

A genetic analysis of weed competitive ability in spring wheat

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Reid, T. A., Navabi, A., Cahill, J. C., Salmon, D. and Spaner, D. 2009. A genetic analysis of weed competitive ability in spring wheat. *Can. J. Plant Sci.* **89**: 591–599. Competition with weeds decreases crop yields globally. Breeding for competitive ability against elevated weed pressure can be difficult because the selection for specific traits which contribute to competitive ability may result in yield losses. The widely studied International Triticeae Mapping Initiative (ITMI) population was used to study the genetics of traits associated with competitive ability in a high latitude (52–53°N) wheat-growing environment in central Alberta, Canada. Grain yield without weed competition and under experimentally sown cultivated oat competition exhibited similar heritability. Grain yield was positively correlated with early season vigour, and negatively correlated with days to maturity in the competitive treatment only. In this study, similar heritability estimates between competition treatments suggest that selection in a weed free environment can lead to improvements in a weedy environment, but some high-yielding lines under competition would be eliminated during selection.

Key words: Wheat, weed competition, competitive ability, International Triticeae Mapping Initiative, genetic correlation

Reid, T. A., Navabi, A., Cahill, J. C., Salmon, D. et Spaner, D. 2009. Génétique de la capacité compétitive du blé de printemps. *Can. J. Plant Sci.* **89**: 591–599. En général, le rendement des cultures diminue quand celles-ci doivent concurrencer les mauvaises herbes. D'autre part, il est difficile d'améliorer la capacité compétitive des cultures en présence d'adventices, car la sélection des caractères responsables d'une telle amélioration peut entraîner une diminution du rendement. Les auteurs ont recouru à la population fort bien étudiée de l'*International Triticeae Mapping Initiative* (ITMI) pour approfondir la génétique des caractères associés à la capacité compétitive du blé à haute latitude (52–53°N), dans les conditions de culture particulières au centre de l'Alberta, au Canada. Le rendement grainier du blé présente la même hérédité en l'absence d'adventices qu'en présence d'avoine semée expérimentalement. Le rendement grainier est positivement corrélé à la vigueur en début de saison et l'est négativement au nombre de jours précédant la maturité, mais uniquement pour l'essai de concurrence. L'hérédité analogue entre les différents scénarios de concurrence estimée dans le cadre de cette étude laisse croire que la sélection sans concurrence de mauvaises herbes peut tout de même conduire à des améliorations en présence d'adventices. Quoiqu'il en soit, certaines lignées très productives en situation de concurrence pourraient être éliminées durant la sélection.

Mots clés: Blé, concurrence des adventices, capacité compétitive, International Triticeae Mapping Initiative, corrélation génétique

Competition with weeds is known to decrease crop yields (Oerke 2006). The study of competitive crop cultivars can be problematic as the concept is vague, difficult to measure, and depends on how competition is defined (Goldberg 1996; Hager 2004). Wheat (*Triticum aestivum* L.) cultivars can suppress weed growth while maintaining their yield (Lemerle et al. 2001b). It has been suggested that a separation between crop tolerance, measured in percent yield loss due to weeds (competitive response), and weed suppression (competitive effect), is important in understanding competitive relationships (Jordan 1993; Didon 2002).

Increased competitiveness in wheat, both tolerance and suppression, is a goal for some wheat-breeding programs, including those directed at low-input environments (Lemerle et al. 2001b; Vandeleur and Gill 2004). Some specific traits are more strongly associated with competitive ability than others, and competitive ideotypes have been developed for a number of geographic regions, though no single set of traits apply in all situations (Lemerle et al. 2006; Mason et al. 2007b).

Taller crops with less-erect leaves and a high leaf area index, or ground cover, are considered more competitive (Richards and Whytock 1993; Huel and Huel 1996; Fischer et al. 2000). Plant height has been widely studied (Challaiah et al. 1986; Thomas et al. 1994; Seefeldt et al.

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Abbreviations: ITMI, International Triticeae Mapping Initiative

1999; Lemerle et al. 2001a), with less attention placed on other traits. Early maturity and greater early-season vigour have been identified specifically for organic agriculture (Mason et al. 2007b).

