

Simultaneous selection for early maturity, increased grain yield and elevated grain protein content in spring wheat

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Abstract

High grain yield and grain protein content, and early maturity are important traits in global bread wheat (*Triticum aestivum* L.)-breeding programmes. Improving these three traits simultaneously is difficult due to the negative association between grain yield and grain protein content and the positive association between maturity and grain yield. We investigated the genetic relationship between maturity, grain yield and grain protein content in a population of 130 early maturing spring wheat lines in a high latitude (52–53°N) wheat-growing region of Canada. Grain protein content exhibited negative genetic correlation with maturity (–0.87), grain fill duration (–0.78), grain fill rate (–0.49), grain yield (–0.93) and harvest index (–0.71). Grain yield exhibited positive genetic correlation with maturity (0.69), rate (0.78) and duration (0.49) of grain fill, and harvest index (0.55). Despite the positive association between maturity and grain yield, and negative association between grain yield and grain protein content, higher yielding lines with medium maturity and higher grain protein content were identified. Broad-sense heritabilities were low (<0.40) for rate and duration of grain fill, grain protein content, spike per m², grains per spike, harvest index and grain yield, and medium to high (>0.40) for grain weight, days to anthesis and maturity, and plant height. Selection for longer preanthesis and shorter grain fill periods may help circumvent the negative association between grain yield and grain protein content. Selection for shorter grain fill periods and higher grain fill rate may be a useful strategy for developing early maturing cultivars with acceptable grain yields in northern wheat-growing regions.

Key words: genetic correlations — heritability — selection index — spring wheat

High grain yield, elevated grain protein content and early maturity are important traits in global bread wheat-breeding programmes. Improving these three traits simultaneously is difficult due to the negative association between grain yield and grain protein content, and the positive association between maturity and grain yield.

The negative association between grain yield and grain protein content is variable across environments and populations. Several studies report genetic correlations between grain yield and grain protein content as $-0.37 \geq r \leq -0.94$ (reviewed by Oury et al. 2003). Stewart and Dwyer (1990) reported an increase in grain yield following selection for this trait in spring wheat on the Canadian prairies from 1961 to 1982. This was accompanied with a decrease in grain protein content. Costa and Kronstad (1994) suggested that the extensive use of semidwarf cultivars with higher harvest indices may have

negatively affected grain protein content in global wheat germplasm. Austin et al. (1980) suggested that grain N uptake is diluted by greater carbohydrate assimilation, resulting in lower grain protein content in high-yielding semidwarf cultivars. Noaman et al. (1990), however, reported that it may be possible to develop winter wheat cultivars with high grain yield and grain protein content due to the occurrence of transgressive segregation for both traits in two winter wheat populations. Fabrizius et al. (1997) also identified progeny (in two crosses of wheat) combining the high yield and protein levels of the parents, and suggested the independent segregation of the genes controlling grain yield and grain protein content.

The positive relationship between grain yield and days to maturity poses another challenge to wheat breeders. Time to anthesis and the subsequent period from anthesis to physiological maturity (grain filling) are the main determinants of maturity in wheat (Duguid and Brule-Babel 1994). The duration and rate of grain filling also determines final grain weight. A better understanding of the grain filling process and its relationship with grain weight and maturity may aid in the development of spring wheat cultivars with high yield and early maturity (Duguid and Brule-Babel 1994). Simultaneous improvement in grain yield and earliness in wheat can be achieved either by selecting for a longer grain fill period or a faster grain fill rate (Sharma 1994). Several studies have demonstrated no association between grain fill duration and grain yield in spring wheat (Nass and Reiser 1975, Bruckner and Froberg 1987, Talbert et al. 2001). However, the rate of grain filling has been found to be positively associated with grain weight and hence grain yield (Nass and Reiser 1975, Bruckner and Froberg 1987, Duguid and Brule-Babel 1994). Przulj and Mladenov (1999) investigated the inheritance of grain fill duration in spring wheat, and found an inconsistent association between this trait and maturity. The gene actions involved in the crosses they studied were mostly additive, with some observable epistasis. There have also been reports on the positive association between grain fill duration and grain protein content in winter (Mou et al. 1994), durum (Knott and Gebeyehou 1987) and spring (Talbert et al. 2001) wheat.

Higher grain yield, increased grain protein content and early maturity are some of the main objectives of a typical wheat-breeding programme in high latitude-growing regions. Simultaneous improvement of several quantitative traits requires an

appropriate multiple-trait selection procedure. Smith (1936) proposed the use of a selection index; a linear function of the different traits, with each trait being given a certain weight according to its importance. Several types of selection indices have been proposed (Baker 1986). Index selection has been reported to be more efficient than single-trait selection methods in increasing aggregate genotypic worth (Wells and Kofoid 1985, Gebre-Mariam and Larter 1996).

