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ORIGINAL PAPER

Molecular mapping of quantitative trait loci for yield and yield components in spring wheat (*Triticum aestivum* L.)

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Abstract An F_1 derived doubled haploid (DH) population of 402 lines from the adapted spring wheat cross Superb (high yielding)/BW278 (low yielding) was developed to identify quantitative trait loci (QTL) associated with yield and yield components. A subset of the population (186 lines) was evaluated in replicated field trials in 2001 and 2002 at six locations in Manitoba and Saskatchewan, Canada. Agronomic parameters, grain yield and yield components including 1,000 grain weight, harvest index, average seed weight spike^{-1}, seed number spike^{-1} and spikes number m^{-2} were measured. A genetic map was constructed with 268 microsatellite marker loci and included two morphological genes, reduced plant height, *Rht-B1b,* and the presence/absence of awns, *B1*. Composite interval mapping was conducted to estimate the location and effect of QTL associated with the evaluated traits. A total of 53 QTL were identified on 12 chromosomes for the 9 evaluated traits with the coefficient of determination ranging from 0.03 to 0.21 of the total variation. The increase in yield and yield components ranged from 4.5 to 17.1% over the population mean. The five grain yield QTL were detected on chromosomes 1A, 2D, 3B, and 5A and showed a combined increase of 34.4%, over the population mean. The alleles from Superb were associated with increased yield for four of the five QTL. This study identified potential chromosome segments for use in marker-assisted selection to improve yield and yield components in spring wheat.

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Introduction

Selection for grain yield has been an important focus of wheat (*Triticum aestivum* L.) breeding programs for decades. Yield is a complex, quantitative trait controlled by a number of genes with low heritability and is significantly influenced by the environment. Quantitative traits provide the greatest challenge for making genetic improvement because plant breeders have little information on the number, location, and contribution of each gene to the final expression of the trait (Koebner and Snape 1999; Mohan et al. 1997). Grain yield can be divided into a number of components including spike number m^{-2}, seed number spike^{-1}, and 1,000 grain weight. Several genes also control yield components however, some components are less environmentally sensitive and have higher heritabilities than grain yield (Bezant et al. 1997). Therefore, it is useful to examine yield components when evaluating grain yield to provide specific information about the genetic control and relationship between yield and its components.

Genetic advance in wheat breeding is largely dependent on the variation created by intervarietal hybridization and historically has lead to small, incremental increases in yield of 0.5% per year (Hucl and Baker 1987). Early generation selection is generally not successful for quantitative traits such as grain yield due to low heritabilities and genotype

by environment interactions (Bernardo 2002). Progress in molecular marker technology and the development of quantitative trait analysis software have permitted researchers to construct genetic maps in wheat to identify and estimate the effects of quantitative trait loci (QTL) associated with important agronomic traits including yield and its components.

In diploid crop species such as maize, rice, and barley, yield and yield components have been shown to map to coincident chromosome regions within a species (Abler et al. 1991; Xiao et al. 1996; Tinker et al. 1996). Wheat, however, is hexaploid with a large genome, which makes it one of the most complex crops for genetic analysis. As a result, QTL analyses of grain yield and its components in wheat are limited and have generally focused on single chromosomes (Hyne and Snape 1991; Berke et al. 1992). Using recombinant chromosome substitution lines, QTL for yield and yield components have been reported on chromosomes 3A (Shah et al. 1999), 4A (Araki et al. 1999), and 5A (Kato et al. 1999, 2000). Börner et al. (2002) used 114 recombinant inbred lines (RIL) of the International Triticeae mapping population and a restriction fragment length polymorphism (RFLP) based map to detect QTL under field and greenhouse conditions for two agronomic and three yield component traits across the entire wheat genome. In total, 56 QTL were identified for the traits of interest when each environment was analyzed separately. Seventeen yield component QTL mapped to chromosomes 2D, 3A, 4A, 5A, and 6B. Börner et al. (2002) also observed coincident QTL for heading, grain number spike^{-1}, 1,000 grain weight, and grain weight spike^{-1}. Huang et al. (2003) studied seven agronomic, yield and yield component traits in a BC_2F_1 population derived from a cross between a winter wheat and a synthetic wheat line. Using advanced backcross QTL (AB-QTL) analysis, Huang et al. (2003) identified a total of 35 QTL for yield and yield components mapped to chromosomes 1A, 1B, 2A, 2B, 2D, 3B, 4D, 5A, 5B, 5D, 6A, 7A, 7B, and 7D. Coincident QTL were observed for all traits and only six of the reported QTL had LOD scores greater than 3.0. Using a population of RIL derived from a cross between a Chinese wheat, Ning 7840, and an American soft red winter wheat, Clark, Marza et al. (2005) identified 206 putative QTL for the 15 yield, yield components, and agronomic traits evaluated when each environment was analyzed separately. Grain yield and yield component QTL were detected on chromosomes 1A, 1B, 2B, 3B, 4A, 4B, 5A, 5B, 6B, 7A, and 7D. These three studies implicate 18 chromosomes controlling yield and yield components.

