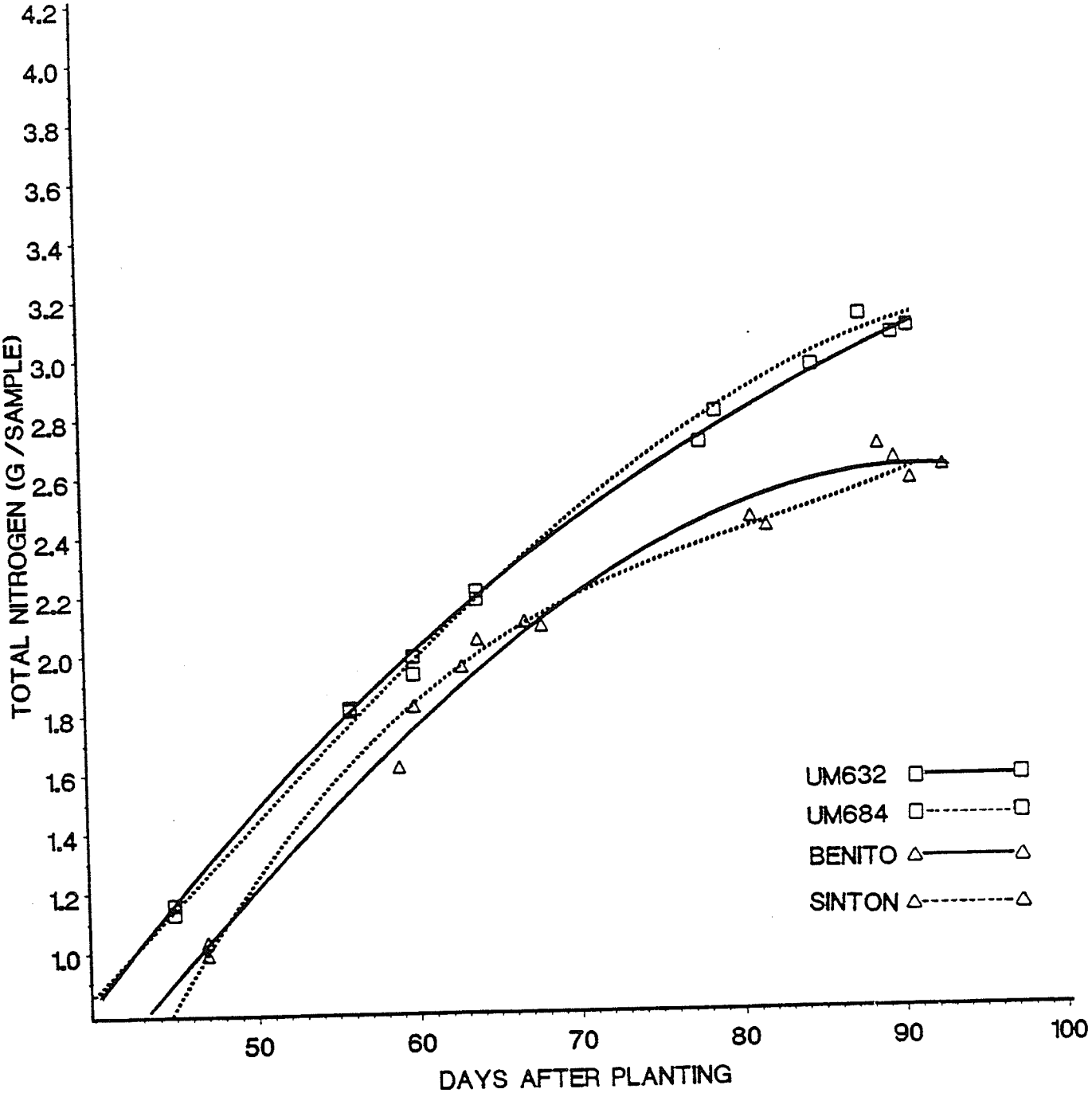

Figure 3. Total accumulated nitrogen in high grain protein concentration, high grain yield versus high grain protein concentration, low grain yield cultivars (1984).

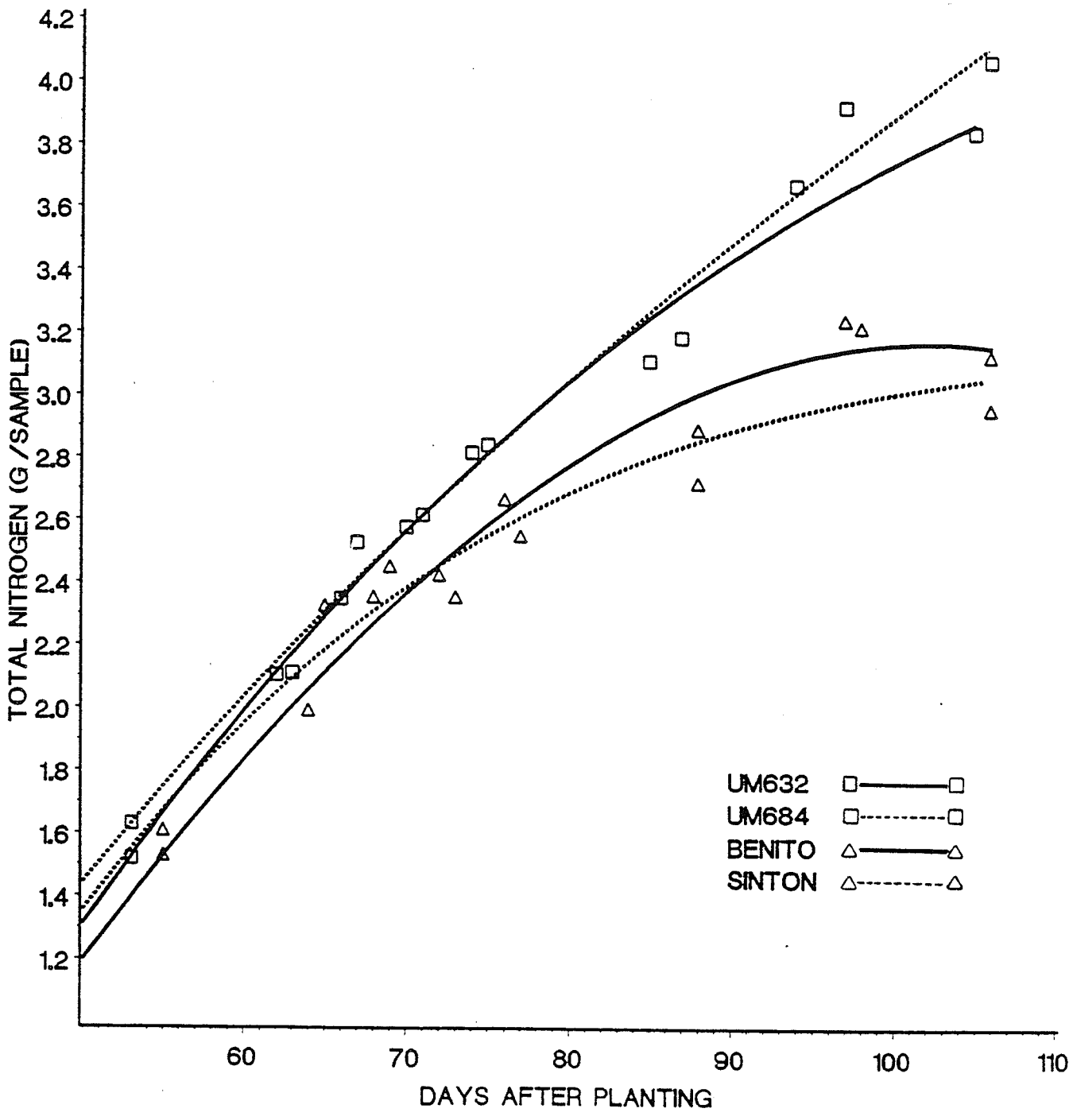

Figure 4. Total accumulated nitrogen in high grain protein concentration, high grain yield versus high grain protein concentration, low grain yield cultivars (1985).

TABLE 7. Comparison of cultivar means for traits related to N uptake and assimilation (1984).

Cultivar	Plant N Anthesis (g/m^2)	Cultivar	Plant N Maturity (g/m^2)	Cultivar	N uptake post-anthesis (g/m^2)
Sinton	13.1 a	UM684	20.2 a	UM684	8.3 a
Glenlea	13.1 a	UM632	20.0 a	UM632	8.2 a
UM841	12.7 ab	Glenlea	18.8 abc	Benito	6.3 b
HY521	12.3 ab	UM841	18.2 bcd	BW90	6.0 bc
UM684	11.9 b	HY521	17.1 cde	Glenlea	5.7 bc
UM632	11.8 b	Sinton	17.1 cde	UM841	5.6 bc
Benito	10.6 c	Benito	16.8 de	HY521	4.8 bc
BW90	10.3 c	BW90	16.3 e	Sinton	4.0 c

TABLE 8. Comparsion of cultivar means for traits related to N uptake and assimilation (1985).

Cultivar	Plant N Anthesis (g/m^2)	Cultivar	Plant N Maturity (g/m^2)	Cultivar	N uptake post-anthesis (g/m^2)
UM841	16.7 a	UM684	26.7 a	UM684	12.8 a
Sinton	15.3 ab	UM632	25.2 a	UM632	11.4 a
HY521	14.9 b	Glenlea	23.1 b	Glenlea	8.6 b
BW90	14.8 b	BW90	23.1 b	BW90	8.3 b
Glenlea	14.5 bc	HY521	22.4 b	HY521	7.5 b
UM684	13.9 bc	UM841	21.7 bc	Benito	7.4 b
UM632	13.8 bc	Benito	20.5 cd	UM841	5.0 c
Benito	13.1 c	Sinton	19.4 d	Sinton	4.2 c

In 1984 (Table 7), TNA for the cultivars ranged from 10.3 to 13.1 g/m^2. Examination of the rank of cultivars indicated that high TNA was more closely associated with high GY than with either high GPC or high GPY. Correlation coefficients confirmed this association as TNA was significantly correlated with GY (r=0.36*) but not correlated with either GPC or GPY (Appendix Table 3).

In 1985 (Table 8) TNA ranged from 13.1 to 16.8 g/m^2. The positive association of TNA with GY detected in 1984, however, was not evident in 1985 from either the rank of cultivars or from phenotypic correlations (Appendix Table 4).

The inconsistent correlation of TNA with GY, GPC and GPY found in this study was also evident from the literature. Seth et al. (1960) found no genotypic differences for TNA among high and low protein cultivars whereas Cox et al. (1985b) found significant genotypic differences in TNA among cultivars. TNA was not correlated with GPC under either low or high N regimes in 96 F_5 lines of the cross Anza x Cajeme 71 (Cox et al. 1985b) or in 30 spring wheat genotype ranging in GPC (Loffler et al. 1985). In both of these studies, however, TNA was found to be correlated with GY. The magnitude of the phenotypic correlation of TNA with GY, found in the 1984 field experiments agreed with the literature values but the magnitude of the resulting coefficient of determination (r^2=0.13) and the inconsistency of the correlation, suggested that TNA would not be a useful predictor of GY in a breeding program.

Total plant nitrogen at maturity (TNM) ranged from 16.3 to 20.2 g/m^2 in 1984 (Table 7) and from 19.4 to 26.7 g/m^2 in 1985 (Table 8). The

high GPC, high GY cultivars UM684 and UM632 consistently ranked highest for TNM over both experimental years. In 1984, TNM for Glenlea did not significantly differ from these two cultivars while in 1985, UM684 and UM632 ranked significantly higher than all other cultivars for TNM. For the remaining six cultivars, TNM appeared to be more closely associated with high GY than with high GPC as Glenlea, HY521 and UM841 generally had a higher TNM than the bread wheats.

Correlation coefficients among the above traits confirmed the positive correlation of TNM with GPY (r=0.97**, 0.95**), GY (r=0.67**, 0.68**) and GPC (r=0.35*, 0.41**). These correlation coefficients and those throughout the physiology section that are presented within one set of parentheses, represent data from the 1984 and 1985 field experiments respectively and are found in Appendix Tables 3 and 4. The high positive correlations detected between TNM and GPY and GY indicated that most of the variability in GPY (r^2=0.94**, 0.90**) could be accounted for by variability in TNM while a smaller proportion of the variability in GY (r^2=0.45**, 0.46**) could be explained by variability in TNM. This strong correlation of TNM with both GPY and GY confirms similar relationships found in other wheat studies (Neales et al. 1963, Cox et al. 1985b, Loffler et al. 1985), but these studies failed to show a correlation between TNM and GPC. The positive correlations found among TNM, GPY, GY and in this study GPC, suggested that selection for TNM could result in improved economic productivity (GPY) and in significant simultaneous improvement in GPC and GY.

Post-anthesis N uptake (PAN) varied widely among cultivars and ranged from 4.0 to 8.3 g/m^2 in 1984 (Table 7) and from 4.2 to 12.8 g/m^2 in 1985

(Table 8). The greater range of PAN observed for the 1985 growing season was associated with the longer grain filling period in 1985 and high levels of available N.

PAN was significantly greater for UM684 and UM632 than for all other cultivars. This suggested that continued N uptake, post-anthesis, was important to achieve high GPY. Few significant differences were detected among the remaining six cultivars. PAN did, however, appear to be more closely associated with GPC than GY, particularly for the 1985 experimental year (Table 8). The high GPC cultivar Sinton however, while accumulating significantly more N by anthesis than other cultivars, consistently accumulated the least N post-anthesis and consequently, TNM for Sinton was low.

Correlation coefficients of PAN with GPY, GPC and GY indicated a highly significant correlation between PAN and GPY for both experimental years (r=0.80**, 0.90**) (Appendix Tables 3 and 4). PAN was also significantly correlated to both GPC (r=0.51**, 0.58**) and GY (r=0.38*, 0.44**) (Appendix Tables 3 and 4).

Although studies in spring wheats have revealed that as much as 92% (Simmons and Moss 1978) and 93% (Loffler et al. 1985) of total plant N is taken up prior to anthesis, many other researchers have found genetic variability for duration of N uptake and frequently, increased PAN has been found to be positively correlated with increased GPC (Neales et al. 1963, Woodruff 1972, Van Sanford and MacKown 1987) and increased GY (Kramer 1979b, Cox et al. 1985b).

Because of the high correlation of PAN with economic productivity (GPY) and its components (GPC and GY), possible explanations for this trait are important. Factors that have been proposed to be associated with the duration of N uptake, have included (1) leaf area duration (Neales et al. 1963, Woodruff 1972), thought to be instrumental in maintaining current root uptake (Smith et al. 1983) and (2) the size of the root mass (Troughton 1968). Troughton (1968) suggested that a larger root mass may be associated with the duration of N uptake by more efficiently extracting diminishing soil nitrate late in the growing season. Finally, the efficiency of nitrate uptake late in the season may also be associated with a more efficient nitrate reductase enzyme with a lower Km for nitrate.

In summary, these results emphasized the importance of N uptake, both TNM and PAN, in attaining the high levels of GY, GPC and GPY achieved by the cultivars UM684 and UM632 and therefore, both traits should prove effective in breeding for simultaneous improvement in GY and GPC.

4.2.2 Assimilation of Dry Matter

The calculation of plant nitrogen involves multiplication of plant dry matter by a nitrogen concentration factor. Therefore, in order to conclude that genotypes are significantly different for N uptake and assimilation, it is necessary to discern whether these differences relate to an increased efficiency of the N uptake and assimilation systems or simply to a greater plant biomass.

Patterns of dry matter accumulation for the high GY cultivars UM632 and UM684 were very similar in both experimental years (Figures 5 and 6). In 1984, Glenlea and HY521 had accumulated significantly more dry matter than both UM684 and UM632 by anthesis. At sequential harvest dates through the season, these differences persisted until mid grain fill when differences among UM684, Glenlea and HY521 became nonsignificant. UM632, however, accumulated dry matter at a lower rate than the remaining three cultivars, resulting in significantly lower total dry matter at maturity (TDM) than for UM684, Glenlea and HY521. In 1985, dry matter differences among these four cultivars at anthesis were nonsignificant. Through the grain filling period however, UM632 and Glenlea accumulated less dry matter than UM684 and HY521 and by maturity, TDM for UM632 and Glenlea was significantly lower than for UM684 and HY521.

Comparison of the seasonal patterns of dry matter accumulation for the high GPC, high GY cultivars UM632 and UM684 versus the high GPC, low GY cultivars Benito and Sinton indicated that Sinton accumulated more dry matter than all cultivars at anthesis in 1984 (Figure 7) while in 1985 (Figure 8) it differed significantly from UM684 and Benito but nonsignificantly from UM632. By mid grain fill (50% moisture), in both experimental years, these differences were overcome and UM684 ranked significantly higher than the remaining cultivars for dry matter accumulation. At physiological maturity, in both experimental years, Benito and Sinton had accumulated significantly less dry matter than UM684. Total dry matter differences between Benito, Sinton and UM632 were only significant in 1985 when UM632 ranked significantly higher than either Benito or Sinton.

