Crop Nitrogen Demand and Grain Protein Concentration of Spring and Winter Wheat

D. B. Fowler*

ABSTRACT

Available soil N and a cultivar's genetic potential are primary factors determining grain protein concentration (GPC). This study focused on important genotypic and environmental factors that determine GPC and yield potential in common wheat (*Triticum aestivum* L.) and investigated the use of GPC as a practical indicator of crop N deficiencies for a wide range of cultivars grown in 16 N fertilizer trials in western Canada. Large GPC responses to added N were accompanied by large increases in grain yield, and similar GPC–grain yield relationships were found at maximum grain yield and 90 and 80% of maximum grain yield. Both genotype and environment influenced the upper limit of yield when N was not limiting. The relationship between GPC and grain yield depended on the part of the N fertilizer response curve sampled, and there was a strong negative correlation between cultivar GPC and maximum potential grain yield. The latter observation indicates that the production of high-yielding cultivars with high GPC is more complicated than simply stacking yield genes in a high-GPC genetic background or vice versa. Large differences amongst cultivars also suggested that the critical GPC–grain yield responses must be known for each cultivar before GPC can be used as a practical postharvest indicator of N sufficiency. Growing season weather had a large influence on GPC–grain yield relationships, and GPC at the point of maximum grain yield increased as the potential grain yield of a cultivar was reduced by environmental limitations. These observations indicate that GPC may be a useful postharvest indicator of N deficiencies for crops that are under N stress, but caution must be used when employing GPC to develop management systems that optimize N fertilizer use.

Both a cultivar's genetic potential and the environment in which it is grown determine GPC. Nitrogen is the basic building block of protein, and as a consequence, levels of soil available N have a large influence on GPC (Eilrich and Hageman, 1973). The large increases in grain yield and GPC achieved with N fertilization stand in sharp contrast to the negative correlation that is normally observed between GPC and grain yield when only cultivar differences are considered. Therefore, the important role that N fertilizer management has to play in optimizing grain yields and the maintenance of grain quality standards must be emphasized in efficient wheat production systems.

Several studies have suggested that the close relationship between GPC and the amount of available soil N may allow GPC to be used as a postharvest indicator of the adequacy of N management (Pierre et al., 1977; Goos et al., 1982). The critical GPC for N sufficiency has been reported to be 8.8% for Stephen's soft white winter (SWW) wheat grown in Oregon (Glenn et al., 1985) and between 11.1 and 12.0% for dryland winter wheat produced on summer fallow in eastern Colorado (Goos et al., 1982). Selles and Zentner (2001) reported that a grain protein concentration of 12.8% was a reliable indicator of N sufficiency in hard red spring (HRS) wheat grown in southwestern Saskatchewan. In contrast, Fowler and Brydon (1989) reported that the N requirements for maximum grain yield are normally met when the GPC–N response curve for Norstar winter wheat reaches approximately 13% under average to good weather conditions in Saskatchewan. Similarly, the critical GPC for spring wheat has been reported as 13.5% for both the eastern prairies (Flaten and Racz, 1997) and Montana (Long and Engel, 1998). This wide range of critical GPC values supports the conclusion drawn by Fowler et al. (1990) that there are important differences in GPC–grain yield relationships that depend on production area (environment) and cereal species and genotypes within species.

The objectives of this study were to quantify the important genotypic and environmental responses that determine GPC and yield potential in common wheat and to determine if GPC can be used as a practical indicator of crop N deficiencies grown under the variable environmental conditions of western Canada.

MATERIALS AND METHODS

A total of 16 fertilizer trials consisting of five spring and five winter wheat cultivars representing the seven wheat quality classes of western Canada were grown on dryland at Saskatoon (52° N, 107° W; Vertic Haploboroll soil), Clair (52° N, 104° W; Udic Haploboroll soils), and Yorkton (51° N, 102° W; Udic Haploboroll soils) and partial irrigation at Saskatoon from 1992 to 1998. The GPC of the wheat quality classes ranged from low-protein soft white spring (SWS) and SWW through Canada prairie spring red (CPSR) and white (CPSW) and hard red winter (HRW) to extra-strong spring (ESS) and high-protein HRS. The cultivars used in these studies were selected to represent the most highly adapted cultivars for these classes in this region. Additional data and new releases resulted in several cultivar changes over the course of this study.