The objectives of this study were to construct a genetic map of the adapted spring wheat cross Superb (high yielding)/BW278 (low yielding) with microsatellite markers and combined with extensive replicated phenotypic data locate and estimate the effects of QTL controlling grain yield. In addition, the association between yield component (1,000 grain weight, seed number spike^{-1}, spikes m^{-2}) and agronomic trait (average seed weight spike^{-1}, harvest index, grain filling time, days to heading and days to maturity) QTL that are coincident with each of the grain yield QTL was determined.

Materials and methods

Plant material

A population of 402 doubled haploid (DH) lines was derived from the spring wheat cross Superb/BW278 using the wheat-maize pollination method (Fedak et al. 1997). Superb [Grandin*2/AC Domain] is a high yielding hard red spring wheat cultivar registered by the Agriculture and Agri-Food Canada (AAFC)—Cereal Research Centre in 2000 and has been used extensively as a parent in the spring wheat breeding program at AAFC. BW278 [AC Domain*2/Sumai 3] is a low yielding breeding line with Fusarium head blight (FHB) resistance incorporated from Sumai 3. The population was selected because it was known to be segregating widely for yield, plant height, presence/absence of awns, leaf spot diseases and FHB. The population of 402 DH lines was divided into two subsets. One subset, referred to as "mapping population", consisted of 186 DH lines. These DH lines came from the two F1 plants producing the largest number of DH lines and were used for detailed mapping of QTL associated with grain yield and yield components. The second subset referred to as the "interval mapping population", consisted of the remaining 216 DH lines derived from five F_1's and was used to provide additional grain yield data.

Field trials

The mapping population was evaluated in replicated field trials at four locations in Manitoba (Brandon, Portage la Prairie, Morden, and Winnipeg) and two locations in Saskatchewan (Melfort and Scott) in 2001 and 2002. The parents, Superb and BW278, and the hard red spring cultivars Roblin, Katepwa and AC Barrie were also included as checks. The field trials were arranged in a 14 × 14 lattice design with two replicates. A common seed source was used for all trials in both years. This seed source was derived by forming a seed composite from trials conducted in 2000 at Morden and Portage la Prairie. Plant height (Ht), days to heading (Hdg), days to Maturity (Mat), grain yield (Yld), and 1,000 grain weight (Tgw) were measured at all locations with the exception of Hdg at Melfort in 2002 and presence/absence of awns was noted at Winnipeg only.

Grain filling time was calculated by subtracting days to heading from the days to physiological maturity.

The plots in Winnipeg and Portage la Prairie consisted of 5 rows, 4.27 m long, spaced 15.2 cm apart. In Brandon, the plots consisted of 4 rows, 4 m long, spaced 22.3 cm apart. The plots in Morden consisted of 5 rows, 4 m long and spaced 17.8 cm apart. The plots in Melfort, SK consisted of 7 rows, 4.2 m long and spaced 17.8 cm apart while the plots in Scott, SK, consisted on 4 rows, 5 m long, and spaced 23 cm apart. All plots were seeded at a rate of 250 seeds m^{-2}. All plots were bordered with a row of fall rye or winter wheat to minimize border effects from neighboring plots. The grain yield from plots was converted to kg ha^{-1} for analysis. Since the mapping population segregated for FHB resistance and susceptibility to leaf spot diseases, Tilt® (propiconazole, Syngenta Crop Production) was applied at the flag leaf stage (Zadoks = 39) for leaf spot disease control and Bravo® (chlorothalonil, Syngenta Crop Production) was applied as close to anthesis as possible (Zadoks = 65–69) for FHB control to eliminate any effects these diseases may have on yield and its components. Fungicides were applied at the recommended field rate. Prior to whole-plot harvest, the above-ground biomass of two, 50 cm row segments was hand harvested from the center rows of each plot at the four Manitoba locations, to measure the yield components: harvest index (Hi), average seed weight $spike^{-1}$ (Asw), seed number $spike^{-1}$ (Sns), and spikes $meter^{-2}$ (Sm2) (Table 1). Two trials in Saskatchewan were lost due to extreme drought (Melfort 2001) and an infestation of wheat stem sawfly (*Cephus cinctus*) (Scott 2002) therefore only ten site-years of data were available for analysis.

