Should spring wheat breeding for organically managed systems be conducted on organically managed land?

Todd A. Reid · Rong-Cai Yang · Donald F. Salmon · D. Spaner

Received: 1 December 2008/Accepted: 23 April 2009/Published online: 10 May 2009 © Springer Science+Business Media B.V. 2009

Abstract Organic spring wheat (Triticum aestivum L.) producers in the northern Great Plains use cultivars which have been bred for conventional management systems or heritage cultivars released before the widespread use of synthetic fertilizers and pesticides. To investigate the feasibility of organic wheat breeding and to determine common genetic parameters for each system, we used a random population of 79 F₆derived recombinant inbred sister lines from a cross between the Canadian hard red spring wheat cultivar AC Barrie and the CIMMYT derived cultivar Attila. The population, including the parents, was grown on conventionally and organically managed land for 3 years. Heritability estimates differed between systems for 6 of the 14 traits measured, including spikes m^{-2} , plant height, test weight, 1,000 kernel weight, grain protein, and days to anthesis. Direct selection in each management system (10% selection intensity) resulted in 50% or fewer lines selected in common for nine traits, including grain yield, grain protein, spikes m^{-2} , and grain fill duration. The results of this study suggest that indirect selection (in

T. A. Reid · R.-C. Yang · D. Spaner (⊠) Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, AB T6G 2P5, Canada e-mail: dean.spaner@ualberta.ca

D. F. Salmon

conventionally managed trials) of spring wheat destined for organically managed production would not result in the advance of the best possible lines in a breeding program. This implies that breeding spring wheat specific to organic agriculture should be conducted on organically managed land.

Keywords Heritability · Organic breeding · Organic management · Quantitative genetics · Spring wheat

Abbreviations

Н	Heritability
BLUP	Best linear unbiased prediction
CIMMYT	International Maize and Wheat
	Improvement Center
NIR	Near-infrared Reflectance
PAR	Photosynthetically active radiation

Introduction

The term "organic agriculture" describes production systems that aim to promote and enhance agroecosystem health while discouraging the use of offfarm inputs. Globally, interest in organic agriculture is increasing due to concerns over a number of factors, including environmental health, agricultural sustainability, pesticide residues, human health, and input costs. Long term market projections indicate that the North American demand for organic products

Alberta Agriculture, Food, and Rural Development, Field Crop Development Centre, Lacombe, AB T4L 1W8, Canada

will continue to grow, eventually overtaking Europe to become the world's largest organic market (Sahota 2006).

Scientific research involving organic production systems is relatively limited. Long-term research relating to soil fertility and biology in various organic cropping systems has been conducted in Europe (Fleissbach et al. 2007; Gosling and Shepherd 2005; Mader et al. 2000), and to a lesser extent in the United States (Harris et al. 1994) and Canada (Entz et al. 2004). Interest in crop breeding and agronomic research for organic production is growing in Canada and the United States. Nonetheless, there are still very few published scientific reports relative to those concerned with conventionally managed cropping systems.

Researchers and farmers often cite weeds as one of the greatest impediments to organic crop production (Barberi 2002; Degenhardt et al. 2005). Studies in Canada and elsewhere have reported higher weed populations, greater aboveground weed biomass, and a greater diversity of weed species in organic cereal crops than in their conventional counterparts (Entz et al. 2001; Leeson et al. 2000; Mason et al. 2007d). In a study of 32 Canadian spring bread wheat (Triticum aestivum L.) cultivars, increased weed abundance on organically managed land contributed to grain yield reductions of $\sim 40\%$ compared to yields on conventionally managed land (Mason et al. 2007d). Increasing crop competitive ability against weeds could be an effective strategy for controlling weeds and improving crop yields in organic grain production systems (Barberi 2002). Several research trials have found competitive ability to differ among wheat genotypes (Lemerle et al. 2001; Wicks et al. 1986), including cultivars registered in Canada (Huel and Hucl 1996; Mason et al. 2007a).

Several research trials have identified plant traits associated with increased competitive ability in wheat, the most compelling of which may be increased plant height (Cousens et al. 2003; Mason et al. 2007a). In contrast, global wheat breeding efforts over the past 50 years have largely been aimed at increasing grain yield, leading to the introduction of height-reducing (*Rht*) genes and the subsequent development of "semi-dwarf" cultivars. Semi-dwarf wheat cultivars exhibit reduced cell size, contributing to smaller root systems, shorter coleoptile lengths and/or smaller leaf areas than traditional cultivars (Gale and Youssefian 1985; Vandeleur and Gill 2004). Thus, semi-dwarf cultivars may not be well-suited for out-competing weeds. Greater yield losses (Cousens et al. 2003) and less weed suppression (Mason et al. 2007b) have been reported in semi-dwarf wheat cultivars under weed competition compared to conventional height cultivars. In Canada, the use of semi-dwarf wheat cultivars is increasing. The semi-dwarf cultivar Superb (released in 2003, Secan 2006) is currently the most widely grown cultivar, representing close to one-fifth of the prairie wheat area only 3 years after its release (CWB 2007).

Other plant traits such as crop biomass, ground cover, flag leaf length, tillering capacity and early season growth were reported to be associated with competitive ability in wheat genotypes from around the world (Hucl 1998; Huel and Hucl 1996; Lemerle et al. 1996). However, these studies were conducted in controlled environments, where plant responses to competition may differ from natural or native conditions. Our research (conducted on organically managed land in central Alberta) suggests that tall plants, fast early season growth, early heading and maturity, and a greater number of fertile tillers are important competitive plant traits for organic environments, where aboveground weed biomass is typically higher and soil fertility is more variable (Mason et al. 2007a; Mason et al. 2007d).

The selection of cultivars for low-input and/or organic environments has not been a priority of past breeding programs. Ceccarelli (1996) suggested that breeders justify selection under optimum conditions because greater environmental variability of low-input conditions reduces heritability. Nevertheless, there have been reports of similar rankings for disease resistance and quality traits in conventional and organic cropping trials (Mader et al. 2000; Mason et al. 2007c), and similar heritability estimates between systems in maize (*Zea mays* L.) (Burger et al. 2008).