Trials that included spring wheat were grown under partial irrigation at Saskatoon in 1992, 1993, 1994, 1995, 1996, 1997, and 1998 and on dryland at Saskatoon in 1996 and 1997 and Clair in 1996, 1997, and 1998. Trials that included winter wheat were grown under partial irrigation at Saskatoon in 1993, 1995, 1997, and 1998 and on dryland at Saskatoon in 1997, Yorkton in 1997 and 1998, and at two locations at Clair in 1997. The cultivars AC Reed, Katepwa, BW90, Roblin, and AC Taber were included in the spring wheat trials starting in 1992. 'Glenlea' replaced BW90 in 1995, 'AC Barrie' was substituted for Roblin in 1997, and 'AC Vista' replaced AC Reed in 1998. 'CDC Ptarmigan', 'CDC Kestrel', S86-101, 'Norstar', and 'Winalta' were included in all winter wheat trials up to 1996 and in Saskatoon and Clair dryland trials in 1997. The winter wheat

Crop Dev. Cent., Univ. of Saskatchewan, Saskatoon, SK, S7N 5A8, Canada. Received 15 Apr. 2002. *Corresponding author (Brian.Fowler@usask.ca).

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Abbreviations: CPSR, Canadian prairie spring red; CPSW, Canadian prairie spring white; GPC, grain protein concentration; HRS, hard red spring; HRW, hard red winter; ESS, extra-strong spring; SWS, soft white spring; SWW, soft white winter.

cultivars CDC Kestrel, CDC Clair, and CDC Osprey were grown in trials under partial irrigation at Saskatoon and dryland at Clair and Yorkton in 1997. The 1998 winter wheat cultivars were Norstar, Winalta, CDC Harrier, CDC Osprey, and CDC Clair.

All trials were direct-seeded into standing stubble from a previous crop (no-till) with a small-plot hoe-press drill. Experimental design was a four-replicate split plot, with N fertilizer rates as the main plots and cultivars as the subplots. Each plot was 5.5 m long and 1.2 m wide. Optimum seeding dates were achieved in all trials, and PO_4 fertilizer was applied with the seed at recommended rates. Nitrogen fertilizer was added as early spring–broadcast ammonium nitrate (34–0–0) at 0, 40, 80, 120, 160, and 240 kg N ha^{-1}. Other soil nutrients were not considered limiting. After removing approximately 30 cm from each end at maturity, the plots were direct-cut with a self-propelled small-plot combine. The outside two rows of each plot were not harvested. Exact plot lengths were recorded before harvest. The GPC was determined from Leco N $\times$ 5.7 (Leco Corp., St. Joseph, MI) (Am. Assoc. of Cereal Chem. Method 46-30) for each plot in each trial. Wheat grain yield and GPC have been reported at 135 g kg^{-1} moisture.

Analyses of variance were conducted to determine the level of significance of differences due to N levels and cultivars in each trial. Regression analyses of treatment means were used to plot curves that best described the response of grain yield and GPC to N fertilizer application. The peak four-parameter Weibull equation was employed to describe the grain yield response:

$$y = a\left(\frac{c-1}{c}\right)^{\frac{1-c}{c}}\left[\frac{x-x_0}{b}+\left(\frac{c-1}{c}\right)^{\frac{1}{c}}\right]^{c-1} e^{-\left[\frac{x-x_0}{b}+\left(\frac{c-1}{c}\right)^{\frac{1}{c}}\right]^{c}}+\frac{c-1}{c} \quad [1]$$

The sigmoidal four-parameter Gompertz equation was used to describe the GPC response to N fertilizer applications:

$$y = y_0 + ae^{-e\exp-\left(\frac{x-x_0}{b}\right)} \quad [2]$$

The peak three-parameter log normal equation was used to describe the relationship between grain yield and GPC using the individual plot data for each cultivar at each location:

$$y = ae\exp\left[-0.05\left(\frac{\ln\left(\frac{x}{x_0}\right)}{b}\right)^2\right] \quad [3]$$

Nonlinear regression procedures outlined by SigmaPlot (SPSS, Chicago, IL) were used to provide least-squares estimates of the regression coefficients in these equations.