The interplay of the large number of factors influencing competitive ability makes improvement through breeding problematic. Breeding efforts have focused on improving one trait at a time (Lemerle et al. 1996) or trying to define competitive response solely on the basis of yield (Cousens et al. 2003a; Lemerle et al. 2006). Alternatively, indirect selection for competitive ability through the selection of known competitive traits has been suggested for upland rice (Zhao et al. 2006c). Selection for these traits in a weed-free environment may result in the improvement of competitive ability in a weedy environment (Zhao et al. 2006a). There may be certain traits that cannot be directly measured in a competitive environment, but would still offer a competitive advantage in weedy situations. For example, improved light interception (i.e., reduced percent transmittance) may provide a competitive advantage to crops (Harbur and Owen 2004). Measuring such a trait in a dense weedy canopy may be biased (Park et al. 2003).

The negative relationship between yield and competitive ability and decreased heritability estimates from increased environmental variation suggest that selection should not be done in naturally weedy environments (Fasoula and Fasoula 1997). However, Huel and Hucl (1996) reported that specific breeding lines that yielded the highest without competition from weeds are not necessarily the highest yielding under competition from weeds. Further to this, ranking wheat cultivars for weed competitive ability may be inconsistent between sites due to site-specific yield limitations and weed density (Lemerle et al. 2001b; Vandeleur and Gill 2004). Despite rank changes between sites, weed-free grain yield may be the best predictor of wheat grain yield under weedy conditions (Cousens and Mokhtari 1998).

The objective of the present study was to determine if genetic parameters associated with competitive ability in spring wheat differed when grown with and without a controlled competitive weed treatment.

MATERIALS AND METHODS

Plant Material

One hundred and eight random recombinant inbred lines from the International Triticeae Mapping Initiative (ITMI) mapping population, provided by Dr. C. O. Qualset (University of California, Davis, CA), and 12 check cultivars (Table 1) were used in this study. The ITMI population was established in 1989 with the goal of developing linkage maps for the major Triticeae species (Sorrells et al. 2005). This population came from a cross between a conventional hexaploid wheat (Opata 85 = Bluejay/Jupateco F 73) and a synthetic hexaploid wheat accession W7984. The synthetic hexaploid wheat is an amphiploid developed from a cross between the

Table 1. Check cultivars employed and their attributes of interest/reason for their inclusion in this study

Variety	Attributes of Interest ² /Reason for Inclusion
Opata	Bread wheat parent in original ITMI population cross
M6	Synthetic parent in original ITMI population cross
Attila	Semi-dwarf, high yield, CIMMYT cultivar (CIMMYT 2008)
AC ^x Barrie	Tall, high yield, Canadian hard red spring wheat ^y (McCaig et al. 1996)
CDC ^w Go	Semi-dwarf, early, high yield, Canadian hard red spring wheat (Hucl 2003)
AC Intrepid	High yield, early, Canadian hard red spring wheat (DePauw et al. 1999)
McKenzie	Tall, high tillering, Canadian hard red spring wheat (Graf et al. 2003)
Park	Tall, commonly used in organic production systems, early maturing, Canadian hard red spring wheat (Kaufmann and McFadden 1968)
Saar	Taller semi-dwarf, high tillering, CIMMYT bread wheat
Sapphire	Semi-dwarf, low tillering, late maturing, New Zealand bread wheat
AC Splendor	Tall, low tillering, Canadian hard red spring wheat (Fox et al. 2007)
Superb	High yield, Semi-dwarf, Potentially competitive, Canadian hard red spring wheat (Secan 2006)

²Attributes such as yield potential, tillering capabilities, maturity characters of the cultivars were determined previously by our research group over various studies.

^yFor a discussion of the attributes of Canada hard red and Canada prairie spring wheat see (Canadian Grain Commission 2007).

^xAC, Agriculture Canada.

^wCDC, Crop Development Center, University of Saskatchewan, Saskatoon SK.

tetraploid Mexican durum wheat cultivar Altar 84 (*Triticum turgidum*) and an accession of diploid goat grass *Aegilops tauschii* (Coss.) Schmal. (Song et al. 2005). The population is genetically diverse for many agronomic traits and has been used to investigate wheat quality traits (Nelson et al. 2006), tillering, growth habit, spike morphology, gross morphology (Li et al. 2002), heading, maturity, plant height, leaf colour (Kulwal et al. 2003), as well as many diseases and pests (Friesen and Faris 2004; Sardesai et al. 2005; Zwart et al. 2006). Several of these traits are thought to contribute to competitive ability (Lemerle et al. 2001a).