The reduction in environmental variability through the widespread use of chemical inputs means individual cultivars can be successful over a large geographic area (Wolfe et al. 2008). In a review, Wolfe et al. (2008) reported that the selection of some traits are similar between organic and conventional breeding programs, but some more complex traits are specific to organic management. For example, Baresel et al. (2008), reported genetic variability in the nitrogen use efficiency of winter wheat. They suggested that cultivars with improved nitrogen uptake during early growth stages, and subsequent efficient translocation, would be more adapted to the timing of nitrogen mineralization on organically managed soils.

Banziger and Cooper (2001) suggested that cultivars developed through formal crop breeding have not been adopted for low-input conditions because few programs have focused on low-input conditions. They further reported that optimally managed onstation experimental trials may be used for assessing highly heritable qualitative traits such as grain size, texture, colour or maturity, but that they would not be useful for most quantitative traits (hence most important agronomic traits) affected by genotype by environment interactions. Our initial studies (e.g. Mason et al. 2007d) provide some evidence of the existence of genotype by environment interaction between organic and conventional conditions.

The applicability to organic agriculture of trials conducted under conventional conditions is questionable. Several studies have reported differences in the performance of wheat cultivars in organic and conventional management systems, with some cultivars better suited to organic management in northern North America (Carr et al. 2006; Mason et al. 2007d; Nass et al. 2003). Murphy et al. (2007) reported that selecting for yield under organic management resulted in genotypic ranks different from conventional management. Przystalski et al. (2008) reported high genetic correlations between management systems, but they identified specific cultivars which exhibited cross-over interactions between systems. They concluded that selection of cultivars should be conducted under conditions which closely match commercial organic farms and should include traits important to organic farmers.

The objective of the present study was to determine if a breeding population of spring wheat exhibited different heritabilities and/or other genetic parameters for agronomic traits under conventionally and organically managed agricultural systems. We were further interested in determining whether selection results would be different between systems.

Materials and methods

A randomly derived recombinant inbred population was created from a cross between the spring wheat cultivar AC Barrie and the CIMMYT spring wheat cultivar Attila. AC Barrie is an awnless, high yielding, high protein, hard red spring wheat (CWRS) cultivar (McCaig et al. 1996) and was the most commonly grown spring wheat cultivar on the Canadian Prairies in the 1990s. Results from the Western Canadian cooperative tests show AC Barrie to be lodging resistant, medium height (93 cm), high yielding (4.05 t ha^{-1}) with high protein (14.0%) and average maturity (108 days) (McCaig et al. 1996). Attila is an awned semi-dwarf bread wheat cultivar widely grown in Southeast Asia (Rosewarne et al. 2008). The 2004 CIMMYT international bread wheat trials report Attila to be high yielding (5.34 t ha^{-1}) and semi-dwarf (84 cm) with average maturity for the regions tested (135 days) (CIMMYT 2008). The original population consisted of 79, F₄ derived F₆ genotypes, which were advanced to F₄ by single seed descent. The population and the two parents were planted in double head rows the year prior in order to multiply seed for experimental use.

The experimental study was conducted from 2005 to 2007 at the University of Alberta Edmonton Research Station (ERS), Edmonton, AB, Canada (53° 34'N, 113° 31'W), with the conventionally managed site less than 1 km from the organically managed site. Different areas at each site were used in subsequent years, in keeping with the research station crop rotation. Plots were seeded on May 6th, 5th, and 14th, on the conventional site and on May 30th, June 1st, and May 24th, on the organic site for 2005, 2006 and 2007, respectively.

On the conventional site, granular fertilizer (11-52–0: N–P₂O₅–K₂O) was banded with the seed during sowing, at a rate of 140 kg ha⁻¹, and broad leaf weeds were controlled using Dyvel[®] (BASF Canada, Mississauga, ON) at a rate of 1.1 l ha⁻¹. No fertilizers or herbicides have been used on the organically managed site since 1999. The 4 year rotation on the conventional site consisted of canola research plots, field pea, triticale/field pea mixture, and cereal research plots. The 3 year rotation on the organic site consisted of barley, triticale/field peas, and cereal research plots. Composted dairy manure had been applied to the organic field in the fall of each year prior to the start of this study, but was not applied during the years of the study because soil nutrient levels were adequate according to soil tests (optimal in 2006, only nitrogen was marginal in 2007) (data not shown). Soil at both sites is classified as Black Chernozemic, which is

typical of central Alberta (Alberta Agriculture Food and Rural Development 2002). Weather data for Edmonton, for each year, were obtained from the Environment Canada data archive at the conclusion of the study (Environment Canada 2008). Plots were seeded with 250 seeds m^{-2} in a randomized complete block design within each management system. In 2005, because of seed limitations, two blocks were grown in the two trials grown that year, and plots were 2 m long by four rows with 23.5-cm row spacing. Three blocks per trial were planted in subsequent years and plot size increased to six rows of 4 m length with similar row spacing.

Data collection

Data recorded for each plot included early season vigour, plant height, number of spikes m^{-2} , grain yield, 1,000 kernel weight, kernels spike⁻¹, test weight, harvest index, grain protein, flag leaf area, weed biomass, and days from seeding to anthesis, and physiological maturity.

Early season vigour was rated visually at the three to four leaf stage, (Zadok's growth stage 13-14) (Zadoks et al. 1974), using a one to five scale based on plant leaf size, number, and overall form, with one being the least vigorous (Mason et al. 2007d). Spikes m⁻² was determined by counting fertile stems from a randomly chosen 0.5 m length of the centre two plot rows. Grain protein content (%) was determined using Near-infrared Reflectance (NIR) spectroscopy using a Monochromator NIR Systems model 6500 (NIRSystems, Inc., Silver Springs, MD, USA). Flag leaf area was recorded using an LI-3000A portable area meter (LI-COR Biosciences, Lincoln, NE) with five different flag leaves selected at random and the mean area recorded. To estimate weed suppressive ability, weed biomass was sampled at wheat physiological maturity from a 625 cm² area of the plot. The weed samples were dried for 3 days at 50°C and dry weight was recorded.