The development of early maturing cultivars with high grain yield is a common objective of spring wheat-breeding programmes in western Canada (Duguid and Brule-Babel 1994). The negative association between grain yield and grain protein content (along with the stringent quality requirements for cultivar registration and shorter growing season) make it extremely difficult to achieve yield gains in the Canada western red spring wheat class (Wang et al. 2002). The present study was designed to examine the relationships among grain yield, maturity and grain protein content in the earliest maturing spring wheat germplasm. The specific objectives were to (i) investigate the genetic variation for maturity, grain yield and grain protein content in a large random population of early maturing wheat genotypes, (ii) study the associations between maturity, grain yield, grain protein content and other important agronomic traits and (iii) identify genotypes not falling within the boundaries of the general interrelationship between maturity, grain yield and grain protein content.

Materials and Methods

The genetic material consisted of 130 spring wheat genotypes from the International Centre for Maize and Wheat Improvement (CIMMYT) in Mexico. Genotypes, including some of the CIMMYT lines released as cultivars in different countries, in addition to inbred lines from different CIMMYT nurseries and yield trials, were selected during 1998 at Ciudad Obregon, Sonora state, Mexico. These genotypes were chosen to represent the earliest maturing lines present among germplasm grown at CIMMYT in that year. This population of 130 lines is hereafter considered as a random population representative of the earliest maturing spring wheat germplasm around the world. Pedigree information of some of these lines is presented in Table 1.

Seed increase was conducted in 1999 and 2000 in Edmonton, AB Canada. Four of the 10 check cultivars ('AC Splendor', 'AC Barrie', 'AC Intrepid' and 'Katepwa') were selected from the Canada western red spring wheat class, with grain protein ranging from 14.1% to

15.0% and days to maturity of 108–110 days, respectively; four ('AC Taber', 'AC Foremost', 'AC Vista' and 'Cutler') from the Canada prairie spring wheat class, with grain protein ranging from 12% to 13% and days to maturity of 106–110 days; and two ('Bluesky' and 'Glenlea') from the Canada western extra strong class with maturities of 108 and 110 days, respectively (Alberta Agriculture, Food and Rural Development (AAFRD) 2005). Field trials were conducted at the Edmonton Research Station of the University of Alberta, Edmonton, AB Canada (53°34'N, 113°31'W) and at the Field Crop Development Centre, Lacombe, AB Canada (52°28'N, 113°45'W), during 2003 and 2004. Soils at both experimental sites were Orthic Black Chernozemics (AAFRD 2004).

The 130 experimental lines and 10 check cultivars were divided into seven groups, each having 20 genotypes. At each of the two locations, the 140 genotypes were planted in a nested split-plot design having two replications with groups as whole plots and genotypes within groups as subplots. Plot size at Edmonton was six rows, 4 m long with row spacing of 0.23 m. Plot size at Lacombe was eight rows, 4 m long with row spacing of 0.14 m. Planting density was 350 seeds per m². Fertilizer was applied according to soil test recommendations. At Edmonton, 196 kg/ha fertilizer as 46-0-0 (N-P₂O₅-K₂O) and 117 kg/ha fertilizer as 8-24-24 (N-P₂O₅-K₂O) was broadcast after sowing during 2003. During 2004, 24 kg/ha 46-0-0 and 25 kg/ha 8-24-24 was applied with the seed in addition to 85 kg/ha 46-0-0 which was banded into the soil in fall 2003. At Lacombe, 110 kg/ha fertilizer as 6-25-30 was applied with the seed during both years (for 2003, 561 kg/ha of 5-25-30 was also banded into the soil during fall 2002). Weeds were controlled by the application of postemergence herbicides [MCPA Amine (500 ml per acre) at Edmonton and Refine/Curtail M (600 ml per acre) at Lacombe].

Data were recorded on days from sowing to anthesis and physiological maturity, plant height, number of spikes per m², grain yield, grain weight and grain protein content. Time of anthesis was determined visually as the day when 75% of the heads in a plot dehisced anthers. Physiological maturity at Edmonton was visually determined as the number of days from sowing to when 75% of the peduncles in a plot completely lost green colour. Grain fill duration was calculated as the difference between days to maturity and anthesis. Grain fill rate was estimated by dividing grain yield per ha by the grain fill duration (Frederick and Bauer 1999). Maturity data and hence grain fill duration and rate were not recorded at the Lacombe site. Harvest Index was calculated (in 2003 only) as a ratio of grain yield and aboveground biomass of a randomly sampled 1 × 2 m row sample harvested just prior to grain harvest. The number of spikes in a randomly sampled 0.5 × 2 m row plot area was counted and recorded as spikes per m². For estimating grain number per spike, number of grains per m² was first estimated from the grain yield and thousand grain weight of a plot, and then divided by spikes per m². Grain protein content (%) was determined using Near-infrared Reflectance (NIR) spectroscopy using a Monochromator NIR Systems model 6500 (NIRSystems, Inc., Silver Springs, MD, USA).

Data were analysed in the MIXED procedure of SAS (SAS Institute 2003) with all effects [Environments, Replications (environments), Groups (replications), Lines, Environments × Lines] considered random. Heterogeneity of error variance was accounted by including the REPEATED/GROUP = ENV statement in PROC MIXED (Piepho 1999). Likelihood ratio testing was used to test if individual variance components were zero. Likelihood ratios were constructed as the difference between the -2 Residual Log Likelihood values of the reduced covariance model (without the effect being tested) and the full covariance model (with the effect being tested) (Yang 2002). Check cultivars were excluded for the purpose of variance and covariance components estimation. Least-square mean values of genotypes, over the four environments, were used to determine the mean, range and standard deviation for each trait.