Experimental Design

The population was grown at two sites in each of 2 yr (2005 and 2006) with two competition treatments in two replications per site. In 2005, the experiment was grown at the University of Alberta Edmonton Research Station (ERS), Edmonton, AB (lat. 53°34'N, long. 113°31'W) (Michener field) and the University of Alberta Ellerslie Research Station, located 10 km south of ERS. The Ellerslie site was planted on 2005 May 25, 15 d later than the Michener site. In 2006, the experiment was grown on two different fields at the ERS (Michener and W240 fields, 1 km distance). The

Michener site was planted on 2006 May 29, 13 d later than the W240 site. Soil at all sites is classified as a Black Chernozem, which is typical of central Alberta (Alberta Agriculture Food and Rural Development 2002). Granular fertilizer (11-52-0: N-P-K) was banded with the seed, during sowing, at a rate of 140 kg ha⁻¹. Competition ranges were cross seeded with Grizzly tame oats (McKenzie and Harder 1995) at a rate of 60 seeds m⁻², with no additional fertilizer placed with the oats. Broad leaf weeds were controlled in both treatments using a commercial mixture of dicamba + MCPA (Dyvel®, BASF Canada, Mississauga, ON) at a rate of 92 and 397 g a.i. ha⁻¹, respectively.

A nested split plot randomized complete block design with two replications was used at each site. Each replication consisted of eight ranges of 30 subplots, where four of the ranges were cross seeded with tame oats and four were not (main plot). Within each replication, 20 subplots (10 subplots each over two ranges), formed 12 incomplete blocks, which were later employed in statistical modelling to adjust for within-replication environmental variation. Subplots consisted of two rows of wheat, 2 m long, 22.5 cm apart, planted at a rate of 250 seeds m⁻². Individual subplots were separated within ranges by an empty crop row, while ranges were separated by a 2-m pathway.

Data Collection

Data recorded for each subplot included early-season vigour, plant height, number of spikes m⁻², grain yield, harvest index, and days from seeding to heading, anthesis, and physiological maturity. Proportion of light captured was recorded for the non-competition treatment only and oat grain yield was recorded for the competition treatment.

Early season vigour was rated visually at the three- to four-leaf stage, which is Zadok's growth stage 13 to 14 (Zadoks et al. 1974), using a 1 to 5 scale based on plant leaf size, number, and overall plant growth habit, with 1 being the least vigorous and 5 the most (Mason et al. 2007b). Spikes m⁻² was determined by counting fertile stems from a 0.5-m length of the two subplot rows. Days to heading was recorded when approximately 75% of the plants in a subplot had spikes emerged from the boot. Likewise, days to anthesis was recorded when 75% of the plants had anthers extruded. Physiological maturity was determined visually as the number of days from seeding to when 75% of the peduncles in a subplot had lost green colour.

A 0.5-m length of the two crop rows was cut near ground level after physiological maturity and each plot was collected into labelled cotton bags. Both wheat and oats were cut and collected in the weed competition treatment. Samples were dried, weighed and threshed to

calculate harvest index and yield. Samples from the weed competition treatment were first separated by crop before weighing and threshing each crop.

Photosynthetically active radiation levels were recorded for the non-competition subplots using a LI-COR LI-191SA Line Quantum Sensor (LI-COR Biosciences, Lincoln, NE). After heading was complete, from Zadok's growth stages 58 to 69 (Zadoks et al. 1974), the sensor was held level between the two rows at ground level and above the subplot with photosynthetically active radiation recorded in $\mu\text{mol s}^{-1} \text{m}^{-2}$. The proportion of light captured was calculated as:

$$\text{Light Captured} = 1 - \frac{\text{PAR Below Canopy}}{\text{PAR Above Canopy}} \quad (1)$$

Data Analyses

All data were analysed using the MIXED procedure of SAS v9.1 (SAS Institute, Inc. 2003). Each environment (site $\times$ year) was subjected to analysis of variance in the mixed model by considering competition as fixed effect and genotype and genotype $\times$ competition as random effects. All multi-location-year data were then subjected to a combined analysis of variance as a mixed model by considering competition as the fixed effect and genotype, environment, genotype $\times$ competition, genotype $\times$ environment, competition $\times$ environment, genotype $\times$ competition $\times$ environment, rep(environment), and incomplete-block(rep $\times$ environment) as random effects. Best linear unbiased predictions (BLUPS) were then estimated for genotype $\times$ competition, across environments, using the estimate statement in the MIXED procedure (Littell et al. 2006).

