Physiological Characteristics of Recent Canada Western Red Spring Wheat Cultivars: Nitrogen Uptake and Remobilization

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Abstract

Genetic yield gains have been difficult to achieve within the CWRS wheat class because of stringent quality requirements, and a growing-season environment of low precipitation and high temperatures. Understanding the physiological basis of yield gains may provide breeders with better insight as to the selection of parents, or provide screening tools to identify desirable genotypes. The objective of the present study was to compare four new CWRS wheat cultivars, which averaged higher yields than Neepawa in three years of multi-location testing within registration trials, both as a group and individually while maintaining or even increasing protein content, with two older cultivars, Neepawa and Marquis, in terms of N uptake and N remobilization. Results indicated that new cultivars had higher N uptake and/or higher N remobilization than old cultivars. Low tissue N concentration at maturity could be a criterion for selecting high-yielding and high-protein cultivars.

Grain protein concentration (GPC) is an important trait of major interest in breeding of bread wheat (T. aestivum L.), because it determines both baking and nutritional properties. Breeding for both high yield and high GPC is very difficult as a negative relationship between yield and GPC was found by many studies (Simmonds 1995; McNeal, et al., 1972; Whitehouse, 1973; Bhatia, 1975; Costa and Kronstad, 1994). Simmonds (1996), therefore, concluded that high yield and high GPC were unattainable simultaneously. However, Kibite and Evans (1984) indicated that the negative relationship between yield and GPC was not primarily driven by genetic factors, but mainly by environmental factors. Cox et al. (1985) found that negative correlations between yield and GPC for some wheat lines were low, although significant, which indicated that simultaneous increase in yield and GPC could be achieved by selection. This is supported by some studies (Davis et al., 1961; Terman et al. 1969; Johnson, 1978; McKendry et al. 1995). Jenner et al. (1991) indicated there is no fundamental conflict on physiological grounds in selecting cultivars for high carbohydrate yield at acceptable, even high, levels of GPC.

GPC is determined by plant total nitrogen (N) uptake and N remobilization to the grain. Many studies found genetic differences in N uptake (Löffler, et al. 1985; Van Sanford and MacKown, 1986; Le et al. 2000; Desai and Bhatia, 1978; McKendry, et al. 1995), while Oscarson et al. (1995) did not find any major differences in NO_3 uptake capacity among wheat grown hydroponically. A positive correlation between N uptake and GPC was found by Beninati and Busch (1992) and McKendry et al. (1995), but not by others (McNeal et al. 1966; Johnson et al. 1967; Desai and Bhatia 1978).

Cultivar difference in N remobilization was also found by some authors (Seth et al. 1960; Johnson et al. 1968; Van Sanford and MacKown, 1987). However, the relationship between plant N metabolism and GPC was not clear. Some reported that N partitioning was associated with GPC (Johnson et al. 1968; Cox et al. 1986; McKendry et al. 1995), but others (McNeal et al. 1972; Woodruff 1972; Van Sanford and MacKown 1987; May et al. 1991) did not support this. Nitrogen harvest index was (grain N at maturity/maximum N uptake, %) used as a selection criterion by some authors (Desai and Bhatia 1978; Cregan and Berkum 1984; Löffler et al. 1985; Jenner et al. 1991; McKendry et al. 1995). Borghi et al. (1987) suggested that both higher biomass yield and efficiency of N remobilization are important traits to overcome the negative relationship between grain yield and GPC.

Some studies suggested to use tissue N (Rostami and Giriaei 1998; Rostami and O'Brien 1996; Sylvester-Bradley 1990) or tissue protein concentrations (Noaman and Taylor 1990; Noaman et al. 1990) as selection criteria for increasing GPC because they were positively correlated with GPC. However, Jenner et al. (1991) indicated that from a physiological point of view, there is little logic in using grain protein percentage as a selection criterion. Delzer et al. (1995) also pointed that selection for grain protein only is questionable because the higher GPC is often associated with lower grain yield.