The confounding effect of the natural weed population in organic trials meant three traits (leaf area index, mean tip angle, and light capture) were recorded only in conventionally managed trials. Leaf area index and mean tip angle were recorded with an LAI-2000 Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, NE). Photosynthetically active radiation (PAR) was recorded using a LI-COR LI-191SA Line Quantum Sensor (LI-COR Biosciences, Lincoln, NE). The sensor was held in the centre of a plot, at ground level and above the canopy, with PAR recorded in μ mol s⁻¹ m⁻². The proportion of light captured was calculated as:

$$Light capture = 1 - \frac{PAR below canopy}{PAR above canopy}$$
(1)

Days to anthesis were recorded when 75% of the plants had anthers extruded. Physiological maturity was determined visually as the number of days from seeding to the point in time when 75% of the peduncles in a plot had lost green colour. Grain fill duration was then calculated as the time from anthesis to physiological maturity.

Statistical analysis

All data were analysed with the MIXED procedure of SAS v9.1 (SAS[®] Institute 2003). The experimental trials were initially analysed separately, with block and genotype considered random. Thereafter, for the purposes of comparing genetic parameters within the two management systems, all six site-years (environments) were considered as one experiment. Each year was considered to be a complete block comprised of replications within each block and the experiment was replicated in time (over years). The data were thus analysed as a split plot, with the fixed effect of management system considered the whole plot, and the random effect of genotype considered the subplot. The data were modeled to:

$$y_{ijk} = \mu + M_i + Y_j + MY_{ij} + G_k + GM_{ik} + GY_{jk}(M_i) + \varepsilon_{ijk}$$
(2)

where M, Y, and G are the management system, year, and genotype, respectively. Only management was considered a fixed effect for the model. The parental cultivars were analysed with the same model, but both management and genotype along with their interaction, were considered fixed effects. For instances where a term resulted in a zero variance estimate, the term was removed from the model. Estimates of variance for the within block replications were always zero and thus are not presented in the model above.

Heritabilities were estimated for each trait pooled over environments, for both organically and conventionally managed environments separately. The variance components were estimated using:

$$y_{ijk} = \mu + E_i + R_j(E_i) + G_k + GE_{ik} + \varepsilon_{ijk}$$
(3)

where E, R, and G are the environment, replicate, and genotype, respectively. Broad sense heritability was then calculated on a plot basis using:

$$H = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2 + \sigma_e^2} \tag{4}$$

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

$$R_e = iH\sigma_{\rm P} \tag{5}$$

where $\sigma_{\rm P}$ is the phenotypic SD, *H* is the broad sense heritability and *i* is the selection intensity (1.755 for 10% selection) (Falconer and Mackay 1996).

Best linear unbiased predictions (BLUPs) were then estimated for genotypes across environments, using the estimate statement in the MIXED procedure (Littell et al. 2006). These were used for estimating observed response to selection for the population, and to calculate Spearman rank correlations using the Spearman option of the CORR procedure in SAS v9.1 (SAS[®] Institute 2003). Best linear unbiased predictions were also estimated separately for the genotypes for each environment and each management system. These BLUPs were used to construct histograms, which were fitted with a three parameter Gaussian curve, to approximate the population distribution using SigmaPlot 10.0 (Sigmaplot 2006).

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

$$r_{Gij} = \frac{\text{Cov}_{Gij}}{\sigma_{Gi}\sigma_{Gj}} \tag{6}$$

(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 SDs of the *i*th and *j*th traits, respectively. Prior to calculating the correlations, data were standardized within management system and year, to minimize differences in scale between traits (Zar 1996), using:

$$Z = \frac{X_i - \mu}{\sigma} \tag{7}$$

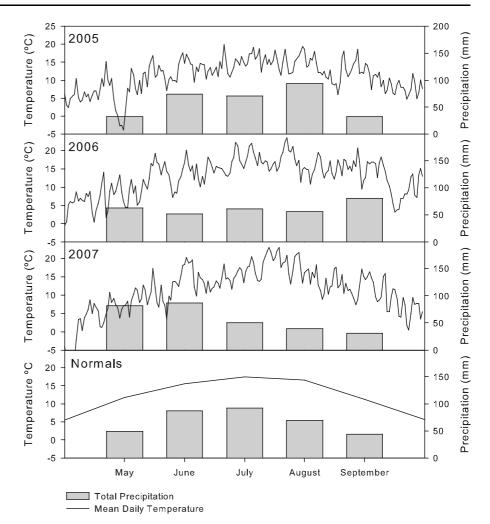
where Z is the standardized data point, X_i is the *i*th observation, μ and σ is the population mean and SD within each year and management system. Variance and co-variance were then estimated using restricted maximum likelihood in the MIXED procedure, and the SE of the correlations were calculated via 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 SE of the correlation. Correlations were considered significantly different from zero if the confidence interval did not include zero (Holland et al. 2003). Results are considered and reported as different only when P < 0.05.

Results

Temperature levels were consistent with normals for the area over the 3 years of the study. Highest temperatures occurred in late July and early August (Fig. 1). Water is the major limiting factor for agriculture production in central Alberta and rainfall over the three study years was variable (Fig. 1), but consistent with normal rainfall patterns. Nevertheless, the month with the highest average rainfall is normally July, which was not the case for any of the years in this study.

On average, the parental genotypes AC Barrie and Attila yielded less grain with greater protein content under organic than under conventional management (Table 1). In the conventional system, AC Barrie had similar grain yield, had 30% more spikes m^{-2} , was 15 cm taller and had 10% greater protein content than Attila. In the organic system AC Barrie had 28% greater yield, had similar spikes m^{-2} , was 17 cm taller, and had 5% greater protein content than Attila.