The interval mapping population was grown in a single replicate trial at Brandon, Morden, Portage la Prairie, and Winnipeg, Manitoba in 2001 and 2002. The parents, Superb and BW278, and the hard red spring cultivars Roblin, Katepwa, and AC Barrie were included as checks. The lines were evaluated in yield plots of the same dimension as described above for each location. Plant height and grain yield were the only measurements collected. Presence/absence of awns was noted at Winnipeg only. The 2002 trial in Brandon suffered from excessive moisture and did not emerge uniformly therefore only seven site-years of data were available for analysis.

Statistical analysis

All traits were analyzed using the procedure MIXED with all effects in the model considered random (site-year, DH line, block, site-year × DH line, and replicate) (SAS v8.2 SAS Institute Inc., Cary, NC, USA). Each site-year was analyzed individually as a separate environment. Further analyses were conducted by combining all years for each site, by combining all sites for each year, and by combining all sites and years. Variance components and best linear unbiased predictors (BLUPs) were obtained by the method of restricted maximum likelihood for all traits and datasets (Littell et al. 1996). The BLUP trait values for each DH line evaluated from each dataset were used for QTL analysis. The broad sense heritability of each trait was estimated from the variance components derived in the PROC MIXED determined as the ratio of genotypic variance to the sum of the genotypic and environmental variance. Pearson correlation coefficients were used to determine the degree of association among the traits of interest.

Construction of the genetic map

Leaf tissue was harvested from a single plant for each DH line and lyophilized for DNA extraction with the Qiagen DNeasy 96 Plant Kit (Qiagen, Mississauga, ON, Canada). DNA was quantified by fluorimetry using Hoechst 33258 stain. Approximately 1,000 microsatellite markers were screened to detect polymorphisms between Superb and BW278. The parents of Superb (Grandin and AC Domain) were also included in the screening to determine the allelic composition of Superb. Genotyping data were obtained using M13 tailing (Schuelke 2000) and fluorescent capillary electrophoresis on an ABI 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) (Somers et al. 2004). Data generated by the ABI3100 was converted to a gel-like image using Genographer (available at http://hordeum.oscs.montana.edu/genographer). Primer sequences for the GWM and GDM microsatellite markers were obtained from Roder et al. (1998) and Pestova et al. (2000). The BARC microsatellite marker sequences were obtained from the USA wheat and barley scab initiative website (http://www.scabusa.org) while the sequences for the WMC, CFA, and CFD microsatellites were obtained from the Grain Genes website (http://wheat.pw.usda.gov).

The polymorphic markers were used to genotype the mapping population. The initial map was constructed using MAPMAKER/EXP version 3.0b (Lincoln et al. 1993; Lander et al. 1987) with a minimum LOD of 3.0 and maximum recombination fraction of 0.35. Marker order was tested using the "compare" and "ripple" commands. The map was verified using JoinMap® 3.0 (Stam 1993).