Although there are not short of studies on N mechanisms, there are lack of consistencies in the results. Clarke et al. (1990) indicated that unless greater variation in N utilization parameters among cultivars can be demonstrated, there seems to be little justification for selection for parameters other than grain yield and protein concentration.

Some recently developed bread wheat cultivars in western Canada have significantly increased yields, while maintaining or increasing percent protein content, relative to earlier cultivars (Wang et al. 2002). These cultivars can be used to study the physiological basis for these genetic improvements in N utilization. A better understanding of these improvements may allow breeders to design more efficient screening methods to develop future high yield and high GPC cultivars. This information may also assist agronomists and producers design soil and crop management practices that will permit full expression of these improved traits.

The objective of this study was to estimate the characteristics of these new cultivars in N utilization in comparison with older cultivars and to identify potential criteria for selection of high yield and high GPC cultivars in the western Canadian semiarid prairie.

MATERIALS AND METHODS

Details of this experiment have been reported by Wang et al. (2002). Two old and four new high-quality CWRS cultivars (T. aestivum L.) were used in this study. Old cultivars were Marquis and Neepawa. Marquis was obtained from the cross Hard Red Calcutta × Red Fife in 1892 and was the first successful widely grown bread wheat cultivar in western Canada (Morrison 1960). Neepawa was registered in 1969 (Campbell 1970) and had 17% higher mean yield than Marquis over five locations in Brown and Dark Brown soil zones over 22 yr (1965-1986) in the WBWC test ($P < 0.001$) (McCaig and DePauw 1995). New cultivars were AC Barrie (McCaig et al. 1996), AC Cadillac (DePauw et al. 1998), AC Elsa (Clarke et al. 1997), and AC Intrepid

(DePauw et al. 1999), which were developed at the Semiarid Prairie Agricultural Research Centre (SPARC), Swift Current, and registered over the period 1994 –1997. All new cultivars had 6-10% higher mean yield than Neepawa over three years and at approximately 10 locations in the WBWC test ($P < 0.05$, Wang et al. 2002).

A field test was conducted on a Swinton loam soil (Orthic Brown Chernozem) near Swift Current, SK, from 1998 to 2000, in a randomized complete block design with four replications. Trials were grown on summerfallow. Each plot was 16 rows, 3 m long, 0.23 m apart, with four rows of winter wheat were seeded between plots (not in 1999). Mono-ammonium phosphate and ammonium sulphate were broadcasted each year before seeding with targets of 112 kg ha^{-1} available N and 67 kg ha^{-1} available P based on soil tests at the end of October in each year prior to spring seeding. The seeding rate was 250 seeds per square metre which was adjusted according to a germination test done prior to seeding. Seeding dates were April 28, 1998, May 26, 1999, and May 9, 2000. There were no irrigations except that 48 mm of water was sprinkled on July 16, 1998. Neutron tubes were installed within 1d after seeding for each plot. Soil moisture was measured once a week during the growing season to a depth of 120 cm (0-10 and 10-20 cm by gravimetric method and 20-35, 35-55, 55-75, 75-95, and 95-120 cm by neutron probe method). Daily maximum and minimum air temperature and precipitation were recorded for the growing season (1 May 1 to 31 July, Campbell et al. 1988) at a weather site located 100 to 200 m from the test.

Phenological development was recorded for each plot every 2-3 d using the Zadoks-Chang-Konzak scale (GS) (Zadoks et al. 1974). For growth analyses, all plants from a random 50-cm row from each plot were sampled at the following growth stages for above-ground biomass: at five main stem leaves (GS 15), flag-leaf ligule visible (GS 39), anthesis complete (GS 69), and physiological maturity (GS 89). In 1999 samples were also taken at soft dough (GS 85). Plants were separated into leaf and stem + sheaths at five main stem leaves; flag, penultimate and lower leaves and stem + sheaths at flag-leaf ligule visible; flag, penultimate and lower leaves, peduncle, stem + sheaths, rachis, glumes and kernel at anthesis complete and physiological maturity. Samples were oven dried at 60 ^{o}C for a minimum of 72 h before weighing. The vegetative components were weighed and ground through a 2-mm screen with a Wiley mill. Grain samples were ground through a Udy Cyclone Sample Mill (Udy Corp., Fort Collins, CO), fitted with a 0.5-mm screen. Kjeldahl N (Williams 1984) and total P using the indophenol procedure (Varley 1966) were determined. Grain yields were determined by harvesting plots (8 central rows in 1999) with a plot combine. GPC (13.5% moisture basis) was determined by near-infrared spectroscopy calibrated with samples from the Grain Research Laboratory (Winnipeg, MB).

