INFLUENCE OF CLIMATE AND CULTIVAR ON GRAIN PROTEIN CONCENTRATION OF WHEAT AND RYE.

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INTRODUCTION

The traditional winter wheat production area of the Canadian prairies has been southwestern Alberta. Only with the recent introduction of a practical snow management system, which utilized no-till seeding into standing stubble immediately after harvest of the previous crop ("stubbling-in"), has the risk of winterkill been reduced sufficiently to provide the opportunity for winter wheat production throughout the remainder of the prairie agricultural region (Fowler, 1983). Winter rye is also adapted to the stubbling-in management system. The no-till aspect of this production system has provided an opportunity to extend rotations and improve soil conservation methods in western Canada.

Most stubble fields on the Canadian prairies are deficient in plant-available-soil nitrogen (N). In high production environments, soil test results often indicate less than 30 kg available N ha^{-1}. Therefore, N fertilization is usually necessary to optimize yield (Fowler et al., 1989a) and maintain protein concentration at acceptable levels (Fowler et al. 1989b). Under these conditions, N fertilizer also becomes the major input cost in the stubbling-in management system (Fowler and Entz, 1986).

Protein is a primary quality component of cereals and its importance is often recognized in the marketplace. This is especially so with wheat where most exporting countries have some segregation of commercial grain lots on the basis of protein concentration. In hard wheat the majority of the variation in loaf volume can be attributed directly to differences in protein concentration. Protein concentration of 11% is usually considered the minimum acceptable for this quality class and premiums are often paid for higher concentrations. The pastry, and to a lesser extent the biscuit, market prefers low protein flour (<11%) from soft wheat. Usually, if large quantities of cereal grains are grown for feed, high protein concentration has a market advantage. Cereal protein contains approximately 17.5% nitrogen (N). Because N is obtained from the soil, plant-available soil N has a direct influence on grain protein yield (Hunter and Stanford, 1973; Olson et al., 1976; Black and Siddoway, 1977).

The central role of N fertilization in the successful production and marketing of stubbled-in winter cereals has made it the focus of numerous research studies in Saskatchewan during the last 14 years. This paper summarizes the results of these genetic and agronomic studies with the objective of providing a detailed characterization of the influence of genotype and environment on wheat and rye grain protein concentration and N-use efficiency.

MATERIALS AND METHODS

A large number of fertilizer trials were conducted during the period 1974 to 1988 as a part of the winter cereal program at the Crop Development Centre, University of Saskatchewan. Details on previous crop, soil type, residual N, cultivar utilized and environmental conditions for each trial, and general experimental details on several of these studies are given in related publications (Darroch, 1988; Entz and Fowler, 1988; 1989a; 1989b; Fowler and Brydon, 1989; Fowler et al., 1989a; 1989b). The most highly adapted wheat and rye cultivars for this region were utilized in these trials and, as a result, there were several cultivar changes over the period of these studies. The two winter wheat cultivars utilized, 'Sundance' and 'Norstar', have similar grain protein concentrations and grain yields (Fowler and de la Roche, 1984). The winter rye cultivars, 'Cougar' and 'Puma', have relative grain yields of 90 and 100%, with grain protein concentration of 9.9 and 9.0%, respectively. Protein yields for the rye cultivars were similar.

Experimental design for the time and rate of N fertilizer application trials was a split plot with fertilizer rate and time of application as the main and sub-plots. Nitrogen treatments were replicated four times in each trial. Nitrogen treatments were applied in the early spring (May 1) and late spring (May 30).

Experimental design for the partial irrigation studies was a split plot with water regimes as the main plots and N fertilizer rates as the sub-plots. Water treatments were irrigation to approximately 130% of the long term average applied using either trickle or flood irrigation techniques. Treatments were replicated three or four times in each trial.

Experimental design for the 'Neepawa' spring wheat, Sundance winter wheat, and Cougar winter rye comparisons was a split plot with N fertilizer rates as the main plots and cultivars as the sub-plots. Treatments were replicated four times in each trial.

Experimental design for the winter wheat cultivar comparisons was a split plot with cultivars as the main plots and nitrogen fertilizer rates as the sub-plots. Cultivars were selected to represent low ('Yorkstar'), intermediate (Norstar and 'Ulianovkia'), and high ('Redwin') protein concentration classes. Treatments were replicated four times in each trial.

With exception of the Porcupine Plain trial, which was seeded into summerfallow, all trials were direct seeded into standing stubble immediately after harvest of the previous crop (between 24 Aug. and 7 Sept. of each year). Phosphate fertilizer (11-51-0 or 11-48-0) was applied with the seed at rates recommended for each soil type. Elements other than phosphorus and N were not considered to be limiting. NItrogen fertilizer was applied as commercial-grade ammonium nitrate (34-0-0) hand-broadcast on the soil surface in the early spring unless otherwise indicated.

In the early spring of each year, mid-row soil samples (0-15, 15-30 and 30-60 cm increments) were collected from plots that had not received N fertilizer in each trial for nitrate analyses by the Saskatchewan Institute of Pedology, soil testing laboratory. Only estimates of NO_3-N were utilized because field trials in both Alberta and Saskatchewan have demonstrated that the relationship between grain yield or protein concentration and NO_3-N plus NH_4-N is no better than for NO_3-N alone (Nuttall et al., 1971; Malhi et al., 1985). Available NO_3-N concentrations were determined colorimetrically by autoanalyzer using cadmium reduction (Technicon Industrial Method #100-70W, Technicon Instrument Corp., Tarrytown, N.Y.). Because soil and fertilizer N were considered to be equally plant-available total available N was calculated for each treatment as the sum of soil NO_3-N to 60 cm depth and added fertilizer N (Heapy et al. 1976; Zentner and Read, 1977; France and Thornley, 1984; Bole and Dubetz, 1986).

Grain protein concentration and protein yield (grain yield x protein concentration) were determined for each plot in each trial. Protein concentrations were determined from Kjeldahl N (N x 5.7) or by the Udy dye method (Udy, 1971). Kjeldahl analyses were utilized to standardize protein concentrations in each trial analyzed by the Udy dye method.

Analyses of variance were conducted to determine the significance of treatment differences within each fertilizer trial. An inverse polynomial equation with a modification for yield depression at high N levels (France and Thornley, 1984) was used to describe the relationship between available N and both grain and grain protein yield. Use of this function to describe the N response curves of grain and grain protein yield has been elaborated on in earlier publications (Fowler et al., 1989a; b).