Two methods were employed to identify critical grain yield–GPC relationships: (i) Maximum grain yield and the N rates required to achieve maximum grain yield and 90 and 80% of maximum grain yield were estimated using the peak four-parameter Weibull equation. These N rates were then used to estimate the GPC at maximum grain yield and 90 and 80% of maximum grain yield using the sigmoidal four-parameter Gompertz equation (Fig. 1). (ii) Grain protein concentration

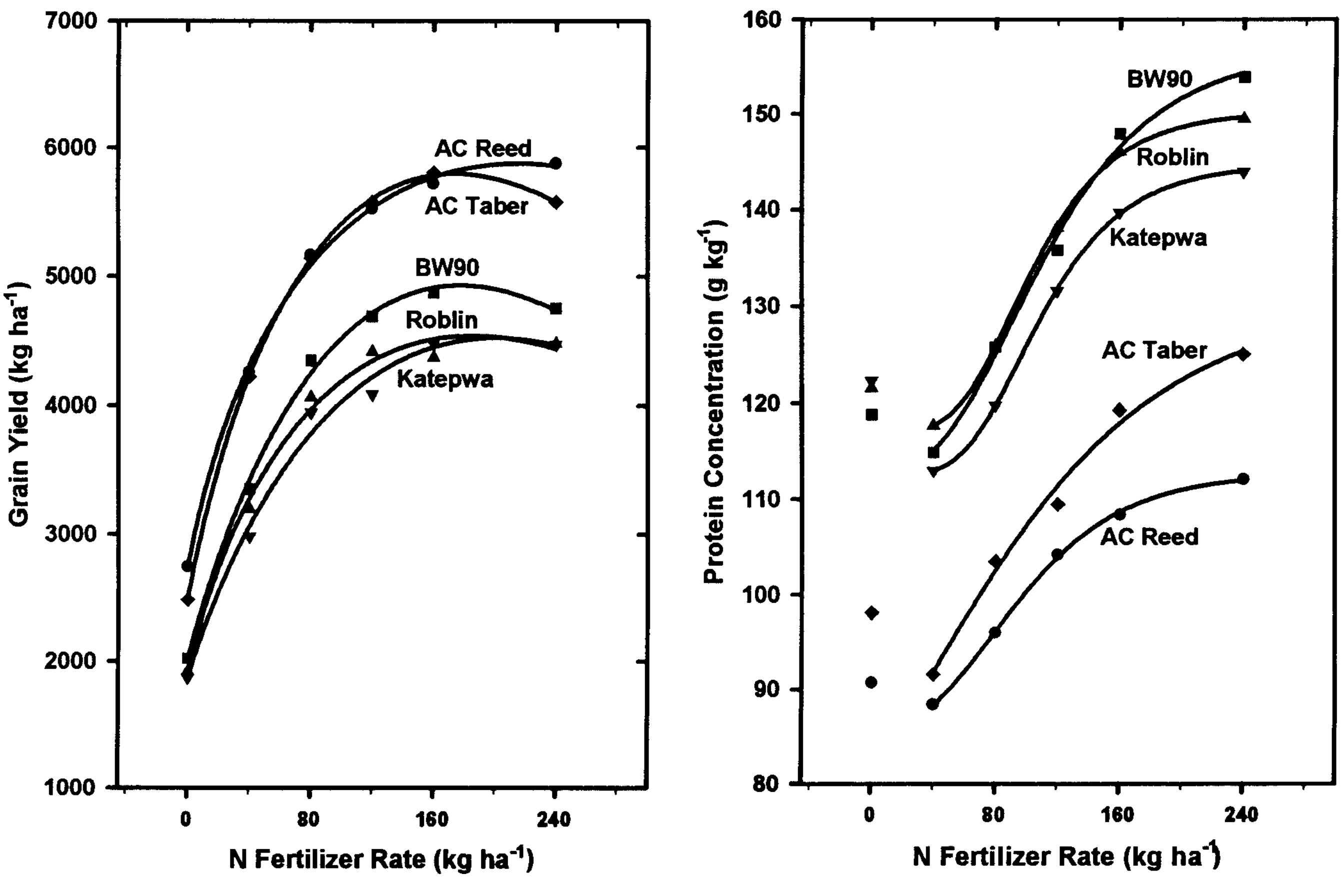

Fig. 1. Grain yield and protein concentration response to N fertilizer for five spring wheat genotypes grown under partial irrigation at Saskatoon in 1994. The peak four-parameter Weibull equation was employed to describe the grain yield response, and the sigmoidal four-parameter Gompertz equation was used to describe the grain protein concentration response to N fertilizer applications.