Statistical analysis

First, all dependent variables were analyzed with the PROC MIXED procedure of SAS (SAS Institute Inc. 1996) with the REML option for each year with cultivars fixed and replications random. Bartlett’s test for homogeneity of errors (Steel et al. 1997) was then performed over years on each variable and a three-years combined analysis was conducted with cultivars fixed and replications, years and cultivar × year interaction random. If the errors were heterogeneous, a REPEATED statement was used to specify a GROUP effect of years. Likelihood ratio c^2 test was used to determine the significance of year difference. A test for the cultivar × year crossover interaction (Azzalini & Cox 1984), as described by Baker (1988), was conducted with $\alpha = 0.158$ for calculating the critical *t*-value (Cornelius et al. 1992). Means comparisons among cultivars were done by Fisher's protected least significant differences (LSD) based on Student's *t* distribution. Single df contrasts were used to compare variable difference between the new group of four cultivars and Neepawa or Marquis using the ESTIMATE statement in the PROC MIXED procedure. An error term of cultivar × year was used for both LSD and contrast comparisons. Pearson's correlation was performed between variables. 'Significance' in the text refers to $P < 0.05$, if the *P* value is not given.

RESULTS AND DISCUSSION

For the three years of this study the mean growing-season (May-July) daily temperature was 14.6 ^{o}C, slightly below the long-term average (1900-2000) of 15.0 ^{o}C, and higher than the average of 14.3 ^{o}C for the period when the new cultivars were evaluated in the WBWC test (1991-1996). The mean precipitation during growing-season was 233 mm, which was higher than the average of 196 mm during 1991-1996, and the long-term average of 168 mm. The soil water content was high in the early growing season each year (Fig. 1). It started to reduce remarkably about boot stage. At or shortly after anthesis complete, the soil moisture was less than 50% of maximum plant extractable soil water at 1.2 m depth (220 mm) and continually to delete until maturity and reached lower limits. Obviously, crops experienced water stress during grain filling in each year.

Over three years, new cultivars had 34% and 6% higher yield than Marquis ($P < 0.001$) and Neepawa ($P = 0.10$), respectively, while no cultivar difference was found for GPC (Table 2). Consequently, new cultivars had 34% and 7% higher protein yield than Marquis ($P < 0.001$) and Neepawa ($P = 0.07$), respectively.

N uptake and remobilization

Above-ground plant attained maximum N uptake at maturity in 1998 and 2000, but at soft dough in 1999. Boatwright and Haas (1961) and Bashir et al. (1997) found that maximum N accumulation was attained at dough stage. The cultivar difference was significant (Table 2). AC Barrie had 13.8% and AC Elsa had 11.9% higher N uptake than Marquis and AC Intrepid ($P < 0.05$), while Neepawa did not differ from new cultivars. The cultivar difference in the proportion of post-anthesis to total N uptake was not significant (data not shown). On the average, only about 10% of total plant N was accumulated after anthesis. On the contrary, McKendry et al. (1995) found two high-yield, high-protein genotypes accumulated significantly higher proportion of their total N after anthesis (43-45%) than other cultivars (21-36%). Austin et al. (1977) and Van Sanford and MacKown (1987) found that the duration of N uptake was related with protein concentration, but Cox et al. (1985) found it was only critical for protein yield. It is widely reported that a smaller proportion of plant N was assimilated post-anthesis under dry conditions compared to that under wet conditions (McNeal et al. 1968; Campbell et al. 1977; McMullan et al. 1988). As the moisture condition of this experiment was well-above the long-term average, it seems that the enhancement of post-anthesis N uptake would be difficult under dryland condition in this region.