These BLUP values were used to calculate population means, 95% confidence limits, and observed response to a 10% selection intensity for each environment. The observed response to selection was estimated as the difference between the mean of the selected lines and the population mean. Significance between the two means was determined using PROC TTEST in SAS (SAS Institute, Inc. 2003). Least-square mean values of genotype $\times$ competition were calculated for the check cultivars for comparison of means, and 95% confidence limits. The terms in the model were the same for the check cultivars as for the random genotypes, except that genotype and genotype $\times$ competition were considered fixed effects for the check cultivars.

For analyses requiring a separation of competition treatments (heritabilities, and genetic correlations) a random model of genotype, genotype $\times$ environment, rep(environment), and incomplete-block(rep $\times$ environment) was used. Random effects estimated to have zero variance were removed from the model for the specific trait being analysed.

Broad sense heritabilities were then estimated for each trait across environments, with and without competition, using:

$$H = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2 + \sigma_e^2} \quad (2)$$

where σ_G^2 , σ_{GE}^2 , and σ_e^2 are the genotype, genotype $\times$ environment, and error variances, respectively. The standard errors of the heritabilities were calculated using the delta method (Holland et al. 2003). Expected genetic gain was estimated as:

$$R_e = iH\sigma_p \quad (3)$$

where σ_p is the phenotypic standard deviation, H is the broad sense heritability and i is the selection intensity (1.755 for 10% selection) (Falconer and Mackay 1996).

Genetic correlations were calculated for all traits within and between competition treatments using:

$$r_{Gij} = \frac{\text{Cov}_{Gij}}{\sigma_{Gi}\sigma_{Gj}} \quad (4)$$

(Bernardo 2002), where r_{Gij} is the genetic correlation between the i th and j th traits, Cov_{Gij} is the genotypic covariance between the i th and j th traits, σ_{Gi} , and σ_{Gj} are the genetic standard deviations of the i th and j th traits, respectively. Environmental correlations were calculated within and between competition treatments using environmental variance and covariance in Eq. 4. Variance and covariance were estimated using restricted maximum likelihood in the MIXED procedure, and the standard errors of the correlations were calculated via the delta method (Holland 2006). For each correlation, 95% confidence intervals were constructed as $r_{gij} \pm z_{(0.05)}\sigma_e$ where r_{gij} is the correlation coefficient, $z_{(0.05)}$ is the ordinate of the standard normal distribution such that the area under the curve from $-\infty$ to $z_{(0.05)}$ equals $1 - 0.05$, and σ_e is the standard error of the correlation. Correlations were considered significantly different from zero if the confidence interval did not include zero (Holland et al. 2003). The differences between correlation coefficients of interest were considered significant where $z_{(0.05)} < (r_1 - r_2)/\sigma_{r_1 - r_2}$ (Zar 1996).

RESULTS

The check cultivars, on average, yielded 22–30% more grain, had greater early-season vigour, and flowered and matured earlier ($P < 0.05$) than the experimental population (Table 2). The presence of a cultivated oat weed analogue in the experimental population furnished an adequate selection screen as a competition treatment, in that the weed analogue treatment reduced grain yield (1.64 t ha^{-1}), spikes m^{-2} (25%) and days to maturity (2 d) ($P < 0.05$) in the random population (Table 2).

Heritability estimates were similar ($P > 0.05$) with and without weed competition for all recorded traits except plant height ($P < 0.01$) (Table 2). Observed response to a 10% selection intensity differed ($P < 0.05$) from the population mean for all measured traits, in both treatments. Observed response to selection was greater ($P < 0.01$) in the weed-free treatment for grain yield, spikes m^{-2} , early-season vigour, days to heading and grain fill duration. As well, environmental correlations between competition treatments for grain yield, spikes m^{-2} , early season vigour, and harvest index were all strong ($r > 0.7$) (Table 3).