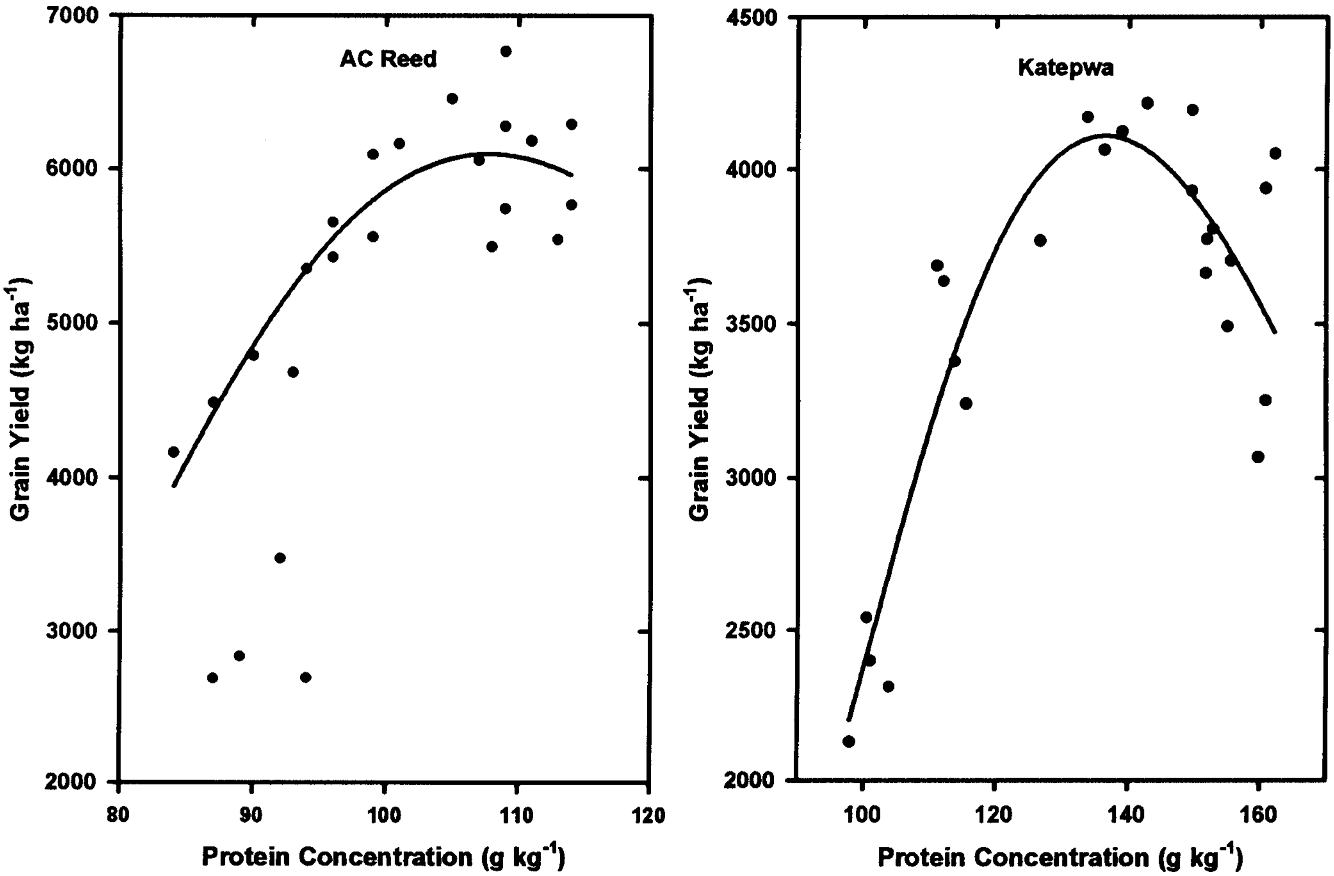

Fig. 2. Relationships between grain yield and protein concentration for AC Reed and Katepwa grown under partial irrigation at Saskatoon in 1994 and 1998, respectively. Grain protein concentration at maximum grain yield and 90 an 80% of maximum grain yield was estimated using the peak three-parameter log normal equation.

at maximum grain yield and 90 an 80% of maximum grain yield was also estimated using the peak three-parameter log normal equation (Fig. 2). Because this study was only concerned with GPC at grain yields that were 80% or more of the maximum, initial decreases in GPC–N responses at low levels of applied N were disregarded to increase the accuracy and simplify curve fitting (Fig. 1 and 2). Estimates of maximum and 90 and 80% of maximum grain yield and GPC at maximum grain yield and 90 and 80% of maximum grain yield for each cultivar in each trial were then subjected to analysis of variance using the General Linear Model procedure of Minitab 13 (Minitab, State College, PA). Adjusted means for these variables are reported.

RESULTS AND DISCUSSION

Early spring soil tests indicated that available NO_3–N in the surface 60 cm of the trials in this study ranged from 16 to 63 kg ha^{-1}, with an average of 40 kg ha^{-1}. Deficiencies in plant available N combined with conditions for growth that were average to excellent produced large grain yield and GPC responses to added N. Analysis of variance for grain yield and GPC indicated that differences due to cultivars and rate of N fertilizer application were significant ($P < 0.05$) for all trials. Nitrogen fertilization was responsible for the largest proportion of variability in GPC (Fowler, 1998b), and large GPC responses to added N were accompanied by increases in grain yield that often more than doubled in response to the first 120 kg ha^{-1} fertilizer N.