The inverse polynomial equation takes the form:

$$Y = \frac{\underline{u}N}{N + \underline{u}/\underline{e}} \quad (1-N/\underline{s}), \qquad [1]$$

where Y = predicted grain or protein yield (kg ha^{-1})
N = total available N (kg N ha^{-1})
$\underline{s}$ = a measure of yield sensitivity to high N levels (larger $\underline{s}$ indicates less sensitivity)
$\underline{u}$ = upper limit of yield achieved in the absence of sensitivity to high levels of N (kg ha^{-1})
$\underline{e}$ = maximum N use efficiency at low levels of N (kg yield kg N^{-1})

Non-linear regression procedures outlined by the SAS Institute (1985) were used to provide least-squares estimates of the regression coefficients $\underline{u}$, $\underline{e}$ and $\underline{s}$. In most cases, limited data prevented the statistical program from converging on reasonable estimates of all three coefficients. In these instances, $\underline{s}$ was held constant at the value (903 for grain and 949 for grain protein yield) determined in earlier studies (Fowler et al., 1989a) and $\underline{u}$ and $\underline{e}$ were successfully estimated.

The Gompertz equation was employed to describe the relationship between protein concentration and available N. Use of this function to describe the protein concentration-N response curve has been detailed in an earlier publication (Fowler et al., 1989b).

The Gompertz equation takes the form:

$$P = \underline{M} + \underline{A} \exp [-\underline{B} \exp (-\underline{K}N)] \qquad [2]$$

where P = predicted protein concentration (14% water)
$\underline{M}$ = minimum protein concentration (%)
$\underline{M} + \underline{A}$ = asymptotic protein concentration achieved at high N levels
$\underline{B}$ = determines N level at which protein concentration reaches $\underline{M} + 0.5\underline{A}$
$\underline{K}$ = coefficient that determines the rate P increases to $\underline{M} + \underline{A}$.
$\underline{N}$ = total available N (kg ha^{-1}).

The coeffficient $\underline{K}$ was held constant at 0.0230 and the coefficient $\underline{M}$ was held constant at 8.4% for wheat and 8.2% for rye (Fowler et al., 1989b). Non-linear regression procedures outlined by the SAS Institute (1985) were used to provide least-squares estimates of the coefficients $\underline{A}$ and $\underline{B}$.

The level of total available N at which maximum protein yield is obtained was calculated from the following equation.

$$N_{MAX} = \frac{u}{\underline{e}} \left(\sqrt{1 + \frac{es}{\underline{u}}} - 1\right) \qquad [3]$$

Maximum yield was estimated by inserting N_{MAX} into Eq. [1].

Nitrogen use efficiency (NUE) for grain protein yield was determined as kg N ha^{-1} recovered as grain N for each 10 kg increment of fertilizer N applied ha^{-1}.

RESULTS AND DISCUSSION

Grain Protein Concentration - N Response Pattern

Problems are often encountered in describing the grain protein concentration-N response curve. Lack of precision in estimates of residual plant-available soil N, the influence of environment in modifying the N cycle, and the fact that most experiments only sample part of the N response curve make it difficult to compare results from different studies. These problems were considered in a 12 year investigation that included forty field trials conducted over a wide range of soil types and environmental conditions in Saskatchewan (Fowler et al., 1989b). In this study, the Gompertz equation (Eq. [2]) provided the most complete description of the relationship between protein concentration and total plant available N. The protein concentration-N response curves for wheat and rye were similar. After an initial lag (lag phase), protein concentration increased rapidly (increase phase), and then tailed off at high N levels (Fig. 1). The length of the initial lag phase of the curve was reflected by the size of the $\underline{B}$ value in Eq. [2] (Table 1). In several trials the lag phase extended beyond the 50 kg ha^{-1} level with the indication that there was an initial decrease in protein concentration (Bole and Dubetz, 1986; Partridge and Shaykewich, 1972). The presence of the initial lag phase indicated that there was a minimum grain protein concentration that was approximately 8.4 and 8.2% for wheat and rye, respectively (Fowler et al., 1989b).