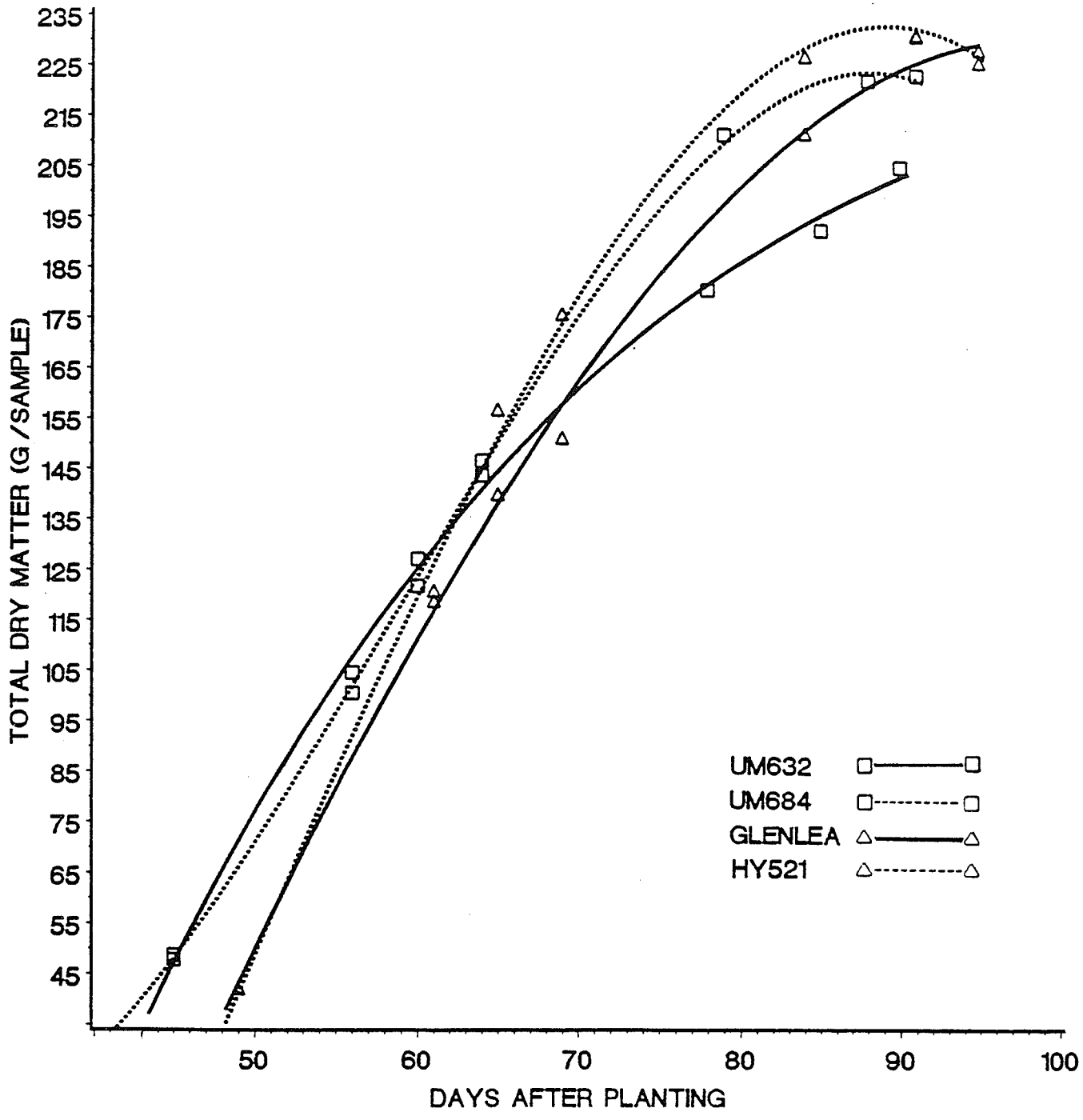

Figure 5. Total dry matter in high grain protein concentration, high grain yield versus low grain protein concentration, high grain yield cultivars (1984).

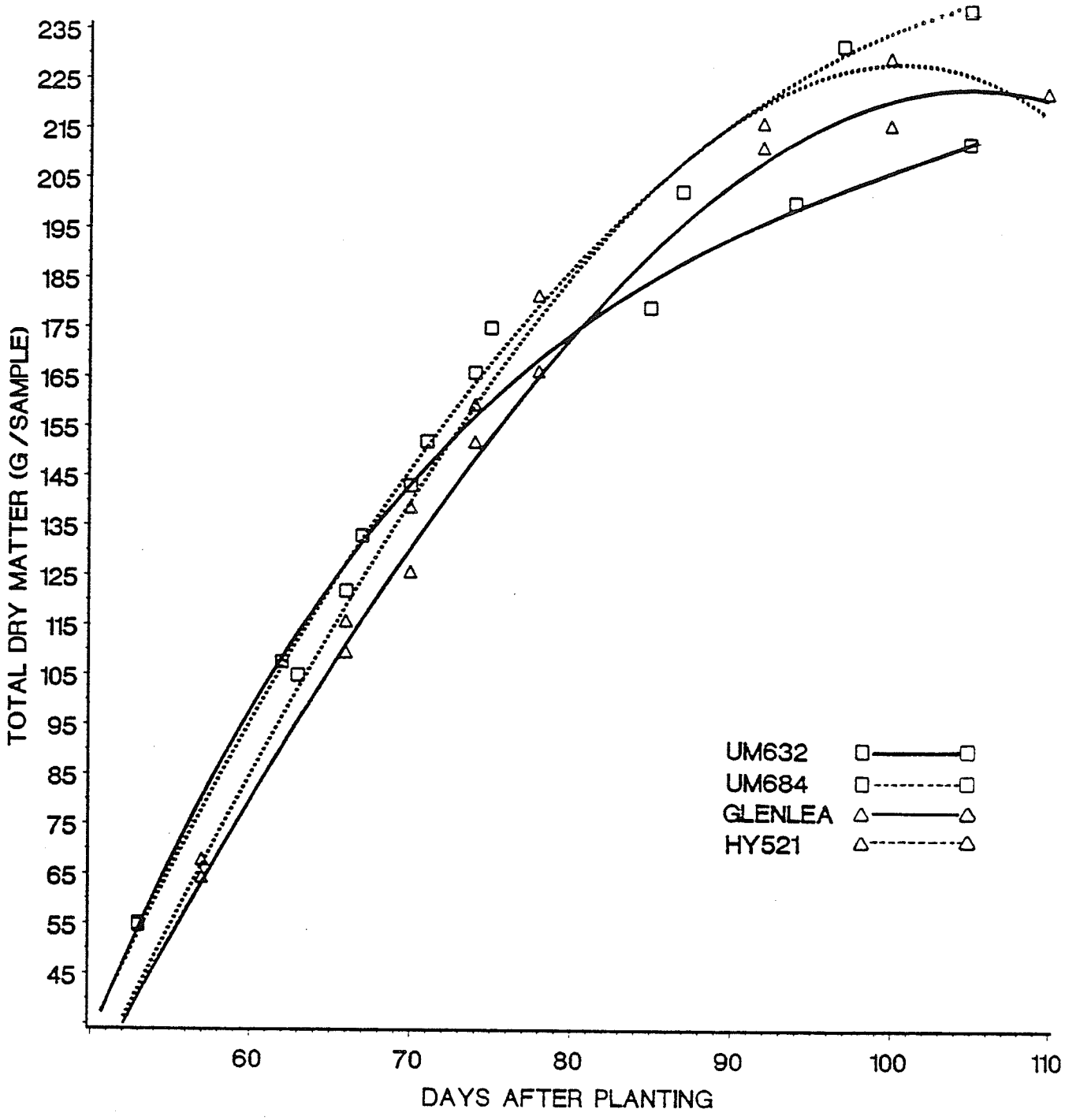

Figure 6. Total dry matter in high grain protein concentration, high grain yield versus low grain protein concentration, high grain yield cultivars (1985).

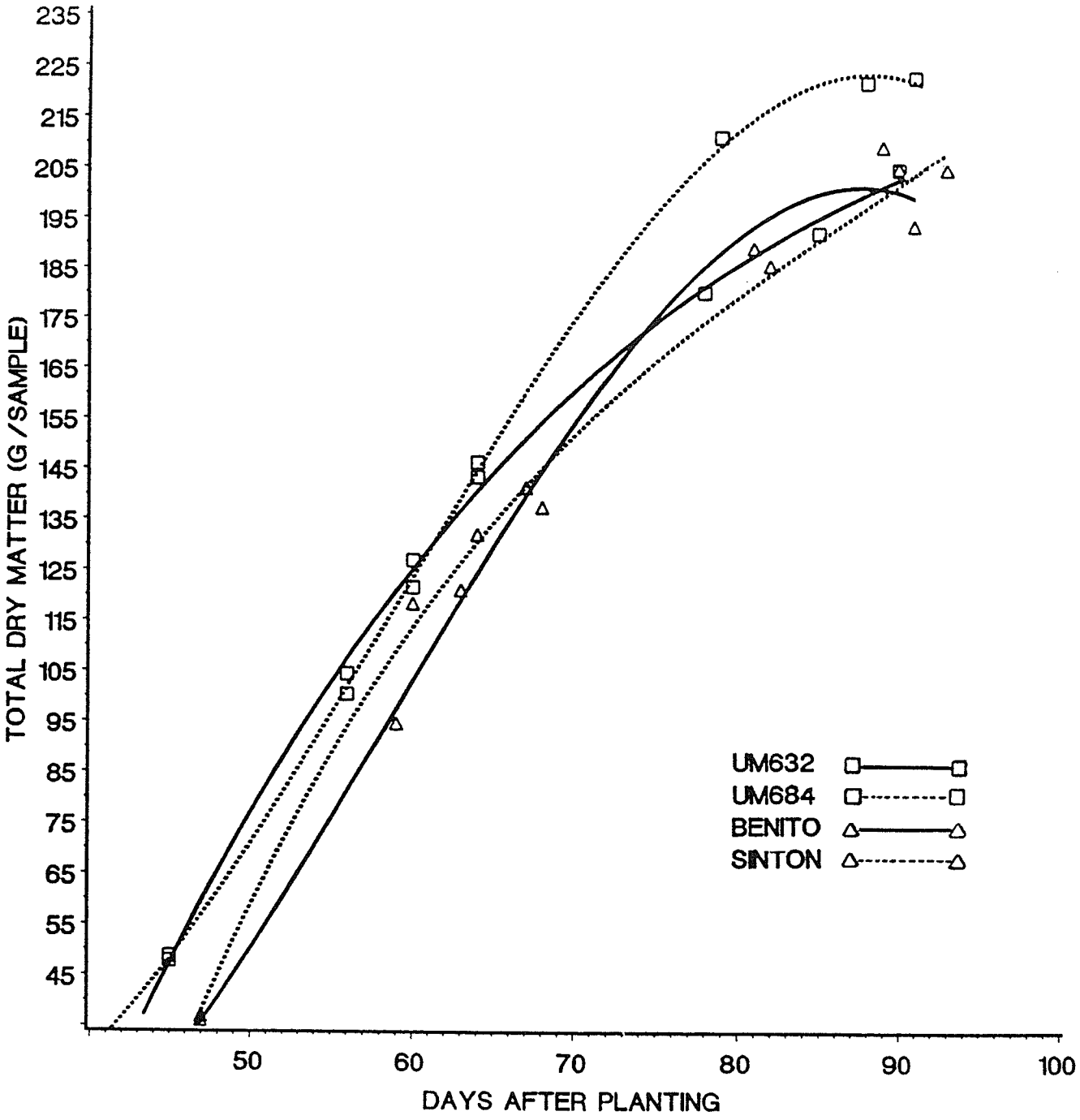

Figure 7. Total dry matter in high grain protein concentration, high grain yield versus high grain protein concentration, low grain yield cultivars (1984).

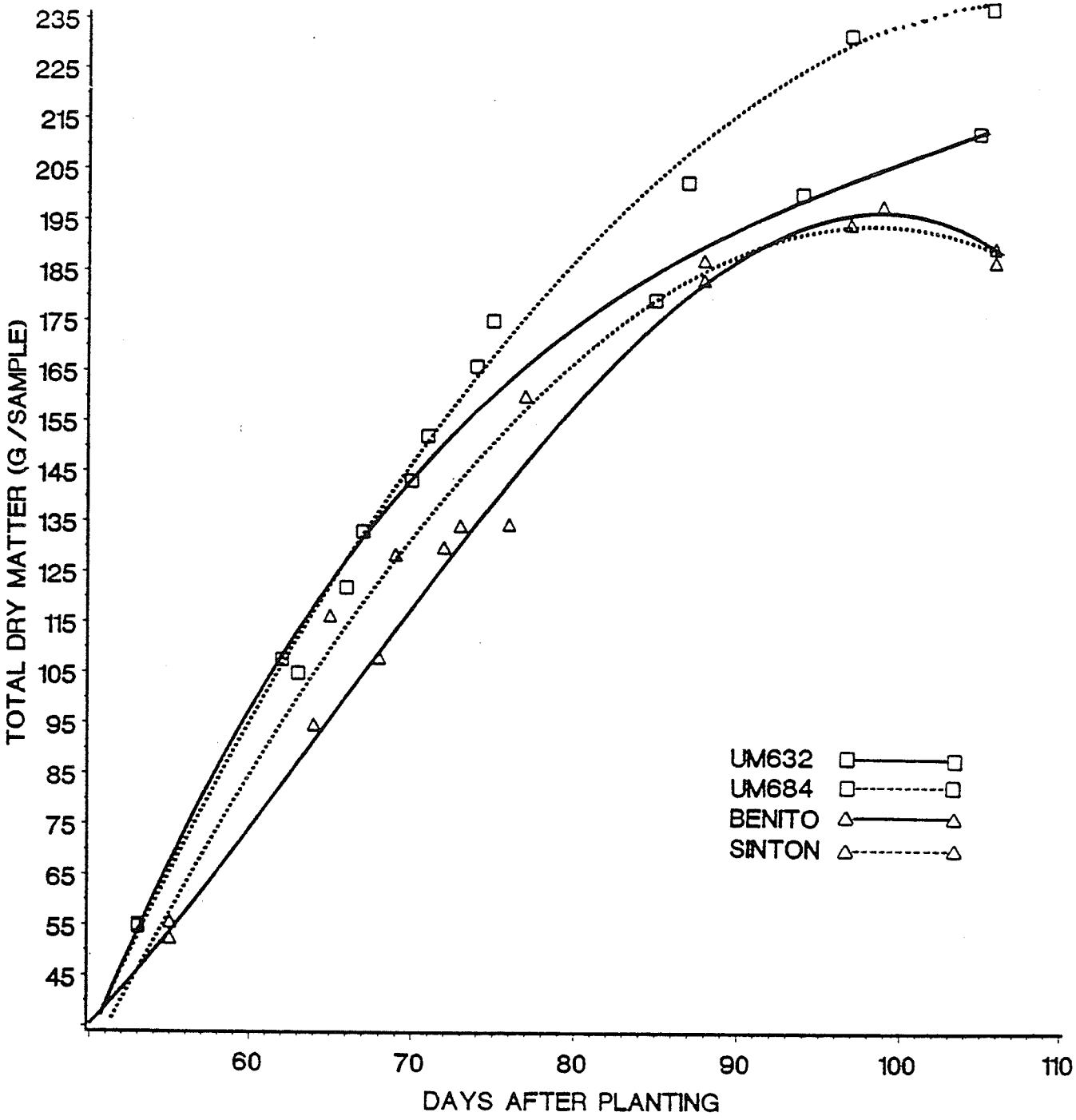

Figure 8. Total dry matter in high grain protein concenration, high grain yield versus high grain protein concentration, low grain yield cultivars (1985).

An examination of cultivar means for dry matter accumulated by anthesis (DMA) indicated that, although significant genotypic differences were detected among the range of cultivars examined, no clear association of DMA with GY or GPY was evident in either 1984 or 1985 (Tables 9 and 10 respectively). DMA ranged from 622 to 792 g/m^2 in 1984 and from 622 to 827 g/m^2 in 1985 and appeared to be negatively correlated with GPC. Correlation coefficients confirmed a moderate negative correlation between DMA and GPC in both 1984 (r=-0.58**) and 1985 (r=-0.46**) (Appendix Tables 3 and 4). Correlations between DMA and GY and GPY indicated the lack of consistent association of DMA with either trait. DMA was weakly correlated with GY in 1984 (r=0.36*) but not in 1985, while no significant correlation was detected between DMA and GPY for either experimental year (Appendix Tables 3 and 4).