For the genetic correlations, grain yield and spikes m^{-2} were not related to early-season vigour in the weed-free treatment ($P > 0.05$), but were in the weed analogue treatment ($P < 0.01$) (Table 4). The proportion of light captured was positively related to grain yield, plant height, and spikes m^{-2} , but not to early-season vigour. Oat grain yield was negatively related to wheat grain yield and spikes m^{-2} , but the correlation was stronger ($P < 0.05$) in the weed analogue treatment. Flowering times were also negatively related to grain yield and spikes m^{-2} in the presence of oats, but not in the weed-free treatment ($P < 0.01$) (Table 5).

The population genotypes were ranked for all recorded traits in both competition treatments. There was very little rank change for plant height, early-season vigour, grain fill duration, and days to maturity in the top 10% of ranked lines (Fig. 1). Many of the highest yielding lines in the non-competitive treatment also yielded highly under competition, and though there was some genotypic rank change, the two highest yielding lines were the same for both competition treatments (Fig. 1). However, lines with the lowest oat grain yield were not among the top 10% of lines for yield.

DISCUSSION

The check cultivars in this study yielded higher, tillered more, and flowered earlier than the ITMI recombinant inbred line population. This was expected because many of the check cultivars used are locally adapted, whereas the ITMI population is not. Even so, the heritability estimates we report are the same between competition treatments for all traits except plant height. These results differ from those of Fasoula and Fasoula (1997) and Zhao et al. (2006b) who reported decreased heritability estimates under competition. For yield, the actual yield of the recombinant inbred line population, and subsequent selection response, was lower under competition than in the weed-free treatment, but the percent increase was higher.

The similar ranking of lines and the similar heritability estimates suggest that selection in a weed-free environment may provide advancement in a weedy environment. The use of a weed-free environment for selection has been suggested for rice (Zhao et al. 2006c). However, while there was some overlap in selected lines,

Table 2. Mean values, 95% confidence intervals (CI), estimates of heritability and selection response (SR) for 10 traits measured on 108 lines of the ITMI population and on 12 spring wheat check cultivars grown in four environments with (C) and without (N) weed analogue competition during 2005–2006. Treatment means, heritabilities, and selection response were tested for equality between treatments using T-tests

Variable		Non-competition		Competition		Heritability estimates		SR _e ^z		SR _o ^z	
		Mean	95% CI	Mean	95% CI	N ^y	C	N	C	N	C
Grain Yield (t ha ⁻¹)	Lines	4.87**	0.18	3.23**	0.15	0.42 (0.05) ^x	0.42 (0.05)	1.22	0.77	1.73**	1.31**
	Checks	6.25**	0.58	4.62**	0.37	— ^w	—	—	—	—	—
Height (cm)	Lines	79	1.2	81	1.2	0.73 (0.03)**	0.58 (0.04)**	10	8	11	11
	Checks	81	5.2	81	4.4	—	—	—	—	—	—
Spikes m ⁻² (<i>n</i>)	Lines	446**	9.0	335**	8.0	0.33 (0.04)	0.29 (0.04)	53	42	84**	75**
	Checks	557**	69.1	471**	43.7	—	—	—	—	—	—
Early season vigour	Lines	3.3	0.1	3.2	0.1	0.42 (0.05)	0.47 (0.05)	0.6	0.7	0.9**	0.8**
	Checks	4.2	0.2	4.1	0.3	—	—	—	—	—	—
Days to heading	Lines	54	0.7	54	0.7	0.91 (0.01)	0.90 (0.01)	−6	−6	−5**	−6**
	Checks	51	1.5	50	1.5	—	—	—	—	—	—
Days to anthesis	Lines	57	0.7	57	0.7	0.89 (0.02)	0.84 (0.02)	−6	−6	−5	−5
	Checks	54	1.6	53	1.7	—	—	—	—	—	—
Days to maturity	Lines	100*	1.0	98*	1.0	0.77 (0.03)	0.78 (0.03)	−8	−7	−9	−8
	Checks	95	3.6	94	3.5	—	—	—	—	—	—
Grain fill duration (d)	Lines	42**	0.5	41**	0.4	0.44 (0.05)	0.31 (0.05)	3	2	5**	4**
	Checks	41	2.3	41	2.1	—	—	—	—	—	—
Harvest index	Lines	0.42	0.01	0.42	0.01	0.40 (0.04)	0.39 (0.05)	0.07	0.06	0.11	0.11
	Checks	0.52	0.03	0.51	0.02	—	—	—	—	—	—
Proportion of light captured	Lines	0.86	0.01	—	—	0.24 (0.05)	—	0.05	—	0.08	—
	Checks	0.86	0.06	—	—	—	—	—	—	—	—
Oat grain yield (t ha ⁻¹)	Lines	—	—	1.65	0.06	—	—	—	—	—	—
	Checks	—	—	1.09	0.17	—	—	—	—	—	—

^zSR_e, expected response from 10% selection; SR_o, observed response from 10% selection.