Broad-sense heritabilities were estimated on a plot basis as: $H = \sigma_G^2 / (\sigma_G^2 + \sigma_{GE}^2 + \sigma_e^2)$, where σ_G^2 , σ_{GE}^2 and σ_e^2 are, respectively, the among-line, line × environment and error variances. The standard errors of the estimated heritabilities were computed employing the

Table 1: Pedigrees/names of selected CIMMYT lines/cultivars grown in four environments in Alberta, Canada during 2003–2004

Line number	Pedigree/name
CIMMYT002	TOBARITO M 97
CIMMYT077	SERI M 82
CIMMYT090	PASTOR
CIMMYT117	ODK16/PDGA//AU/JTS179/3/NAC /4/OPATA/5/CNO79/PRL
CIMMYT131	PRL/VEE#6//VEE/MYNA
CIMMYT151	CEP8927
CIMMYT158	KAUZ*2//K134(60)/VEE
CIMMYT217	CHEN/AEGILOPS SQUARROSA (TAUS)//BCN
CIMMYT248	BOW/PRL//BUC/3/LUAN
CIMMYT250	RABE/PARUS//PARUS
CIMMYT259	WEAVER/ROBLIN
CIMMYT274	CMH73A.497/2*CNO79//CMH76.173/CNO79
CIMMYT276	CMH81.38/2*KAUZCAL/NH //H567.71/3/2*NING 7840/
CIMMYT304	Not available
CIMMYT312	'NG8319//SHA4/LIRA'

delta method (Holland et al. 2003). Selection response for 10% of the population being selected was calculated as: $R = ih\sigma_p$, where σ_p is the phenotypic standard deviation, H is the broad-sense heritability and i is the selection intensity (1.755 for 10% of the population selected; Falconer and Mackay 1996). Genetic and phenotypic correlations among the traits, and their standard errors, were estimated using multivariate REML implemented in the MIXED procedure (Holland 2005). The estimated genetic [$\hat{r}_{g(xy)}$] and phenotypic [$\hat{r}_{p(xy)}$] correlations between traits x and y are given by:

$$\hat{r}_{g(xy)} = \frac{\hat{\sigma}_{G(xy)}}{\sqrt{\hat{\sigma}_{G(x)}^2 \cdot \hat{\sigma}_{G(y)}^2}}$$

and

$$\hat{r}_{p(xy)} = \frac{\hat{\sigma}_{P(xy)}}{\sqrt{\hat{\sigma}_{P(x)}^2 \cdot \hat{\sigma}_{P(y)}^2}} = \frac{\hat{\sigma}_{G(xy)} + \hat{\sigma}_{GE(xy)} + \hat{\sigma}_{e(xy)}}{\sqrt{(\hat{\sigma}_{G(x)}^2 + \hat{\sigma}_{GE(x)}^2 + \hat{\sigma}_{e(x)}^2) \cdot (\hat{\sigma}_{G(y)}^2 + \hat{\sigma}_{GE(y)}^2 + \hat{\sigma}_{e(y)}^2)}}$$

where $\hat{\sigma}_{G(xy)}$ and $\hat{\sigma}_{P(xy)}$ are the estimated genetic and phenotypic covariances between traits x and y ; $\hat{\sigma}_G^2$ and $\hat{\sigma}_P^2$ are the estimated genetic and phenotypic variances; $\hat{\sigma}_{GE(xy)}$ and $\hat{\sigma}_{e(xy)}$ are the estimated genotype \times environment and experimental error covariances between traits x and y ; while $\hat{\sigma}_{GE}^2$ and $\hat{\sigma}_e^2$ are the estimated genotype \times environment and experimental error variances, respectively. Correlations were considered significantly different from zero ($P < 0.05$) if their approximate 95% confidence intervals did not contain zero (Holland et al. 2003). Confidence intervals were constructed as $r \pm z_{(0.05)}\sigma_e$, where r is the correlation coefficient, $z_{(0.05)}$ is the value from standardized normal distribution table at $P = 0.05$ and σ_e is the standard error of the correlation coefficients.

Selection indices for four traits were constructed as: $I = b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4$, where b is the index coefficient and X the BLUPs of genotypes for the respective trait. The vector of Smith-Hazel index coefficients b was calculated as: $b = P^{-1}Ga$ (Baker 1986), where P^{-1} is the inverse of the estimated phenotypic variance-covariance matrix for the four traits; G is the estimated genetic variance-covariance matrix, and a is the vector of relative economic weights of the traits included in the index. The relative economic values were assigned as reciprocals of the genotypic standard deviation of the traits, hence all traits were roughly given equal value (R. J. Baker, personal communication). Two selection indices, both having protein, yield and grain fill duration in common, but differing in either maturity or anthesis, were constructed. The economic values of grain yield, protein and days to anthesis were given positive signs while those of maturity and grain fill duration were given negative signs. The expected response to selection based on index was calculated as: $R_I = iGb'/\sqrt{b'Pb}$ (Baker 1986), where b' is the transposition of b . The observed genetic gain was calculated as the difference between the mean of the selected top 10% lines and that of the entire population.