Each year on average, the AC Barrie × Attila population yielded less grain under organic than under conventional management (P < 0.01). However, in conventional management, the population distributions were narrower, and were less variable over years (Fig. 2). In 2006, decreased precipitation Fig. 1 Weather data from the Edmonton International Airport for each year of the experiment and the 40 years normal for the months of the growing season. Data obtained from the Environment Canada weather data archive (Environment Canada 2008)



after planting on the organically managed land created increased weed pressure (data not shown) which reduced wheat growth and yield. In 2007, the organic plots had low weed competition (data not shown) which resulted in increased growth and yield for the organic wheat. Interestingly, Attila consistently yielded less grain than AC Barrie in organically managed trials while the reverse was true under conventional management. In contrast to grain yield, the population distributions for protein content were similar between systems (Fig. 3).

Conventionally managed trials, on average, yielded double the amount of grain, and with less recorded weed biomass, than organic trials (Table 1). No other traits differed statistically between the systems. The ranges of measured variables tended to be greater in conventional with the exception of harvest index, weed biomass, and flowering times (Table 1). The experimental population exhibited statistically similar heritability estimates for grain yield, kernels spike⁻¹, harvest index, flag leaf area, weed biomass, early season vigour, days to maturity, and grain fill duration under both management systems (Table 2). Lower heritability estimates occurred in the organic system for spikes m⁻², plant height, test weight, thousand kernel weight, and protein content, whereas days to anthesis had a higher heritability estimate under organic management (Table 2). Five traits had different observed responses to selection (kernels spike⁻¹, harvest index, weed biomass, days to maturity, and grain fill duration), with no observed difference in heritability estimates between systems for those traits.

Spearman rank correlations were high (>0.70) between the systems for seven of the measured traits (Table 3). Grain yield (0.33), early season vigour

Variable	AC Barrie ^a		Attila ^a		Diff. between parents ^b		Population mean ^a		SE of diff.	Conventional		Organic	
	Conv ^c	Org	Conv	Org	Conv	Org	Conv	Org		Min	Max	Min	Max
Grain yield (t ha ⁻¹)	4.54*	2.68*	4.83**	2.09**	-0.29	0.59*	3.88*	1.85*	0.67	4.19	5.22	1.80	2.63
Spikes m ⁻²	536	322	414	336	122*	-14	454	343	83	387	520	303	396
Plant height (cm)	86	84	71	67	15*	17**	76	74	7.2	64	92	66	88
Test weight (kg hl ⁻¹)	81	79	81	77	0	2	80	76	2.5	76	82	73	79
Kernels spike ⁻¹	31	28	39**	32**	-8**	-4	40	32	3.0	32	48	25	39
1,000 kernel weight (g)	37*	40*	38	38	-1	2**	36	36	1.2	31	41	30	41
Harvest index (%)	45	45	49	42	-4	3	47	42	2.3	42	50	33	49
Flag leaf area (cm ²)	19	15	16	10	3	5	18	14	3.4	13	22	9	17
Grain protein (%)	14.1**	15.2**	12.8**	14.4**	1.3**	0.8**	13.0	14.8	0.58	11.6	15.1	13.7	16.1
Weed biomass (g m ⁻²)	0	10	1**	20**	-1	-10	1*	13*	3.5	0.2	2	12	16
Early season vigour	4	4	3	3	1	1*	3	3	0.1	3	4	3	3
Days to anthesis	59	53	58	53	1	0	59	53	3.3	56	63	48	58
Days to maturity	90	90	95	90	-5	0	94	92	3.5	88	100	85	101
Grain fill duration (days)	32*	37*	37	37	-5*	0	35	39	3.9	29	38	34	44
Leaf area index	2.93	d	2.44	_	0.49	-	2.58	-	_	1.75	3.73	_	-
Mean tip angle	60.7	_	58.5	_	2.25	-	59.0	-	_	50.1	65.9	-	-
Light capture	0.88	-	0.91	-	0.03	-	0.81	_	-	0.79	0.81	_	_

 Table 1
 Least square means of AC Barrie and Attila and the population derived from a cross between the two, grown under organic and conventional management in Edmonton, AB, Canada from 2005 to 2007, and the range of the population for 17 agronomic traits

^a Statistical differences tested between management systems

^b Statistical differences tested between AC Barrie and Attila

^c Conv Conventionally managed system, Org Organically managed system

^d Trait not measured in the organically managed system

*, ** Significant at P = 0.05 and P = 0.01, respectively

(0.26), and weed biomass (0.22) suppressive ability had the three lowest rank correlations between systems (Table 3). Direct selection in each management system (10% selection intensity) resulted in 50% or fewer lines selected in common for nine traits, including grain yield, and grain protein, (Table 3). If the top yielding eight lines (10%) of the population were selected from each management system (based on our results) one line would be in common. Selecting the top 12 (15%) and 16 (20%) lines based on yield resulted in four and eight lines in common, respectively. This suggests that selecting in the two management systems would result in large differences between systems for lines retained for further yield trials in a breeding program. The difference in the relative ranking of lines between systems was also large for other agronomically important traits (Table 3; Fig. 4).

Among yield components, grain yield was moderately correlated (0.4 < r < 0.8) with 1,000 kernel weight in organically managed land. Alternately, in conventionally managed land, grain yield was moderately correlated with kernels spike⁻¹ (Table 4). Spikes m⁻² was negatively correlated to kernels spike⁻¹ in both systems.

Heritability estimates for weed biomass suppressive ability, and early season vigour did not differ from zero in either conventionally or organically managed systems (Table 1). This suggests that the environmental and statistically unaccounted variation in weed biomass suppressive ability and compensation for increased weed biomass was far greater than the genotypic variation to suppress or withstand weed pressure. Perhaps as a result of this, under organic management, weed biomass levels were not correlated to any of the eight measured traits. However,

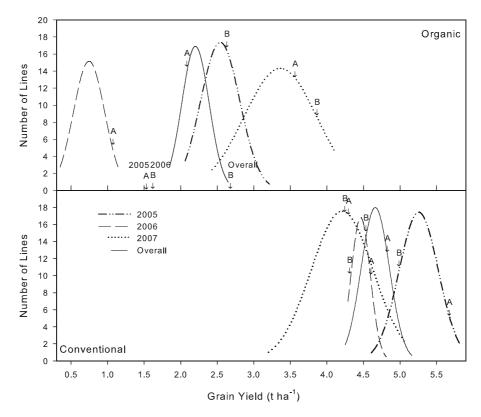


Fig. 2 Population distribution of grain yield for both management systems for each year and across years, with *arrows* showing the position of each parent (A Attila, B AC Barrie) for each distribution

under conventional management, weed biomass levels were negatively correlated with grain yield, plant height, test weight, and flag leaf area (Table 5). Days to maturity in organically managed trials was negatively correlated with grain yield, kernels spike⁻¹, and flag leaf area. In conventionally managed trials, the correlations were positive.