The typical nonlinear GPC–N response pattern (Fowler, 1998a), which includes the three phases designated as zones of minimum percentage, poverty adjustment, and luxury consumption by Macy (1936), were observed in these trials (Fig. 1). Low GPC was associated with low levels of residual soil available N and favorable growing conditions. In these instances, N fertilization stimulated large increases in grain yield that produced a *lag phase* (zone of minimum percentage) in the GPC–N response curve. The lag phase was longest when cultivars with high grain yield potentials were grown under low levels of available soil N. Under these conditions, the correction of severe N stress by the addition of fertilizer N often produced an initial decrease in the GPC–N response curve (Partridge and Shaykewich, 1972; Terman, 1979; Goos et al., 1982; Bole and Dubetz, 1986; Fowler and Brydon, 1989) that extended beyond the 40 kg ha^{-1} N level. The most extreme example of an initial decrease in GPC associated with the lag phase in this study occurred in the 1993 partial irrigation trial at Saskatoon. Very low residual N levels in the soil and favorable growing conditions resulted in a decrease in GPC from 119 to 101 g kg^{-1} with the first 40 kg ha^{-1} fertilizer N for both Winalta winter wheat and AC Taber spring wheat. Nitrogen fertilizer applications of >120 kg ha^{-1}

Table 1. Number of trials and average maximum grain yields (Ymax) and protein concentrations at maximum grain yield (Pmax) and 90% (P90) and 80% (P80) of maximum grain yield for eight spring and seven winter wheat genotypes. Grain yields were estimated using the peak four- parameter Weibull equation, and protein concentrations were estimated the using the sigmoidal four-parameter Gompertz equation (see Fig. 1).