The relative efficiency of index selection over direct selection for trait x was calculated as: $R_I/R_x = [b'G \cdot \sigma_{P(x)}]/\sqrt{b'Pb} \cdot \sigma_{G(x)}^2$ (Baker 1986), where $\sigma_{P(x)}$ and $\sigma_{G(x)}^2$ are the phenotypic standard deviation and genetic variance of trait x , respectively.

Results

Environmental conditions and mean grain protein content varied across locations and years (data not shown). Overall, grain protein content was about 2% greater in Edmonton (in both years) than Lacombe. Grain protein content at both locations was higher in 2004 than 2003 and was associated with low grain yields.

Lines differed ($P < 0.01$) for all traits measured (Table 2). The effect of environment was significant on all measured traits, while that of line \times environment was significant ($P < 0.01$) for all traits except spikes per m^2 , grains per spike and harvest index. Environment effects contributed the most to the observed variation in the measured traits, followed by line effects and line \times environment interaction effects. All traits exhibited a wide range of variation (Table 3). Maturity varied from 95 to 114 days in the experimental lines, a range of 6 days greater than the check cultivars. Similar variation occurred for grain yield (2.43–5.36 t/ha) and percentage grain protein (10.8–14.7%) in the experimental population. Broad-sense heritabilities across environments were low (< 0.40) for grain fill duration, grain protein content, spike per m^2 , grains per spike, grain fill rate, harvest index and grain yield, and medium to high (> 0.40) for grain weight, days to anthesis and maturity and plant height (Table 3).

For a selection intensity of 10%, the expected genetic gain (as a percentage of the population mean μ) in the studied population was 3% for anthesis, 4% for maturity and grain fill duration, 6% for spikes per m^2 , 8% for grain fill rate, grains per spike and grain weight, 13% for plant height, 10% for grain yield and 5% for grain protein content (Table 3). The observed genetic gain from one cycle of selection was higher than the expected gain for all traits except plant height. The expected genetic gain from selection based on index including maturity was 4.1 days (4% of μ) for maturity and 0.89 (7% of μ) for protein (with relative efficiencies of 114% and 127% over single trait selection for these traits). An expected decrease of 422 kg/ha in yield was observed for selection based on this index. Selection based on index including anthesis resulted in an expected change of 0.13 (1% of μ) in

Table 2: Variance component estimates for 11 traits measured on a population of 130 early maturing spring wheat lines in four environments in Alberta, Canada during 2003–2004

Trait	Variance components				
	Environment	Rep (Env)	Groups (Rep)	Line	Env \times line
Days to anthesis	32**	0.02	0.04**	2.5**	0.8**
Spikes per m^2	33 506**	298**	138	1363**	236
Grains per spike	277.4**	2.5	0.09	2.64**	0.00
Plant height	18.2*	1.62**	1.89**	48.4**	3.82**
Grain fill rate	143.8**	0.00**	75.3**	90.1**	97.3**
Grain fill duration	13.5**	0.02	0.16	3.4**	2.7**
Days to maturity	48.3**	0.06	0.16*	8.7**	3.2**
Grain weight	11.2**	0.00	0.09	7.95**	2.25**
Harvest index	0.001*	0.00*	0.00	0.001**	0.00
Grain yield	1.33*	0.02*	0.09**	0.11**	0**
Grain protein	1.6**	0	0.1**	0.81**	0.20**

*, **Significant at $P = 0.05$ and $P = 0.01$, respectively, based on likelihood test ratio.

Table 3: Mean values, standard deviations (SD), ranges, heritabilities and selection response (R) for 11 traits measured on a population of 130 early maturing spring wheat lines and 10 check cultivars grown in four environments in Alberta, Canada during 2003–2004

Trait	Mean	SD	Minimum	Maximum	Heritability	R_e^1	R_o^1
Days to anthesis							
Lines	67	1.7	63	70	0.63 (0.04) ²	2.3	2.7
Checks	66	1.4	64	68	–	– ³	–
Spikes per m ² (n)							
Lines	490	62	380	720	0.14 (0.03)	28	61
Checks	530	88	400	660	–	–	–
Grains per spike (n)							
Lines	27	5	15	39	0.14 (0.03)	2.2	4.6
Checks	25	4	19	31	–	–	–
Plant height (cm)							
Lines	79	7	66	106	0.71 (0.03)	10	9.6
Checks	91	10	76	105	–	–	–
Grain fill rate (kg/ha/day)							
Lines	129	15	82	162	0.32 (0.06)	11	13
Checks	133	8	121	147	–	–	–
Grain fill duration (days)							
Lines	42	2	34	48	0.29 (0.04)	1.5	2.2
Checks	40	3	36	44	–	–	–
Days to maturity							
Lines	106	3.3	95	114	0.54 (0.04)	3.6	5.2
Checks	103	4.6	97	110	–	–	–
Grain weight (mg)							
Lines	41	2.9	32	49	0.49 (0.04)	3.4	4.5
Checks	41	3.3	36	46	–	–	–
Harvest index							
Lines	0.50	0.04	0.39	0.57	0.35 (0.05)	0.03	0.04
Checks	0.48	0.04	0.44	0.55	–	–	–
Grain yield (t/ha)							
Lines	4.33	0.46	2.43	5.36	0.38 (0.04)	0.45	0.55
Checks	4.31	0.36	3.56	4.77	–	–	–
Grain protein (%)							
Lines	12.4	0.8	10.8	14.7	0.29 (0.04)	0.7	1.2
Checks	12.3	0.8	11.0	13.3	–	–	–
Index (maturity)	–29.9	2.3	–34.6	–22.8	0.60 (0.04)	2.2	–
Index (anthesis)	–17.5	1.4	–20.4	–13.0	0.63 (0.04)	1.5	–