N harvest index (grain N at maturity/maximum N uptake, %) differed significantly among cultivars ($P < 0.001$, Table 2). As a group, new cultivars were higher than both Marquis ($P < 0.001$) and Neepawa ($P < 0.05$). AC Intrepid, which had a relatively low N uptake, had the highest N harvest index. Löffler and Busch (1982) indicated that selection for N harvest index was an effective way to improve yield and GPC. Clarke et al. (1990) suggested that N harvest index may be useful for selecting parents for breeding high-yield and high GPC cultivars.

Above-ground vegetative (non-grain) N reached the maximum at anthesis complete and no cultivar difference was found (data not shown). On the average, the maximum vegetative N was 15.1 g m^{-2}. At physiological maturity, vegetative N was left only about one-third of the maximum accumulation. All cultivars had a similar vegetative N (4.1 g m^{-2}), except Marquis which had significantly ($P < 0.001$) higher N left at maturity (5.9 g m^{-2}). We assume the loss of N (maximum vegetative N - vegetative N at maturity) is remobilized N although it also can be due to dead leaves falling from the plant, to volatilization (Wetselaar and Farquhar 1980; Parton et al. 1988) and to sampling error. All cultivars had significantly higher remobilized N than Marquis ($P < 0.001$), which only had 9.0 g m^{-2}, while AC Elsa (11.8 g m^{-2}) and AC Barrie (11.6 g m^{-2}) were significantly higher than Neepawa (10.6 g m^{-2}). All cultivars had significantly higher N remobilization efficiency (remobilized N/maximum vegetative N, %) than Marquis ($P < 0.001$), while new cultivars, as a group, were higher than Neepawa at the level of $P = 0.10$ (Table 2).
In contrast with N remobilization efficiency, dry matter remobilization efficiency was low and cultivar difference was not significant (Table 2). Marquis was only slightly lower than other cultivars ($P = 0.06$). Clarke et al. (1990) indicated that N uptake, harvest index and translocation were strongly associated with dry matter production and partitioning. Correlation analysis showed that maximum N uptake and dry matter was significantly correlated ($r = 0.90$, $P = 0.01$, $n = 6$). It seems that the characteristic of high N uptake could be simply achieved by breeding high biomass cultivars. Although, N harvest index was also correlated with harvest index ($r = 0.89$, $P = 0.02$, $n = 6$), N remobilization efficiency was not significantly correlated with dry matter remobilization efficiency ($r = 0.75$, $P = 0.08$, $n = 6$). Jenner et al. (1991) indicated the rate and duration of both starch and protein deposition in the endosperm of wheat are essentially independent events, controlled and influenced by different factors. High (carbohydrate) yield and high protein yield should be selected as independent traits.

Table 2 showed that both Marquis ($P < 0.001$) and Neepawa ($P < 0.05$) had significantly higher vegetative N concentration at maturity than new cultivars. From this standpoint, old cultivars were inefficient at remobilizing N. A possible reason for the genetic difference in N remobilization efficiency is that they differ in the rate of protein synthesis (Seth et al. 1960). Cregan and Berkum (1984) suggested that the affinity of the developing seed for N could be an important factor to achieve maximum N movement from vegetation to seed. Another possibility is that the poor N remobilization is related to the smaller sink size (small kernel size and less kernels per spike) in old cultivars compared to new cultivars (Wang et al. 2002). Peña (1996) indicated that head size and grain size maybe associated with the capacity of the grain sink (size) to assimilate differential amounts of translocated N.