As mentioned earlier, accumulated N at any sampling period is a function of the plant dry matter at that sampling period and the nitrogen concentration. Correlation coefficients for DMA and total plant N at anthesis (TNA), discussed earlier, for both 1984 (r=0.74**) and 1985 (r=0.83**) (Appendix Tables 3 and 4), clearly showed that TNA was more closely a function of DMA than it was a function of the relative level of GY or GPY of the cultivar. This relationship was expected and is in agreement with similar results in other wheat studies (Austin et al. 1977a, Cox et al. 1985b).

DMA was negatively correlated with GPC (noted earlier) and with the post-anthesis N accumulation (PAN) in both 1984 (r=-0.54**) and 1985 (r=-0.48**) (Appendix Tables 3 and 4). Since Troughton (1968) has noted that the greater the shoot growth, the smaller the proportion of photo-

TABLE 9. Comparison of cultivar means for traits related to seasonal accumulation of dry matter (1984).

Cultivar	Dry matter Anthesis (g/m^2)	Cultivar	Dry matter Maturity (g/m^2)	Cultivar	Dry matter post-anthesis (g/m^2)
Glenlea	792 a	HY521	1496 a	UM684	776 a
HY521	778 a	Glenlea	1479 a	HY521	717 ab
Sinton	777 a	UM841	1472 a	UM841	703 ab
UM841	770 a	UM684	1461 a	Glenlea	687 abc
UM684	686 b	Sinton	1343 b	UM632	684 abc
BW90	669 bc	UM632	1343 b	Benito	648 abc
UM632	659 bc	Benito	1270 b	BW90	600 bc
Benito	622 c	BW90	1269 b	Sinton	565 c

TABLE 10. Comparison of cultivar means for traits related to seasonal accumulation of dry matter (1985).

Cultivar	Dry matter Anthesis (g/m^2)	Cultivar	Dry matter Maturity (g/m^2)	Cultivar	Dry matter post-anthesis (g/m^2)
UM841	827 a	HY521	1571 a	UM684	863 a
Sinton	764 b	UM684	1552 a	HY521	810 ab
HY521	761 b	Glenlea	1462 b	Glenlea	742 bc
BW90	754 bc	UM841	1397 bc	UM632	687 cd
Glenlea	720 bc	UM632	1394 bc	Benito	623 de
UM632	707 bc	BW90	1363 c	BW90	609 de
UM684	689 c	Benito	1245 d	UM841	570 e
Benito	622 d	Sinton	1227 d	Sinton	464 f

synthates used for root development, it may be reasonable to assume that cultivars with a large above ground biomass at anthesis could have a proportionately smaller root mass than cultivars with a smaller above ground biomass at anthesis. From similar correlations, Cox et al. (1985b) further proposed that this smaller root biomass would have a reduced capacity to accumulate nitrogen late in the season when residual soil nitrate levels are diminished, hence the negative correlation with PAN. Although this study does not involve the range of plant heights of the Cox et al. (1985b) study, the same arguments may apply. This emphasizes the need to know more about the mechanisms of N uptake and particularly the necessity for more study of the root systems.

Total dry matter at maturity (TDM) on a unit area basis ranged from 1269 to 1496 g/m^2 in 1984 (Table 9) and from 1227 to 1571 g/m^2 in 1985 (Table 10). Examination of the cultivar ranks for TDM suggested that TDM was more closely associated with GY than with GPC. In both experimental years, cultivars with high GY, with the exception of UM632 in 1984, assimilated more TDM than cultivars with low GY. Differences were significant in 1984 whereas in 1985, TDM for the lower yielding cultivar BW90, did not differ significantly from the high GY cultivars. This association was confirmed as correlation coefficients for TDM and GY ($r=0.89^{**}$, 0.95^{**}) were highly significant (Appendix Tables 3 and 4). TDM was also positively correlated with GPY ($r=0.40^{*}$, $r=0.60^{**}$) (Appendix Tables 3 and 4) but the association was not as strong as that for GY.

The importance of TDM as a predictor of GY hinges on the fact that GY is a function of TDM and harvest index. Many wheat studies have

reported a significant positive correlation between GY and TDM (Tehlan et al. 1979, McVetty and Evans 1980a,b, Baker and Gebeyehou 1982, Loffler and Busch 1982), although the magnitude of the correlation differs with the genetic material studied and with the environment in which it is grown. Therefore, breeding efforts to enhance TDM , while maintaining harvest index could result in significant GY improvement.

A significant correlation between TDM and GPY (r=.70**) has also been found in the literature (Bhatia 1975). Austin et al. (1977a) similarly concluded that it should be easier to select for enhanced nitrogen uptake from among heavy than from among light genotypes as TDM was significantly correlated with TNM (r=0.79**).

In this study, TDM was also significantly correlated with total plant N at maturity (TNM) in both experimental years (r=0.51**, 0.75**) (Appendix Tables 3 and 4). A close examination of cultivar means, however, suggested that despite this positive correlation, UM632 and UM684 were more efficient at accumulating N per unit dry matter than were the other cultivars. Whereas, as reported earlier, TNM for UM632 and UM684 was significantly higher than for the other high GY cultivars (with the exception of Glenlea in 1984), TDM differences among the high GY cultivars were nonsignificantly different. In fact, UM632 accumulated significantly less TDM than other high GY cultivars in 1984, yet TNM was significantly higher. As there is a causal connection between increased TDM and TNM because of their mutual dependence on photosynthetic carbon fixation, these data suggested that UM632 and UM684 were more efficient at nitrate uptake and reduction relative to dry matter accumulation, than were the other cultivars investigated.

Examination of cultivar means for DMA and TDM indicated that from 49 to 58% of TDM in 1984 and from 48 to 62% of TDM in 1985 was accumulated prior to anthesis. Therefore, approximately 40 to 50% of TDM was accumulated (primarily in the grain), post-anthesis.

The range of cultivar means for post-anthesis accumulated dry matter (PADM) was from 565 to 776 g/m^2 in 1984 (Table 9) and from 464 to 863 g/m^2 in 1985 (Table 10). This difference over years reflected the longer grain filling period in 1985 and the subsequently higher GY. The rank of cultivar means for PADM in both experimental years was, as expected, more closely associated with high GY than with high GPC. High GY cultivars ranked highest for PADM in both experimental years with the expection of UM841 which had significantly lower PADM in in 1985 than in 1984.

A correlation coefficient of r=0.77** for both experimental years (Appendix Tables 3 and 4), confirmed the positive correlation between PADM and GY while the correlations between PADM and GPC were nonsignificant. GPY, a function of GY and GPC was also significantly correlated with PADM (r=0.59**, 0.68**) indicating the role of PADM in accumulating grain protein on a unit area basis.

As PADM is a function of net assimilation rate and leaf area index, the duration of leaf area should also be critical to PADM and therefore, GY (Watson 1952). Many studies have shown this relationship between leaf area duration and hence PADM with GY (Lupton et al. 1967, Yoshida 1972, Khalifa 1973). Bingham (1967) and Yoshida (1972) concluded that maintaining leaf area and PADM was as important as sink size in determining GY.

As leaf area duration is equally important for the post-anthesis N uptake (PAN) reported earlier, it is useful to examine PAN in light of PADM to determine if there is greater cultivar efficiency of N uptake post-anthesis or if PAN is simply a function of PADM. Correlation coefficients over two years indicated a positive correlation between PADM and PAN (r=0.63**, 0.76**) and between PADM and total plant N at maturity (TNM) (r=0.62**, 0.76**) and indicated that much of the variability in TNM was associated with variability in PAN. Examination of cultivar means for PAN and PADM in both experimental years, however, suggested that while UM632 and UM684 did not differ significantly from the high GY cultivars HY521 and Glenlea for PADM, they did have significantly greater PAN than either HY521 or Glenlea. The ratios of PAN:PADM for UM632 (1.2, 1.7) and UM684 (1.1, 1.5) for 1984 and 1985 respectively, are significantly higher than the ratios for Glenlea (.8, 1.2) and HY521 (.7, .9) at P=0.05. These ratios further indicated that the high GY, high GPC cultivars UM632 and UM684, more efficiently accumulated N per unit photosynthate fixed than did the high GY, low GPC cultivars Glenlea and HY521. The low GY, high GPC cultivars BW90 and Benito were intermediate for this ratio while Sinton did not differ significantly from the low GPC cultivars.

The higher TNM and PAN of UM632 and UM684 relative to TDM and PADM will, however, result in enhanced grain N only if a significant proportion of that plant N is remobilized into the developing grain.

4.2.3 Nitrogen Remobilization

The extent and efficiency of remobilization of N from the vegetative tissue is a function of the maximum amount of nitrogen accumulated in the vegetative tissue and the amount of vegetative N remaining at maturity.

The period of maximum vegetative nitrogen accumulation varied with both genotype and year. In 1984, the high GY, low GPC cultivars, Glenlea, HY521 and UM841, achieved a maximum for vegetative N approximately 4 days post-anthesis as did the low GY, high GPC cultivars, Benito , Sinton and BW90. UM632 and UM684 accumulated vegetative nitrogen significantly longer, achieving a maximum 8 days post-anthesis. Results were similar for 1985 with the exception that UM632, UM684 and BW90 reached maximum vegetative N 12 days post-anthesis while all other cultivars reached this point 8 days post-anthesis. This clearly reflected the year effect as well as the greater duration of N uptake of the high GY, high GPC cultivars. These results also suggested that remobilization efficiency values, calculated with anthesis N as an estimate of maximum vegetative nitrogen (Cox et al. 1986, Van Sanford and MacKown 1987), will be underestimated.

Maximum vegetative N varied little among the cultivars tested in 1984, ranging from 11.4 to 12.9 g/m^2 (Table 11), yet significant cultivar differences were clearly evident. In 1985 it ranged from 13.0 to 16.5 g/m^2 (Table 12) and reflected the significant year effect. Again, cultivar differences were significant. Maximum vegetative N was posi-

TABLE 11. Comparison of cultivar means for traits related to remobilization of plant N (1984).

Cultivar	Vegetative N maximum (g/m^2)	Cultivar	Vegetative N maturity (g/m^2)	Cultivar	Vegetative N remobilized (g/m^2)	Cultivar	Remobilization efficiency (%)	Cultivar	Grain N from remobilization (%)
Glenlea	12.9 a	HY521	4.1 a	Glenlea	8.9 a	BW90	72.4 a	HY521	66.4 a
HY521	12.7 ab	UM841	4.0 ab	Sinton	8.7 ab	UM684	72.4 a	Sinton	64.5 ab
Sinton	12.3 abc	Glenlea	4.0 ab	UM684	8.7 ab	UM632	72.3 a	BW90	63.4 ab
UM684	12.0 abc	Sinton	3.6 bc	HY521	8.6 ab	Sinton	70.7 ab	Glenlea	60.4 abc
UM841	11.7 bc	Benito	3.5 cd	UM632	8.3 ab	Benito	69.1 abc	Benito	59.3 abc
UM632	11.5 c	UM684	3.3 cd	BW90	8.3 ab	Glenlea	68.9 abc	UM841	54.3 bc
BW90	11.4 c	UM632	3.2 cd	Benito	7.9 ab	HY521	67.4 bc	UM684	51.6 c
Benito	11.4 c	BW90	3.1 d	UM841	7.6 b	UM841	65.3 c	UM632	50.1 c

TABLE 12. Comparison of cultivar means for traits related to remobilization of plant N (1985).

Cultivar	Vegetative N maximum (g/m^2)	Cultivar	Vegetative N maturity (g/m^2)	Cultivar	Vegetative N remobilized (g/m^2)	Cultivar	Remobilization efficiency (%)	Cultivar	Grain N from remobilization (%)
HY521	16.5 a	UM841	5.3 a	UM684	11.3 a	UM632	75.7 a	Sinton	69.8 a
UM841	16.3 ab	HY521	5.2 a	HY521	11.2 a	UM684	74.2 ab	UM841	66.7 a
Glenlea	15.8 ab	Glenlea	5.0 a	UM632	11.0 a	Sinton	72.8 abc	HY521	65.5 a
UM684	15.2 bc	BW90	4.2 b	UM841	11.0 a	BW90	70.2 bcd	Glenlea	60.0 ab
Sinton	14.6 c	Benito	4.1 bc	Glenlea	10.8 a	Benito	68.9 cd	Benito	54.2 b
UM632	14.5 c	Sinton	4.0 bc	Sinton	10.7 a	Glenlea	68.5 d	BW90	52.8 b
BW90	14.2 c	UM684	3.9 bc	BW90	10.0 ab	HY521	68.1 d	UM632	50.8 b
Benito	13.0 d	UM632	3.5 c	Benito	8.9 b	UM841	67.4 d	UM684	49.9 b

tively correlated with GY (r=0.41**, r=0.85**) and negatively correlated with GPC (r=-0.54**, r=-0.72**) in both experimental years (Appendix Tables 3 and 4). This positive correlation with GY, however, may have simply reflected the greater dry matter at this sampling period as a highly significant positive correlation was detected between maximum vegetative N and the sample date dry matter (r=0.82**, r=0.70**). This was similar to the association found between TNA and DMA, discussed earlier. In summary then, the high GY cultivars had significantly more N available for remobilization to the grain than the low GY cultivars.

Vegetative N at maturity represents the residual N remaining in the vegetative tissue (leaves, culms and nongrain spike parts) at maturity and is one measure of the plants efficiency at translocating N from the vegetative tissue to the grain.

Vegetative N at maturity ranged from 3.1 to 4.1 g/m^2 in 1984 (Table 11) and from 3.5 to 5.3 g/m^2 in 1985 (Table 12) and appeared to be associated with high GY and low GPC. In both experimental years, the high GY and low GPC cultivars retained significantly more N in the vegetative tissue at maturity than high GPC cultivars. Low residual vegetative N at maturity also appeared to be important for combining high GPC with high GY as UM632 and UM684 did not differ significantly from BW90, the lowest cultivar in 1984 and retained the least residual vegetative N at maturity of all of the cultivars investigated in 1985.

Correlation coefficients of vegetative N at maturity with GY, GPC and GPY confirmed that this trait was moderately correlated with GY (r=0.38*, 0.43**) and negatively correlated with GPC (r=-0.49**,

-0.71**) while correlations with GPY were nonsignificant. It can be concluded therefore, that in addition to accumulating vegetative nitrogen, the plant must be able to effectively remobilize it from the vegetative tissue to the grain during grain fill in order to enhance GPC.

The high GY, low GPC cultivars Glenlea, HY521 and UM841 accumulated more vegetative N than the high GPC cultivars but also retained more N in the vegetative tissue at maturity than the high GPC cultivars. This suggested that the high GY cultivars were less efficient at remobilizing N to the developing grain than the high GPC cultivars. The high GY, high GPC cultivars, UM632 and UM684, were intermediate with respect to the maximum amount of vegetative N accumulated but appeared to be the most efficient of the cultivars investigated at remobilizing N from the vegetative tissue at maturity.

This correlation of high GPC with reduced vegetative N at maturity has also been found by Johnson et al. (1967) and Rao et al. (1977). From both of these studies, it was concluded that remobilization efficiency was important for increased GPC.

The difference between maximum vegetative N and vegetative N at maturity was taken as the amount of vegetative N remobilized to the developing grain. The absolute amount of N remobilized varied little among the cultivars studied, ranging from 7.6 to 8.9 g/m^2 in 1984 (Table 11) and from 8.9 to 11.3 g/m^2 in 1985 (Table 12). The similarity of the cultivars for remobilized N indicated that, although high GPC cultivars accumulated less vegetative N than the low GPC cultivars, the high GPC cultivars were more efficient at remobilizing N from the vegetative tis-

sue. This resulted in nonsignificant cultivar differences for net N remobilized. The ability to accumulate vegetative N and the ability to efficiently remobilize that N, represent two complementary physiological strategies which, if combined into one plant, should enhance GPC. It appeared from this study, that the high GPC cultivars attain the levels of GPC reported through the remobilization of amounts of N equal to those of the low GPC cultivars, while maintaining higher levels of post-anthesis N uptake (PAN) than the low GPC cultivars.

Remobilization efficiency has been defined differently by various workers and is frequently underestimated by taking anthesis as the period of maximum accumulation of vegetative N. It was clear from this study that the point of maximum vegetative N occurs after anthesis and is genotype specific. From a comparison of the relative rank of cultivars for total plant N at anthesis (TNA) and maximum vegetative N for both experimental years, it was quite evident that TNA should not be substituted for maximum vegetative N when calculating remobilization efficiency. In this study, remobilization efficiency has been measured as (maximum vegetative N - vegetative N at maturity)/maximum vegetative N X 100 and has been reported as a percentage.

Remobilization efficiency varied from 65.3 to 72.4% in 1984 (Table 11) and from 67.4 to 75.7% in 1985 (Table 12). For both experimental years it was evident that cultivars with high GPC more efficiently remobilized N than cultivars with low GPC. For both experimental years, the high GY , low GPC cultivars ranked lowest with respect to remobilization efficiency.