Three traits, measured only in conventional trials (leaf area index, mean tip angle, and light capture), were not correlated to grain yield under organic management. However, grain protein in organically managed land was correlated to light capture and leaf area index (Table 6).

Discussion

Our study employed an experimental wheat population at the developmental stage, within a single seed descent breeding program, where a preliminary yield trial would normally occur to select lines for replicated multi-location trials. To the best of our knowledge, there has been no direct comparison of a random recombinant inbred spring wheat breeding population between conventional and organic management in North America.

We found heritability estimates for various agronomic traits were either similar between the two systems or lower in the organic system (with one exception). This suggests that, at best, breeding under organic conditions would produce similar genetic gains to conventional breeding. Nevertheless, breeding directly within organically managed systems would result in lower genetic gains than on conventionally managed land for some traits. Burger et al. (2008) reported heritability estimates for yield that were similar between organic and conventional systems for populations of maize. Reduced heritability estimates were predicted for plants grown in competitive or stressful environments (Fasoula and Fasoula 1997), but there were exceptions to this under both artificially induced weed competition in spring wheat (Reid, unpublished data) and under imposed drought stress in rice (Bernier et al. 2007).

Fig. 3 Population distribution of grain protein

levels for both management systems for each year and across years, with *arrows* showing the position of each parent (*A* Attila, *B* AC Barrie) for each distribution

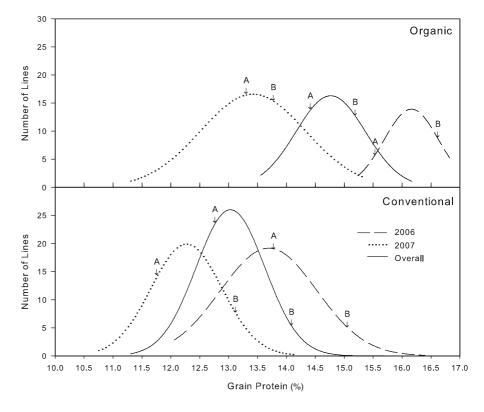


Table 2 Estimates of heritability, their SEs, and selection responses (SR) for 14 agronomic traits in a population derived from a cross between AC Barrie and Attila grown under

organic and conventional management in Edmonton, AB, Canada from 2005 to 2007 $\,$

Variable	Heritabilit	y estimate	(%)		SR_e^a		SR _o ^a		
	Conv ^b	SE ^c	Org ^b	SE	Conv	Org	Conv	Org	
Grain yield (t ha ⁻¹)	22	5	14	5	0.25	0.13	0.54	0.47	
Spikes m ⁻²	22**	5	4**	4	30	6	54**	35**	
Plant height (cm)	67**	4	43**	5	9	7	12	11	
Test weight (kg hl ⁻¹)	51**	5	26**	6	1.4	1.0	1.8	1.8	
Kernels spike ⁻¹	47	5	37	6	5	4	7*	5*	
1,000 kernel weight (g)	59**	5	39**	5	3	3	4	4	
Harvest index (%)	31	5	37	6	2	5	3**	6**	
Flag leaf area (cm ²)	36	5	32	6	11	9	3	3	
Grain protein (%)	62**	6	31**	8	0.83	0.45	1.1	0.8	
Weed biomass (g m ⁻²)	7	4	2	2	-0.13	-0.45	-0.3**	-0.9**	
Early season vigour	6	3	4	3	0.1	0.1	0.3	0.2	
Days to anthesis	37*	6	53*	5	-1	-3	-2**	-4**	
Days to maturity	35	5	44	5	-2	-4	-4*	-6*	
Grain fill duration (days)	21	6	27	5	1	2	3*	4*	

^a SR_e Expected response from 10% selection, SR_o observed response from 10% selection

^b Conv Conventionally managed system, Org Organically managed system

^c SE Standard error of the heritability estimate

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

Table 3 Spearman rank correlations (r_s) and the numbers of lines in common at three selection intensities, for 14 agronomic traits in a population derived from a cross between AC Barrie and Attila grown under organic and conventional management in Edmonton, AB, Canada from 2005 to 2007

Trait	Rank (r _s)	Lines selected in common						
		10% ^a (8) ^b	15% (12)	20% (16)				
Grain yield	0.33	1	4	8				
Spikes m ⁻²	0.63	4	7	8				
Plant height	0.86	7	9	10				
Test weight	0.70	3	6	9				
Kernel spike ⁻¹	0.75	3	5	11				
1,000 kernel weight	0.80	4	7	8				
Harvest index	0.63	3	5	7				
Flag leaf area	0.40	4	7	8				
Grain protein	0.77	4	6	6				
Weed biomass	0.22	2	3	4				
Early season vigour	0.26	0	3	5				
Days to anthesis	0.82	5	11	11				
Days to maturity	0.73	5	8	12				
Grain fill duration	0.57	2	4	6				

^a Selection intensity applied within each system

^b Maximum number of lines selected from the population of 79 lines at the given selection intensity (10, 15, 20%)

Direct selection in each management system (up to 20% selection intensity) resulted in 50% or fewer lines selected in common for nine traits, including economically important traits such as grain yield, grain protein, spikes m⁻², and grain fill duration. Of those nine traits, seven had Spearman rank correlations below 0.70. This suggests that selecting in the two management systems would result in large differences between systems for lines retained for further yield trials in breeding programs. The difference in the relative ranking of lines between systems was also large for other agronomically important traits. Loschenberger et al. (2008) recommended growing conventional and organic trials in parallel, on advanced breeding material, to obtain a more accurate analysis. In our study, observed response to selection did not differ between systems for traits with differing heritability estimates. This suggests that genetic gain may not differ between the two systems, but would be more difficult to predict under organic conditions. Over years, the mean and population distributions for grain yield were more variable in organic trials. Variable cultivar performance differences were observed between organic farms in Europe (Przystalski et al. 2008).