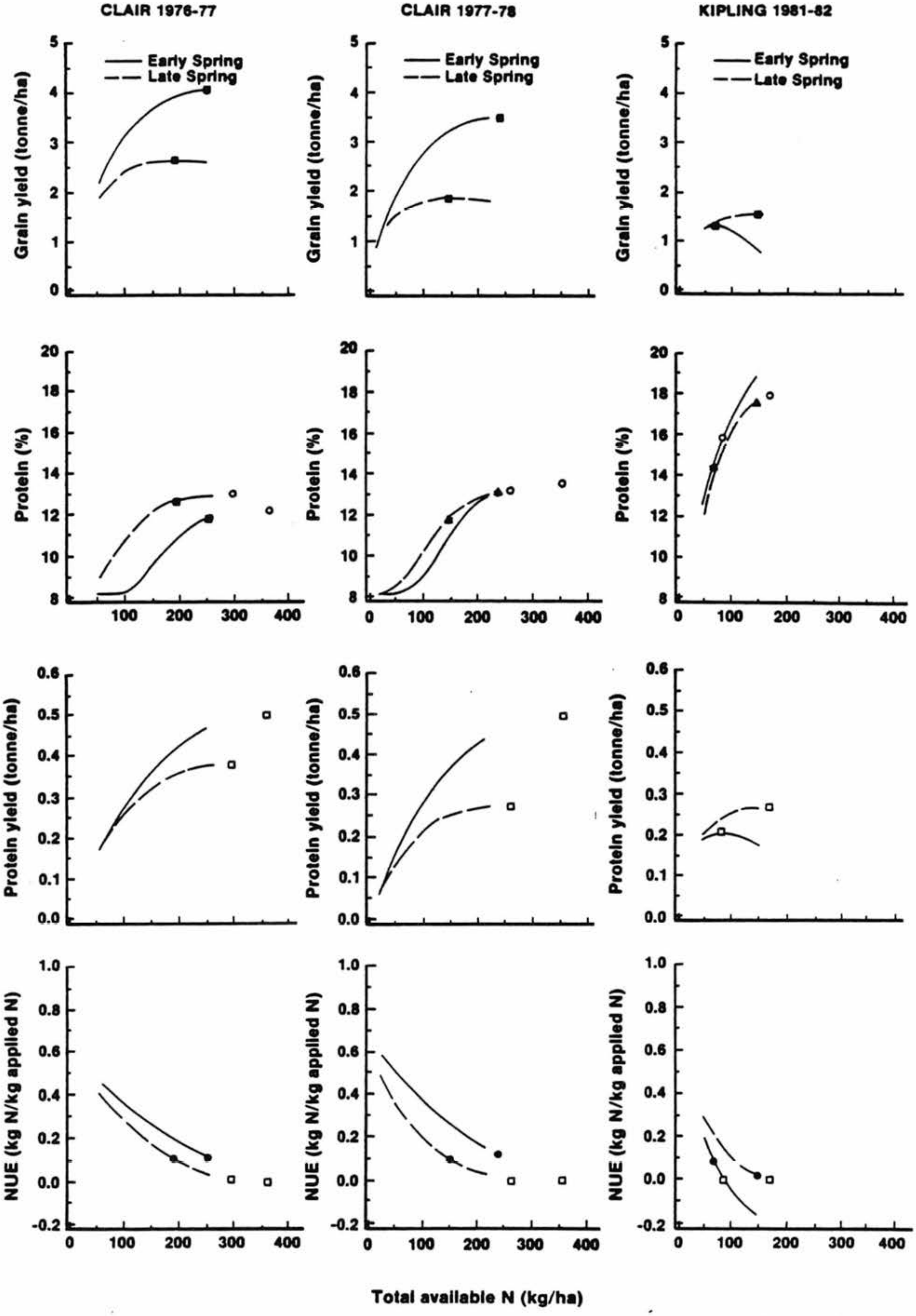

Figure 1. Norstar winter wheat grain yield, grain protein yield, and grain protein concentration response to total available N and nitrogen use efficiency (NUE) for grain protein production for early and late spring N fertilization. Total available N level at which maximum grain (●) and grain protein (o) yields were achieved.

Table 1. Estimated regression coefficients (Eq. [2]) and reductions in sums of squares due to model (r^2) for grain protein concentration in a) date of N fertilization, b) partial irrigation, c) wheat and rye comparison, and d) winter wheat cultivar comparison trials.

Trial	Treatment	Regression Coefficient A	 B	r^2
a) Date of N fertilization (Fig. 1)				
Clair 1976/77	Early spring	4.1	36.8	.870
	Late spring	4.9	6.7	.987
Clair 1977/78	Early spring	5.3	20.6	.998
	Late spring	5.1	9.8	.992
Kipling 1981/82	Early spring	11.7	2.9	.999
	Late spring	10.4	2.9	.999
b) Partial irrigation (Fig. 2)				
Clair 1985/86	Irrigation	3.1	1.7	.991
	Dryland	3.6	1.2	.984
Outlook 1985/86	Irrigation	4.8	4.5	.978
	Dryland	5.5	2.8	.996
Saskatoon 1987/88	Irrigation	6.8	2.9	.999
	Dryland	6.7	0.3	.997
c) Wheat and rye comparisons (Fig. 3)				
Clair 1976/77	Winter wheat	4.0	9.2	.959
	Spring wheat	6.0	1.7	.997
	Winter rye	3.2	22.8	.850
Clair 1977/78	Winter wheat	5.4	9.6	.999
	Spring wheat	7.8	1.5	.994
	Winter rye	3.2	12.8	.983
Saskatoon 1977/78	Winter wheat	7.6	4.5	.999
	Spring wheat	8.8	1.1	.999
	Winter rye	6.5	8.6	.981
d) Winter wheat cultivar comparisons (Fig. 4).				
Paddockwood 1985/86	Norstar	2.9	7.0	.970
	Ulianovkia	3.1	1.5	.997
	Redwin	4.2	1.5	.999
Porcupine Plain 1985/86	Norstar	3.7	<170	.999
	Ulianovkia	3.8	<170	.999
	Redwin	4.4	<170	.999
	Yorkstar	2.8	<170	.999

Table 2. Estimated regression coefficients (Eq. [1]) and reduction in sums of squares due to model (r^2) for grain yield in a) date of N fertilization, b) partial irrigation, c) wheat and rye comparison, and d) winter wheat cultivar comparison trials.

Trial	Treatment	Regression Coefficient			r^2
		u	*e*	*s*	
a) Date of N fertilization (Fig. 1)					
Clair 1976/77	Early spring	9137	58	903	.999
	Late spring	4528	67	903	.996
Clair 1977/78	Early spring	7402	56	903	.990
	Late spring	2734	80	903	.996
Kipling 1981/82	Early spring	3412	66	217	.987
	Late spring	2293	66	903	.986
b) Partial irrigation (Fig. 2)					
Clair 1985/86	Irrigation	7292	98	518	.998
	Dryland	3973	150	518	.998
Outlook 1985/86	Irrigation	6950	110	518	.999
	Dryland	5292	130	518	.999
Saskatoon 1987/88	Irrigation	2733	69	635	.999
	Dryland	436	141	635	.997
c) Wheat and rye comparisons (Fig. 3)					
Clair 1976/77	Winter wheat	6647	69	914	.998
	Spring wheat	3856	88	914	.985
	Winter rye	7345	93	914	.996
Clair 1977/78	Winter wheat	9926	55	778	.997
	Spring wheat	4158	133	1102	.997
	Winter rye	10789	66	768	.999
Saskatoon 1977/78	Winter wheat	2300	142	1348	.997
	Spring wheat	1321	93	1348	.991
	Winter rye	3830	76	1348	.998
d) Winter wheat cultivar comparisons (Fig. 4)					
Paddockwood 1985/86	Norstar	8139	47	506	.999
	Ulianovkia	4219	48	663	.999
	Redwin	2808	46	1656	.997
Porcupine Plain 1985/86	Norstar	42773	20	1037	.999
	Ulianovkia	26849	21	1037	.999
	Redwin	11566	19	1037	.995
	Yorkstar	9639	20	1037	.990

Table 3. Estimated regression coefficients (Eq. [1]) and reduction in sums of squares due to model (r^2) for grain protein yield in a) date of N fertilization, b) partial irrigation, c) wheat and rye comparison, and d) winter wheat cultivar comparison trials.