Correlation coefficients for remobilization efficiency with GPC (Appendix Tables 3 and 4) confirmed that remobilization efficiency was positively correlated with GPC (r=0.52**, 0.62**) in both experimental years. Correlations of this trait with GY were effectively zero while correlations with GPY were nonsignificant in 1984 and significant (r=0.41**) in 1985. Much of variability in remobilization efficiency, as expected, was accounted for by variability in vegetative N at maturity (r=-0.73**, -0.89**) and therefore, selecton for low residual vegetative N would effectively select for remobilization efficiency while being much less labour intensive.

From the literature, it remains unclear as to whether the more efficient and complete translocation of nitrogen from the vegetative tissue to the grain is the physiological basis for higher GPC. Although McNeal et al. (1966, 1968, 1972) and Halloran (1981a) have failed to find significant genotypic effects for N remobilization efficiency, Johnson et al. (1967), and Rao et al. (1977) have both linked increased N remobilization efficiency to high GPC, while Cox et al. (1986) found N remobilization efficiency to be marginally correlated with GPC (r=0.25*). Remobilization efficiency in the latter study, however, was based on anthesis N and therefore may have underestimated this trait. From this study of 8 wide ranging cultivars, N remobilization efficiency was positively correlated with GPC and may in fact have a role in high GY and high GPC, as UM632 and UM684 did not differ significantly from the highest ranked cultivar (BW90) in 1984 and ranked highest among the cultivars studied for N remobilization efficiency in 1985.

Grain N derived from remobilization from the vegetative tissue ranged from 50.1 to 64.4% in 1984 (Table 11) and from 49.9 to 69.8% in 1985 (Table 12). These values were comparable to those reported by Spiertz and Ellen (1978) and Gregory et al. (1981) but were much lower than the maximum value of 83% reported by Van Sanford and MacKown (1987). Clearly, this value is very much genotype and/or environment specific and represents the physiological strategy used by a specific genotype to accumulate grain N.

A range of physiological strategies for accumulating grain N was evident from the 8 cultivars investigated in this study. The high GPC cultivars tended, over the two years, to rely less on N remobilized from the vegetative tissue and more on N uptake during grain fill, whereas, the high GY, low GPC cultivars tended to derive a greater percentage of their grain N from remobilized N and consequently less from uptake during grain fill (Tables 11 and 12). Sinton remains the exception, accumulating more nitrogen in the vegetative tissue and efficiently remobilizing that nitrogen to the developing grain (Tables 11 and 12) while at the same time, relying the least among the cultivars investigated, on post-anthesis N uptake (Tables 7 and 8).

A second measure of nitrogen translocation or the nitrogen partitioning efficiency is the nitrogen harvest index (NHI), taken as the ratio of grain N/total plant N at maturity (TNM). NHI ranged from 76.5 to 83.6% in 1984 (Table 13) and from 75.8 to 86% in 1985 (Table 14) and appeared to be more closely associated with high GPC than with high GY. The high GPC, high GY cultivars partitioned N into the grain most efficiently, ranking highest for NHI in both experimental years. Low GPC

TABLE 13. Comparison of cultivar means for nitrogen harvest index and harvest index (1984).

Cultivar	Nitrogen harvest index (%)	Cultivar	Harvest index (%)
UM632	83.6 a	UM632	41.4 a
UM684	83.4 a	UM841	40.5 a
BW90	81.0 ab	Glenlea	38.3 b
Glenlea	79.3 bc	HY521	38.1 b
Benito	79.3 bc	UM684	38.0 b
Sinton	79.0 bc	Benito	36.2 c
UM841	78.4 bc	BW90	35.9 c
HY521	76.5 c	Sinton	34.9 c

TABLE 14. Comparison of cultivar means for nitrogen harvest index and harvest index (1985).

Cultivar	Nitrogen harvest index (%)	Cultivar	Harvest index (%)
UM632	86.0 a	UM841	46.9 a
UM684	85.7 a	Glenlea	45.3 b
BW90	82.3 b	UM684	44.5 bc
Benito	80.3 bc	HY521	44.4 bc
Sinton	79.5 c	UM632	44.1 bc
Glenlea	78.4 cd	Sinton	43.3 cd
HY521	76.7 de	BW90	42.3 d
UM841	75.8 e	Benito	42.2 d

cultivars generally ranked lowest for NHI although Glenlea did not differ significantly in either year from Benito and Sinton.

Correlation coefficients for NHI and GY, GPC and GPY confirmed that NHI was more closely related to GPC than to GY. In both experimental years, NHI was significantly correlated with both GPC (r=0.55**, r=0.84**) and GPY (r=0.59**, 0.71**) but was not correlated with GY (Appendix Tables 3 and 4). The literature on wheat on the relationship of NHI with GPC has been quite contradictory with researchers finding NHI and GPC positively correlated (Cox et al. 1986), not significantly correlated (Desai and Bhatia 1978, Loffler and Busch 1982) and negatively correlated (Loffler et al. 1985). NHI has been more consistently correlated with GPY (Desai and Bhatia 1978, Loffler and Busch 1982, Loffler et al. 1985 and Cox et al. 1986). The lack of a significant correlation between NHI and GY, found in this study, disagreed with much of the literature on wheat where a significant positive correlation was generally detected between these two traits (Desai and Bhatia 1978, Loffler and Busch 1982, Loffler et al. 1985 and Cox et al. 1986). The differences between this study and those previously reported were attributed to the greater range of GY, GPC and GPY in the cultivars selected for this study, relative to those in the literature.

Finally, NHI was also found to be highly significantly correlated to N remobilization efficiency (r=0.64**, 0.84**) and negatively correlated to vegetative N at maturity (r=-0.75**, -0.85**), as expected. The calculation of both NHI and vegetative N at maturity require only a harvest sample while the calculation of remobilization efficiency requires monitoring vegetative tissue for the point of maximum vegetative N in addi-

tion to the harvest sample. The high correlation of both NHI and vegetative N at maturity with N remobilization efficiency in addition to their higher correlation with GPC, suggested that selection for both high NHI and/or low vegetative N at maturity would effectively select for remobilization efficiency without the amount of labour required to select for N remobilization efficiency per se.

GPC is not only influenced by the amount of N partitioned into the grain but also by the amount of carbohydrate partitioned into the grain or by the harvest index (HI). HI is defined as the ratio of GY/TDM (above ground) and ranged from 34.9 to 41.4% in 1984 (Table 13) and from 42.2 to 46.9% in 1985 (Table 14). The increased HI in 1985 was closely associated with the increased GY detected for that year as TDM over years remained relatively constant. This may have been linked to the moisture conditions late in the 1985 growing season, favorable for greater duration of leaf activity and photosynthetic carbon fixation. HI appeared to be associated with high GY as the high GY cultivars frequently did not differ significantly from one another for HI but had a significantly higher HI in both experimental years than the low GY, high GPC cultivars, Benito and BW90. Sinton differed significantly from all high GY cultivars in 1984 but was only significantly lower than UM841 and Glenlea in 1985.

Correlation coefficients for both experimental years (Appendix Tables 3 and 4), confirmed that HI was highly correlated with GY (r=0.76**, 0.71**) but was inconsistently correlated with both GPY and GPC. In 1984, HI was significantly correlated with GPY (r=0.60**) but was not correlated with GPC, while in 1985, HI was not correlated with GPY but

was significantly inversely correlated with GPC (r=-0.52**). HI has frequently been found to be correlated with increased GY, (Syme 1970, Singh and Stoskopf 1971, Syme 1972, Fischer and Kertesz 1976, Loffler and Busch 1985) and where correlations were significant, this study also reflected the positive correlations found in the literature for HI and GPY (McNeal et al. 1972, Bhatia 1975, Loffler and Busch 1982, Loffler et al. 1985) and the negative correlations found for HI and GPC (McNeal et al. 1972, Bhatia 1975, Loffler and Busch 1982, Loffler et al. 1985). Kramer (1979a,b) has also reported a negative correlation between HI and GPC but further reported that this was more a function of "plant type" genes than of "protein genes". He suggested that the smaller vegetative N reservoir associated with increased HI in addition to the larger quantity of grain biomass produced, resulted in lower GPC. He further found that when GPC was assessed on a constant HI basis, the negative correlation between GPC and HI decreased. Cox et al. (1986) attempted to eliminate the influence of plant type genes on GPC by computing the ratio of NHI/HI. Although the values were moderate, correlations between this ratio and GPC were positive and significant (r=0.39* to r=0.45**).

A similar ratio calculated from the NHI and HI data of this study also showed a significant positive correlation with GPC in both experimental years (r=0.50**, 0.90**) (Appendix Tables 3 and 4) but at the same time, was negatively correlated with GY (r=-0.69**, -0.46**) and was nonsignificantly and moderately correlated (r=0.42**) with GPY in 1984 and 1985 respectively. Therefore, although selection based on this ratio should be useful for increasing GPC, it would not effectively select for increased GY and GPY and therefore would be of little use in most wheat breeding programs.

Examination of the combined NHI and HI data indicated that the high GY, high GPC cultivars, UM632 and UM684, differed from the low GY, high GPC cultivars Benito, Sinton and BW90 in having a HI comparable to the high GY cultivars while maintaining the NHI of the high GPC cultivars. This suggested therefore, that breeders must select for a high efficiency for partitioning both nitrogen and carbon into the grain in order to simultaneously improve both GY and GPC. HI was significantly, although moderately, correlated with NHI in 1984 ($r=0.31^*$) but not in 1985 (Appendix Tables 3 and 4) but has been shown in other studies, to be highly correlated with NHI (Loffler and Busch 1982, Loffler et al. 1985, Cox et al. 1986). This indicated therefore, that it should be possible to improve GY while maintaining GPC by selecting for increased HI while maintaining NHI levels.

4.3 Inheritance Study

4.3.1 Preliminary Analyses

The frequency distribution of each generation for each trait measured was tested against a normal distribution, with mean and variance equal to the sample mean and variance, using the Kolmogorov Smirnov D-statistic. The analyses indicated that the data from each generation approximated the normal distribution and consequently, no transformation of the data was required.

Analyses of variance for the UM684/Sinton cross indicated that variances for grain protein concentration (GPC) in the segregating F_2 generation of .457 and .398 for the Winnipeg and Portage locations respectively were significantly greater that the mean variance of the nonsegregating parental and F_1 generations (.240, .150) for these two locations. It was therefore concluded that UM684 and Sinton were different genetic sources of grain protein.

Analyses of variance for reciprocal F_1 values for both crosses at both experimental locations indicated that there were no significant reciprocal F_1 differences for most traits measured. Significant reciprocal F_1 differences were, however, detected for GPC and grain yield (GY) at one location of the HY521/Sinton cross. At Winnipeg, GPC was significantly higher when the female parent was Sinton, while GY on the other hand, was significantly higher when the female parent was HY521. Since these reciprocal differences were not consistent over locations, it was assumed that these traits, as well as those for which reciprocal differences were not detected, were predominantly under nuclear genetic control and therefore were analysed as such.

Variances of the means (i.e. standard errors squared) of each generation for all traits were tested for homogeneity using a Bartlett's test and were found to be heterogeneous. Consequently all genetic means analyses reported result from weighted least squares analyses.

Preliminary genetic data used for means and variance analyses are presented in Appendix Tables 5 through 12 and provide the reader with generation means, variances of the means (standard errors squared) and generation variances for each cross, location and trait analysed.

It was clear from the preliminary data that for all traits and both experimental locations, the variances of the segregating generations were large in comparison to the variances for the nonsegregating parental and F_1 generations. The mean variance of the parents and F_1 was taken as an estimate of the environmental component of the observed variability for each trait and therefore, it was concluded that there was a large genetic component of the phenotypic variability. Analyses of variance verified the significance of this genetic component of the phenotypic variability for all traits analysed.

4.3.2 Means Analyses of Grain Protein Related Traits

The means for total plant nitrogen at maturity (TNM), nitrogen harvest index (NHI), grain protein concentration (GPC) and grain protein yield (GPY), were analysed using the joint scaling test of Cavalli (1952) outlined by Mather and Jinks (1977).

4.3.2.1 Total Plant Nitrogen at Maturity. The mean F_1 values for TNM indicated that gene action governing the expression of this trait in the HY521/UM684 cross was confounded by heterosis as the F_1 mean exceeded that of the higher parent (Appendix Table 5). Generation means analysis, as outlined by Mather and Jinks (1977), is not designed to accomodate overdominance and therefore, the analysis was run without the F_1 values in order to decrease its confounding effect. It was recognized

that this confounding effect will persist to the F_2 but will be very much reduced because of the reduction by 1/2 of the heterozygosity in the F_2. F_2 values were therefore included in the analyses.

Analyses of P_1, P_2, F_2, B_1, B_2 and F_3 generation means for the HY521/UM684 cross indicated that TNM had both additive and dominance genetic effects (Table 15). The dominance effect was large relative to the additive effect and was for increased TNM but again, the magnitude of this value may have reflected a degree of overdominance. Epistasis was nonsignificant.

Overdominance was not evident in the HY521/Sinton cross (Table 16) and therefore the analyses were run with parental, F_1, F_2, B_1, B_2 and F_3 generation means. The sign on the additive component (d) was negative and reflected the consistent use of the parent with high GPC (Sinton) as P_1 and the parent with low GPC (HY521) as P_2 for the analyses of all traits. The negative value associated with the 'd' estimate simply indicated that for the HY521/Sinton cross, P_2 actually accumulated more N by maturity than P_1, hence the negative sign associated with the P_1-P_2 estimator.

Gene effects for TNM were primarily additive but again, a significant dominance component for increased TNM was evident for both locations. Nonallelic gene action also influenced the expression of TNM. At both the Winnipeg and Portage locations, additive x additive epistasis (i) was significant, while at Portage there was also a significant additive x dominance (j) component detected. The importance of the latter, however, was unclear as it was not consistent over locations. The consis-

TABLE 15. Means analyses results for total plant N at maturity (TNM), nitrogen harvest index (NHI), grain protein concentration (GPC) and grain protein yield (GPY) for the HY521/UM684 cross.

Location	Parameter	TNM	NHI	GPC	GPY
Winnipeg					
	m	2.96 ± .02	72.4 ± .2	15.3 ± .03	12.3 ± .1
	d	0.03 ± .01	3.1 ± .2	1.5 ± .03	0.7 ± .1
	h	0.15 ± .06	1.0 ± .5	-0.2 ± .06	0.6 ± .3
	χ^2	6.71 (3df)	7.86 (4df)	8.44 (4df)	6.22 (3df)
	P(.05)	7.81	9.49	9.49	7.81
Portage					
	m	2.68 ± .03	72.5 ± .4	15.4 ± .04	11.4 ± .1
	d	0.09 ± .03	2.3 ± .2	1.5 ± .04	0.5 ± .1
	h	0.19 ± .08	4.5 ± .8	-0.2 ± .08	0.6 ± .3
	i	-	2.7 ± .5	-	-
	χ^2	3.81 (3df)	7.70 (3df)	7.88 (4df)	4.71 (3df)
	P(.05)	7.81	7.81	9.49	7.81

TABLE 16. Means analyses results for total plant N at maturity (TNM), nitrogen harvest index (NHI), grain protein concentration (GPC) and grain protein yield (GPY) for the HY521/Sinton cross.

Location	Parameter	TNM	NHI	GPC	GPY
Winnipeg					
	m	2.78 ± .04	70.6 ± .3	14.9 ± .04	10.9 ± .2
	d	-0.61 ± .02	2.6 ± .2	1.1 ± .04	-1.9 ± .1
	h	0.37 ± .06	-2.0 ± .6	-0.4 ± .08	1.5 ± .4
	i	0.13 ± .05	-	-	0.6 ± .3
	χ^2	7.16 (3df)	7.54 (4df)	2.86 (4df)	1.23 (3df)
	P(.05)	7.81	9.49	9.49	7.81
Portage					
	m	1.96 ± .04	75.5 ± .2	15.0 ± .03	8.2 ± .2
	d	-0.68 ± .03	2.3 ± .2	1.1 ± .04	-2.8 ± .1
	h	0.30 ± .07	-0.9 ± .5	-	1.4 ± .3
	i	0.11 ± .05	-	0.2 ± .06	0.7 ± .2
	j	0.52 ± .10	-	-	2.2 ± .4
	χ^2	3.12 (2df)	1.20 (4df)	6.91 (4df)	3.24 (2df)
	P(.05)	5.99	9.49	9.49	5.99

tent significance of the additive x additive component over locations indicated that the genes governing TNM in Sinton differ from those of UM684 where no epistasis was detected but should have little consequence for the breeder as this component can be fixed, along with the additive effects, by traditional plant breeding methods.

In summary, gene effects for TNM appears to consist of both an additive component and a dominance component for high TNM. An additive x additive component also played a role in the inheritance of this trait but its influence appears to be genotype specific.

4.3.2.2 Nitrogen Harvest Index. NHI was governed by both additive and dominant genes in the HY521/UM684 cross (Table 15). Dominance was for high NHI. A significant additive x additive nonallelic component was detected for the Portage location but, as this was not consistent over locations, its relative contribution to the expression of genes for NHI in UM684 remains unclear.