Nass et al. (2003) reported that AC Barrie performed well under organic management. Therefore,

Fig. 4 Genotypic ranks changes observed in the top 10% lines ranked under each management system (*O*: Organic; *C*: Conventional) for seven traits measured in both systems. Rank was assigned according to the desired direction of selection (e.g. rank one for grain yield was the highest yielding)

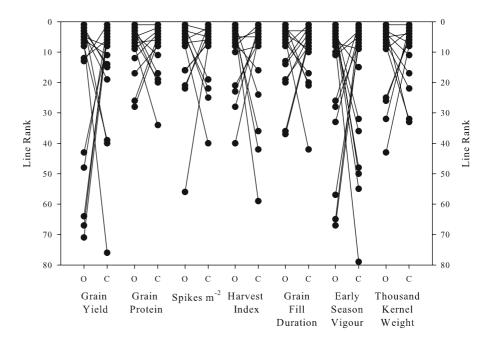


Table 4 Genetic correlations (r) for eight agronomic traits, calculated using data standardized within management system, measured in a population derived from a cross between AC

Barrie and Attila grown under organic and conventional management in Edmonton, AB, Canada from 2005 to 2007

	Grain yield	Spikes m ⁻²	Kernel spike ⁻¹	1000 Kernel weight	Plant height	Harvest index	Flag leaf area	Grain protein
Grain yield		_a	_	0.45	_	0.72	0.53	-0.38
Spikes m ⁻²	-		-0.94	_	-0.61	_	_	_
Kernel spike ⁻¹	0.33	-0.56		-	_	0.58	0.59	-0.91
1000 kernel weight	-	-	_		-	-	0.29	0.31
Plant height	0.27	-0.38	_	0.68		-0.44	_	_
Harvest index	-	_	0.33	-0.40	-0.65		0.71	-0.79
Flag leaf area	0.58	-0.41	0.42	-	0.53	-0.26		-0.55
Grain protein	-	_	-0.67	0.62	0.56	-0.60	-	

Values above the diagonal represent organically managed system; values below the diagonal represent conventionally managed system

^a Correlation not different from zero (P > 0.05)

Table 5 Genetic correlations (r) between eight agronomic traits and each of weed biomass, early season vigour, days to anthesis, days to maturity, and grain fill duration, all calculated using standardized data within management systems, measured

in a population derived from a cross between AC Barrie and Attila grown under organic and conventional management in Edmonton, AB, Canada from 2005 to 2007

	Grain y	yield	Plant height		Test w	eight	Kernel 1,000 kernel spike ⁻¹ weight		Harves	t index	Flag leaf area		Grain protein			
	Conv ^a	Org	Conv	Org	Conv	Org	Conv	Org	Conv	Org	Conv	Org	Conv	Org	Conv	Org
Weed biomass	-0.72	_ ^b	-0.52	-	-0.32	_	_	-	-	-	0.41	-	-0.45	-	-	-
Early season vigour	-	-	0.35	-	0.41	-	-0.61	-	-	0.81	-	0.42	-	0.49	0.83	-
Days to anthesis	0.57	-0.28	0.23	-	-	-	-	-	-	-	-0.55	-0.70	0.41	-0.57	-	0.31
Days to maturity	0.84	-0.28	-	-	-	-	0.41	-0.31	-	-	-	-0.74	0.53	-0.60	-	0.29
Grain fill duration	0.75	-	-	-	-	-	0.64	-0.40	-	-	-	-0.55	0.43	-0.43	-0.42	-

^a Conv Conventionally managed system, Org Organically managed system

^b Correlation not different from zero (P > 0.05)

AC Barrie was a logical choice as a parent to initiate breeding for organic agriculture. Parental selection is an important first step for breeding in organic systems (Wolfe et al. 2008). The introduction of height reduction genes is common in conventional wheat breeding (Worland and Snape 2001) and the population used in this study was segregating for height. Mason et al. (2007b) reported that semi-dwarf wheat

Table 6 Genetic and phenotypic correlations, between 17 traits measured in the conventionally managed system, and grain yield and grain protein measured in the organically managed system, calculated using data standardized within management system, on a population derived from a cross between AC Barrie and Attila grown under organic and conventional management in Edmonton, AB, Canada from 2005 to 2007

Conventional	Organic	grain yield	Organic grain protein			
	Genetic	Phenotypic	Genetic	Phenotypic		
Grain yield (t ha ⁻¹)	0.56	0.10	_ ^a	-		
Spikes m ⁻²	-	-	0.36	-		
Plant height (cm)	_	-	0.28	0.20		
Test weight (kg hl)	0.44	-	-	-		
Kernel spike ⁻¹	_	-	-0.72	-0.28		
1,000 kernel weight	-	-	0.53	0.25		
Harvest index (%)	0.29	0.18	-0.81	-0.27		
Flag leaf area (cm ²)	-	-	_	_		
Grain protein (%)	_	-0.13	1	0.47		
Early season vigour	-	0.08	0.47	-		
Weed biomass (g)	-0.43	-0.08	_	_		
Days to anthesis	_	-0.20	0.29	0.17		
Days to maturity	-	-	-	-		
Grain fill duration	-	-	-	-0.14		
Leaf area index	-	-	0.38	0.14		
Mean tip angle	-	-	-	-		
Light capture	-	-	0.90	-		

^a Correlation not different from zero (P > 0.05)

cultivars were not as competitive against weeds as tall cultivars. In this study, AC Barrie yielded higher in organic systems whereas Attila, a semi-dwarf cultivar, yielded more grain in the conventional system.