Trial	Treatment	Regression Coefficient			r^2
		u	e	s	
a) Date of N fertilization (Fig. 1)					
Clair 1976/77	Early spring	2119	3.6	949	.999
	Late spring	1003	4.1	949	.999
Clair 1977/78	Early spring	1953	3.8	949	.986
	Late spring	610	3.9	949	.999
Kipling 1981/82	Early spring	477	8.9	292	.997
	Late spring	415	8.9	949	.999
b) Partial irrigation (Fig. 2)					
Clair 1985/86	Irrigation	1100	7.0	871	.998
	Dryland	530	10.6	871	.999
Outlook 1985/86	Irrigation	605	8.5	871	.998
	Dryland	488	10.8	871	.999
Saskatoon 1987/88	Irrigation	696	4.9	505	.999
	Dryland	67	4.8	786	.999
c) Wheat and rye comparisons (Fig. 3)					
Clair 1976/77	Winter wheat	866	5.5	1418	.998
	Spring wheat	566	8.8	1418	.990
	Winter rye	1008	5.4	1418	.998
Clair 1977/78	Winter wheat	4045	4.6	656	.997
	Spring wheat	721	15.0	1302	.999
	Winter rye	1699	5.5	795	.999
Saskatoon 1977/78	Winter wheat	384	8.0	2792	.999
	Spring wheat	215	14.9	2792	.996
	Winter rye	1277	4.4	800	.992
d) Winter wheat cultivar comparisons (Fig. 4)					
Paddockwood 1985/86	Norstar	610	4.3	2491	.999
	Ulianovkia	497	5.2	824	.999
	Redwin	398	4.7	2491	.998
Porcupine Plain 1985/86	Norstar	1989	3.0	1342	.999
	Ulianovkia	1813	3.0	1342	.993
	Redwin	1083	2.8	1342	.993
	Yorkstar	820	1.6	1342	.997

Limited variation in the size of the coefficients that determined minimum grain protein concentration (M) and the rate at which protein concentration increased to its asymptote (K) in Eq. [2] indicated these two variables were under strong genotypic control in both wheat and rye (Fowler et al., 1989b). In contrast, large experiment effects indicated that the relative length of the initial lag phase (B) and the asymptotic protein concentration (A) were both under greater environmental influence (Fowler et al., 1989b).

Critical Growth Stages and the Effect of Environment

Studies on the influence of rate and time of N fertilization have identified the general grain yield, grain protein yield, and grain protein concentration-N response patterns for stubbled-in Norstar winter wheat grown in Saskatchewan (Fowler and Brydon, 1989). As indicated in the previous section, there is a minimum N level required for plant growth that yields grain with a protein concentration of approximately 8.4 and 8.2% for wheat and rye, respectively. When conditions are favorable for growth, the correction of severe N stress through N fertilization results in proportional increases in grain and grain protein yield. Consequently, minimum protein concentration is maintained for the first increments of added N giving rise to the lag phase in the protein concentration-N response curve. Once other environmental or genotypic factors become limiting to growth and subsequent increases in grain yield, excess N is utilized mainly for grain protein production and the protein concentration-N response curve enters an increase phase. Delays in the availability of N to the plant as a result of late spring applications (Clair trials Fig. 1) or prolonged dry periods following spring fertilization have the effect of limiting grain yield potential. If accessed later, the fertilizer N becomes surplus to the plants minimum N requirements for growth at lower total N levels. This results in a more rapid increase in grain protein yield than total grain yield, lower B values and a shift of the protein concentration-N response curve to the left (Clair trials Fig. 1, Table 1).

The importance of critical growth stages in determining grain yield, grain protein yield, and grain protein concentration was investigated further in detailed studies conducted on stubbled-in winter wheat in Saskatchewan (Entz and Fowler, 1988). Root zone and profile extractable soil water, precipitation, pan evaporation, and growing degree days were monitored throughout the growing season. Variation in pan evaporation during the 2 week period immediately prior to anthesis (Zadok stage 46 to 65) accounted for 72 and 71% of the variability in grain and grain protein yield, respectively. When measurements of root zone extractable soil water at anthesis (Zadok stage 65) and pan evaporation two weeks prior to maturity (Zadok stage 83 to 91) were included in the equation, the amount of variability in grain yield accounted for rose to 91%. Pan evaporation for the 2 week period immediately prior to anthesis and temperature in the 2 week period immediately after anthesis (Zadok stage 65 to 74) together explained 82% of the variability observed in grain protein yield in these trials. Protein concentration was negatively correlated with soil water at all development stages considered, but was most dependent on root zone water at elongation (Zadok stage 31). Measures of root zone water at elongation and pan evaporation during the 2 weeks prior to maturity explained 73% of the variability observed in grain protein concentration. Stepwise addition of other environmental variables considered in this study did not provide additional information on grain yield, grain protein yield, or grain protein concentration.

The effects of N and water on grain protein concentration were further clarified in field studies conducted in Saskatchewan between 1984 and 1988. Partial irrigation of stubbled-in winter wheat significantly increased grain and grain protein yield over comparable dryland treatments in these trials (Fig. 2). The addition of water also increased the length of the lag phase (B in Eq. [2]) of the protein concentration-N response curve (Fig. 2, Table 1). In contrast to the differences observed in the length of the lag phase, the asymptotic maximums (A) of the protein concentration-N response curves for dryland and irrigation treatments were often similar. Consequently, removal of the factor most limiting grain yield, i.e., water limitations in this instance, resulted in a delay of the protein concentration increase phase of the N response curve. Once limits on the expression of yield potential were reimposed, the protein concentration-N response proceeded in a manner similar to that observed for dryland treatments.

Investigations into the interaction between N and water in determining the agronomic performance of stubbled-in winter wheat have also assisted in the identification of growth stages and environmental factors that have a major influence on protein concentration. Grain yield is considered a good measure of the cumulative influence of environment upon plant growth, i.e., the more favorable the environment the greater the yield. Environmentally induced changes in grain protein yield have been shown to be closely related to changes in grain yield (r=0.93**; Fowler et al., 1989b). However, maximum grain protein yield was not significantly correlated with either the asymptotic protein concentration (A) or the relative length of the lag phase (B) in Eq. [2] (Fowler et al; 1989b). Length of the initial lag phase (B) of the protein concentration-N response curve was correlated with dry matter at anthesis (r=0.97**) and root zone extractable water at stem elongation (r=0.85**) indicating that, as pre-anthesis growing conditions improve, more N is required to produce an increase in grain protein concentration above the minimum 8.4% (Entz and Fowler, 1989b). In contrast to the lag phase (B), identification of the critical growth stages and important environmental factors determining the asymptotic maximum protein concentration (A) has proven more difficult. Asymptotic protein concentration (A) has been shown to be negatively correlated (r=-0.67**) with water availability from May 1 to anthesis (Entz and Fowler, 1989b). However, explanation of the positive influence that evaporation during the 2 weeks prior to maturity has in determining protein concentration (Entz and Fowler, 1988), and the size of A, requires an understanding of the factors determining grain yield and grain protein yield.