Genotype†	Market class‡	Number of trials	Ymax	Pmax	P90	P80
			kg ha^{-1}	g kg^{-1}		
Spring wheat						
Katepwa	HRS	12	3906	149	124	115
Roblin	HRS	7	4073	154	133	122
AC Barrie	HRS	5	4111	159	135	124
Glenlea	ESS	9	4344	139	114	106
BW90	HRS	3	4419	155	139	131
AC Taber	CPSR	12	5257	125	105	100
AC Reed	SWS	10	5317	116	99	92
AC Vista	CPSW	2	5589	127	103	93
Winter wheat						
Winalta	HRW	6	4580	134	116	108
S86-101	HRW	4	5140	122	103	95
Norstar	HRW	6	5232	122	103	95
CDC Harrier	HRW	2	5310	120	106	96
CDC Osprey	HRW	5	5344	134	119	107
CDC Kestrel	HRW	7	5507	116	101	94
CDC Clair	HRW	5	5589	132	119	107
CDC Ptarmigan	SWW	4	5844	107	89	83
SD§			309	5.6	8.1	7.1

† BW90 and S86-101 are not registered cultivars.
‡ HRS, hard red spring; ESS, extra-strong spring; CPSR, Canadian prairie spring red; SWS, soft white spring; CPSW, Canadian prairie spring white; HRW, hard red winter; SWW, soft white winter.
§ SD, standard deviation.

were required before the GPC of these two cultivars exceeded the level found at the 0 kg ha^{-1} N rate in this trial (data not shown). In contrast, the lag phase of the GPC response curve became shorter as environmental limitations increased or cultivar grain yield potential decreased, and it often disappeared entirely in trials grown in fields with high levels of residual soil available N and/or under moderate or high drought stress.

Once cultivar yield potential or environmental factors other than available N became limiting to plant growth, excess N was utilized mainly for grain protein production, and the GPC–N response curve entered an *increase phase* (zone of poverty adjustment). During this phase, GPC increased rapidly, even under favorable growing conditions. However, the response curve turned up at lower N levels and tailed off at higher GPC under poor compared with good growing conditions (data not shown).

The GPC response to increased N quickly diminished to near zero when cultivar yield potential or environmental factors, such as moisture, limited grain yield. The end of the increase phase and the start of the *maximum phase* (zone of luxury consumption) of the GPC–N response curve usually occurred at approximately the same N rate as maximum grain yield was achieved (Fowler et al., 1990). A detrimental effect (Goos et al., 1982; Fowler et al., 1989) that resulted in yield depression was observed at high N levels.

Different GPC–grain yield relationships were associated with each of the three phases of the GPC–N response curve. The lag phase of the response curve often had a negative slope. From the end of the lag phase to the point of maximum grain yield there was a positive correlation between grain yield and GPC that was due to increased N availability. Beyond the point of maximum grain yield, the correlation between GPC and grain yield was once again either nonsignificant or negative. Consequently, the relationship between GPC and grain yield depended on the region of the response curve sampled.

The peak four-parameter Weibull equation was employed to describe the grain yield response, and the sigmoidal four-parameter Gompertz equation was used to describe the GPC response to N fertilizer applications for each of the 99 genotype–trial comparisons made in this study (examples given in Fig. 1). Average reductions in sums of squares due to model were 97.2 and 98.9%, respectively, indicating that these equations provided an excellent fit to the observed data. Maximum grain yield (Table 1) and the N rates required to achieve maximum grain yield and 90 and 80% of maximum grain yield were estimated for each cultivar in each trial using the peak four-parameter Weibull equation. These N rates were then used to estimate the GPC at maximum grain yield and 90 and 80% of maximum grain yield using the sigmoidal four-parameter Gompertz equation. The GPC at maximum grain yield and 90 an 80% of maximum grain yield was also estimated by fitting the grain yield and GPC data for each of the 99 genotype–trial comparisons to the peak three-parameter log normal equation (examples given in Fig. 2). In this instance, average reduction in sums of squares due to model was 66.8%. The two approaches used the same database and arrived at similar estimates of maximum grain yield and GPC at maximum grain yield and 90 and 80% of maximum grain yield (Tables 1 and 2).