N remobilization in different plant parts

In flag leaf, N accumulation reached a maximum at anthesis complete. There was no cultivar difference in remobilized N, which averaged 2.2 g m^{-2} (Table 3). New cultivars had significantly higher N remobilization efficiency than Marquis, but not than Neepawa. Both old cultivars had significantly higher N concentration than new cultivars at maturity ($P < 0.001$).

Penultimate leaf accumulated the maximum N content at flag ligule visible in 1999 and 2000, but at anthesis complete in 1998. The average N remobilization was slightly lower than flag leaf (1.8 g m^{-2}) (Table 3). Contrast comparison showed that Marquis was lower than ner cultivars at the level of ($P = 0.05$). Penultimate leaf had lower N remobilization efficiency. Both old cultivars had significantly lower N remobilization efficiency ($P < 0.05$) and higher ($P < 0.01$) N concentration at maturity than new cultivars.

Lower leaves accumulated the maximum N content at flag leaf ligule visible. The average N remobilization was 2.6 g m^{-2} and cultivar difference was not significant (Table 3). The average N remobilization for new cultivars was 87.8, which was significantly higher than Marquis ($P < 0.01$). Again, both old cultivars had significantly ($P < 0.01$) higher N concentration at maturity than new cultivars indicating that old cultivars had poorer N remobilization even in lower leaves.

Peduncle attained the maximum N accumulation at anthesis complete. The average N remobilization and remobilization efficiency for new cultivars were 2.3 g m^{-2} and 68.7%, respectively which were significantly ($P < 0.001$) higher than Marquis (Table 4). Both Marquis ($P < 0.001$) and Neepawa ($P < 0.05$) had significantly higher N concentration at maturity than new cultivars.

Stem + sheaths attained maximum N accumulation also at anthesis complete. New cultivars had significantly higher N remobilization efficiency than both Marquis and Neepawa, but the difference in N concentration at maturity between Neepawa and new cultivars was not significant (Table 4).

Both glumes and rachis accumulated the maximum N content at anthesis complete and results were very similar (Table 5). Marquis had significantly lower N remobilization, N remobilization efficiency and higher N concentrations at maturity than new cultivars. No difference was found between Neepawa and new cultivars in any traits.

Results showed that stem + sheaths remobilized highest N among different plant parts. Flag, penultimate, total lower leaves and peduncle were similar, followed by glumes, and rachis had the lowest. Nitrogen partitioning was reported from different plant parts, such as leaves (Gregory et al. 1981; Van Sanford and MacKown 1987), stem (Simpson et al. 1983), glumes (Jenner et al. 1991), rachis (Berecz et al. 1997; Halloran and Lee 1979; Simpson et al. 1983; Waters et al. 1980) and roots (Dalling et al. 1976). Berecz et al. (1997) indicated that flag leaf and uppermost internode has the greatest relative N depletions compared to glumes, rachis and flag leaf sheaths. Waters et al. (1980) found that flag leaf was a major contributor to the grain N. Van Sanford and MacKown (1987) reported that 10 to 19% and 10 to 26% of the N accumulated by the developing spikes were remobilized from flag leaves and peduncle, respectively. However, Jenner et al.

(1991) indicated that glumes may contribute 15% to the grain but, more importantly, they act as a temporary depository for N early in grain filling, and as a site for transfer of N from xylem to phloem. In order to improve N translocation efficiency, Peña (1996) suggested to breed culivars with improved glumes photosynthetic capacity (accumulate and translocate N to grain).

New cultivars significantly increased N remobilization efficiency from every part of the plant compared to Marquis. Although new cultivars had higher overall N remobilization efficiency over Neepawa ($P = 0.10$) (Table 2), it did not appear on any plant parts except penultimate leaf and stem + sheaths (Table 3). The chemical analysis of tissue N concentration at maturity should be a better indicator on genetic difference in N remobilization efficiency based on per dry weight unit because plant parts are often lost during growth season, especially for leaves. As Neepawa had significantly higher N concentration than new cultivars in flag and penultimate leaves (Table 3) and peduncle (Table 4), new cultivars seems increased N remobilization over Neepawa through these plant parts.

