Apparent vernalization requirement of high yielding spring wheat

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Controlled environment studies have demonstrated that the high yield potential of certain spring wheat (*Triticum aestivum* L.) cultivars may result from a moderate vernalization requirement. The objective of this study was to determine whether apparent vernalization responses of cultivars could be detected when comparing the development of early and late-seeded crops. The effect of delayed seeding on 9 or 10 spring wheat cultivars was studied at Saskatoon over a period of four years. Within years, the earliest and latest dates of seeding differed by a minimum of 22 days. Vernalization effects were apparent in 1983 and 1986 but not in 1985 and 1987. In 1983 and 1986 Growing Degree Day accumulation 14 days after seeding (GDD14) averaged 44 for the earliest date of seeding compared to 120 GDD or more for the later seeding dates. However, the GDD14 for the earliest date of seeding was 121 in 1985 and 134 in 1987. Apparent vernalization effects were manifested by higher main stem leaf number, increased spikelet production and delayed spike emergence. Cultivars were ranked in the following order for apparent vernalization sensitivity: Fielder = Pitic 62 > HY402 > HY320 > Genesis > HY912 > Leader > Glenlea > Neepawa > Katepwa > Siete Cerros > Potam. Fielder had the greatest vernalization requirement and Potam the least. On average, delayed seeding resulted in increased grain yields, but this observation was not consistent over years.

INTRODUCTION

Low-temperature promotion of flowering (vernalization) in wheat is usually associated with the winter growth habit. This, however, is a generalization. Facultative and certain spring wheat cultivars can be vernalized.

Vernalization requirement in wheat is controlled by alleles at five loci. The dominant allele confers insensitivity to vernalization. Of the five loci, Vrn1 has the greatest effect and appears to be epistatic to the other genes (Law et al., 1976). Vrn1, Vrn2, Vrn3, Vrn4 and Vrn5 have been assigned to chromosomes 5AL, 2B, 5DL, 5B and 7BS, respectively. Winter habit cultivars carry recessive alleles at all five loci. Spring genotypes which carry Vrn1 alone or in combination with dominant alleles at the other loci exhibit very little or no vernalization response while genotypes carrying vrn1 and a combination of dominant alleles at the other loci exhibit varying levels of vernalization response. For instance, the hard red spring wheat cultivars Cadet, Rescue, and Cypress are thought to have the following genotypes, respectively: Vrn1 vrn4 vrnx, vrn1 Vrn3 Vrn4, and vrn1 vrn3 Vrn4 (Roberts and Larson, 1985). Cypress has the largest vernalization response, followed by Rescue and Cadet.

Spring wheat genotypes which are vernalization-sensitive may be vernalized by temperatures as high as 10-13°C. If not vernalized, sensitive genotypes typically produce more leaves and spikelets and head out later (Wall and Cartwright, 1974). As a result, an unfulfilled vernalization requirement may increase yield potential while delaying maturity. The relatively high sensitivity of the cultivar Pitic 62 (Wall and Cartwright, 1974; Jedel et al., 1986) appears to be linked to its yield instability under certain growing conditions (Walton, 1968; Baker and Gebeyehou, 1982). Other late maturing high yielding spring wheat cultivars (eg. Fielder, Biggar and Genesis) may behave in a manner similar to that of Pitic 62 when not fully vernalized. Canadian Western Red Spring wheat cultivars that have been tested for vernalization response (Benito, Cadet, Glenlea, Marquis, Neepawa, Prelude, Reward, Sinton, Thatcher) range from insensitive to slightly sensitive (Pugsley, 1971; Major and Whelan, 1985; Jedel et al., 1986).

The objective of this study was to determine whether suspected cultivar differences in vernalization response could be detected with delayed seeding.

MATERIALS AND METHODS

Results from two series of experiments are presented here. In the first series, nine spring wheat (*Triticum aestivum* L.) genotypes were tested over a 3-year period. Seeding dates within years were as follows: 15 May, 27 May and 6 June 1985; 2 May, 19 May and 2 June 1986; 29 April, 13 May, 23 May and 2 June 1987. Standard small plot techniques were used in the performance of these experiments; details are published elsewhere (Baker, 1990).

Data collection proceeded as follows:

1. Plant Haun stage (Haun, 1973) was measured 25-39 days after seeding. Means of 3 plants per plot were used for the purpose of statistical analysis.

2. Leaf number was measured on the main culm following flag leaf emergence. Means of 3 plants per plot were used for the purpose of statistical analysis.

3. Days to spike emergence were recorded as the time of seeding to the time when 50% of the culms in a plot had emerged spikes.