Grain Protein Concentration and Yield Potential

Both genotype (Tables 1 and 2) and environment influenced the upper limit of yield when N was not limiting. Maximum grain yields for individual trials ranged from an average of 4140 kg ha^{-1} on dryland at Saskatoon in 1998 to 6767 kg ha^{-1} under partial irrigation at Saskatoon in 1992 for spring wheat

Table 2. Number of trials and average maximum grain yields (Ymax) and protein concentrations at maximum grain yield (Pmax) and 90% (P90) and 80% (P80) of maximum grain yield for eight spring and seven winter wheat genotypes. Grain yields and protein concentrations were estimated the using the peak three-parameter log normal equation (see Fig. 2).

Genotype	Number of trials	Ymax	Pmax	P90	P80
		kg ha^{-1}	g kg^{-1}		
Spring wheat					
Katepwa	12	3942	142	124	113
Roblin	7	4022	153	129	120
AC Barrie	5	4168	148	128	120
Glenlea	9	4391	134	111	105
BW90	3	4240	157	140	132
AC Taber	12	5212	123	104	96
AC Reed	10	5305	113	98	91
AC Vista	2	5668	124	104	96
Winter wheat					
Winalta	6	4563	132	115	111
S86-101	4	5187	115	100	93
Norstar	6	5142	119	102	95
CDC Harrier	2	5211	120	102	96
CDC Osprey	5	5197	129	112	107
CDC Kestrel	7	5392	112	98	93
CDC Clair	5	5450	129	115	109
CDC Ptarmigan	4	5839	102	89	83
SD		313	6.1	5.6	6.0

and from 2793 kg ha^{-1} under dryland at Yorkton in 1997 to 6457 kg ha^{-1} under partial irrigation at Saskatoon in 1993 for winter wheat. As the maximum potential grain yield (Ymax) of a genotype increased due to more favorable environmental conditions, which in this case was primarily increased water availability, the GPC at the point of maximum grain yield (Pmax) decreased. For example, every tonne per hectare increase in maximum grain yield due to improved growing conditions produced a 12.5 and 7.9 g kg^{-1} decrease in GPC for Katepwa [Pmax (g kg^{-1}) = 201.4 − 0.0125 × Ymax (kg ha^{-1}); r^2 = 0.68] and AC Taber (Pmax (%) = 169.1 − 0.00786 × Ymax (kg ha^{-1}); r^2 = 0.70], respectively. Similar GPC–grain yield relationships were found at 90 and 80% of maximum grain yield.

There were large differences in GPC and maximum grain yield (Tables 1 and 2) among the genotypes considered in this study. For example, average GPC at maximum grain yield ranged from 107 g kg^{-1} for CDC Ptarmigan to 159 g kg^{-1} for AC Barrie while average maximum grain yield ranged from 3906 kg ha^{-1} for Katepwa to 5844 kg ha^{-1} for CDC Ptarmigan (Table 1). The often reported strong negative correlation between cultivar GPC and grain yield (Terman et al., 1969; Terman, 1979) was especially evident in these comparisons, translating into more than a one-third tonne-per-hectare reduction in maximum potential grain yield for every 10 g kg^{-1} increase in GPC [Ymax (kg ha^{-1}) = 9593 − 35 × Pmax (g kg^{-1}); r^2 = 0.76]. Among western Canadian wheat market classes, the GPC at maximum grain yield was lower for the high-yielding SWW wheat cultivar CDC Ptarmigan than for the cultivars that represented the SWS, HRW, CPSR, and CPSW classes. In turn, the GPC at maximum grain yield was lower for cultivars that represented the HRW, CPSR, and CPSW classes than for the HRS cultivars, which had a very low maximum grain yield potential.