For the HY521/Sinton cross, a simple additive - dominance model adequately fit the data for both locations (Table 16). Dominance gene effects, however, were for lower NHI, which indicated that Sinton differs from UM684 in genes governing the expression of NHI.

In summary, both additive and dominance gene effects governed the expression of NHI but the degree and direction of dominance was genotype specific. The role of epistasis in the inheritance of NHI remains unclear.

4.3.2.3 Grain Protein Concentration. A highly significant additive genetic effect was detected for GPC over both locations of the HY521/UM684 cross (Table 15). Dominance gene effects for low GPC were also significant although the magnitude of the contribution of this component was small in comparison to the additive genetic component. For both locations, the simple additive-dominance model adequately described the data and therefore, it was concluded that epistatic effects do not contribute significantly to the expression of genes for GPC in the HY521/UM684 cross.

For both locations of the HY521/Sinton cross, a highly significant additive component of the means was again detected for GPC (Table 16). At Winnipeg, a dominance component for low GPC was also significant but this was not consistent over locations. This may have been due to a combination of environmental influences on the expression of these genes and their dispersion within the parents which may have resulted in the cancellation of dominance gene effects at Portage. A simple additive-dominance model did not adequately explain the means data for the Portage location and therefore the model was extended to the six parameter epistatic model. Of the three interaction components, only the additive x additive component ,(i),was significant which again for a plant breeder, is of little consequence as it can be fixed with selection.

The inheritance of GPC detected in this study and particularly in the HY521/UM684 cross, is in agreement with much of the literature which also suggests the importance of additive and partial dominance gene effects for low GPC in both winter wheat (Chapman and McNeal 1970,

Johnson et al. 1963, Diehl et al. 1978) and spring wheat (Halloran 1981b, Sampson et al. 1983). The possible role of additive x additive epistasis in the HY521/Sinton cross is also in agreement with similar findings in wheat (Sampson et al. 1983). This study, however, differs from the work of Hsu and Sosulski (1969) and Cowley and Wells (1980), who found dominant genes for high GPC in spring wheat.

Finally, the significant reciprocal F_1 differences detected for GPC for one location of the HY521/Sinton cross suggested that there may be some maternal influence on the expression of genes for GPC. This maternal influence however, appears to be small and genotype specific. The possible role of maternal inheritance for GPC was also proposed by Millet et al. (1984) who found some evidence for maternal inheritance of GPC in very high protein wild wheats.

4.3.2.4 Grain Protein Yield. Overdominance was detected for GPY for both locations of the HY521/UM684 cross (Appendix Table 7), and as such, the F_1 was not included in the generation means analyses.

A simple additive-dominance model adequately explained GPY from P_1, P_2, F_2, B_1, B_2 and F_3, at both locations (Table 15). Partial dominance was for high GPY. The dominance component however, was roughly equal to the additive component possibly reflecting some residual overdominance in the F_2 but also indicating its relative importance. Epistasis did not significantly contribute to GPY for this cross.

Grain protein yield for the HY521/Sinton cross (Table 16) was more complexly inherited. A significant additive component was detected, the

negative sign for which indicated that under spaced conditions, GPY for HY521 (P_2) was higher than for Sinton (P_1). A large significant dominance component, again for increased GPY, was also detected. Epistasis also significantly influenced GPY. A consistent additive x additive component was detected over both locations while additive x dominance (j) inter-allelic interactions were significant only for the Portage location. The relative importance of the additive x dominance inter-allelic interactions in the inheritance of GPY therefore, remains questionable.

In summary, the inheritance of GPY is significantly influenced by additive, dominance and epistatic gene effects, the latter being genotype specific. The large dominance component relative to the additive component, suggested that efforts to improve this trait would be most effective in advanced generations where the dominant component would be significantly reduced.

4.3.3 Means Analyses for Grain Yield and Related Traits

Generation means for grain yield (GY) and its two physiological components, total dry matter (TDM), and harvest index (HI), were analysed using the joint scaling test of Cavalli (1952) as outlined by Mather and Jinks (1977).

4.3.3.1 Total Dry Matter. A significant additive component for total dry matter (TDM) was detected for both locations of the HY521/UM684 cross (Table 17). The negative sign associated with this estimate again simply indicated that under spaced conditions, HY521 (P_2) accumulated more TDM than UM684 (P_1). A large degree of dominance for high TDM was also detected for this cross. The simple additive-dominance model adequately fit the data and therefore it was concluded that epistasis did not significantly influence the expression of genes for TDM.

A highly significant additive genetic component was again detected for TDM in the HY521/Sinton cross (Table 18). Again, the negative sign associated with this estimate indicated that HY521 (P_2) accumulated more TDM than Sinton (P_1). A large, highly significant dominance component for high TDM was also detected. As the simple additive-dominance model did not adequately fit the data, the complexity of the model was increased to include the nonallelic interations. Additive x additive epistasis influenced TDM over both locations while the additive x dominance component was significant for only the Portage location.

It was concluded that both additive and dominance genetic effects influenced TDM with partial dominance for increased TDM. The influence of nonallelic interactions on the expression of the trait appeared to be genotype specific and additive in nature and therefore would not hinder a breeding program. Finally, TDM was more complexly inherited in the HY521/Sinton cross than in the HY521/UM684 cross which indicated that these two sources of high GPC differed in genes determining the accumulation of dry matter.

TABLE 17. Means analyses results for total dry matter (TDM), harvest index (HI) and grain yield (GY) for the HY521/UM684 cross.

Location	Parameter	TDM	HI	GY
Winnipeg				
	m	185.5 ± 1.4	43.3 ± .2	80.3 ± 0.7
	d	-13.2 ± 1.4	1.1 ± .2	-3.6 ± 0.7
	h	9.8 ± 2.8	0.9 ± .4	5.3 ± 1.7
	χ^2	9.30 (4df)	6.71 (3df)	6.83 (3df)
	P(.05)	9.49	7.81	7.81
Portage				
	m	167.3 ± 2.0	42.9 ± .2	73.3 ± 1.1
	d	-16.5 ± 2.0	0.8 ± .2	-5.1 ± 0.9
	h	11.5 ± 4.1	1.0 ± .5	4.7 ± 2.3
	χ^2	9.24 (4df)	2.14 (3df)	1.63 (3df)
	P(.05)	9.49	7.81	7.81

TABLE 18. Means analyses results for total dry matter (TDM), harvest index (HI) and grain yield (GY) for the HY521/Sinton cross.

Location	Parameter	TDM	HI	GY
Winnipeg				
	m	173.7 ± 2.7	43.0 ± 0.1	73.9 ± 1.2
	d	-48.3 ± 1.5	1.4 ± 0.2	-18.4 ± 0.6
	h	24.1 ± 4.2	-	11.1 ± 1.9
	i	8.6 ± 3.3	-	4.8 ± 1.4
	χ^2	6.57 (3df)	10.74 (5df)	6.58 (3df)
	P(.05)	7.81	11.07	7.81
Portage				
	m	124.4 ± 3.1	42.4 ± 0.1	55.9 ± 1.3
	d	-55.1 ± 1.8	0.9 ± 0.2	-22.7 ± 0.9
	h	33.3 ± 4.5	-	7.2 ± 2.2
	i	17.0 ± 3.6	-	4.3 ± 1.6
	j	40.7 ± 6.4	-	14.3 ± 2.7
	χ^2	0.83 (2df)	8.10 (5df)	4.89 (2df)
	P(.05)	5.99	11.07	5.99

4.3.3.2 Harvest Index. Overdominance for harvest index (HI) was detected in the HY521/UM684 cross as evidenced by the greater mean of the F_1, relative to the higher parent (Appendix Table 9). As such, means analyses for both locations were carried out without the F_1 generation in an effort to minimize the confounding influence of this type of gene action on the results.

A simple additive-dominance model adequately fit the data for P_1, P_2, F_2, B_1, B_2 and F_3 (Table 17). The magnitude of the dominance component was large relative to the additive component and was in the direction of increased HI. Epistasis was nonsignificant.

Overdominance was not detected for HI in the HY521/Sinton cross and therefore the means analyses were carried out on all seven generations. HI was found to be simply inherited, with only an additive component significantly influencing the expression of this trait (Table 18).

In summary, HI was found to be relatively simply inherited, but the nature of the gene effects appeared to be genotype specific. The simple additive-dominance model with dominance for high HI, detected for the HY521/UM684 cross, agreed with other reports in the literature for the inheritance of HI (Bhatt 1976, Nanda et al. 1982, Singh et al. 1986). It appeared from this study however, that the dominance component is genotype specific. Epistasis did not significantly influence the expression of HI in this study. This is in agreement with reports in the literature (Nanda et al. 1982, Singh et al. 1986) and therefore, improvement in HI with selection should be relatively easy.

4.3.3.3 Grain Yield. Overdominance again confounded the means analyses for GY for the HY521/UM684 cross (Appendix Table 11). Consequently, the analyses for both locations were performed on six generations with the F_1 generation excluded. The results are presented in Table 17.

For both locations, a simple additive-dominance model adequately fit the generation means data. The dominance component was large relative to the additive component and was in the direction of increased GY. The magnitude of this estimate, however, may have been partially influenced by residual overdominance in the F_2, particularly for the Winnipeg location. Epistasis, although tested, did not significantly influence the expression of genes for GY in this cross.

Overdominance for GY was not detected in the F_1 data for the HY521/Sinton cross (Appendix Table 12) and therefore, generation means analyses were performed on all seven generations.

Additive, dominance and epistatic gene effects were all found to significantly influence the expression of GY in the HY521/Sinton cross (Table 18). A highly significant additive component was detected for both locations, the negative sign for which indicated that under spaced conditions, HY521 (P_2), had a higher GY than Sinton. Dominance effects for increased GY were also highly significant and again, large in magnitude relative to the additive component. This indicated the relative importance of dominance in the inheritance of GY for this cross. Nonallelic additive x additive (i) genetic interactions were detected over both locations while additive x dominance (j) interactions were significant only at the Portage location and therefore, were presumed to

be of less importance to the inheritance of GY than the additive x additive interactions.

In summary, GY appeared to be conditioned by both additive and dominant genes with partial dominance for increased GY. These results were in agreement with those reported in literature (Stuber et al. 1962, Walton 1971, Chapman and McNeal 1971), but were contrary to those of Halloran (1981b) who found dominance for low GY. In addition to additive and dominance genetic effects, significant additive x additive and additive x dominance interactions were detected for GY in the HY521/Sinton cross. These findings are also supported in the literature where epistatic genes for GY have frequently been reported (Ketata et al. 1978, Singh and Singh 1978, Singh et al. 1986). The complexity of the inheritance of GY and the predominance of dominance genetic effects, confirms what breeders have found when selecting for GY per se, namely that selection is most effective in advanced generations where dominance is reduced due to homozygosity.

4.3.4 Variance Analyses for Grain Protein Related Traits

The generation variances for TNM, NHI, GPC and GPY, were analysed as outlined by Mather and Jinks (1977) and provided estimates of the additive (D), dominance (H) and environmental (E) components of the phenotypic variance. In addition, a fourth component (F), which arose from the partitioning of the variation in the backcross generations, was

estimated. The F component was not different from zero in the analyses of all traits for both crosses at both locations and therefore, only the D, H and E components of variance are reported.

4.3.4.1 Total Plant Nitrogen at Maturity. Analyses of variance for TNM for the HY521/UM684 cross for both locations detected significant additive and dominance components to the observed variation (Table 19). This trait was largely under genetic control as evidenced by the collective magnitude of the additive and dominance components relative to the environmental component of the variation. The large dominance component relative to the additive component, however, indicated that selection for TNM would be most effective in advanced generations where the dominance variance is minimal.

Similarly, for the HY521/Sinton cross at both locations (Table 20), there was a large genetic component of the observed variation relative to the environmental component, with both significant additive and dominance components. Dominance variance was again large relative to additive variance and therefore, early generation selection for TNM would be ineffective.

4.3.4.2 Nitrogen Harvest Index. The phenotypic variance observed for NHI also consisted of significant additive, dominance and environmental components of variance for both locations of the HY521/UM684 cross (Table 19). Additive genetic variance, which represents the proportion of the variance that can be fixed with selection, was larger than the

TABLE 19. Variance components analyses results for total plant N at maturity (TNM), nitrogen harvest index (NHI), grain protein concentration (GPC) and grain protein yield (GPY) for the HY521/UM684 cross.

Location	Component	TNM	NHI	GPC	GPY
Winnipeg					
	D	11.26 ± 1.18	8.03 ± 1.21	4.78 ± 0.67	19.39 ± 2.47
	H	32.09 ± 2.61	6.43 ± 2.67	2.85 ± 1.48	59.10 ± 5.46
	E	5.03 ± 0.31	6.61 ± 0.32	1.22 ± 0.18	9.42 ± 0.65
	χ^2	1.57 (5df)	1.63 (5df)	0.50 (5df)	6.84 (5df)
	P(.05)	11.07	11.07	11.07	11.07
Portage					
	D	13.62 ± 3.06	8.41 ± 0.83	5.73 ± 1.52	19.58 ± 2.51
	H	25.85 ± 6.77	3.16 ± 1.84	5.75 ± 3.37	74.45 ± 5.55
	E	7.18 ± 0.80	7.82 ± 0.22	1.40 ± 0.40	9.05 ± 0.66
	χ^2	10.53 (5df)	0.78 (5df)	2.61 (5df)	7.08 (5df)
	P(.05)	11.07	11.07	11.07	11.07

TABLE 20. Variance components analyses results for total plant N at maturity (TNM), nitrogen harvest index (NHI), grain protein concentration (GPC) and grain protein yield (GPY) for the HY521/Sinton cross.

Location	Component	TNM	NHI	GPC	GPY
Winnipeg					
	D	7.30 ± 3.12	10.60 ± 2.19	8.91 ± 0.46	36.36 ± 2.97
	H	16.05 ± 6.89	11.93 ± 4.83	-	17.85 ± 6.56
	E	5.93 ± 0.82	5.64 ± 0.57	1.48 ± 0.15	17.22 ± 0.78
	χ^2	10.94 (5df)	5.38 (5df)	0.61 (6df)	9.91 (5df)
	P(.05)	11.07	11.07	12.59	11.07
Portage					
	D	10.44 ± 2.53	4.96 ± 2.10	54.72 ± 1.53	24.19 ± 2.10
	H	14.44 ± 5.59	9.02 ± 4.53	-	8.89 ± 4.46
	E	4.81 ± 0.66	5.61 ± 0.55	20.40 ± 0.50	10.71 ± 0.53
	χ^2	7.19 (5df)	4.95 (5df)	6.72 (6df)	4.58 (5df)
	P(.05)	11.07	11.07	12.59	11.07

dominance component and therefore, indicated that selection for this trait would be successful.

For the HY521/Sinton cross (Table 20), both additive and dominance variances were again significant but the dominance component was proportionately larger than that for the HY521/UM684 cross. The significance of this is questionable, however, as the variability in the dominance estimate itself was also larger.

4.3.4.3 Grain Protein Concentration. Analyses of the generation variances for GPC indicated that, for the HY521/UM684 cross (Table 19), the genetic component was large relative to the environmental component of the variance. Both additive and dominance variance contributed significantly to the genetic variance for GPC. The precision and magnitude of the dominance estimate, however, indicated that a large proportion of the genetic variation could be fixed with selection.

For the HY521/Sinton cross (Table 20), the heritable variation for GPC was entirely additive and therefore, the trait would respond well to selection. In addition, the magnitude of the environmental component relative to the additive component suggested that early generation selection would be successful.

4.3.4.4 Grain Protein Yield. The phenotypic variation observed for GPY in the HY521/UM684 cross (Table 19), again consisted of a sizable heritable component relative to the environmental component of variation. The dominance component however, was large relative to the additive com-

ponent and therefore, selection would be most effective in the more homogenous advanced generations where dominance variance is minimized.

The variance observed for GPY in the HY521/Sinton cross (Table 20) again indicated a large genetic component of the phenotypic variation. The dominance component was relatively smaller in this cross but the larger standard error associated with the estimate render further conclusions questionable.

In summary, for the grain protein related traits investigated, phenotypic variation was partitioned into predominantly genetic variation suggesting that progress from selection was possible in all traits. However, the proportion of the genetic variance that was additive and therefore fixable, varied with the trait and genotype investigated.

4.3.5 Variance Analyses for Grain Yield and Related Traits

The generation variances for TDM, HI and GY were also analysed as outlined by Mather and Jinks (1977). Again, the F component estimated from the backcross generations was not different from zero for all traits in both crosses at both locations and therefore, only D, H and E estimates are presented.

4.3.5.1 Total Dry Matter. The phenotypic variance of TDM for the experimental generations of the HY521/UM684 cross was partitioned into sig-

nificant additive, dominance and environmental components (Table 21). Again the heritable variation was large relative to the environmental variation but the very large dominance component relative to the additive component for this cross indicated that selection for TDM would be most effective in advanced generations.