4. Growing Degree Days (GDD) using a base temperature of 5°C were calculated from meteorological data collected by the Saskatchewan Research Council at the University of Saskatchewan. GDD were calculated for the time to spike emergence as well as the time to physiological maturity (90% of the spikes in a plot devoid of green colour).

5. Grain yield was determined by combining each plot in its entirety with a small-plot combine.

In each of the three years a six-replication randomized complete block design was used for each date of seeding. Data were expressed as the difference between the later and the earliest date of seeding (i.e. SD3-SD1, SD2-SD1) with the exception of grain yield which was expressed on a percent basis. Within years, combined analysis of variance were conducted across seeding dates. Where genotype x seeding date interactions are not significant at P=0.05, main effect means are presented. Crossover interactions were tested for significance as outlined by Baker (1988).

In the second series of experiments, 10 spring wheat genotypes were planted at an early (4 May) and a late (28 May) date at Saskatoon in 1983. A randomized complete block design with 4 replications was used. Plot techniques were the same as those used in Experiment 1. Spikelet counts and grain yield determinations were performed on the main stem, T1 and T2 tillers for 5 plants per plot. Prior to analysis of variance, data were averaged over plants and tillers.

RESULTS AND DISCUSSION

Study 1.

The long-term optimal seeding date for hard red spring wheat at Saskatoon is mid-May. In 1985, higher grain yields were achieved with an early June planting (Table 1). Delayed seeding resulted in fewer leaves being formed on the main stem and a reduction in the time to spike emergence (DSE). At later seeding dates the wheat crop is exposed to larger daily heat accumulations, accelerating plant development. The cultivars Fielder and HY320 exhibited the least reduction in DSE when seeding was delayed. When expressed on a Growing Degree Day scale (GDD5), Fielder and HY320 exhibited a significantly larger GDD increase with an early June planting than did the remaining cultivars (Table 1).

Table 1. Seeding date effects on spring wheat crop development expressed as differences from the earliest date of seeding, Saskatoon 1985.

Seeding date	Haun (units)	Leaf no. (no.)	DSE (days)		DSE GDD5 (units)		Grain yield (%)
SD2-SD1		-0.5	-4.6		-11.1		14.8
SD3-SD1		-0.3	-6.2		31.3		39.5
Cultivar			SD2-SD1	SD3-SD1	SD2-SD1	SD3-SD1	
Fielder	0.09	-0.3	-2.5	-3.2	10.0	59.0	18.8
HY320	0.06	-0.5	-3.7	-4.3	-6.7	46.7	34.1
Genesis	0.13	-0.3	-4.8	-6.2	-22.5	24.7	27.5
HY912	0.30	-0.3	-4.5	-6.7	-9.5	26.3	21.9
Siete Cerros	0.36	-0.8	-5.7	-8.0	-20.7	12.0	41.5
Glenlea	0.17	-0.5	-4.3	-7.0	-8.0	22.5	59.6
Katepwa	0.23	-0.3	-6.0	-7.0	-22.0	30.0	7.7
Neepawa	0.13	-0.6	-6.0	-6.7	-22.0	33.3	15.8
Leader	0.25	-0.5	-4.0	-7.0	1.0	27.0	17.5
SE	0.04	0.1	0.2		2.2		4.5

Seeding date 1 (SD1)=15 May, SD2=27 May, SD3=06 June.
Haun rating = plant development 25-39 d after seeding.
DSE=Days to 50% spike emergence.
GDD5=Growing Degree Days with a base temperature of 5°C.

In 1986 Fielder, HY320 and Genesis exhibited significant increases in leaf number with delayed seeding (Table 2). An increase in leaf number is characteristic of an extended vegetative period resulting from an unmet vernalization requirement (Wall and Cartwright, 1974). The vernalization requirement of Fielder, HY320 and Genesis is also apparent from the significantly smaller reduction in DSE (Table 2) arising from delayed seeding, relative to the other cultivars. When contrasting the earliest and latest seeding dates Fielder, HY320 and Genesis stand apart from the other cultivars in that they have positive GDD5 values while the other cultivars have negative values. Delayed seeding (02 June) increased the grain yield of most non-CWRS cultivars with the exception of Fielder and Genesis (Table 2).

Table 2. Seeding date effects on spring wheat crop development expressed as differences from the earliest date of seeding, Saskatoon 1986.