Reports in the literature suggest that from 50 to 80% of the grain protein N is derived from vegetative tissue produced during the pre-anthesis period (Spiertz and Vos, 1985) with the remaining N being supplied by uptake after anthesis. Under moist soil conditions, wheat may continue to take up N until near maturity but, under dry conditions, very little N is taken up after anthesis (Gregory et al., 1979). Field trials conducted with stubbled-in winter wheat have shown that, under average Saskatchewan conditions, 70% of the total dry matter and 90% of the total plant N is accumulated by anthesis (Darroch, 1988). Maximum grain yield is determined primarily by kernels m^{-2} (Fowler et al., 1989a; Entz and Fowler, 1989a) and high dry matter production in the pre-anthesis period is required to establish high kernels m^{-2} (Entz and Fowler, 1989a). The only adjustments in yield potential to take place after

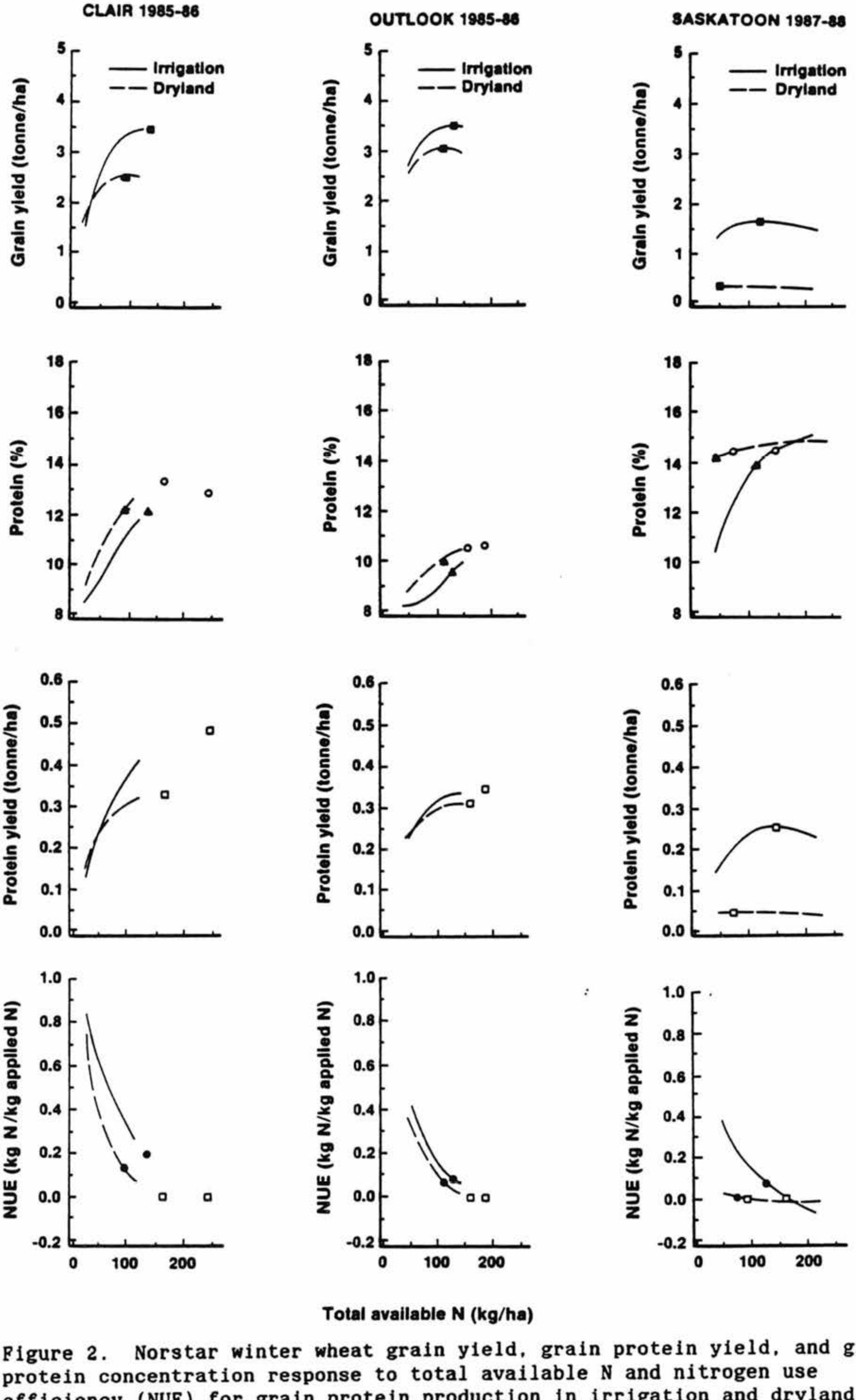

Figure 2. Norstar winter wheat grain yield, grain protein yield, and grain protein concentration response to total available N and nitrogen use efficiency (NUE) for grain protein production in irrigation and dryland trials. Total available N level at which maximum grain (●) and grain protein (o) yields were achieved.

anthesis are compensation for adverse environmental conditions through tiller loss, floret abortion (blasting) and/or as a last resort reduced seed size. Consequently, under Saskatchewan growing conditions, most of the protein N is in position for remobilization in the plant by anthesis. In contrast, dry matter yield at anthesis only determines the maximum yield potential of the crop. The period after anthesis determines the level of expression of this yield potential.

Observations from timing of N fertilization trials further demonstrate the important influence on protein concentration that arises because the period of maximum N assimilation occurs prior to anthesis and grain carbohydrate synthesis occurs after anthesis. As described earlier, delayed N application normally shifts the protein concentration-N response curve to the left (Fig. 1). However, the reverse situation was observed in a field trial at Kipling in 1981-82 that experienced low early and high later season drought stress (Fowler and Brydon, 1989). In this trial, increased N rate decreased grain yield except for late spring applications where the check yield was maintained even at high N rates (Kipling Fig. 1). These observations indicate that, as normally occurs, the late spring applied fertilizer N was not available before N became severely limiting to plant growth. Consequently, in the absence of N-stimulated luxuriant spring growth, plants in late spring applied N plots did not sustain the same level of damage from the subsequent extended drought as plants in plots with high levels of available N from earlier fertilizer applications. Reductions in grain protein yield were also associated with early N applications. This suggests that, while N uptake most certainly occurred early in the season, the resulting drought-induced sensitivity to high levels of N also interfered with N translocation to the developing seed. However, contrary to the normal increase in the length of the lag phase (B̲) associated with early spring N fertilization (Clair trials Fig. 1), early spring N fertilization produced a shorter lag phase (B̲) than late spring N applications in the Kipling trial (Fig. 1, Table 1).