Similarly, for the HY521/Sinton cross, both additive and dominance components of the variation for TDM were significant and large relative to the environmental component (Table 22). The magnitude of the dominance component again suggested the advantage of selection for TDM in advanced generations although once again, the precision of the dominance estimates was poor.

4.3.5.2 Harvest Index. Generation variance analyses for HI for the HY521/UM684 cross (Table 21) partitioned the observed variance into significant additive, dominance and environmental components. The magnitude of the collective additive and dominance components suggested that much of the phenotypic variance was heritable. The additive component of the heritable variation was large compared to the dominance component but again, the standard error associated with the dominance estimate was large.

Genetic variance for HI for the HY521/Sinton cross (Table 22) was entirely additive and significantly larger than the environmental component. This suggested that good progress could be made in HI with selection. The lack of dominanace variance for this trait indicated that early generation selection for HI would be successful.

TABLE 21. Variance components analyses results for total dry matter (TDM), harvest index (HI) and grain yield (GY) for the HY521/UM684 cross.

Location	Component	TDM	HI	GY
Winnipeg				
	D	6.80 ± 2.71	9.24 ± 1.48	7.86 ± 3.02
	H	11.10 ± 6.02	6.73 ± 3.28	20.49 ± 6.69
	E	1.63 ± 0.72	3.14 ± 0.39	4.20 ± 0.80
	χ^2	8.35 (5df)	2.48 (5df)	10.31 (5df)
	P(.05)	11.07	11.07	11.07
Portage				
	D	6.48 ± 3.05	8.87 ± 1.20	8.76 ± 2.58
	H	13.24 ± 6.74	4.47 ± 2.64	15.75 ± 5.69
	E	3.48 ± 0.80	2.87 ± 0.31	8.13 ± 0.68
	χ^2	10.46 (5df)	1.61 (5df)	7.46 (5df)
	P(.05)	11.07	11.07	11.07

TABLE 22. Variance components analyses results for total dry matter (TDM), harvest index (HI) and grain yield (GY) for the HY521/Sinton cross.

Location	Component	TDM	HI	GY
Winnipeg				
	D	6.19 ± 2.63	7.18 ± 1.04	8.48 ± 2.97
	H	10.67 ± 5.81	-	20.31 ± 6.56
	E	1.97 ± 0.69	3.55 ± 0.34	3.98 ± 0.78
	χ^2	7.78 (5df)	3.11 (6df)	9.91 (5df)
	P(.05)	11.07	12.59	11.07
Portage				
	D	9.19 ± 0.76	8.84 ± 1.20	10.62 ± 1.82
	H	3.75 ± 1.39	-	7.10 ± 4.01
	E	2.08 ± 0.11	3.16 ± 0.39	6.63 ± 0.48
	χ^2	0.23 (5df)	4.11 (6df)	3.71 (5df)
	P(.05)	11.07	12.59	11.07

4.3.5.3 Grain Yield. Generation variances for GY for the HY521/UM684 cross (Table 21), were partitioned into significant additive, dominance and environmental components. As expected, the environmental component for GY was larger than for other traits measured. A dominance component, significantly larger than the additive component, reflected the large dominance component detected in the means analyses reported earlier and confirmed the need for advanced generation selection when the selection criterion is GY per se.

Similarly, for the HY521/Sinton cross (Table 22), significant additive and dominance variance components indicated the magnitude of the heritable component of the phenotypic variance. The dominance component was significantly larger than the additive component for the Winnipeg location but was lower at the Portage location. The standard error associated with the Portage estimate, however, was greater than 50% of the estimate and consequently further conclusions are not justified.

In summary, the phenotypic variance of GY and the related traits investigated was predominantly heritable but the relative size of the additive and dominance components varied with both trait and genotype investigated. For both TDM and GY, the large dominance component of the observed variation suggested that selection for these traits should be delayed to advanced generations when the dominance variance is negligible due to homozygosity. Finally, the magnitude of the standard errors associated with the D and H estimates for all traits investigated, compared to those for (d) and (h) estimated from the means analyses reported earlier, clearly illustrated the decreased precision associated with analyses based on second degree statistics, (variances).

4.3.6 Heritability

The extent to which selection for a particular trait is likely to be effective is determined by the heritability of that trait or, the proportion of the total phenotypic variation for the trait that is genetic. This is termed heritability in the broad sense and is the ratio of the heritable variance, both the additive and non-additive components, over the overall phenotypic variance. Of particular interest to the plant breeder is the narrow sense heritability because it represents that portion of the genetic variance that will respond to selection or is fixable. It is defined as the ratio of the additive genetic variance over the total phenotypic variance.

4.3.6.1 Total Plant Nitrogen at Maturity. F_2 broad sense heritabilities for TNM ranged from 0.65 to 0.73 for the HY521/UM684 cross and from 0.56 to 0.65 for the HY521/Sinton cross (Table 23). These estimates are significantly larger than the broad sense estimate reported by Austin et al. (1977a) from an analysis of variance or 47 winter wheat genotypes but may simply reflect the differences in the genetic material and analytical technique used. Heritability in the narrow sense for TNM reflected the large dominance component of the heritable variation in both crosses and ranged from 0.30 to 0.33 for the HY521/UM684 cross and from 0.27 to 0.38 for the HY521/Sinton cross. The consistency of these narrow sense estimates over genotype and location suggested that TNM is moderately heritable and can therefore be improved with selection although the rate of improvement would be slow.

TABLE 23. Estimates of broad and narrow sense heritabilities for total N at maturity (TNM), nitrogen harvest index (NHI), grain protein concentration (GPC) and grain protein yield (GPY).

Cross	Location	Heritability[1]	TNM	NHI	GPC	GPY
HY521/UM684	Winnipeg	Broad sense	.73	.46	.72	.72
		Narrow sense	.30	.33	.55	.29
	Portage	Broad sense	.65	.39	.76	.76
		Narrow sense	.33	.33	.50	.26
HY521/Sinton	Winnipeg	Broad sense	.56	.59	.75	.57
		Narrow sense	.27	.38	.75	.46
	Portage	Broad sense	.65	.46	.57	.57
		Narrow sense	.38	.24	.57	.48

[1] Estimates calculated according to Warner (1952).

4.3.6.2 Nitrogen Harvest Index. F_2 broad sense heritability for NHI for the HY521/UM684 cross ranged from 0.39 to 0.46 while for the HY521/Sinton cross broad sense estimates for the F_2 ranged from 0.46 to 0.59 (Table 23). These estimates are somewhat lower than those reported by Loffler and Busch (1982) which ranged from 0.59 to 0.65. Differences were again attributed to differences in both the genetic material and the analytical technique used. Narrow sense heritability estimates were similar at 0.33 for both locations of the HY521/UM684 cross and ranged from 0.24 to 0.38 for the HY521/Sinton cross. Narrow sense estimates of this order of magnitude, although lower than a breeder would desire, are sufficiently large to enable reasonable progress from selection.

4.3.6.3 Grain Protein Concentration. GPC for the two crosses under investigation proved to be highly heritable (Table 23). Broad sense heritability estimates for the F_2, ranged from 0.72 to 0.76 for the HY521/UM684 cross and from 0.57 to 0.75 for the HY521/Sinton cross. These estimates are of the same order of magnitude as those reported in both winter wheat (Haunold et al. 1962b, Stuber et al. 1962) and spring wheat (Baker et al. 1968, Hsu and Sosulski 1969, and Loffler and Busch 1982). Narrow sense heritability estimates for the HY521/UM684 cross ranged from 0.50 to 0.55 and reflected the significant dominance component of the genetic variation detected for this genotype. Narrow sense heritability for the HY521/Sinton cross equalled the broad sense estimates (0.57 and 0.75) and reflected the lack of a dominance component of variance for this cross. These estimates were similar in magnitude to those reported for GPC in winter wheat (Lofgren et al. 1968) and in

spring wheat (Halloran 1981b), but were higher than those reported by Sampson et al. (1983) which ranged from 0.25 to 0.50. These differences may reflect the F_2 - F_3 parent-offspring regression techniques used by Sampson et al. (1983), a difference in the genetic material, or both. The magnitude of the narrow sense heritability estimates obtained from this study for GPC however, suggested that good progress could be expected from selection and that early generation selection for GPC would be successful.

4.3.6.4 Grain Protein Yield. Broad sense heritabilities for GPY ranged from 0.72 to 0.76 for the HY521/UM684 cross and equalled 0.57 for both locations of the HY521/Sinton cross (Table 23). These data closely resembled broad sense estimates for GPY reported by Loffler and Busch (1982) but were significantly higher than similar estimates reported by Cox et al. (1985a) which ranged from 0.21 to 0.27. Narrow sense estimates for the HY521/UM684 cross ranged from 0.26 to 0.29 and clearly relected the large dominance variance component reported for this trait earlier. Narrow sense heritability estimates for the HY521/Sinton cross were higher, ranging from 0.46 to 0.48 and indicated that good progress could be expected if selection were practiced for GPY.

4.3.6.5 Total Dry Matter. Broad sense heritability estimates for TDM ranged from 0.65 to 0.79 for the HY521/UM684 cross and from 0.73 to 0.75 for the HY521/Sinton cross (Table 24). Narrow sense estimates reflected the magnitude of the dominance component of variance and ranged from 0.32 to 0.44 for the HY521/UM684 cross and from 0.40 to 0.60 for the

TABLE 24. Estimates of broad and narrow sense heritabilities for total dry matter (TDM), harvest index (HI) and grain yield (GY).

Cross	Location	Heritability [1]	TDM	HI	GY
HY521/UM684	Winnipeg	Broad sense	.79	.67	.68
		Narrow sense	.65	.49	.30
	Portage	Broad sense	.65	.66	.51
		Narrow sense	.32	.53	.27
HY521/Sinton	Winnipeg	Broad sense	.75	.50	.70
		Narrow sense	.40	.50	.32
	Portage	Broad sense	.73	.58	.52
		Narrow sense	.60	.58	.39

[1] Estimates calculated according to Warner (1952).

HY521/Sinton cross. The broad sense heritability estimates were of the approximate magnitude of those reported by Loffler and Busch (1982), but were significantly larger than the 0.40 broad sense heritability estimate reported by Austin et al. (1977a) and than those reported by Cox et al. (1985a) which ranged from 0.32 to 0.44. The discrepency with the results of Cox et al. (1985a) was again attributed to differences in genetic material and analytical technique used. The magnitude of the heritability estimates, particularly the narrow sense estimates, suggested that good progress could be expected in TDM if selection was practised for this trait in the advanced generations.

4.3.6.6 Harvest Index. HI for the two crosses investigated proved to be highly heritable in both the broad and narrow sense (Table 24). Broad sense heritabilities ranged from 0.66 to 0.67 for the HY521/UM684 cross and from 0.50 to 0.58 for the HY521/Sinton cross. Narrow sense heritability estimates for the HY521/UM684 cross were lower due to the significant dominance variance for HI reported earlier and ranged from 0.49 to 0.53 while for the HY521/Sinton cross, they equalled the broad sense estimates of 0.50 and 0.58 due to a zero dominance variance for the cross. The literature reports equally high broad sense heritabilities for HI, ranging from 0.48 to 0.80 (Bhatt 1976) and from 0.60 to 0.80 (Loffler and Busch 1982). Singh et al. (1986), however, using different genetic material reported much lower broad sense and narrow sense heritability estimates for HI (0.39 and 0.28 respectively). In summary, heritability estimates for HI again indicated that much of the variance associated with the trait was additive and therefore, good progress

could be expected with selection for HI and that this selection could be successfully practised in early generations as the dominance variance associated with the trait was small.

4.3.6.7 Grain Yield. F_2 broad sense heritability estimates for GY ranged from 0.51 to 0.68 for the HY521/UM684 cross and from 0.52 to 0.70 for the HY521/Sinton cross (Table 24). These values are similar in relative magnitude to those reported for both spring wheat (Loffler and Busch 1982, Wells and Kofoid 1986, and Singh et al. 1986) and winter wheat (Stuber et al. 1962, Austin et al. 1977a).

Narrow sense heritability estimates for both crosses reflected the large dominance variance associated with GY. Estimates ranged from 0.27 to 0.30 for the HY521/UM684 cross and from 0.32 to 0.39 for the HY521/Sinton cross and are in close agreement with narrow sense estimates from F_2 - F_3 parent-offspring regression values for winter wheat (Guthrie et al. 1984) but differed markedly from the estimates of Stuber et al. (1962) and Sunderman et al. (1965) who reported estimates of 0.53 and 0.07 respectively for winter wheat. The results of this study also differ significantly from the narrow sense heritability estimate for GY of 0.62 reported by Singh et al. (1986) for spring wheat. These estimates clearly demonstrated that heritability estimates are a function of the procedure used and the nature of the parental material studied. The range of estimates reported here reinforce the fact that heritability estimates are unique and a property of a specific population in a specific experiment and therefore, should be interpreted only in terms of general orders of magnitude.

In summary, a comparison of the relative magnitudes of the narrow sense heritability estimates for TDM, HI and GY detected in this study suggested that progress could be made for all three traits with selection but that progress would be comparatively slower if selection were based on GY per se rather than on TDM or HI.

5. GENERAL DISCUSSION AND CONCLUSIONS

5.1 Physiology Study

Simultaneous improvement in grain yield (GY) and grain protein concentration (GPC) in spring wheats requires a better understanding of the negative relationship that is frequently observed between these two traits. Although a sound physiological basis to account for this correlation of end products is lacking, it no doubt results from a more basic genetic association between nitrogen and carbon supply.

From a physiological point of view, one of the keys to increasing GPC while maintaining GY must be to increase the accumultion of nitrogen in the grain. Two approaches to do this would appear to be to increase the nitrogen (N) accumulation in the plant and/or to increase the redistribution of accumulated N from the vegetative tissue to the developing grain. The extent of success in using either or both of these components of N metabolism as a selection criterion in the improvement of GPC is dependent on their positive relationship with GPC and the nature and extent of genetic variability for these and related traits.

This study examined genotypic variability in the components of nitrogen accumulation and redistribution through a comparison of contrasting cultivars, varying widely in levels of GPC and GY. Included in the

range of cultivars examined were two experimental genotypes developed at the University of Manitoba and unique among the cultivars studied in their combination of high GPC and high GY. This combination resulted in a grain protein yield (GPY) for these cultivars that was significantly higher than that for any cultivar studied. GY and GPC differences among other cultivars were compensatory with respect to GPY, resulting in few significant differences in GPY among the remaining six cultivars.

Cultivar comparisons made for traits related to N uptake and accumulation indicated that although significant genetic variability existed for total N accumulated at anthesis (TNA) and at maturity (TNM), only TNM was significantly correlated to GY, GPY and GPC. As all cultivars were grown at comparable nitrogen levels, TNM was considered an index of cultivar efficiency of N uptake under nonlimiting N conditions. The high GPC, high GY cultivars UM632 and UM684, clearly were more efficient in seasonal N uptake than any of the remaining cultivars. For the remaining six cultivars, TNM was more closely correlated with GY and GPY than with GPC, although correlations were significant for all comparisons. As over 90% of the variability in GPY was associated with variability in TNM in both experimental years, the need to breed for increased TNM was clear.

Three distinctive physiological strategies for accumulating total N were evident from this study. High GY, low GPC cultivars accumulated more N by anthesis than low GY, high GPC cultivars, while at the same time, generally ranked lower among the cultivars studied for post-anthesis N uptake. The high GPC, low GY cultivars generally accumulated less N by anthesis and relied more heavily on post-anthesis N uptake

than the low GPC cultivars. These two strategies were compensatory resulting in comparable levels of GPY. Sinton, also having high GPC and low GY, remained the clear exception in this study, accumulating significantly more N pre-anthesis and relying least among the 8 cultivars on post-anthesis N uptake. Again, the result of these two different strategies was compensatory in that Sinton did not differ significantly from Benito in either year for TNM.

The third strategy, evident for UM632 and UM684, indicated that these two strategies are complementary, under independent genetic control and can be successfully combined into one cultivar. UM632 and UM684 combined the TNA of the high GY cultivars with post-anthesis uptake significantly higher than all cultivars studied. The resulting high GPC, high GY and consequently high GPY of these cultivars clearly indicated that, among the cultivars investigated, this combination of strategies maximized seasonal N uptake and more effectively exploited available soil N than either strategy independently.

The lack of significant total dry matter differences (TDM) among the high GY cultivars differing in GPC reinforced the idea that UM632 and UM684 were better able to efficiently utilize their environment with respect to N uptake relative to TDM than were other cultivars.

The reasons for the enhanced N uptake efficiency of UM632 and UM684, particularly as it is related to the greater duration of N uptake in these two cultivars, remain unclear. Factors that have been proposed to be associated with the duration of N uptake have included increased leaf area duration (Neales et al. 1963, Woodruff 1972) and the size of the

root mass (Troughton 1968). Although leaf area duraton was not monitored in this study, the amount of dry matter accumulated post-anthesis and the GY levels of UM632 and UM684 suggested that the leaves continued to fix carbon throughout much of the grain filling period. The lack of significant differences among the high GY cultivars for post-anthesis dry matter accumulation however, suggested that leaf area duration alone could not explain differences in the duration of N uptake post-anthesis.