Seeding date	Haun (units)	Leaf no. (no.)	DSE (days)		DSE GDD5 (units)		Grain yield (%)	
SD2-SD1		0.8	-7.5		36.5		11.3	
SD3-SD1		1.0	-9.1		-8.2		5.1	
Cultivar			SD2-SD1	SD3-SD1	SD2-SD1	SD3-SD1	SD2/SD1	SD3/SD1
Fielder	-0.16	1.9	-3.3	-2.5	87.3	69.8	5.4	-6.5
HY320	-0.19	1.7	-4.7	-4.0	73.5	54.8	13.4	11.7
Genesis	-0.38	1.8	-5.2	-6.8	66.5	24.0	22.5	-0.4
HY912	-0.12	0.7	-8.5	-10.3	23.0	-20.7	7.1	11.2
Siete Cerros	-0.21	0.1	-9.0	-11.2	17.5	-35.3	12.4	16.5
Glenlea	-0.19	0.3	-8.7	-11.0	22.2	-28.8	7.4	10.8
Katepwa	0.19	0.5	-9.7	-12.2	8.8	-47.7	11.3	-2.2
Neepawa	-0.08	0.3	-10.2	-13.2	0.8	-59.0	6.7	-1.8
Leader	-0.03	0.5	-8.2	-11.2	28.7	-31.0	15.8	7.0
SE	0.06	0.2	0.2		4.0		3.7	

Seeding date 1 (SD1)=2 May, SD2=19 May, SD3=02 June.
Haun rating = plant development 25-39 d after seeding.
DSE=Days to 50% spike emergence.
GDD5=Growing Degree Days with a base temperature of 5°C.

In 1987 HY320 and Genesis produced slightly more leaves with delayed seeding while most other cultivars, including Fielder, produced fewer (Table 3). Similarly, HY320 and Genesis tended to a smaller reduction in DSE with delayed seeding (SD2 vs SD1 and SD4 vs SD1). On average, HY320 and Genesis exhibited increases in GDD to spike emergence with delayed seeding while most of the other cultivars did not. Highest grain yields were achieved with an early June planting.

Table 3. Seeding date effects on spring wheat crop development expressed as differences from the earliest date of seeding, Saskatoon 1987.

Seeding date	Haun (units)	Leaf no. (no.)		DSE (days)		DSE GDD5 (units)	Grain yield (%)
SD2-SD1		-0.1		-4.3		-11.6	52.2
SD3-SD1		0.1		-7.3		-17.2	-1.5
SD4-SD1		-0.3		-6.4		13.9	71.8
Cultivar			SD2-SD1	SD3-SD1	SD4-SD1		
Fielder	-0.33	-0.2	-4.2	-7.3	-6.3	-3.9	41.1
HY320	-0.35	0.6	-2.8	-6.2	-5.2	10.9	37.5
Genesis	-0.32	0.2	-2.7	-6.2	-4.0	12.5	30.0
HY912	-0.27	0.1	-3.8	-5.7	-4.8	5.4	36.3
Siete Cerros	-0.19	-0.4	-5.7	-9.3	-10.7	-35.5	54.5
Glenlea	-0.42	-0.2	-4.8	-7.5	-6.3	-9.4	53.1
Katepwa	-0.26	-0.4	-5.3	-8.0	-7.3	-11.9	30.1
Neepawa	-0.33	-0.2	-4.8	-7.7	-7.0	-5.2	36.0
Leader	-0.41	-0.2	-4.3	-7.8	-5.8	-7.6	48.8
SE	0.06	0.1		0.4		3.3	4.1

Seeding date 1 (SD1)=29 April, SD2=13 May, SD3=23 May, SD4=02 June.
Haun rating = plant development 25-39 d after seeding.
DSE=Days to 50% spike emergence.
GDD5=Growing Degree Days with a base temperature of 5°C.

Averaged over the three years, Siete Cerros and Glenlea exhibited, proportionally, the largest increases in grain yield with delayed seeding. Grain yields of the CWRS cultivars Katepwa and Neepawa changed the least with seeding date (Tables 1 to 3).

Seedling development, as measured with the Haun scale, failed to reveal cultivar differences consistent with contrasting vernalization responses (Tables 1 to 3).

It is apparent from the data presented in Tables 1,2 and 3 that the largest vernalization responses were observed in 1986. As a measure of seedling cold temperature exposure, GDD5 were calculated for the 14 day period following each seeding date:

1985	1986	1987
SD1 121 GDD	SD1 45 GDD	SD1 134 GDD
SD2 93 GDD	SD2 200 GDD	SD2 109 GDD
SD3 134 GDD	SD3 128 GDD	SD3 157 GDD
		SD4 204 GDD

The earliest planting in 1986 accumulated the least GDD during the 14 days after seeding, resulting in the largest GDD differential between earliest and latest plantings over the three year period. The relatively large seeding date differences in seedling cold temperature exposure in 1986 are consistent with the vernalization responses documented in Table 2.