¹ R_e , expected response from 10% selection; R_o , observed response from 10% selection;

²Standard error of the heritability estimate.

³–, Not estimated.

percentage grain protein content and of 60 kg/ha (1.4% of μ) in grain yield. The expected changes in protein and yield from this index were very small, but both protein and yield did increase. Both indices had higher heritabilities (Table 3) than all individual traits except days to anthesis. Hence, the expected genetic gain will be higher if selection is based on index than on individual traits. The index (including maturity) values were significantly correlated with maturity (–0.78), protein (0.73), yield (–0.59) and grain fill duration (–0.64), further suggesting that selection based on index values is likely to generate considerable genetic gain in each trait. The correlation between the index (including anthesis) values and individual trait values were, however, lower (0.36, 0.11, 0.08 and –0.29 with anthesis, protein, yield and grain fill duration, respectively).

Grain yield exhibited a positive genetic correlation with grains per spike, grain fill duration and rate, harvest index and days to anthesis and maturity (Table 4). Percentage grain protein content was negatively correlated with grain yield, days to anthesis and maturity, grains per spike, and duration and rate of grain fill period. All the traits showed almost similar phenotypic associations but with lower correlation coefficients (Table 4). The general interrelationships of maturity, grain yield and grain protein content were also revealed when

simultaneous improvement in maturity, yield and protein was attempted through index selection. Selection based on higher index values resulted in early maturity and increased percentage grain protein content but decreased grain yield, while selection based on lower index values resulted in the reverse.

The cultivar ‘AC Splendor’ was the earliest maturing check cultivar with the highest mean grain protein content among the check cultivars (Table 5). ‘AC Foremost’ had the highest grain yield among the check cultivars. Lines identified based on their superiority over check cultivars for maturity, grain yield and/or protein content, and based on their departure from the general interrelationships for these traits, are presented in three groups (Table 5). There were three lines (CIMMYT250, CIMMYT259 and CIMMYT274), which matured roughly 10 days earlier than the population mean, had 2% higher grain protein content but 18–44% lower grain yield than the population mean (Table 5). CIMMYT274 and CIMMYT276 had significantly higher grain protein content than ‘AC Splendor’. Group II lines had average maturity but 11–20% higher grain yield than the population mean. There were five lines (Group III) which roughly yielded as much as the population mean, had 0.8–2.3% greater grain protein content and were 1–6 days earlier maturing (with the exception of CIMMYT131) than the population mean.

Table 4: Genetic (G) and phenotypic (P) correlation coefficients for 11 traits measured on a population of 130 early maturing spring wheat lines grown in four environments in Alberta, Canada during 2003–2004

Trait	Coefficient	Spikes per m ²	Grains per spike	Plant height	Grain fill rate	Grain fill duration	Maturity	Grain weight	Harvest index	Grain yield	Grain protein
Anthesis	G	-0.42*	0.63*	0.03	0.63*	0.39*	0.82*	0.07	0.08	0.66*	-0.56*
	P	-0.22*	0.24*	0.10	0.38*	0.04	0.60*	0.12*	0.14*	0.41*	-0.21*
Spikes per m ²	G		-0.79*	-0.28*	-0.37	-0.19*	-0.44*	-0.32*	-0.02	-0.44*	0.49*
	P		-0.61*	-0.18*	-0.32	0.09*	-0.09	-0.16*	-0.10*	-0.18*	0.13*
Grains per spike	G			0.10	0.52*	0.34*	0.68*	-0.22	0.20	0.80*	-0.93*
	P			0.07	0.59*	0.06	0.21*	-0.12*	0.16*	0.39*	-0.19*
Plant height	G				0.35*	-0.33*	-0.15	0.11	-0.64*	0.01	0.08
	P				0.32*	-0.25*	-0.11	0.13*	-0.31*	0.17*	-0.02
Grain fill rate	G					-0.14	0.47*	0.24	0.14	0.78*	-0.49*
	P					-0.37*	0.00	0.19*	0.16*	0.84*	-0.18*
Grain fill duration	G						0.70*	0.17	0.63*	0.49*	-0.78*
	P						0.75*	0.01	0.26*	0.12*	-0.20*
Maturity	G							0.15	0.45*	0.69*	-0.87*
	P							0.11	0.25*	0.45*	-0.31*
Grain weight	G								0.21	0.25*	-0.09
	P								0.10	0.22*	-0.06
Harvest index	G									0.55*	-0.71*
	P									0.33*	-0.28*
Grain yield	G										-0.93*
	P										-0.34*

*Significant at P = 0.05.