The observations made in this study help us to understand the limitations in our ability to select for both grain yield and GPC in wheat breeding programs. Wheat quality standards in western Canada have been maintained by a restrictive cultivar registration system that only allows the commercial release of lines with quality characteristics that are equal to or better than designated check cultivars for each quality class. The HRS class has been the mainstay of the western Canadian wheat industry, and there has been nearly 100 yr of intensive breeding effort concentrated on improving cultivars in this class (DePauw et al., 1995). The breeding efforts on the rest of the quality classes have been much less intensive, and the intermediate-GPC classes—ESS, CPSR, and CPSW—have only been seriously pursued in the last 15 to 20 yr (DePauw, 1995). Interestingly, in spite of all the attention in the last century, modern cultivars of the HRS wheat class have the lowest maximum grain yield potential (Tables 1 and 2). In contrast, the SWW wheat cultivar CDC Ptarmigan, which originated from a group of three lines selected from a single hard wheat × soft wheat cross in a HRW breeding program, had the highest maximum grain yield potential of all the cultivars considered in this study. These observations indicate that, while improvements have been made within classes, even small increases in grain yield are extremely difficult to achieve when breeding programs are also expected to maintain or improve GPC. Certainly, the production of high-yielding cultivars with high GPC is more complicated than simply stacking yield genes in a high-GPC genetic background or vice versa.

Part of the explanation for the negative relationship between cultivar grain yield potential and GPC lies in the fact that the amount of N available to a plant for protein production depends on a substrate-inducible, relatively unstable enzyme, nitrate reductase, which is regulated by the level of available soil N (Eilrich and Hageman, 1973). Cultivars growing side by side have access to similar amounts of available soil N, and GPC is determined by the ratio of grain protein yield to total grain yield. As a result, higher-yielding cultivars will have lower GPC than lower-yielding cultivars unless they have an increased ability to extract N from the soil, translocate it to the grain, or use it in protein synthesis. However, these observations do not explain the strong negative correlation between cultivar GPC and maximum potential grain yield observed in the present study where plant available N was not limiting. The higher energy requirements for protein compared with carbohydrate synthesis (Penning de Vries et al., 1974) and/or critical genetic adjustments that limit grain yield potential may provide possible explanations for this negative relationship. Whatever the cause, the general rule in effective breeding programs appears to be that the higher a cultivar's relative GPC is, the lower its maximum grain yield potential.

Grain Protein Concentration as a Postharvest Indicator of Crop Nitrogen Deficiencies

This study focused on important genotypic and environmental interactions that determine the GPC and yield potential in common wheat. From a practical standpoint, the results indicate that GPC may be a useful postharvest indicator of N deficiencies for crops grown under high N stress, but caution must be used when the goal is to optimize N management systems. The following limitations should be kept in mind:

1. High GPC can be associated with severe N deficiency in high production environments, i.e., high GPC does not always indicate N sufficiency. Under these conditions, the first few increments of added N produce large increases in grain yield and reductions in GPC.
2. The grain yield response curves flatten out at maximum grain yield (Fig. 2), with the result that large differences in GPC often translate into small differences in grain yield, thereby reducing the usefulness of this part of the GPC–grain yield response curve for postharvest assessment of N sufficiency. Grain protein concentration at 80 and 90% of maximum grain yield is much more sensitive

to changes in N availability, suggesting that GPC in this region of the response curve would be a more practical indicator of N deficiency. Coincidentally, the GPC at maximum grain yields (Tables 1 and 2) of hard red wheat cultivars were higher in this study than those identified as postharvest indicators of N sufficiency by other researchers (Goos et al., 1982; Flaten and Racz, 1997; Long and Engel, 1998; Selles and Zentner, 2001). The GPC identified in the earlier reports was more in line with the GPC at 90% of maximum grain yield in the present study, a point which would also be expected to provide a more realistic estimate of maximum economic grain yield.

3. Growing season weather conditions have a large influence on both GPC and grain yield, which makes the GPC–grain yield relationships environment specific. As the maximum potential grain yield of a genotype was reduced by environmental factors, which in this case was primarily water availability, the protein concentration at the point of maximum grain yield increased.
4. There are large differences among wheat cultivars in their GPC at maximum grain yield (Tables 1 and 2). Therefore, the critical GPC–grain yield responses must be known for each cultivar before GPC is of value as a postharvest indicator of N sufficiency.
5. There is a strong negative correlation between cultivar GPC and maximum potential grain yield. The most direct solution to this GPC–grain yield dilemma is to simply increase the rate of N fertilization to meet GPC targets when cultivars with high yield potential are grown. However, N may have to be applied at rates above those required to achieve maximum grain yield to meet premium GPC targets when hard wheat cultivars with high grain yield potentials are produced.

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