Consideration of dry matter differences among cultivars at anthesis (DMA), however, suggested that differences in root mass may have contributed to the increased N uptake efficiency of UM632 and UM684. Troughton (1968) has noted that the greater the shoot growth, the smaller the proportion of photosynthate available for root development and therefore, it may be reasonable to asssume that UM632, UM684 and Benito, which have significantly less DMA, may have a proportionately larger root mass than the cultivars UM841, HY521 and Glenlea, which have proportionately higher DMA. This results in the argument, similar to that of Cox et al. (1985b), that those cultivars with a larger root mass will be better able to extract nitrate late in the growing season when nitrate concentrations will be appreciably diminished. In addition, the Km for the nitrate reductase enzyme for UM632 and UM684 may be lower than Km for the low GPC cultivars, thereby giving the enzyme a greater affinity for the lower nitrate concentrations, late in the growing season. The purely speculative nature of these conclusions emphasizes the need to know more about the mechanisms of N uptake and particularly, the necessity for more study of the root systems.

In crops like spring wheat, which are extensively grown under climatic conditions where plants face receeding soil nitrogen and moisture availability during the grain filling period, the effective partitioning of N between the vegetative tissue and the grain becomes equally as important as N uptake for accumulating N in the grain. As such, N remobilization traits among the eight cultivars were studied in an attempt to establish whether or not significant cultivar variability for the components of N remobilization existed and if so whether or not it was correlated with GPC and/or GPY.

Both cultivar variability for the traits associated with N remobilization, and differential strategies for accumulating N in the grain were evident from an analysis of these eight cultivars. Cultivars with high GY and low GPC (Glenlea, HY521 and UM841) accumulated significantly more N in the vegetative tissue at the point of maximum vegetative nitrogen than cultivars with low GY and high GPC (Benito and BW90) while retaining more residual vegetative nitrogen at maturity. Consequently, although both groups remobilized comparable amounts of vegetative N to the grain, the high GPC, low GY cultivars remobilized N more efficiently than the low GPC, high GY cultivars. This, coupled to the greater duration of uptake post-anthesis of the high GPC, low GY cultivars, resulted in the significantly higher GPC of these cultivars.

Sinton was the exception among the high GPC, low GY cultivars in that it accumulated vegetative nitrogen comparably to the high GY cultivars but retained less residual vegetative N at maturity than these cultivars and therefore, had a remobilization efficiency comparable to the high GY, high GPC cultivars. Sinton however relied the least of any cultivar

on post-anthesis N uptake, thereby resulting in GPC levels nonsignificantly different or somewhat lower than those of Benito and BW90.

The high GY, high GPC cultivars UM632 and UM684 again successfully combined these two strategies thereby maximizing remobilization efficiency. These cultivars, particularly UM684, accumulated vegetative N in amounts comparable to the maximum vegetative N levels of the high GY cultivars, while retaining the least vegetative N at maturity of all the cultivars investigated. UM632 and UM684 had a significantly higher remobilization efficiency than the high GY cultivars studied. This high remobilization efficiency, when coupled to a high uptake efficiency resulted in the high N utilization efficiency observed for UM632 and UM684.

The reliance on remobilized N to supply the needs of the developing grain can, however, be detrimental to the plant. Sinclair and de Wit (1975) refer to the strategy of low post-anthesis N accumulation and high N remobilization as being self-destructive. Gregory et al. (1981) confirmed this in winter wheat with the observation that maximum photosynthesis was inversely linearly correlated with N remobilized from the vegetative tissue, particularly the flag leaf. They concluded that continued production of dry matter in cereals during grain growth and hence GY, depends on the availability and uptake of sufficient N to prevent significant decreases in the N content of leaves and consequently in the rate of photosynthesis. This relative importance of the components of N and dry matter accumulation in the grain appeared to be confirmed in this data. Sinton, which relied most on remobilized N during grain fill, accumulated the least dry matter and N post-anthesis while culti-

vars such as UM632 and UM684, which relied the least on remobilized N during grain fill, ranked significantly higher for both post-anthesis N and dry matter uptake.

The partitioning of carbon to the grain appeared from this study to be important for both GY and the simultaneous improvement in GY and GPC. Total dry matter (TDM) and harvest index (HI) were both found to be highly correlated with GY.

The ability to accumulate dry matter and subsequently partition it into the grain was found to be independent of the ability to partition N into the grain (NHI). These results suggested therefore, that TDM and HI could be increased without adversely affecting NHI. The importance of breeding for both HI and NHI was evident from the relative rank of cultivars for these traits. Cultivars with high GY ranked significantly higher for HI than cultivars with low GY while cultivars with high GPC ranked significantly higher for NHI than low GPC cultivars. UM632 and UM684, which combined high GY and high GPC, successfully combined high HI with high NHI. This indicated therefore that it should be possible to breed for simultaneous improvements in carbon and N partitioning to the grain and in so doing, simultaneously improve GY and GPC. It was clear from this study, that N uptake and redistribution are independent, complementary physiological strategies for accumulating N in the grain. As these strategies are independent of one another, they can be manipulated separately and where there is genetic control, as was evident from this study, they should be able to be combined into one cultivar through plant breeding, to generate a cultivar that has a higher N use efficiency than cultivars possessing either strategy alone.

Similarly, the accumulation and redistribution of dry matter are complementary physiological strategies for increasing GY, and when combined with complementary strategies for N accumulation and redistribution, should result in a cultivar combining both high GY with high GPC and thereby generating higher economic yield.

From this study, it was clear that GPC would be most readily improved by enhancing grain N while maintaining yield levels. This could most effectively be carried out by selection for increased TNM to improve the N uptake efficiency, followed by selection for NHI to increase the N utilization efficiency. The role of leaf area duration relative to enhanced duration of N uptake should be more thoroughly investigated to determine whether or not visually monitoring and selecting cultivars for delayed senescence would result in the enhanced duration of N and dry matter accumulation necessary for high GY and high GPC. Similarly, GY can be increased by increasing TDM and/or HI. Within the range of material studied, selection for high TDM followed by selection for high HI to improve the dry matter use efficiency, should result in increased GY, provided the TDM remains high. The high positive correlations detected between TDM and TNM suggested that these two traits can be selected for simultaneously. Finally, the lack of significant correlation between HI and NHI suggested that improvements could be made in either of these indicies without a subsequent decline in the other. Simultaneous improvements in these four traits should be quite possible based on the material studied and when successfully combined into one cultivar, should lead to simultaneous improvements in both GY and GPC.

5.2 Inheritance Study

The extent of possible improvement in grain yield (GY), grain protein concentration (GPC) and grain protein yield (GPY) in spring wheat depends on a knowledge of the amount of genetic variation present, in these and related traits, in relation to environmental variation. The genetic variation and in particular, the additive genetic variance, sets the upper limit on the progress that can be made. In turn, the strategy the breeder uses to improve these traits is dependent on the type of genetic variation governing the phenotypic expression of the trait. Both the extent and type of genetic variance can change with the genetic material under consideration. Therefore, a knowledge of the inheritance of GY, GPC, GPY and related traits in locally adapted material is essential to developing a strategy for improving these economically important traits in cultivars being developed for western Canadian growing conditions.

Conclusions drawn from the physiology study indicated that in addition to selection based on GY and GPC per se, simultaneous improvement in these two traits should be possible by breeding for a combination of increased total plant N at maturity (TNM) and total dry matter (TDM), to maximize the efficiency of nitrogen and carbon uptake and assimilation and increased nitrogen harvest index (NHI) and harvest index (HI) to maximize the efficiency of nitrogen and carbon utilization. As such the inheritance of TNM, NHI, TDM, and HI were studied in addition to GPC, GY and GPY in crosses of a common low GPC, high GY maternal parent (HY521) to two sources of high GPC (UM684 and Sinton). UM684 was selected as it

successfully combined high GY and high GPC, while Sinton represented the standard Canada Western Red Spring bread wheat class. A third cross between the two high GPC cultivars UM684 and Sinton was made to determine if these two cultivars differed in their genes for high GPC. From an analysis of the variances of the F_2 relative to the mean of the parental and F_1 generations of the UM684/Sinton cross it was concluded that UM684 and Sinton were different genetic sources of GPC.

Genetic analyses of TNM, NHI, GPC and GPY indicated that these grain protein related traits were primarily under genetic control in both the HY521/UM684 and HY521/Sinton crosses with additive genetic effects being significant for all traits. Dominance and epistatic genetic effects were both trait and genotype specific. Analysis of all traits related to GPC confirmed that UM684 and Sinton were different genetic sources of high protein.

Genetic analyses of TNM indicated that the trait was controlled by both additive and dominance genes, the latter exerting a greater influence in the HY521/UM684 cross than in the HY521/Sinton cross. Epistasis was also important in the inheritance of TNM in the HY521/Sinton cross but was primarily of the additive x additive type and therefore, could be easily fixed along with the additive genes by conventional plant breeding methods.

Genetic variance analyses for TNM also indicated the large genetic component of the phenotypic variation as evidenced by the high broad sense heritabilities for TNM, particularly for the HY521/UM684 cross. Narrow sense heritabilities, however, indicated that much of the genetic

variance in this material was dominance variance and therefore cannot be fixed with conventional pureline stategies. Genetic advance based on narrow sense heritability and a 10% selection intensity indicated that for populations grown at Winnipeg, selection in the F_2 for TNM would increase TNM by 7.8% of the F_2 popultion mean for the HY521/UM684 cross and by 7.7% of the F_2 population mean for the HY521/Sinton cross. These estimates reflect a realistic estimate of progress as they are based on only the additive portion of the genetic variance thereby excluding dominance variance which would otherwise confound the predicted progress.

Additive genetic effects were predominant for NHI in both crosses, with the magnitude and direction of the dominance component being determined by the genotype. Variance analyses again suggested that much of the phenotypic variance was genetic although broad sense heritabilities reflected the proportionately larger environmental component for NHI than for TNM. The reason for this was not clear. Narrow sense heritabilities, larger than those for TNM reflected the larger additive variance for this trait and indicated that much of the genetic variance could be fixed with selection. Calculations of genetic advance with selection indicated that the rate of progress would be slow, with one round of selection improving the F_2 population mean by 2.8% in the HY521/UM684 cross and by 3.3% in the HY521/UM684 cross. This rate of progress however, reflected the small parental differences for NHI and as small differences were associated with significantly more efficient partitioning of N to the grain, increases of 3% per cycle would prove quite worthwhile.

From the means analyses for GPC, it was clear that the phenotypic expression of this trait was conditioned primarily by additive genetic effects. Dominance for low protein was evident in the HY521/UM684 cross, but was absent in the HY521/Sinton cross. Additive variance was the major component of the genetic variance and this was reflected in the moderately high narrow sense heritabilities for both crosses. Gain from selection based on these heritability estimates and a 10% selection intensity, indicated that moderate improvement could be made in GPC with selection ranging from 4.4% of the F_2 population mean for the HY521/UM684 cross to 7.1% of the F_2 population mean for the HY521/Sinton cross. The larger expected gain predicted for the HY521/Sinton cross, reflected the lack of domiance variance and subsequent larger narrow sense heritability for GPC in this cross. Again, these estimates more realistically predict gains made when selection is practised for GPC as the confounding effect of the unfixable dominance component is removed through the use of the narrow sense heritability estimate.

Finally, means analyses for GPY indicated significant additive and dominance genetic effects controlling this trait in both crosses. Additive x additive epistasis was also significant for the HY521/Sinton cross, but should not hinder breeding for GPY as it can be fixed along with the additive genes. Epistasis, however, may confound the predicted advance from selection. Variance analyses indicated that much of the genetic variation for GPY was dominance variance and therefore would restrict the rate of progress possible in this trait. Narrow sense heritabilities are therefore correspondingly lower for the HY521/UM684 cross than for the HY521/Sinton cross as the dominance variance in the

former cross was significantly larger than the additive variance. Predicted gains in GPY from selection for this trait were large due to the higher phenotypic standard deviations detected. An increase of 7.4% of the F_2 mean was predicted for the HY521/UM684 cross and 12.9% of the F_2 mean for the HY521/Sinton cross, reflecting again, the high narrow sense heritability of the latter cross. Selection based on GPY should result in good progress in GPY and if the theshold levels of GPC, necessary to meet the "Marquis" type quality standards of the Canada Western Red Spring wheat class are maintained, could significantly improve GY while maintaining GPC in this class.

Genetic analyses of TDM and HI indicated that in the genetic material investigated, these two GY related traits were predominantly determined by additive genetic effects governing their phenotypic expression in both crosses. Dominance and epistasis were of secondary importance and were again both trait and genotype specific.

Additive gene effects were found for TDM with significant dominance for high TDM in both crosses. Epistasis was also significant for the HY521/Sinton cross but was of the additive x additive type and therefore could be fixed with selection. Phenotypic variance was predominantly genetic, as reflected by high broad sense heritabilities but consisted of a large dominance component, thereby reducing narrow sense heritability and limiting progress from selection. Selection for TDM, based on a 10% selection intensity would result in good progress in this trait amounting to 17% of the F_2 population mean for the HY521/UM684 cross and 11.2% of the F_2 population mean for the HY521/Sinton cross. As the limit to HI is approached, genetic improvement in GY will depend largely

on detecting and exploiting genetic variation in TDM. These results suggested that selecting for TDM could be quite a successful strategy.

Genetic analyses of HI indicated that this trait is relatively simply inherited being governed primarily by additive genetic effects in both crosses. Dominance for high HI was detected in the HY521/UM684 cross but not in the HY521/Sinton cross. Variance analyses indicated that phenotypic variance was predominantly genetic and primarily additive in nature. High narrow sense heritability estimates further suggested that good progress could be made in HI with selection. Calculation of genetic advance with a 10% selection intensity confirmed this conclusion as improvements of 4.5% and 5.3% could be expected in the F_2 population means of the HY521/UM684 and HY521/Sinton crosses respectively, with selection for increased HI. This would correspond to an increase in HI of 2.0 and 2.3% for each cross respectively. Given that small HI differences resulted in significant increases in carbon partitioning efficiency in this study, this level of progress would be quite worthwhile.

The genetic study of GY per se indicated that the phenotypic expression of this trait was governed by significant additive and dominance components in both crosses. Additive x additive epistasis was significant for only the HY521/Sinton cross. Phenotypic variance was again largely genetic and consisted primarily of dominance variance, as evidenced by the moderately low narrow sense heritability estimates for GY. This suggested that progress could be made with selection for GY but would be most effective when delayed until advanced generations. Predicted advance from selection ranged from 7.9 to 9.2% of the population means for the HY521/UM684 and HY521/Sinton crosses respectively.

This represented a gain in GY per plant of from 6.6 to 7.2 g/plant for these two crosses respectively.

In summary, it remains for selection studies to be performed using each of the GPC and GY related traits reported here as a selection criterion for improving GPC and GY in order to determine realized gain in GY and GPC from selection. Analysis of this type should provide more information to determine a selection index for the simultaneous improvement of GY and GPC.

In addition, further research should be carried out with this material in order to determine if the N utilization efficiency associated with UM632 and UM684 persists over all N levels, as literature reports (Moll et al. 1982, Cox et al. 1985b, 1986), have suggested that efficiency of N uptake and partitioning is a function of N level. Investigations under different levels of soil N would enable the breeder to select a soil N level where both N uptake and N utilization efficiency could be improved simultaneously.

From this study, the accumulation of plant N (TNM) and its subsequent redistribution to the developing grain (NHI), were found to be independent, genetically controlled, complementary physiological strategies for accumulating nitrogen in the grain that, when combined into one cultivar, significantly increased GPC. Similarly, the accumulation of plant dry matter (TDM) and the subsequent partitioning of it into the grain (HI) were also found to be independent, complementary, physiological strategies, that when combined into one cultivar, significantly increased GY. When these four strategies were combined at least in part

into one cultivar, as was evident from data based on UM632 and UM684, the net result was cultivars that were more efficient at both nitrogen and carbon uptake and assimilation and nitrogen and carbon utilization. In the case of UM632 and UM684, this led to significant improvement in both GY and GPC simultaneously and therefore, significantly higher GPY.

A range of genetic variability for each of these traits clearly existed within the material studied and the nature of the genetic variation and magnitude of the narrow sense heritabilities indicated that progress could be made in all traits, particularly in the GY related traits, TDM and HI. Predicted genetic advance for TNM and NHI although lower than that for TDM and HI, indicated that significant progress in these traits could also be possible with selection. In addition, the correlation of TNM with both GPC and GPY and with GY, suggested that improvement in this trait while maintaining or increasing NHI could clearly result in increased GPC and GY simultaneously. The positive correlation of TNM with TDM and HI, as well as the lack of a significant correlation between NHI and HI, suggested that it should be quite possible to increase these traits simultaneously.