Moisture availability during the growing season is one of the major factors limiting crop productivity on the Canadian prairies. On average, only 20% of the moisture used by stubbled-in winter wheat comes from soil moisture reserves and most of this reserve will have been depleted by anthesis (Entz and Fowler, 1989b). Consequently, water utilized after anthesis is mostly derived from intermittent rainfall events. Average growing season pan evaporation is approximately three times precipitation resulting in a very large water demand and considerable drought stress in most seasons. These observations underline the importance of growing season rainfall distribution relative to plant growth stage in this region. Ten-fold differences in maximum grain yield of Norstar have been attributed to environmental differences experienced by stubbled-in winter wheat trials in Saskatchewan (Fowler et al., 1989a). This grain yield increase required a 3.2-fold increase in N emphasizing the unpredictable nature of crop N demands in Saskatchewan. Maximum protein concentration at high levels of N have been observed to vary from 11.4 to 20.3% for Norstar winter wheat and 9.5 to 15.5% for Puma winter rye (Fowler et al., 1989b). Under average to good environmental conditions, the maximum N requirements of the Norstar winter wheat plant can be expected to have been met when the grain protein concentration reaches approximately 13.0% (Fowler and Brydon, 1989). The protein concentration-N response curve reaches a maximum near this level unless spring environmental conditions favorable for plant growth an N uptake are followed by extreme drought that severely limits grain yield. Under these conditions, maximum protein concentrations will range from 15.0 to 20.3% for Norstar winter wheat.

Genotypic Effects

Significant ($P \leq 0.01$) differences in grain yield, grain protein yield, and grain protein concentration were observed among Neepawa spring wheat, Cougar winter rye, and Sundance winter wheat in the three trials reported on in this study (Fig. 3). However, a significant ($P \leq 0.05$) cultivar by N fertilizer rate interaction for all three characters indicated that the response to increased N levels was not always the same for these cultivars. The grain yield advantage was in the order Cougar, Sundance, and Neepawa over most of the N response curve considered (Fig. 3). Differences among cultivars were not as clear for grain protein yield, especially at lower total N levels. In all instances, Cougar had the highest grain yield and the longest lag phase ($\underline{B}$) in the protein concentration-N response curve (Table 1). Neepawa had the lowest grain yield and the shortest lag phase. Cultivar rankings for protein concentration did not change over the entire range of N rates considered (Fig. 3). These observations clearly established a genetic advantage for protein concentration that was in the decreasing order Neepawa, Sundance, and Cougar.

Nitrogen fertilizer trials that included only winter wheat cultivars demonstrated why the expression of genetic differences in grain protein concentration is not always as clear as indicated in the previous study (Table 1). Differences among winter wheat cultivars were significant ($P \leq 0.05$) for grain yield, grain protein yield, and grain protein concentration in both the Paddockwood and Porcupine Plain trials. The close relationship between grain yield and grain protein yield was evident in both trials, however, differences among cultivars were more obvious for grain protein yield in the Porcupine Plain trial than the Paddockwood trial (Fig. 4). While the magnitude of the differences changed considerably between trials, grain and grain protein yield rankings were similar for cultivars common to these two trials (Fig. 4). Norstar had the largest grain and grain protein yield advantage in the Paddockwood trial. As expected, the higher yield potential of Norstar was reflected in a larger lag phase ($\underline{B}$) of the protein concentration-N response curve (Fig. 4, Table 1). A high residual soil-N level did not allow for a reliable estimate of the lag phase in the Porcupine Plain trial. While cultivar rankings were similar in the two trials, the difference in protein concentration between Norstar and Ulianovkia was much smaller with the high N rates experienced at Porcupine Plain (Fig. 4). The lower yield potential, high protein concentration of Redwin when produced in Saskatchewan was evident in both trials. In contrast, the soft white winter wheat cultivar Yorkstar produced both low grain yield and low protein concentration in the Porcupine Plain trial (Fig. 4).

The following general conclusions can be drawn from the observations that have been made on the effects of environmental and cultivar variability on the protein concentration-N response curve (Eq.[2]). Only when total plant available soil N levels are extremely low, or environmental conditions are very favorable, is it possible to obtain an accurate estimate of the minimum protein concentration ($\underline{M}$) for a cultivar. The transition from the lag ($\underline{B}$) to the increase ($\underline{K}$) phase of the protein concentration-N response curve of a cultivar occurs when N is no longer the factor most limiting grain yield.