^yN, non-competitive treatment. C, competitive treatment.

^x Standard error of the heritability estimate.

^w—, Not estimated.

*, **Significant at *P* = 0.05 and *P* = 0.01 respectively (T-Test).

Table 3. Environmental correlations (r_{env}) between treatments for traits measured in competitive and non-competitive environments

Trait	r_{env}
Grain yield	0.74
Plant height	0.96
Spikes m^{-2}	0.79
Early season vigour	0.95
Harvest index	0.76
Days to heading	0.99
Days to anthesis	0.99
Days to maturity	0.97
Grain fill duration	0.90

our results suggest that the use of a weed-free environment would result in discarding some lines which yielded better under competition.

The complexity of competitive ability itself does not allow for direct selection as it cannot be explained by a single trait (Lemerle et al. 1996). Oat competition in this experiment reduced wheat yield, which has been reported previously (Harker 2001). Defining competitive ability as decreased yield loss under weedy conditions puts breeding for it on familiar ground, i.e., single trait selection, without removing the possibility for weed suppression (Huel and Hucl 1996; Lemerle et al. 2001b). However, in this study, the two top-yielding lines were the same for both treatments, but these lines were not among the top 10% of lines for reduced oat yield.

We found a strong negative relationship between wheat grain yield and oat grain yield, but the correlation alone does not provide an explanation of the underlying mechanisms involved (Fasoula and Fasoula 1997; Mason and Spaner 2006). Light capture is considered an important aspect of competitive success with other competitive traits often related to the increased capture of light (Coleman et al. 2001; Cousens et al. 2003b; Harbur and Owen 2004). In this study, light capture measured in the weed-free treatment was negatively related to oat grain yield, suggesting that lines able to capture more light may be more competitive. Measuring light capture in a weedy environment is not practical (Park et al. 2003), but the trait, though difficult to measure directly, can still confer a competitive advantage (Harbur and Owen 2004).

Tillering capacity is one of the more plastic traits in wheat, and genotypes with a higher tillering capacity are considered more competitive (Hucl and Baker 1993) though this is still debated (Mason et al. 2007a). We found a positive relationship between spikes m^{-2} and grain yield under competition and a negative relationship between spikes m^{-2} and oat yield. Interestingly, early-season vigour was related to increased wheat grain yield and spikes m^{-2} under competition only and also negatively related to oat grain yield. Rapid early growth is associated with competitive ability (Huel and Hucl 1996; Lemerle et al. 2001a). The near simultaneous emergence of the oats and wheat in this study may

Table 4. Genetic correlations ($P < 0.05$) made within and between competitive treatments for six agronomic traits measured on 108 lines of the ITMI population for four locations in Alberta, Canada

		Grain yield		Plant height		Spikes m^{-2}		Early season vigour		Harvest index		Light capture	
		N ^z	C	N	C	N	C	N	C	N	C	N	C
Plant height	N	0.31	0.31										
	C	0.29	0.26										
Spikes m^{-2}	N	0.42	0.42	NS ^y	NS								
	C	0.43	0.61	NS	NS								
Early season vigour	N	NS	0.44	NS	NS	NS	0.61						
	C	NS	0.48	NS	NS	NS	0.68	NS	NS				
Harvest index	N	0.75	0.65	NS	NS	NS	NS	NS	NS	NS	NS		
	C	0.66	0.57	-0.24	-0.24	NS	NS	NS	NS	NS	NS	NS	NS
Light capture	N	0.67	0.47	0.53	0.45	0.77	0.38	NS	NS	NS	NS	NS	NS
	C	-0.33	-0.75	-0.24	NS	-0.36	-0.89	-0.77	-0.78	NS	NS	-0.58	-0.58

^zN, non-competitive treatment. C, competitive treatment.

^yNS, not significantly different from zero ($P=0.05$).