Delayed heading due to unmet vernalization requirements can result in increased leaf and spikelet numbers and, under certain growing conditions, higher grain yield (Wall and Cartwright, 1974). In years where late summer rainfall is significant, delayed maturity is associated with increased grain yield (Cutforth et al. 1990). Delayed heading, however, would be detrimental to grain yield and quality in a situation where post-anthesis abiotic or biotic stresses were severe and grain-filling was curtailed. An example of a biotic stress that would adversely affect late-heading spring wheats would be a leaf rust infestation affecting cultivars with only partial genetic resistance, in mid- to late July. This scenario was a reality in 1986 and 1991. Severe post-anthesis drought or an early fall frost are forms of abiotic stress that would adversely affect cultivars with delayed heading.

Data in Tables 4,5 and 6 are the differences between GDD accumulated prior to spike emergence and GDD accumulated between spike emergence and physiological maturity. A positive value indicates that the pre-spike emergence period (PrSE) was longer than the post-spike emergence period (PsSE). The general trend in all three years was for PrSE to increase relative to PsSE as seeding was delayed. Fielder and HY320 exhibited the largest difference between PrSE and PsSE in 1985 (Table 4) and 1986 (Table 5). Genesis behaved similarly to Fielder and HY320 in 1985 but not in 1986. Cultivars with smaller vernalization responses (Tables 1 and 2) tended to have PsSE which were longer than PrSE (negative values) or suffered less curtailment of PsSE relative to PrSE with late seeding. The cultivars Katepwa, Neepawa and Siete Cerros fell in the latter category.

Statistically significant cultivar x seeding date interaction was detected for approximately half of the traits measured in 1985-1987. In a number of cases these interactions involved significant cultivar cross-overs. In 1986 Genesis switched ranks with Glenlea, Siete Cerros and HY912 for percent grain yield response to delayed seeding (Table 2). The majority of significant cultivar cross-overs were for PrSE-PsSE differential. In 1985 HY320 switched ranks with Genesis and HY912 (Table 4). In 1986, for the same trait, HY320 switched ranks with Neepawa and Leader; Genesis with Neepawa, Katepwa, Glenlea and Siete Cerros; Neepawa with Glenlea (Table 5). In 1987 Siete Cerros switched ranks with HY320, Fielder, Neepawa and Katepwa (Table 6).

Table 4. Difference between pre-spike emergence and post-spike emergence GDD5, Saskatoon 1985.

	SD1	SD2	SD3
Fielder	133.0	146.3	257.0
HY320	79.0	65.5	190.3
Genesis	131.5	81.5	171.3
HY912	104.5	85.3	136.5
Siete Cerros	68.2	48.0	89.3
Glenlea	61.2	37.5	109.2
Katepwa	64.7	1.2	89.5
Neepawa	50.3	-1.7	96.2
Leader	75.2	69.0	97.7
SE		4.1	
Average	85.3	59.2	137.4

GDD5=Growing Degree Days with a base temperature of 5°C.
Seeding date 1 (SD1)=15 May, SD2=27 May, SD3=06 June.

Table 5. Difference between pre-spike emergence and post-spike emergence GDD5, Saskatoon 1986.

	SD1	SD2	SD3
Fielder	11.3	99.7	173.8
HY320	-30.0	50.0	129.0
Genesis	-61.0	30.5	33.0
HY912	-18.3	16.2	32.7
Siete Cerros	-14.3	-4.3	-31.3
Glenlea	-29.0	6.7	12.7
Katepwa	-16.5	-4.2	-29.5
Neepawa	4.7	11.0	-23.3
Leader	-7.5	48.3	16.5
SE		6.5	
Average	-17.9	28.2	34.8

GDD5=Growing Degree Days with a base temperature of 5°C.
Seeding date 1 (SD1)=02 May, SD2=19 May, SD3=02 June.

Table 6. Difference between pre-spike emergence and post-spike emergence GDD5, Saskatoon 1987.

	SD1	SD2	SD3	SD4
Fielder	40.8	-8.8	-9.0	35.2
HY320	34.0	7.0	6.0	35.3
Genesis	63.0	61.5	47.7	90.0
HY912	81.2	48.8	85.0	98.3
Siete Cerros	82.0	12.2	16.7	-7.5
Glenlea	60.7	-5.8	3.2	41.7
Katepwa	55.5	-17.3	4.7	25.5
Neepawa	58.3	-7.3	9.2	27.0
Leader	84.8	20.2	28.2	69.8
SE		6.5		
Average	62.2	12.2	21.2	46.1

GDD5=Growing Degree Days with a base temperature of 5°C. Seeding date 1 (SD1)=29 April, SD2=13 May, SD3=23 May, SD4=02 June.