In conclusion, new high-yield, high-protein cultivars improved N utilization mainly by increasing N remobilization. Some new cultivars also increased total N uptake. To achieve high N uptake, breeders could simply select lines with high biomass. To obtain high N remobilization, selections traits could be N remobilization efficiency from different plant parts, especially higher parts, such as flag leaf, peduncle and chaff, and be larger reproductive sink size (kernel number per head and kernel weight). Tissue N concentration at maturity could be an indicator on genetic difference in N remobilization efficiency based on per unit dry weight.

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Table 1. Growing season (May-July) air temperature and precipitation for Swift Current, SK

	Mean Daily Temperature				Precipitation			
	May (^{o}C)	June (^{o}C)	July (^{o}C)	Mean (^{o}C)	May (mm)	June (mm)	July (mm)	Total (mm)
1998	12.6	14.0	20.1	15.6	38.1	90.5	85.0[z]	213.6
1999	9.9	14.1	16.4	13.5	93.9	86.2	60.3	240.4
2000	10.9	13.9	19.1	14.6	65.3	52.2	127.0	244.5
Mean (1998-2000)	11.1	14.0	18.6	14.6	65.8	76.3	90.8	232.9
Long-term (1900-2000)	10.9	15.4	18.6	15.0	44.2	72.9	51.0	168.1
Mean (1991-1996)[y]	10.5	15.4	17.0	14.3	50.0	90.5	55.5	195.6

[z] 48 mm of irrigation on July 16, 1998.

[y] The four new cultivars were evaluated for registration for three years during the 1991 - 1996 period in the WBWC test (not the same years for each cultivar).

Table 2. Grain yield, protein concentration (GPC), grain protein yield (GPY), maximum N uptake (NUP), N harvest index (NHI), N remobilization efficiency (NRE), dry matter remobilization efficiency, and non-grain dry matter N concentration at maturity (CON) for new and old CWRS cultivars.

	Yield (t ha^{-1})	GPC (%)	GPY (t ha^{-1})	NUP (g m^{-2})	NHI (%)	NRE (%)	DRE (%)	CON (%)
Significance								
Cultivar (C)	***	0.18	***	*	**	**	0.20	***
Year (Y)	***	0.34	0.07	0.64	**	0.10	0.15	*
C × Y	**^{z}	0.08	0.06	0.61	0.99	0.86	0.49	*
New vs. Neepawa	0.10	0.71	0.07	0.90	*	0.10	0.39	*
New vs. Marquis	***	0.30	***	*	***	***	0.06	***
LSD (0.05)	0.3	0.5	0.05	1.4	5.1	4.2	11.0	0.09
Cultivar					*New*			
AC Barrie	3.8	15.8	0.59	18.2	68.6	72.6	14.1	0.61
AC Cadillac	3.8	15.3	0.58	17.3	65.1	74.0	14.1	0.58
AC Elsa	3.8	15.8	0.60	17.9	69.8	74.6	18.0	0.59
AC Intrepid	3.7	15.4	0.58	16.0	70.2	74.4	20.6	0.57
Mean	3.8	15.6	0.59	17.4	68.4	73.9	16.7	0.59
					Old			
Neepawa	3.6	15.5	0.55	17.3	62.2	71.2	20.3	0.66
Marquis	2.8	15.8	0.44	16.0	53.0	61.3	8.3	0.84

*, **, *** Significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$ probability levels, respectively. Other probabilities given.

[z] Crossover interaction: three of the four new cultivars yielded significantly more than Neepawa in 1998, but not in 1999 or 2000.

Table 3. N remobilization (NRM), N remobilization efficiency (NRE), N concentration at maturity (CON) in flag, penultimate and lower leaves for new and old CWRS cultivars.