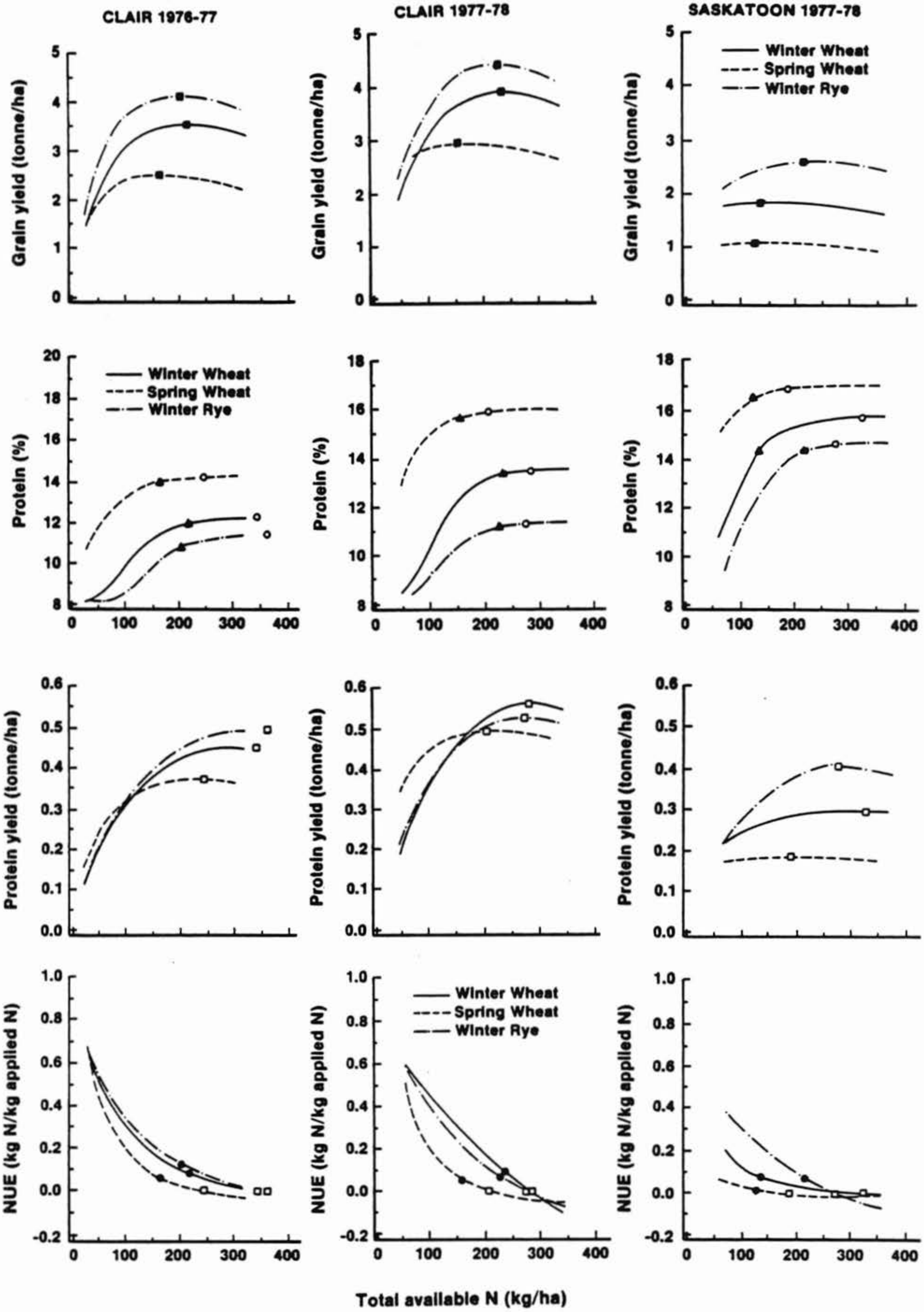

Figure 3. Grain yield, grain protein yield, and grain protein concentration response to total available N and nitrogen use efficiency (NUE) for grain protein production of Sundance winter wheat, Neepawa spring wheat, and Cougar winter rye. Total available N level at which maximum grain (•) and grain protein (o) yields were achieved.

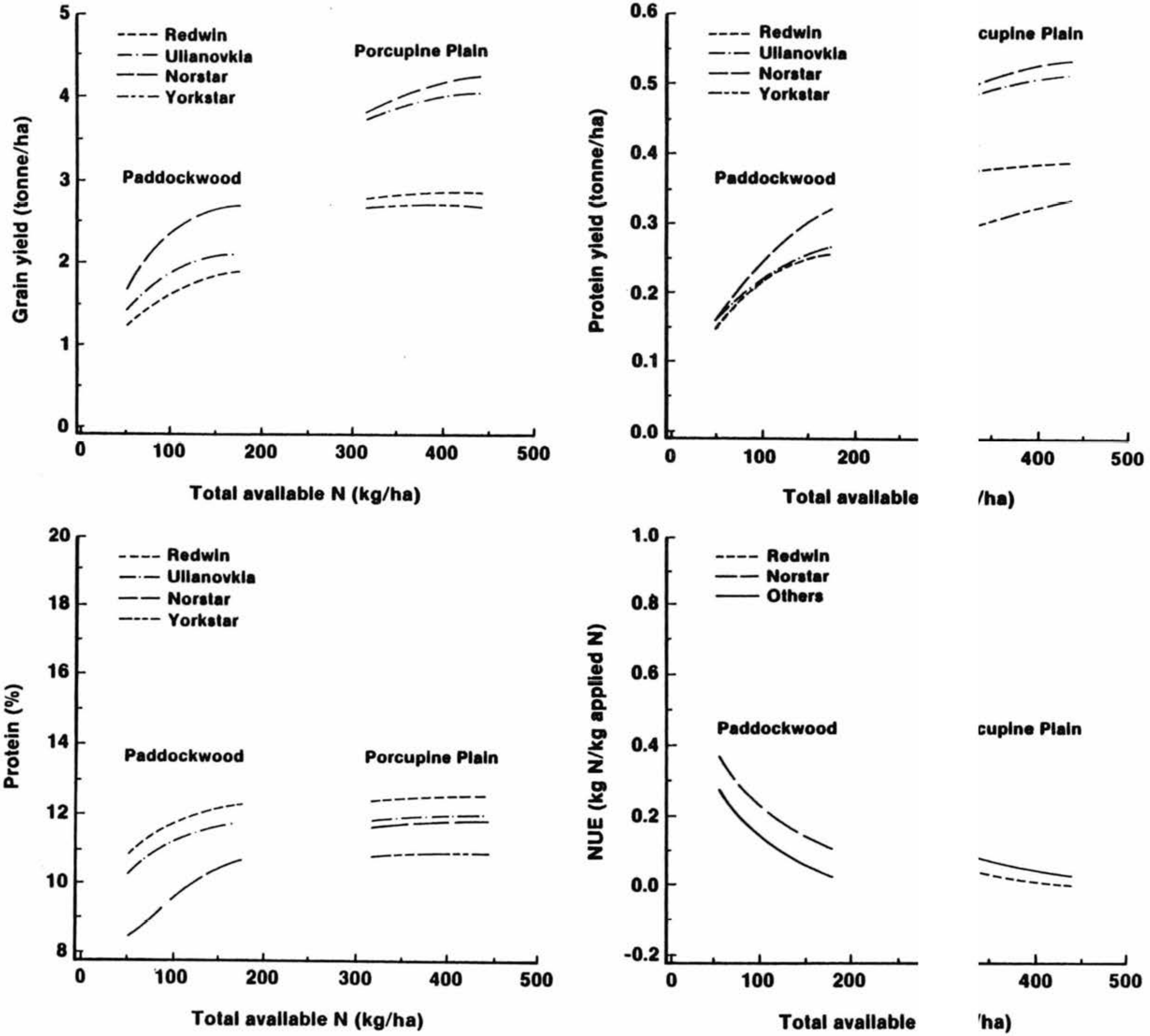

Figure 4. Grain yield, grain protein yield, and grain protein concen on response to total available N and nitrogen use efficiency (NUE) for gr protein production of several winter wheat cultivars grown at two loc

Therefore, cultivar differences in protein concentration at low N levels are largely a function of differences in grain yield potential and cultivars with low yield potential will start into the increase phase of the protein concentration-N response curve at lower total available N levels. The negative relationship between grain yield and protein concentration will mask the expression of genotypic differences in protein concentration until the N requirements for grain yield have been met. Consequently, the most reliable estimates of genotypic differences in protein concentration should be arrived at once the increase phase of the N response curve has been completed. The end of the increase phase of the N response curve occurs at total plant available N levels that approximate those required for maximum grain yield (Fig. 1, 2, and 3). These observations emphasize the importance of ensuring that N fertilization is in excess of normal grain yield requirements when the identification of genotypic differences in protein concentration is an objective. Values of asymptotic maximum protein concentration ($\underline{A}$) are determined from data that meet these requirements. Consequently, differences in $\underline{A}$ values should provide a reliable estimate of differences due to genetic variability for protein concentration among cultivars. However, it must be emphasized that precise estimates of $\underline{A}$ will only be obtained from cultivar-N fertilizer trials that include several N levels in excess of those required for maximum grain protein yield.