Weed biomass was much greater in the organic trials of this experiment. However, in our trials weed biomass suppressive ability and early season vigour were not heritable traits in both management systems. This could have resulted from inherent field variability, especially in an uncontrolled organic system. In the conventional system weeds were largely controlled through herbicide application, making genetic variation difficult to estimate. Higher weed biomass levels in organic systems were reported previously (Leeson et al. 2000). Different levels of natural weed pressure can affect which competitive traits are more important (Mason et al. 2007a). In this study, plant height was the most important trait for reducing weed biomass levels. This suggests that semi-dwarf wheats may not be appropriate for organic farming systems.

In this study selection based on nine traits resulted in few lines being commonly selected in between management systems even though six of those traits had similar heritabilities in both systems. The similar heritability estimates suggests there will be similar genetic gain in both systems, however, the selection of different lines between systems implies the genetic gain is being achieved though different paths. Breeding programs, whether in conventional or organic systems, do not make selections based on only one trait (Wolfe et al. 2008). Organic breeding will require selections based on traits specifically required for organic agriculture, and therefore selection in an environment requiring the expression of those traits (Loschenberger et al. 2008; Murphy et al. 2007; Przystalski et al. 2008).

The negative relationship between flowering time and grain yield under organic management in the present study suggests that earliness is an advantage in organic systems. This agrees with previous reports which concluded that earliness confers a competitive advantage to spring wheat in central Alberta (Mason et al. 2007d), even when seeding dates are the same (Reid, unpublished data).

Conclusions

The results of this study suggest that, for certain agronomic traits, variability in organic management systems may reduce the precision of genetic parameters commonly estimated in breeding programs. Therefore, prediction of potential gains from selection in organically managed fields is difficult; but direct selection should result in observable gains. This study demonstrated that selection in conventionally managed land for the purposes of developing cultivars for organic production does not result in the same genotypes being selected for each system for all traits. Based on the results of the study, we believe selection of spring wheat cultivars for organic production systems should be done on organically managed land. Creating a population from parents exhibiting different morphological and/or physiological traits of potential interest for organic systems may result in greater differences in selection results between the two systems.

Acknowledgments F1 seed of the original population was kindly provided by Dr. Ron DePauw of Agriculture and Agri-Food Canada, Swift Current, SK. We thank Cliff Therou for the management of the fields at the Edmonton research station and Dr James Holland for assistance in the statistical analysis and genetic correlation calculations. Thanks also to Dr. Alireza Navabi, Klaus Strenzke, Brian Bowen, Alana Kornelsen, Carla Ollenberger, Holly Yorston, and the many others contributing to this project. Todd Reid was supported by a Canadian Wheat Board Post-Graduate Fellowship. Our research group was supported by NSERC Discovery and Collaborative grants, Western Grain Research Foundation (Check-off and Endowment Fund grants), and we gratefully acknowledge additional grant support from the Alberta Crop Industry Development Fund and the Alberta Agricultural Research Institute.

References

- Alberta Agriculture Food and Rural Development (2002) Soil group map of Alberta, vol 2007. Alberta Agriculture, Food, and Rural Development, Alberta
- Banziger M, Cooper M (2001) Breeding for low input conditions and consequences for participatory plant breeding: Examples from tropical maize and wheat. Euphytica 122:503–519. doi:10.1023/A:1017510928038
- Barberi P (2002) Weed management in organic agriculture: are we addressing the right issues? Weed Res Oxf 42:177– 193. doi:10.1046/j.1365-3180.2002.00277.x
- Baresel JP, Zimmermann G, Reents HJ (2008) Effects of genotype and environment on N uptake and N partition in organically grown winter wheat (*Triticum aestivum* L.) in Germany. Euphytica 163:347–354. doi:10.1007/s10681-008-9718-1
- Bernardo R (2002) Breeding for quantitative traits in plants. Stemma Press, Woodbury
- Bernier J, Kumar A, Ramaiah V et al (2007) A large-effect QTL for grain yield under reproductive-stage drought stress in upland rice. Crop Sci 47:507–518
- Burger H, Schloen M, Schmidt W et al (2008) Quantitative genetic studies on breeding maize for adaptation to organic farming. Euphytica 163:501–510. doi:10.1007/ s10681-008-9723-4
- Carr PM, Kandel HJ, Porter PM et al (2006) Wheat cultivar performance on certified organic fields in Minnesota and North Dakota. Crop Sci 46:1963–1971. doi:10.2135/ cropsci2006.01-0046
- Ceccarelli S (1996) Adaptation to low high input cultivation. Euphytica 92:203–214. doi:10.1007/BF00022846
- CIMMYT (2008) 37th International Bread Wheat, Grain yield, Plant Height, Days to Maturity. http://www.cimmyt.org/ wpgd/index.htm