Study 2

In 1983, the early planting was exposed to 44 GDD in the 14 days following seeding compared to 119 GDD for the late planting. The cultivars HY402, Pitic 62 and HY320 exhibited the largest increases in spikelet number with delayed seeding (Table 7). Furthermore, HY402 and Pitic 62 were characterized by spike emergence responses (Table 8) consistent with vernalization responses observed in the previous study (Tables 1 and 2). The Chinese cultivar Ko-Chuan appears to have a fairly strong vernalization requirement. Delayed seeding reduced the spikelet number of the early maturing CIMMYT cultivar Potam and resulted in a sharp reduction in its time to spike emergence. Controlled environment studies of Potam have shown the growth and development of this cultivar to be relatively more temperature-driven than that of other genotypes (Hucl and Baker, 1990). Ko-Chuan and Pitic 62 suffered yield reductions when late-seeded while the remaining cultivars exhibited yield increases.

Table 7. Seeding date effects on the spikelet number and spike yield of 10 spring wheat cultivars, Saskatoon 1983.

Cultivar	SD1	SD2	SD2-SD1	SD1	SD2	SD2/SD1
	Spikelets/spike (no.)			Grain yield/spike (g)		(%)
HY402	17.4	19.4	2.1	1.160	1.283	10.6
Pitic 62	18.2	20.8	2.6	1.387	1.170	-15.6
HY320	16.3	18.6	2.3	1.017	1.240	22.0
Ko-Chuan	19.6	20.3	0.7	1.270	1.137	-10.5
Ko-Fong	18.5	19.2	0.7	1.160	1.263	8.9
Siete Cerros	16.7	17.4	0.8	1.063	1.320	24.1
Ingal	14.6	15.5	0.9	0.480	0.603	25.7
Potam	15.0	14.0	-1.0	0.787	0.973	23.7
Glenlea	16.1	17.3	1.2	1.113	1.203	8.1
Neepawa	12.8	13.7	0.9	0.757	0.863	14.1
SE		0.4				

SD1=seeding date1=04 May, SD2=28 May.

Table 8. Seeding date effect on spring wheat development expressed as differences from the earliest date of seeding, Saskatoon 1983.

Cultivar	DSE (days)	DSE GDD5 (units)
HY402	-9.8	86.3
Pitic 62	-7.0	121.0
HY320	-10.5	67.5
Ko-Chuan	-6.8	116.8
Ko-Fong	-9.8	76.0
Siete Cerros	-14.5	15.0
Ingal	-10.0	-36.5
Potam	-19.5	-57.5
Glenlea	-10.5	65.5
Neepawa	-12.0	45.3
SE	2.9	25.9

SD1=seeding date1=04 May, SD2=28 May.
DSE=days to 5% spike emergence.
GDD5=Growing Degree Days with a base temperature of 5°C.

Averaged over experiments, the cultivars under evaluation can be ranked in the following (descending) order for vernalization sensitivity:

Fielder = Pitic 62 > HY402 > HY320 > Genesis > HY912 > Leader > Glenlea > Neepawa > Katepwa > Siete Cerros > Potam.

Fielder and Pitic 62 are rated equal for vernalization response by Jedel et al. (1986). Cutforth et al. (1990) concluded that HY320 has a greater vernalization requirement than Neepawa. Pitic 62, HY402 and Potam are included in the above ranking because they have been used as parents in the development of a number of Canadian spring wheat cultivars:

Genesis = HY320/HY402 where HY402 = Pitic 62/Gaines
Biggar = HY320 (reselection of hard kernel lines)
AC Taber= HY320*3/BW553

Bluesky = Potam/Glenlea

Based on the pedigrees of Biggar and AC Taber one might expect that those Canada Prairie Spring wheat cultivars will also have a vernalization requirement since they are closely related to HY320. Bluesky is a very early maturing Utility wheat adapted to the Peace River region of Alberta.

In conclusion, clear evidence of vernalization response in high yielding spring wheats was obtained in two years out of four. In most instances delayed heading and increased leaf production, manifestations of unmet vernalization requirements, were associated with higher grain yield. The cultivars Fielder and HY320 had the largest apparent vernalization requirement while Katepwa, Neepawa and Siete Cerros had the least. Vernalization requirement is a varietal characteristic that, along with resistance to lodging, shattering and diseases, should be taken into account when producers select wheat cultivars for their production areas.

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