N-Use Efficiency for Protein Production

Grain and grain protein yield-N response curves are very similar in shape (Fig. 1,2,3, and 4). Observations made in the present studies have demonstrated that changes in grain yield are also usually accompanied by changes in grain protein yield. For example, any environmental or genotypic factor that increased grain yield also increased grain protein yield (Fig. 1,2,3, and 4).

The first increments of N fertilizer stimulated the greatest increases in grain protein N (Fig. 1,2,3, and 4). At low levels of residual soil N, the N use efficiency (NUE) for grain protein production has been shown to be as high as 80%. The NUE for grain protein production drops off rapidly for subsequent increments of N fertilizer, approaching zero for maximum grain yield and reaching zero when maximum grain protein yield is achieved (Fig. 1,2, and 3). Maximum grain yield coincides with the end of the increase phase of the protein concentration-N response curve. Consequently, it can be concluded that high grain protein concentration can only be achieved at the expense of nitrogen use efficiency for grain and grain protein yield. Therefore, management systems designed for the production of cereals with high grain protein concentration will have very low NUE's for grain and grain protein yield and high levels of N will be left unharvested. In high moisture environments, especially where water leaching and surface runoff are problems, management of this residual N could have extremely important environmental implications, i.e., nitrate pollution. Consequently, while high protein concentration can be achieved under intensive management systems in high moisture environments, semi-arid climates like that of western Canada provide ecologically safer environments for the production of cereal grains with high protein concentration.

ACKNOWLEDGEMENTS

The authors would like to acknowledge the financial support of the Canada-Saskatchewan Economic Regional Development Agreement (ERDA).

REFERENCES

Black, A.L. and F.H. Siddoway. 1977. Winter wheat recropping on dryland as affected by stubble height and nitrogen fertilization. Soil Sci. Soc. Am. J. 41: 1186-1490.

Bole, J.B. and S. Dubetz. 1986. Effect of irrigation and nitrogen fertilizer on the yield and protein content of soft white spring wheat. Can. J. Plant Sci. 66: 281-289.

Darroch, B.A. 1988. The effects of genotype and environment on grain protein of winter wheat in Saskatchewan. Ph.D. diss. Univ. of Sask., Saskatoon, Sask.

Entz, M.H. and D.B. Fowler. 1988. Critical stress periods affecting productivity of no-till winter wheat in western Canada. Agron. J. 80: 987-992.

Entz, M.H. and D.B. Fowler. 1989a. Influence of crop water environment and dry matter accumulation on grain yield of no-till winter wheat. Accepted. Can. J. Plant Sci.

Entz, M.H. and D.B. Fowler. 1989b. Response of winter wheat to N and water: Growth, water use, yield and grain protein. Submitted. Can. J. Plant Sci.

Fowler, D.B. 1983. The effect of management practices on winter survival and yield of winter wheat produced in regions with harsh winter climates. pp. 238-282. In D.B. Fowler, L.V. Gusta, A.E. Slinkard and B.A. Hobin (eds.). New Frontiers in Winter Wheat Production. Div. Comm. Rel., Univ. of Saskatchewan, Saskatoon, Sask., Can.

Fowler, D.B. and J. Brydon. 1989. No-till winter wheat production on the Canadian prairies: Timing of nitrogen fertilization. Submitted Agron. J.

Fowler, D.B., J. Brydon, and R.J. Baker. 1989a. Nitrogen fertilization of no-till winter wheat and rye. 1. Yield and agronomic responses. Agron. J. 81: 66-72.

Fowler, D.B., J. Brydon, and R.J. Baker. 1989b. Nitrogen fertilization of no-till winter wheat and rye. 2. Influence on grain protein. Agron. J. 81:72-77.

Fowler, D.B. and I.A. de la Roche. 1984. Winter wheat production on the North-Central Canadian Prairies: potential quality classes. Crop Sci. 24: 873-876.

Fowler, D.B. and M.H. Entz. 1986. Role of winter wheat in tillage systems. p. 147-172. In Proc. Tillage and Soil Conserv. Symp., Indian Head Exp. Farm, Indian Head, Sask.

France, J. and J.H.M. Thornley. 1984. Mathematical models in agriculture. pp. 144-151. Butterworths, London, England.

Gregory, P.J., Crawford, D.V. and McGowan, M. 1979. Nutrient relations of winter wheat. 1. Accumulation and distribution of Na, Ca, Mg, P, S and N. J. Agric. Sci., Camb. 93: 485-494.

Heapy, L., J.A. Robertson, D.K. McBeath, V.M. von Maydell, H.C. Love, and G.R. Webster. 1976. Development of a barley yield equation for central Alberta. I. Effects of soil and fertilizer N and P. Can. J. Soil Sci. 56: 233-247.

Hunter, A.S. and G. Stanford. 1973. Protein content of winter wheat in relation to rate and time of nitrogen fertilizer application. Agron. J. 65: 772-774.

Malhi, S.S., M. Nyborg, D.R. Walker, and D.H. Laverty. 1985. Fall and spring soil sampling for mineral N in north-cental Alberta. Can. J. Soil Sci. 65: 339-346.

Nuttall, W.F., H.G. Zandstra, and K.E. Bowren. 1971. Exchangeable ammonium and nitrate nitrogen related to yields of Conquest barley grown as second or third corp after fallow in northeastern Saskatchewan. Can. J. Soil Sci. 51: 371-377.

Olson, R.A., K.D. Frank, E.J. Derbert, A.F. Dreier, D.H. Sander, and V.A. Johnson. 1976. Impact of residual mineral N in soil on grain protein yields of winter wheat and corn. Agron. J. 68: 769-772.

Partridge, V.R. and C.F. Shaykewich. 1972. Effects of nitrogen, temperature, and moisture regime the yield and protein content of Neepawa wheat. Can. J. Soil Sci. 52: 179-185.

Spiertz, J.H.J. and J. Vos. 1985. Grain growth and its limitation by carbohydrate and nitrogen supply. In W. Day and R.K. Atkins (eds.). Wheat Growth and Modelling. Plenum Press. pp. 129-141.

Statistical Analysis Systems (SAS) Institute. 1985. The ANOVA, GLM, and NLIN procedures. In: SAS User's Guide: Statistics, Version 5 Edition. Statistical Analysis Systems Institute Inc., 1985. Cary, N.C. 956 pp.

Udy, D.C. 1971. Improved dye method for estimating protein. J. Am. Oil Chem. Soc. 48: 29-33.

Zentner, R.P. and D.W.L. Read. 1977. Fertilizer decisions and soil moisture in the brown soil zone. Can. Farm Econ. 12: 8-13.