- Cousens RD, Rebetzke GJ, Barnett AG (2003) Dynamics of competition between wheat and oat: II. Effects of dwarfing genes. Agron J 95:1305–1313
- CWB (2007) 2005–06 Statistical tables, vol 2007. Canadian Wheat Board, Canada
- Degenhardt R, Martin R, Spaner D (2005) Organic farming in Central Alberta: current trends, production constraints and research needs. J Sustain Agric 27:153–173. doi:10.1300/ J064v27n02_10
- Entz MH, Guilford R, Gulden R (2001) Crop yield and soil nutrient status on 14 organic farms in the eastern portion of the northern Great Plains. Can J Plant Sci 81:351–354
- Entz MH, Penner KR, Vessey JK et al (2004) Mycorrhizal colonization of flax under long-term organic and conventional management. Can J Plant Sci 84:1097–1099
- Environment Canada (2008) Canadian Climate Data, vol 2008. Government of Canada, Canada
- Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Pearson Education Ltd, Harlow
- Fasoula DA, Fasoula VA (1997) Competitive ability and plant breeding. Plant Breed Rev 14:89–138
- Fleissbach A, Oberholzer H-R, Gunst L et al (2007) Soil organic matter and biological soil quality indicators after 21 years of organic and conventional farming. Agric Ecosyst Environ 118:273–284. doi:10.1016/j.agee.2006.05.022
- Gale MD, Youssefian S (1985) Dwarfing genes in wheat. In: Russell GE (ed) Progress in plant breeding. Butterworths, London, pp 1–35
- Gosling P, Shepherd M (2005) Long-term changes in soil fertility in organic arable farming systems in England, with particular reference to phosphorus and potassium. Agric Ecosyst Environ 105:425–432. doi:10.1016/ j.agee.2004.03.007
- Harris GH, Hesterman OB, Paul EA et al (1994) Fate of legume and fertilizer nitrogen-15 in a long-term cropping systems experiment. Agron J 86:910–915
- Holland JB (2006) Estimating genotypic correlations and their standard errors using multivariate restricted maximum likelihood estimation with SAS Proc MIXED. Crop Sci 46:642–654. doi:10.2135/cropsci2005.0191
- Holland JB, Nyquist WE, Cervantes-Martinez CT (2003) Estimating and interpreting heritability for plant breeding: an update. Plant Breed Rev 22:9–112
- Hucl P (1998) Response to weed control by four spring wheat genotypes differing in competitive ability. Can J Plant Sci 78:171–173
- Huel DG, Huel P (1996) Genotypic variation for competitive ability in spring wheat. Plant Breed 115:325–329. doi: 10.1111/j.1439-0523.1996.tb00927.x
- Leeson JY, Sheard JW, Thomas AG (2000) Weed communities associated with arable Saskatchewan farm management systems. Can J Plant Sci 80:177–185
- Lemerle D, Verbeek B, Cousens RD et al (1996) The potential for selecting wheat varieties strongly competitive against weeds. Weed Res Oxf 36:505–513. doi:10.1111/j.1365-3180.1996.tb01679.x
- Lemerle D, Gill GS, Murphy CE et al (2001) Genetic improvement and agronomy for enhanced wheat competitiveness with weeds. Aust J Agric Res 52:527–548. doi:10.1071/AR00056

- Littell RC, Milliken GA, Stroup WW et al (2006) SAS for mixed models, 2nd edn. SAS® Institute Inc., Cary
- Loschenberger F, Fleck A, Grausgruber H et al (2008) Breeding for organic agriculture: the example of winter wheat in Austria. Euphytica 163:469–480. doi:10.1007/ s10681-008-9709-2
- Mader P, Edenhofer S, Boller T et al (2000) Arbuscular mycorrhizae in a long-term field trial comparing lowinput (organic, biological) and high-input (conventional) farming systems in a crop rotation. Biol Fertil Soils 31:150–156. doi:10.1007/s003740050638
- Mason H, Goonewardene L, Spaner D (2007a) Competitive traits and the stability of wheat cultivars in differing natural weed environments on the northern Canadian Prairies. J Agric Sci 146:21–33
- Mason H, Navabi A, Frick B et al (2007b) Cultivar and seeding rate effects on the competitive ability of spring cereals grown under organic production in northern Canada. Agron J 99:1199–1207. doi:10.2134/agronj2006.0262
- Mason H, Navabi A, Frick B et al (2007c) Does growing organic Canadian hard red spring wheat under organic management alter its breadmaking quality? Renew Agric Food Syst 22:157–167. doi:10.1017/S1742170507001688
- Mason HE, Navabi A, Frick BL et al (2007d) The weedcompetitive ability of Canada Western Red Spring Wheat cultivars grown under organic management. Crop Sci 47:1167–1176
- McCaig TN, DePauw RM, Clarke JM et al (1996) AC Barrie hard red spring wheat. Can J Plant Sci 76:337–339
- Murphy KM, Campbell KG, Lyon SR et al (2007) Evidence of varietal adaptation to organic farming systems. Field Crops Res 102:172–177. doi:10.1016/j.fcr.2007.03.011
- Nass HG, Ivany JA, MacLeod JA (2003) Agronomic performance and quality of spring wheat and soybean cultivars under organic culture. Am J Altern Agric 18:164–170. doi:10.1079/AJAA200348
- Przystalski M, Osman A, Thiemt EM et al (2008) Comparing the performance of cereal varieties in organic and non-

organic cropping systems in different European countries. Euphytica 163:417–433. doi:10.1007/s10681-008-9715-4

- Rosewarne GM, Singh RP, Huerta-Espino J et al (2008) Quantitative trait loci for slow-rusting resistance in wheat to leaf rust and stripe rust identified with multi-environment analysis. Theor Appl Genet 116:1027–1034. doi: 10.1007/s00122-008-0736-0
- Sahota A (2006) Overview of the global market for organic food and drink. In: Willer H, Yussefi M. (eds) The world of organic agriculture statistics and emerging trends 2006. International Federation of Organic Agriculture Movements (IFOAM) and Research Institute of Organic Agriculture FiBL, Bonn, Germany SAS[®] Institute (2003) Release 9.1. SAS[®] Institute Inc., Cary
- Secan (2006) Superb Canada western red spring wheat, vol 2008. Secan: Canada's Seed Partner, Kanata
- Sigmaplot (2006) SigmaPlot for Windows version 10.0. Systat Software Inc, San Jose
- Vandeleur RK, Gill GS (2004) The impact of plant breeding on the grain yield and competitive ability of wheat in Australia. Aust J Agric Res 55:855–861. doi:10.1071/ AR03136
- Wicks GA, Ramsel RE, Nordquist PT et al (1986) Impact of wheat cultivars on establishment and suppression of summer annual weeds. Agron J 78:59–62
- Wolfe MS, Baresel JP, Desclaux D et al (2008) Developments in breeding cereals for organic agriculture. Euphytica 163:323–346. doi:10.1007/s10681-008-9690-9
- Worland T, Snape JW (2001) Genetic basis of worldwide wheat varietal improvement. In: Bonjean AP, Angus WJ (eds) The world wheat book. Lavoisier Publishing, Paris, pp 59–100
- Zadoks JC, Chang TT, Konzak CF (1974) Decimal code for growth stages of cereals. Weed Res Oxf 14:415–421. doi: 10.1111/j.1365-3180.1974.tb01084.x
- Zar JH (1996) Biostatistial analysis. Prentice Hall, Upper Saddle River