Table 5: Least-square mean values for eight traits of selected spring wheat lines based on maturity, grain yield and protein, and check cultivars grown in four environments in Alberta, Canada during 2003–2004

Genotype	Grains per spike (n)	GFR (kg/ha/day)	GFD (days)	Maturity (days)	Grain weight (mg)	HI	Grain yield (t/ha)	Grain protein (%)
Experimental lines								
Mean	27	129	42	106	41	0.50	4.33	12.4
Group I (early maturity or high yield potential)								
CIMMYT090	30	152	43	110	41	0.52	5.36	10.8
CIMMYT250	19	114	37	95	42	0.45	3.50	14.0
CIMMYT259	22	122	36	95	41	0.44	3.56	13.8
CIMMYT274	15	82	40	98	38	0.40	2.43	14.6
Group II (average maturity with high grain yield potential)								
CIMMYT002	33	153	39	103	37	0.52	4.80	12.1
CIMMYT077	26	147	42	107	39	0.53	5.20	11.9
CIMMYT117	26	133	42	105	46	0.54	4.81	12.6
CIMMYT151	27	162	41	107	40	0.47	5.05	11.3
CIMMYT217	23	137	43	106	46	0.54	4.90	11.6
CIMMYT304	31	141	40	106	38	0.54	4.81	11.9
Group III (high grain protein potential with average yield potential)								
CIMMYT131	22	117	44	109	44	0.50	4.29	13.7
CIMMYT158	26	128	41	102	43	0.51	4.34	13.2
CIMMYT248	25	157	39	105	45	0.51	4.51	13.7
CIMMYT276	24	148	37	101	39	0.45	4.06	14.7
CIMMYT312	27	140	37	100	41	0.50	4.15	13.3
Check cultivars								
Mean	25	133	40	104	41	0.48	4.31	12.3
AC Splendor	24	121	36	97	36	0.44	3.56	13.3
AC foremost	26	129	44	109	42	0.55	4.77	11.5
Cutler	26	147	40	101	41	0.51	4.41	12.5
SE (difference)	4	14	2	2	2	0.03	0.31	0.6

GFD, grain fill duration; GFR, grain fill rate; HI, harvest index.

Discussion

Within a large random population of early maturing spring wheat lines grown in a high latitude environment, we found (i) a strong positive association between maturity and grain yield, (ii) a strong negative association between maturity and grain protein content and (iii) a strong negative association between grain yield and grain protein content. The negative association of grain protein content with maturity suggests that one important objective of spring wheat-breeding programmes in high northern latitudes (early maturity and high grain protein

content) can be readily achieved simultaneously. However, simultaneous improvements in protein and yield, and early maturity and yield will be extremely difficult, due to the strong negative associations of these traits.

Despite the negative association between grain yield and grain protein content in the present study, some lines departed from the general interrelationships of maturity, yield and protein content. Lines with average grain yield but significantly higher grain protein than the population mean were identified (CIMMYT131, CIMMYT248 and CIMMYT276).

Similarly, lines with average maturity and significantly higher grain yield than the population mean were also identified (CIMMYT077, CIMMYT151 and CIMMYT217). The existence of such lines, and the considerable genetic variability exhibited for maturity, grain yield and grain protein content, suggests the possibility of simultaneously improving the three traits. The presence of such outlying genotypes has also been reported previously. Fabrizio et al. (1997) identified progeny combining high grain yield and protein in two crosses of wheat. Costa and Kronstad (1994) reported moderate correlations between grain yield and protein, and concluded that these two traits could be improved simultaneously. Mesfin et al. (2000) did not find any association of grain protein with grain yield, days to heading and plant height in two hard red spring wheat populations, and concluded that they could select lines with high protein and acceptable yield, but with later maturity and taller plants. Löffler et al. (1985) identified hard red spring wheat genotypes close to the population mean for grain protein, but significantly higher than the mean for grain yield.

The high positive genetic and phenotypic associations between grain yield and grain fill rate and grains per spike indicate that the latter two traits contribute more than grain fill duration and grain weight to high yield potential. Grain number per spike was the major contributing factor to increased grain yield, as was also reported by Austin et al. (1989), Siddique et al. (1989), Slafer and Andrade (1993) and Hucl and Baker (1987). The negative association between harvest index and grain protein content observed in this study has been previously reported (Kramer 1979, Löffler and Busch 1982, Costa and Kronstad 1994). Extensive use of semidwarf cultivars as a means to increase grain yield has been suggested to be the cause of this negative relationship (Austin et al. 1980, Costa and Kronstad 1994).