	Flag leaf			Penultimate leaf			Lower leaves		
	NRM (g m^{-2})	NRE (%)	CON (%)	NRM (g m^{-2})	NRE (%)	CON (%)	NRM (g m^{-2})	NRE (%)	CON (%)
Significance									
Cultivar (C)	0.10	0.31	***	*	0.14	***	0.17	0.14	**
Year (Y)	0.05	**	0.54	**	0.05	0.89	*	***	*
C × Y	0.36	0.53	0.08	0.31	**[z]	**[y]	0.42	0.32	***[x]
New vs. Neepawa	0.15	0.36	***	0.50	*	**	0.53	0.73	**
New vs. Marquis	0.60	*	***	0.05	*	***	0.51	**	***
LSD (0.05)	0.4	4.0	0.22	0.4	6.3	0.18	0.5	4.9	0.17
AC Barrie	2.2	89.0	1.23	1.9	84.0	1.20	3.0	87.0	1.22
AC Cadillac	2.2	89.1	1.11	1.7	85.2	1.01	2.7	88.7	1.15
AC Elsa	2.5	90.2	0.97	2.2	87.9	1.04	2.2	87.5	1.12
AC Intrepid	2.0	89.5	1.16	1.6	84.5	1.16	2.4	88.1	1.21
Mean	2.2	89.5	1.12	1.8	85.4	1.10	2.6	87.8	1.18
Neepawa	2.0	88.1	1.49	1.9	80.7	1.35	2.7	86.1	1.36
Marquis	2.2	85.9	1.68	1.6	80.3	1.51	2.4	81.1	1.54

*, **, *** Significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$ probability levels, respectively. Other probabilities given.

[z] C × Y crossover interaction: Marquis was significantly higher than Neepawa in 1998 only.

[y] C × Y crossover interaction: AC Barrie was significantly higher than AC Intrepid in 2000 only.

[x] C × Y crossover interaction: AC Barrie was significantly higher than AC Cadillac and AC Intrepid in 2000 only.

Table 4. N remobilization (NRM), N remobilization efficiency (NRE) and N concentration at physiological maturity (CON) in peduncle and stem + sheaths for new and old CWRS cultivars.

	Peduncle			Stem + sheaths		
	NRM (g m^{-2})	NRE (%)	CON (%)	NRM (g m^{-2})	NRE (%)	CON (%)
Significance						
Cultivar (C)	***	***	***	0.19	***	**
Year (Y)	0.90	*	0.25	0.48	0.11	0.19
C × Y	0.24	0.13	0.14	0.15	0.91	*^{z}
New vs. Neepawa	0.46	0.44	*	0.25	*	0.26
New vs. Marquis	***	***	***	*	***	**
LSD (0.05)	0.6	10.2	0.08	1.5	5.2	0.11
Cultivar			*New*			
AC Barrie	2.4	67.8	0.57	4.7	74.5	0.51
AC Cadillac	2.2	68.0	0.52	5.4	77.2	0.50
AC Elsa	2.4	69.1	0.52	5.1	77.9	0.51
AC Intrepid	2.0	70.0	0.50	4.7	77.8	0.49
Mean	2.3	68.7	0.53	5.0	76.9	0.50
			Old			
Neepawa	2.1	66.2	0.61	4.3	72.4	0.55
Marquis	1.2	42.3	0.83	3.5	63.2	0.68