The nature of the genetic effects governing all traits indicated that all traits could be improved with conventional pureline breeding strategies. The predominance of additive genetic effects for many of the traits suggested that one or more cycles of recurrent selection would enable greater recombination, break possible linkage blocks and aid in the accumulation of favorable alleles into one genotype. This sort of extensive recombination should result in greater progress in combining complementary physiological strategies.

The labour associated with using NHI and TNM as selection criteria is such that it would normally be prohibitive for screening segregating generations as it would require N analysis on both the grain and straw. The use of near infrared reflectance spectroscopy for both seed and vegetative tissue analyses (Loffler and Busch 1983), would markedly decrease labour costs but may not reduce them to an economically feasible level as tissue samples would still need to be ground. These criteria could however, be effectively used for screening parental material for differing physiological strategies of nitrogen accumulation and redistribution so that crosses could be more effectively planned. Differing, yet complementary, strategies in the parents coupled to recurrent selection breeding techniques and selection for TDM and HI in addition to the conventional end products GPC and GY in the offspring, should result in improvements in GY while maintaining GPC. Where selection is also practised for GPY in addition to the threshold GPC necessary for the Canada Western Red Spring wheat class, simultaneous improvements in both GY and GPC may be expected.

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APPENDIX TABLE 1. Coefficients of the components of means (Mather and Jinks 1977).

Generation	m	[d]	[h]	[i]	[j]	[l]
P_1	1	1	0	1	0	0
P_2	1	-1	0	1	0	0
F_1	1	0	1	0	0	1
F_2	1	0	.50	0	0	.250
F_3	1	0	.25	0	0	.063
B_1	1	.50	.50	.25	.250	.250
B_2	1	-.50	.50	.25	-.250	.250

APPENDIX TABLE 2. Coefficients of the components of variance (Mather and Jinks 1977).

Generation	Component			
	D	H	F	E
P_1	0	0	0	1
P_2	0	0	0	1
F_1	0	0	0	1
F_2	.500	.250	0	1
F_3	.750	.188	0	1
B_1	.250	.250	-.500	1
B_2	.250	.250	.500	1

APPENDIX TABLE 3. Phenotypic correlation coefficients among cultivar traits (1984, N=40).

Trait [1]	GPY	GPC	NHI	HI	RATIO	TNM	TDM	TNA	DMA	PAN	PADM	MATVN	REMEFF
GY	0.58**	-0.42**	NS	0.76**	-0.69**	0.67**	0.89**	0.36*	0.36*	0.38*	0.77**	O.38*	NS
GPY		0.48**	0.59**	0.60**	NS	0.97**	0.40*	NS	NS	0.80**	0.59**	NS	NS
GPC			0.55**	NS	0.50**	0.35*	-0.50**	NS	-0.58**	0.51**	NS	-0.49**	0.52**
NHI				0.31*	0.33*	0.40*	NS	-0.39*	-0.45**	0.66**	NS	-0.75**	0.64**
HI					-0.79**	0.62**	0.39*	NS	NS	0.50**	0.48**	NS	NS
RATIO						-0.36*	-0.45**	-0.38*	NS	NS	-0.33*	-0.57**	0.51**
TNM							0.52**	0.31*	NS	0.73**	0.62**	NS	NS
TDM								0.44**	0.54**	NS	0.76**	0.50**	-0.36*
TNA									0.74**	-0.42**	NS	0.56**	NS
DMA										-0.54**	NS	0.54**	-0.33*
PAN											0.63**	NS	NS
PADM												NS	NS
MATVN													-0.73**

*,**Significant at $P \leq 0.05$. and $P \leq 0.01$. respectively.
[1] GY=grain yield; GPY=grain protein yield; GPC=grain protein concentration; NHI=nitrogen harvest index; HI=harvest index; RATIO=NHI/HI; TNM=total plant N at maturity; TDM=total dry matter; TNA=total plant N at anthesis; DMA=total dry matter at anthesis; PAN=post-anthesis accumulated N; PADM=post-anthesis accumulated dry matter; MATVN= vegetative N at maturity; REMEFF=remobilization efficiency.

APPENDIX TABLE 4. Phenotypic correlation coefficients among cultivar traits (1985, N=40).

TRAIT [1]	GPY	GPC	NHI	HI	RATIO	TNM	TDM	TNA	DMA	PAN	PADM	MATVN	REMEFF
GY	0.52**	-0.35**	NS	0.71**	-0.46**	0.68**	0.95**	NS	NS	0.44**	0.77**	0.43**	NS
GPY		0.61**	0.71**	NS	0.42**	0.95**	0.60**	NS	NS	0.90**	0.68**	NS	0.41**
GPC			0.84**	-0.52**	0.90**	0.41**	NS	-0.48**	-0.46**	0.58**	NS	-0.71**	0.61**
NHI				NS	0.83**	0.47**	NS	-0.48**	-0.39*	0.62**	NS	-0.85**	0.84**
HI					-0.72**	NS	0.46**	0.33*	0.34*	NS	NS	0.34*	NS
RATIO						NS	NS	-0.53**	-0.46**	0.41**	NS	-0.80**	0.65**
TNM							0.75**	NS	NS	0.86**	0.76**	NS	NS
TDM								NS	NS	0.54**	0.87**	0.40*	NS
TNA									0.83**	-0.59**	-0.32*	0.50**	-0.36*
DMA										-0.48**	-0.35*	0.40*	NS
PAN											0.76**	NS	0.32*
PADM												NS	NS
MATVN													-0.89**

*,**Significant at $P \leq 0.05$. and $P \leq 0.01$. respectively.
[1] GY=grain yield; GPY=grain protein yield; GPC=grain protein concentration; NHI=nitrogen harvest index; HI=harvest index; RATIO=NHI/HI; TNM=total plant N at maturity; TDM=total dry matter; TNA=total plant N at anthesis; DMA=total dry matter at anthesis; PAN=post-anthesis accumulated N; PADM=post-anthesis accumulated dry matter; MATVN= vegetative N at maturity; REMEFF=remobilization efficiency.

APPENDIX TABLE 5. Summary of preliminary data for total N at maturity (TNM) and nitrogen harvest index (NHI) per plant for the HY521/UM684 cross.

		TNM (g)			NHI (%)		
Location	Generation	Mean	$(S.E.)^2$	Variance	Mean	$(S.E.)^2$	Variance
Winnipeg							
	P_1	3.03	.0012	.044	75.8	.200	7.2
	P_2	2.90	.0014	.057	69.7	.146	6.6
	F_1	3.13	.0015	.052	74.4	.205	7.2
	F_2	3.04	.0006	.186	72.7	.041	6.5
	B_1	3.01	.0008	.163	74.4	.046	13.5
	B_2	3.05	.0007	.156	71.3	.045	10.7
	F_3	2.97	.0014	.102 (V_1F_3)	72.9	.100	10.0 (V_1F_3)
				.114 (V_2F_3)			9.3 (V_2F_3)
Portage							
	P_1	2.71	.0023	.068	77.8	.249	7.5
	P_2	2.56	.0026	.078	73.2	.270	8.1
	F_1	2.82	.0028	.084	77.2	.273	8.2
	F_2	2.69	.0009	.201	75.2	.049	11.4
	B_1	2.69	.0011	.178	76.3	.057	9.1
	B_2	2.57	.0010	.175	74.1	.054	9.3
	F_3	2.64	.0019	.121 (V_1F_3)	73.3	.119	6.0 (V_1F_3)
				.112 (V_2F_3)			8.9 (V_2F_3)

APPENDIX TABLE 6. Summary of preliminary data for total N at maturity (TNM) and nitrogen harvest index (NHI) per plant for the HY521/Sinton cross.

Location	Generation	TNM (g) Mean	TNM (g) $(S.E.)^2$	TNM (g) Variance	NHI (%) Mean	NHI (%) $(S.E.)^2$	NHI (%) Variance
Winnipeg							
	P_1	2.28	.0019	.067	73.6	0.188	6.6
	P_2	3.52	.0019	.068	67.5	0.183	6.6
	F_1	3.18	.0017	.058	69.0	1.124	4.2
	F_2	2.92	.0006	.143	69.8	0.053	13.4
	B_1	2.71	.0006	.112	70.5	0.052	11.5
	B_2	3.03	.0006	.119	68.5	0.064	11.8
	F_3	2.91	.0009	.070 (V_1F_3)	70.4	0.117	8.5 (V_1F_3)
				.068 (V_2F_3)			9.5 (V_2F_3)
Portage							
	P_1	1.38	.0015	.053	77.6	.163	5.7
	P_2	2.75	.0015	.054	73.2	.169	6.1
	F_1	2.26	.0014	.050	74.4	.159	5.9
	F_2	2.08	.0006	.135	75.0	.055	11.5
	B_1	1.94	.0008	.115	76.4	.061	9.2
	B_2	2.36	.0008	.117	73.9	.059	8.8
	F_3	2.06	.0013	.089 (V_1F_3)	75.3	.086	4.5 (V_1F_3)
				.069 (V_2F_3)			6.2 (V_2F_3)

APPENDIX TABLE 7. Summary of preliminary data for grain protein concentration (GPC) and grain protein yield (GPY) per plant for the HY521/UM684 cross.

Location	Generation	GPC (%) Mean	GPC (%) $(S.E.)^2$	GPC (%) Variance	GPY (g) Mean	GPY (g) $(S.E.)^2$	GPY (g) Variance
Winnipeg							
	P_1	16.8	.0034	.117	13.1	.024	0.839
	P_2	13.8	.0026	.106	11.4	.025	1.033
	F_1	15.0	.0044	.149	13.3	.029	1.013
	F_2	15.2	.0015	.471	12.7	.011	3.362
	B_1	15.9	.0015	.329	12.7	.014	3.057
	B_2	14.5	.0013	.273	12.4	.013	2.816
	F_3	15.4	.0014	.297 (V_1F_3)	12.5	.026	1.815 (V_1F_3)
				.256 (V_2F_3)			2.061 (V_2F_3)
Portage							
	P_1	17.0	.0065	.197	12.0	.029	0.883
	P_2	13.8	.0047	.141	10.9	.028	0.851
	F_1	15.2	.0048	.144	12.4	.035	1.060
	F_2	15.3	.0028	.648	11.9	.016	3.652
	B_1	16.0	.0027	.430	11.7	.021	3.347
	B_2	14.6	.0024	.412	11.5	.019	3.291
	F_3	15.3	.0049	.385 (V_1F_3)	11.6	.034	1.994 (V_1F_3)
				.227 (V_2F_3)			2.193 (V_2F_3)

APPENDIX TABLE 8. Summary of preliminary data for grain protein concentration (GPC) and grain protein yield (GPY) per plant for the HY521/Sinton cross.

		GPC (%)			GPY (g)		
Location	Generation	Mean	$(S.E.)^2$	Variance	Mean	$(S.E.)^2$	Variance
Winnipeg							
	P_1	15.96	.0037	.129	9.55	.047	1.649
	P_2	13.83	.0055	.162	13.52	.047	1.677
	F_1	14.45	.0067	.193	12.49	.051	1.729
	F_2	14.74	.0025	.631	11.59	.015	3.803
	B_1	15.25	.0016	.351	10.89	.014	3.080
	B_2	14.14	.0019	.351	12.69	.017	3.129
	F_3	14.90	.0057	.520 (V_1F_3)	11.36	.037	2.536 (V_1F_3)
				.335 (V_2F_3)			3.087 (V_1F_3)
Portage							
	P_1	16.25	.0060	.201	6.11	.030	1.046
	P_2	14.12	.0057	.204	11.69	.032	1.156
	F_1	15.08	.0056	.209	9.75	.029	1.077
	F_2	15.03	.0023	.484	8.79	.012	2.407
	B_1	15.66	.0023	.352	8.23	.013	1.994
	B_2	14.53	.0022	.330	9.90	.013	1.922
	F_3	14.86	.0053	.344 (V_1F_3)	8.75	.027	1.703 (V_1F_3)
				.323 (V_2F_3)			1.676 (V_2F_3)

APPENDIX TABLE 9. Summary of preliminary data for total dry matter (TDM) and harvest index per plant for the HY521/UM684 cross.

Location	Generation	TDM (g) Mean	(S.E.)^2	Variance	HI (%) Mean	(S.E.)^2	Variance
Winnipeg							
	P_1	176.1	5.086	150.73	44.3	.109	3.8
	P_2	198.0	6.377	261.46	42.2	.082	3.3
	F_1	196.6	6.210	211.14	44.9	.089	2.8
	F_2	191.5	2.586	812.16	44.0	.017	5.4
	B_1	180.7	2.894	630.89	44.0	.045	4.4
	B_2	198.4	3.029	666.47	43.1	.018	4.0
	F_3	184.6	5.154	554.61 (V_1F_2)	43.7	.057	5.7 (V_1F_2)
				218.40 (V_2F_3)			3.8 (V_2F_3)
Portage							
	P_1	156.5	12.631	378.93	43.9	.080	2.4
	P_2	186.0	12.576	377.34	42.0	.113	2.9
	F_1	184.9	14.626	438.78	43.9	.117	3.4
	F_2	173.4	3.887	1072.65	43.4	.023	5.4
	B_1	161.5	5.180	898.11	43.7	.028	4.5
	B_2	180.8	4.967	844.35	43.0	.024	4.1
	F_3	166.8	7.734	582.40 (V_1F_2)	42.8	.080	5.5 (V_1F_2)
				384.32 (V_2F_3)			4.5 (V_2F_3)

APPENDIX TABLE 10. Summary of preliminary data for total dry matter (TDM) and harvest index per plant for the HY521/Sinton cross.

Location	Generation	TDM (g) Mean	TDM (g) $(S.E.)^2$	TDM (g) Variance	HI (%) Mean	HI (%) $(S.E.)^2$	HI (%) Variance
Winnipeg							
	P_1	133.2	6.326	221.4	44.9	.109	3.8
	P_2	232.2	8.136	292.9	42.1	.098	3.5
	F_1	200.2	5.968	202.9	43.2	.090	3.1
	F_2	183.0	3.349	853.9	43.1	.026	6.6
	B_1	164.4	2.926	643.8	43.5	.027	5.9
	B_2	210.5	3.388	626.8	42.1	.035	6.5
	F_3	182.9	4.902	495.6 (V_1F_3)	42.6	.062	4.8 (V_1F_3)
				239.7 (V_2F_3)			4.4 (V_2F_3)
Portage							
	P_1	86.6	6.597	230.9	43.4	.085	3.0
	P_2	196.7	6.032	217.2	42.2	.092	3.3
	F_1	157.5	5.023	185.9	42.5	.078	2.9
	F_2	142.4	3.696	768.8	42.5	.038	7.9
	B_1	127.6	3.671	550.7	42.3	.039	5.9
	B_2	162.3	3.415	512.3	42.0	.043	6.4
	F_3	31.2	8.862	642.1 (V_1F_3)	42.5	.060	5.2 (V_1F_3)
				465.6 (V_2F_3)			3.8 (V_2F_3)

APPENDIX TABLE 11. Summary of preliminary data for grain yield (GY) per plant for the HY521/UM684 cross.

Location	Generation	GY (g) Mean	GY (g) $(S.E.)^2$	GY (g) Variance
Winnipeg				
	P_1	78.0	1.168	40.88
	P_2	83.5	1.274	52.26
	F_1	88.2	1.362	47.68
	F_2	83.2	0.440	138.38
	B_1	80.2	0.540	117.65
	B_2	85.4	0.522	114.76
	F_3	80.2	0.885	74.03 (V_1F_3)
				58.77 (V_2F_3)
Portage				
	P_1	68.7	2.758	82.74
	P_2	78.8	2.576	77.28
	F_1	82.0	3.181	95.44
	F_2	75.2	0.711	164.24
	B_1	73.5	0.851	149.46
	B_2	78.6	0.968	144.60
	F_3	73.3	1.488	84.11 (V_1F_3)
				101.87 (V_2F_3)

APPENDIX TABLE 12. Summary of preliminary data for grain yield (GY) per plant for the HY521/Sinton cross.

Location	Generation	GY (g) Mean	GY (g) $(S.E.)^2$	GY (g) Variance
Winnipeg				
	P_1	59.9	1.278	44.74
	P_2	97.8	1.147	41.31
	F_1	86.5	1.421	48.33
	F_2	78.8	0.524	133.72
	B_1	71.5	0.539	118.62
	B_2	88.7	0.625	115.63
	F_3	77.9	0.920	7.95 (V_1F_3)
				5.85 (V_2F_3)
Portage				
	P_1	37.6	1.583	55.40
	P_2	82.9	1.825	65.71
	F_1	64.7	2.159	79.90
	F_2	58.6	0.508	105.19
	B_1	52.7	0.525	78.67
	B_2	68.2	0.469	70.40
	F_3	59.2	1.155	64.74 (V_1F_3)
				79.71 (V_2F_3)