Based on the positive association between grain fill duration and grain protein content, Talbert et al. (2001) suggested that selection for early heading and longer grain fill duration may help circumvent the undesirable negative association between grain yield and grain protein content. In the present study, however, grain fill duration and grain protein content were negatively correlated. By accounting for the associations of grain protein content with days to anthesis and grain fill duration, and of grain fill duration with grain yield, it may be more appropriate to select for delayed flowering and shorter grain fill duration. As grain protein content and days to anthesis were moderately correlated in the present study, delayed flowering may not be associated with lower grain protein accumulation. Indeed, delayed flowering may have a positive effect on grain protein content if accompanied with shorter grain fill duration. Furthermore, as the association between grain fill duration and grain yield was also moderate, the decrease in grain yield due to shorter grain fill duration may be only moderate. If the delayed flowering involves longer spike growth period, then the increased number of spikelets per spike and high percentage of fertile florets (as a result of greater partitioning of assimilates towards spike compared with that of stem) is expected to increase grain yield (Siddique et al. 1989, Slafer et al. 2001, Gonzalez et al. 2003). A longer vegetative period (planting to anthesis) may also serve to increase grain yield through increased grains per spike and grain weight, as reported by Gebeyehou et al. (1982) in durum wheat and Bingham (1969) in bread wheat.

The positive genetic association between maturity and grain fill duration, in the present study, was much higher than that between anthesis and grain fill duration. This, coupled with the observation that grain yield had stronger association with grain fill rate compared to that with grain fill duration, again suggests that selecting for a longer spike growth period and a shorter grain fill duration with higher grain fill rate may aid in selecting for early maturity and high grain yield. This is supported by the fact that genetic yield gains in wheat over time have been generally attributed to increased numbers of grains per spike rather than grain weight (Hucl and Baker 1987, Austin et al. 1989, Siddique et al. 1989, Slafer and Andrade 1993).

Results of the present study suggest the possibility of developing early maturing spring wheat without negatively affecting grain yield and grain protein content, through selection for shorter grain fill duration. However, a point of concern is the low heritability of grain fill duration, implying that genetic gain in this trait would require multi-environment testing. This problem may be solved by indirect selection for shorter grain fill duration through delayed anthesis and early maturity, both exhibiting high heritabilities. To better understand the processes leading to the departure from the normal interrelationships of maturity, grain yield and grain protein, we have embarked upon studies examining outlying genotypes identified in this study.

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References

- Alberta Agriculture, Food and Rural Development (AAFRD), 2004: Soil Group Map of Alberta. Available at: <http://www1.agric.gov.ab.ca/soils/soils.nsf/soilgroupmap?readform>, accessed on 26 September 2005.
- Alberta Agriculture, Food and Rural Development (AAFRD), 2005: Cereal and Oilseed Yield and Performance Data. Available at: [http://www1.agric.gov.ab.ca/\\$department/deptdocs.nsf/all/crop80?opendocument](http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/crop80?opendocument), accessed on 26 September 2005.
- Austin, R. B., J. Bingham, R. D. Blackwell, L. T. Evans, M. A. Ford, C. L. Morgan, and M. Taylor, 1980: Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *J. Agric. Sci. Camb.* **94**, 675–689.
- Austin, R. B., M. A. Ford, and C. L. Morgan, 1989: Genetic improvement in the yield of wheat: a further evaluation. *J. Agric. Sci.* **112**, 295–301.
- Baker, R. J., 1986: Selection Indices in Plant Breeding. CRC Press, Boca Raton, Florida.
- Bingham, J., 1969: The physiological determinants of grain yield in cereals. *Agric. Prog.* **44**, 30–42.
- Bruckner, P. L., and R. C. Frohberg, 1987: Rate and duration of grain fill in spring wheat. *Crop Sci.* **27**, 451–455.
- Costa, J. M., and W. E. Kronstad, 1994: Association of grain protein concentration and selected traits in hard red winter wheat populations in the Pacific Northwest. *Crop Sci.* **34**, 1234–1239.