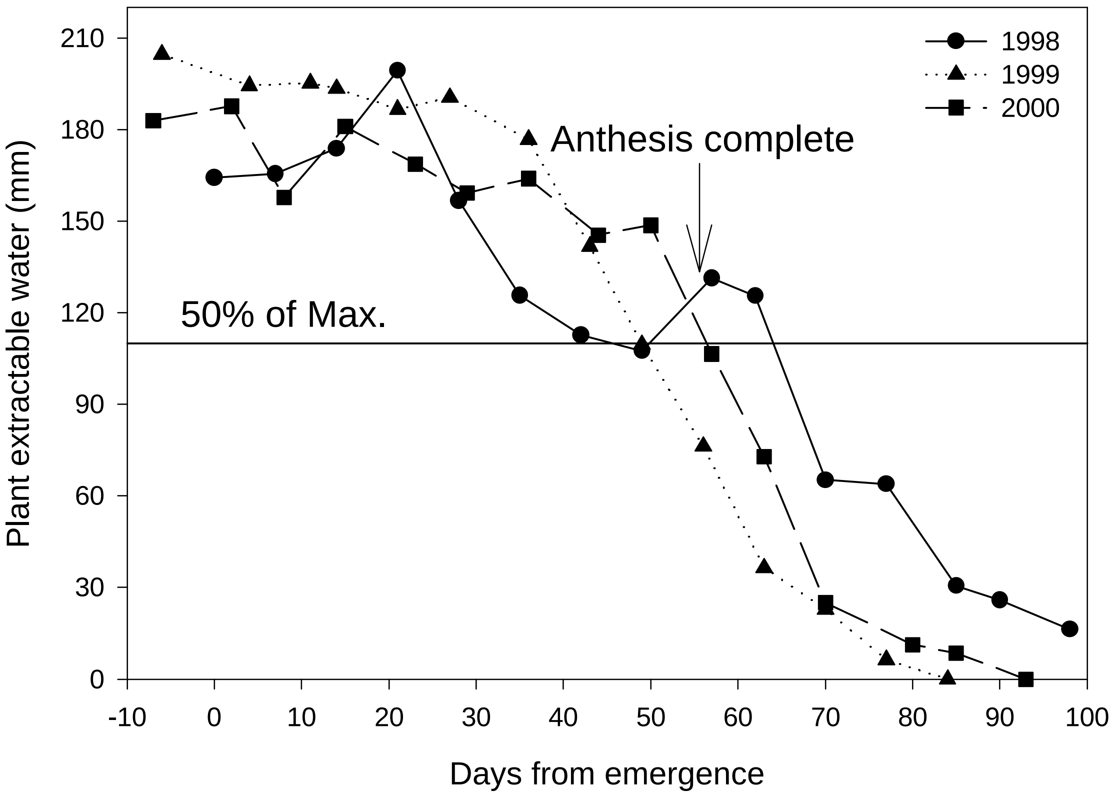
*, **, *** Significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$ probability levels, respectively. Other probabilities given.

[z] C × Y crossover interaction: AC Barrie was significantly higher than all other new cultivars in 1999 only.

Table 5. N remobilization (NRM), N remobilization efficiency (NRE) and N concentration at physiological maturity (CON) in glumes and rachis for new and old CWRS cultivars.

	Glumes			Rachis		
	NRM ($g\ m^{-2}$)	NRE (%)	CON (%)	NRM ($g\ m^{-2}$)	NRE (%)	CON (%)
Significance						
Cultivar (C)	**	0.08	***	**	***	***
Year (Y)	0.98	0.99	*	0.15	0.07	*
C × Y	0.54	0.23	0.40	0.31	0.37	0.60
New vs. Neepawa	0.21	0.98	0.49	0.58	0.94	0.90
New vs. Marquis	***	**	***	***	***	***
LSD (0.05)	0.3	9.5	0.08	0.05	11.8	0.06
Cultivar				*New*		
AC Barrie	1.3	69.8	0.51	0.2	51.7	0.53
AC Cadillac	1.1	70.0	0.52	0.2	62.0	0.48
AC Elsa	1.3	65.5	0.62	0.2	56.5	0.46
AC Intrepid	1.1	71.1	0.51	0.2	58.4	0.44
Mean	1.2	69.1	0.54	0.2	57.2	0.48
				Old		
Neepawa	1.1	69.1	0.56	0.2	58.0	0.48
Marquis	0.8	57.8	0.76	0.1	25.5	0.79

*, **, *** Significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$ probability levels, respectively. Other probabilities given.



Plant extractable water (mm)
210
180
150
120
90
60
30
0
-10
0
10
20
30
40
50
60
70
80
90
100
Days from emergence
1998
1999
2000
Anthesis complete
50% of Max.