Table 5. Genetic correlations made within and between competitive treatments using the 108 lines of the ITMI population for four locations in Alberta, Canada. Six agronomic traits and oat grain yield are correlated to flowering times and grain fill duration

		Days to heading		Days to anthesis		Days to maturity		Grain fill duration	
		N ^z	C	N	C	N	C	N	C
Grain yield	N ^z	NS ^y	NS	NS	NS	NS	NS	NS	NS
	C	−0.33	−0.35	−0.39	−0.38	−0.27	−0.35	NS	NS
Plant height	N	0.33	0.34	0.26	0.30	0.30	0.28	0.25	NS
	C	0.32	0.32	0.25	0.28	0.27	0.25	0.22	NS
Spikes per m ²	N	NS	NS	NS	NS	NS	NS	NS	NS
	C	−0.56	−0.57	−0.62	−0.62	−0.54	−0.61	−0.29	−0.41
Early season vigour	N	−0.84	−0.85	−0.86	−0.86	−0.83	−0.9	−0.57	−0.71
	C	−0.86	−0.88	−0.86	−0.85	−0.89	−0.93	−0.67	−0.79
Light capture	N	0.44	0.42	0.30	0.30	0.36	0.36	NS	NS
Oat grain yield	C	0.64	0.66	0.70	0.69	0.60	0.64	0.30	0.32

^zN, non-competitive treatment; C, competitive treatment.

^yNS, not significantly different from zero ($P=0.05$).

highlight the importance of early season vigour to wheat competitive ability, because cultivated oats have a high suppressive ability during early growth (Seavers and Wright 1999). Rapid early growth in wheat could increase light capture, conferring a competitive advantage (Coleman et al. 2001; Harbur and Owen 2004), but a relationship between rapid early growth and light capture was not observed in this study.

In addition, we found the flowering times and maturity of wheat were negatively correlated with wheat grain yield under competition and positively correlated with oat grain yield. Early-maturing wheat has been correlated with increased yield in competitive organic farming systems (Mason et al. 2007b) and early heading

associated with competitive ability (Huel and Huel 1996). Flowering in wheat is influenced by photoperiod, vernalization, and earliness per se genes (Iqbal et al. 2006). Cousens et al. (2003a) reported reduced time to flower did not increase competitive ability. This study supports the idea of early-maturing wheat aiding in both the suppressive and tolerant aspects of competitive ability in wheat, but how flowering times assist in the suppression of weeds is still not clear (Mason et al. 2007a).

In this study, similar heritability estimates between competition treatments suggest that selection in a weed-free environment can lead to improvements in a weedy environment, but some high-yielding lines under competition would be eliminated during selection. Use of a weed-free environment allows for the selection of traits that cannot be measured in a weedy environment, e.g., light capture. Early-season vigour and early maturity both help wheat escape the negative effects of weed pressure in a northern grain-growing region. Our study is somewhat limited, as it cannot be related to field-scale crop competitive conditions owing to the small plot size employed. A similar study using a population derived from locally adapted cultivars employing a larger plot size is warranted.

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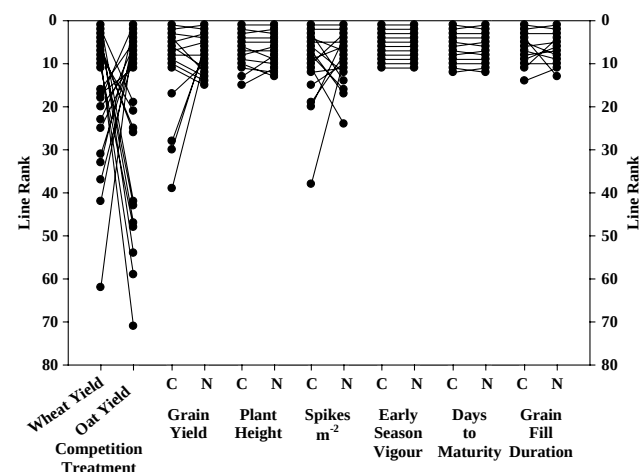


Fig. 1. Genotypic rank changes observed in the top 10% of lines ranked under each treatment condition (C, competitive treatment; N, non-competitive treatment) for selected traits measured in both treatments and between wheat yield and oat yield suppression in the competition treatment. Rank was assigned according to the desired direction of selection (e.g., rank 1 for grain yield was the highest yielding whereas rank 1 for oat yield was the lowest yielding).

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