- Duguid, S. D., and A. L. Brule-Babel, 1994: Rate and duration of grain filling in five spring wheat (*Triticum aestivum* L.) genotypes. *Can. J. Plant Sci.* **74**, 681—686.
- Fabrizius, M. A., M. Cooper, and K. E. Basford, 1997: Genetic analysis of variation for grain yield and protein concentration in two wheat crosses. *Aust. J. Agric. Res.* **48**, 605—614.
- Falconer, D. S., and T. F. C. Mackay, 1996: Introduction to Quantitative Genetics, 4th edn. Prentice Hall, Harlow, London, p. 379.
- Frederick, J. R., and P. J. Bauer, 1999: Physiological and numerical components of wheat yield. In: E. H. Satorre, and G. A. Slafer (eds), *Wheat, Ecology and Physiology of Yield Determination*. 55. Haworth Press, NY.
- Gebeyehou, G., D. R. Knott, and R. J. Baker, 1982: Relationships among durations of vegetative and grain filling phases, yield components, and grain yield in durum wheat cultivars. *Crop Sci.* **22**, 287—290.
- Gebre-Mariam, H., and E. N. Larter, 1996: Genetic response to index selection for grain yield, kernel weight and per cent protein in four wheat crosses. *Plant Breed.* **115**, 459—464.
- Gonzalez, F. G., G. A. Slafer, and D. J. Miralles, 2003: Floret development and spike growth as affected by photoperiod during stem elongation in wheat. *Field Crops Res.* **81**, 29—38.
- Holland, J. B., 2005: Correlations Estimated from Incomplete Block Designs in Multiple Environments. Available at: <http://www4.ncsu.edu/%7Ejholland/correlation/correlation.html>, accessed on 12 April 2005.
- Holland, J. B., W. E. Nyquist, and C. T. Cervantes-Martinez, 2003: Estimating and interpreting heritability for plant breeding: an update. *Plant Breed. Rev.* **22**, 9—111.
- Hucl, P., and R. J. Baker, 1987: A study of ancestral and modern Canadian spring wheats. *Can. J. Plant Sci.* **67**, 87—97.
- Knott, D. R., and G. Gebeyehou, 1987: Relationships between the lengths of the vegetative and grain filling periods and agronomic characters in three durum wheat crosses. *Crop Sci.* **27**, 857—860.
- Kramer, T. H., 1979: Environmental and genetic variation for protein content in winter wheat (*Triticum aestivum* L.). *Euphytica* **28**, 209—218.
- Loffler, C. M., and R. H. Busch, 1982: Selection for grain protein, grain yield, and nitrogen partitioning efficiency in hard red spring wheat. *Crop Sci.* **22**, 591—595.
- Loffler, C. M., T. L. Rauch, and R. H. Busch, 1985: Grain and plant protein relationships in hard red spring wheat. *Crop Sci.* **25**, 521—524.
- Mesfin, A., R. C. Frohberg, K. Khan, and T. C. Olson, 2000: Increased grain protein content and its association with agronomic and end-use quality in two hard red spring wheat populations derived from *Triticum turgidum* L. var. *dicoccoides*. *Euphytica* **116**, 237—242.
- Mou, B., W. E. Kronstad, and N. N. Saulescu, 1994: Grain filling parameters and protein content in selected winter wheat populations: II. Associations. *Crop Sci.* **34**, 838—841.
- Nass, H. G., and B. Reiser, 1975: Grain filling period and grain yield relationships in spring wheat. *Can. J. Plant Sci.* **55**, 673—678.
- Noaman, M. M., G. A. Taylor, and J. M. Martin, 1990: Indirect selection for grain protein and grain yield in winter wheat. *Euphytica* **47**, 121—130.
- Oury, F. X., P. Berard, M. Brancourt-Hulmel, C. Depatureaux, G. Doussinault, N. Galic, A. Giraud, E. Heumez, C. Lecomte, P. Pluchard, B. Rolland, M. Rousset, and M. Trottet, 2003: Yield and grain protein concentration in bread wheat: a review and a study of multi-annual data from a French breeding program. *J. Genet. Breed.* **57**, 59—68.
- Piepho, H.-P., 1999: Stability analysis using the SAS system. *Agron. J.* **91**, 154—160.
- Przulj, N., and N. Mladenov, 1999: Inheritance of grain filling duration in spring wheat. *Plant Breed.* **118**, 517—521.
- SAS Institute, 2003: Release 9.1. SAS Institute Inc. Cary, NC, USA.
- Sharma, R. C., 1994: Early generation selection for grain-filling period in wheat. *Crop Sci.* **34**, 945—948.
- Siddique, K. H. M., R. K. Belford, M. W. Perry, and D. Tennant, 1989: Growth, development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. *Aust. J. Agric. Res.* **40**, 473—487.
- Slafer, G. A., and F. H. Andrade, 1993: Physiological attributes related to the generation of grain yield in bread wheat cultivars released in different eras. *Field Crops Res.* **31**, 351—367.
- Slafer, G. A., L. G. Abeledo, D. J. Miralles, F. G. Gonzalez, and E. M. Whitechurch, 2001: Photoperiod sensitivity during stem elongation phase as an avenue to raise potential yield in wheat. *Euphytica* **119**, 191—197.
- Smith, H. F., 1936: A discriminant function for plant selection. *Ann. Eugen. (London)* **7**, 240—250.
- Stewart, D. W., and L. M. Dwyer, 1990: Yields and protein trends of spring wheat (*Triticum aestivum* L.) on the Canadian prairies, 1961—1982. *Can. J. Plant Sci.* **70**, 33—44.
- Talbert, L. E., S. P. Lanning, R. L. Murphy, and J. M. Martin, 2001: Grain fill duration in twelve hard red spring wheat crosses: genetic variation and association with other agronomic traits. *Crop Sci.* **41**, 1390—1395.
- Wang, H., T. N. McCaig, R. M. DePauw, F. R. Clarke, and J. M. Clarke, 2002: Physiological characteristics of recent Canada western red spring wheat cultivars: yield components and dry matter production. *Can. J. Plant Sci.* **82**, 299—306.
- Wells, W. C., and K. D. Kofoid, 1985: Selection indices to improve an intermating population of spring wheat. *Crop Sci.* **26**, 1104—1109.
- Yang, R.-C., 2002: Likelihood-based analysis of genotype-environment interactions. *Crop Sci.* **42**, 1434—1440.