QTL analysis

Composite interval mapping (CIM) analysis (Zeng 1993, 1994) was performed using Windows QTL Cartographer v2.0 (Wang et al. 2004 http://statgen.ncsu.edu/qtlcart/WQTLCart.htm). Forward stepwise regression with backward elimination was used to search for QTL and identify

Table 1 Summary of the agronomic traits and yield and yield components measured for the Superb/BW278 mapping population in 2001 and 2002

Trait[a]	Abbreviation	Environments evaluated[b]	Method of measurement
Plant height	Ht	B01, B02, Me02, M01, M02, P01, P02, S01, W01, W02	Average plant height measured from the soil surface to tip of spike, excluding awns (cm)
Days to heading	Hdg	B01, B02, M01, M02, P01, P02, S01, W01, W02	Assessed as the number of days from planting until emergence of 50% of the inflorescences in each plot (days)
Days to maturity	Mat	B01, B02, Me02, M01, M02, P02, S01, W01, W02	Assessed as the number of days from planting to physiological maturity (days)
Grain yield	Yld	B01, B02, Me02, M01, M02, P01, P02, S01, W01, W02	Weight of grain harvested per unit area (kg ha^{-1})
Thousand grain weight	Tgw	B01, B02, Me02, M01, M02, P01, P02, S01, W01, W02	Weight of a 1,000 grain sample (g)
Harvest index	Hi	B01, B02, M01, M02, P01, P02, W01, W02	Grain weight from a one meter row/total aboveground biomass harvested from a 1 m row
Average seed weight $spike^{-1}$	Asw	B01, B02, M01, M02, P01, P02, W01, W02	Grain weight from a one meter row/number of spikes harvested from a 1 m row (g)
Spikes m^{-2}	Sm2	B01, B02, M01, M02, P01, P02, W01, W02	Number of spikes per meter square
Seed number $spike^{-1}$	Sns	B01, B02, M01, M02, P01, P02, W01, W02	Seed weight per spike/individual grain weight (no.)
Grain filling time	Gft	B01, B02, M01, M02, P01, P02, S01, W01, W02	Period of time between date of heading and date of maturity (days)

[a] Traits Hi, Asw, Sm2, Sns were calculated from the eight Manitoba locations only

[b]Environment codes: *B* Brandon, *MB, M* Morden, *MB, Me* Melfort, *SK, P* Portage la Prairie, *MB, S* Scott, *SK, W* Winnipeg, *MB, 01* 2001, *02* 2002

cofactors for CIM analysis. The threshold for $P(F_{in})$ and $P(F_{out})$ were set at 0.05, based on the ability to repeatedly detect the same QTL with similar effects across all environments. CIM analysis was completed using the standard model (Model 6). Window size was set at 10 cM and the maximum number of cofactors was used to control the genetic background for each trait. Empirical LOD thresholds were estimated using 1,000 permutations (Churchill and Doerge 1994). A QTL was declared for a trait when the LOD score was greater than the threshold LOD score in a minimum of four environments and was also detected in the site, year, and overall data sets.

QTL analysis for grain yield and yield components revealed major effects from two morphological genes including *Rht-B1b* and the presence/absence of awns, *B1* (Table 2). The effect of *Rht-B1b* and *B1* were additive on all traits and showed no evidence of epistasis. All of the lines were phenotypically classified based on the factors plant height (tall/short) and awns (presence/absence). ANOVA was used to determine the additive effects of these factors on all BLUP trait values of each line. The additive effect on all traits for each line was derived from the LS means of the ANOVA and used to adjust the BLUP trait values. The adjusted BLUP trait values were used with CIM to reveal other important QTL controlling yield and yield components. The coefficient of determination of each QTL represents the variation in line performance based on the adjusted BLUP values.

Interval mapping

The interval mapping population was genotyped with 6–12 markers from each interval identified in the QTL analysis as being associated with grain yield. BLUP estimates were also obtained for the 216 DH lines using the MIXED procedure with a random effects model. Since these lines were only evaluated in single replicate trials, the BLUP trait values for each line from the 7 site-years was averaged to determine the line performance.

Results

Quantitative traits

Frequency distributions were generated for all traits evaluated in the field trials (data not shown). Normal distributions were observed for all traits except for plant height, which showed a bimodal segregation pattern (ratio = 1:1, $\chi^2 = 0.36$, $P < 0.05$) and was mapped as a Mendelian gene to chromosome 4BS (*Rht-B1b*) (Fig. 1). The mapping population size was reduced to 178 DH lines since plant height for 8 lines was intermediate and could not be categorically determined. This population is hereafter referred to as the mapping population(178). The effect of *Rht-B1b* and *B1* on all traits evaluated was additive and there were no instances of epitasis between the genes.

Table 2 Effects of the *Rht-B1b* and *B1* genes on yield, yield component and agronomic traits measured in the Superb/BW278 mapping population based on BLUP trait values across all environments

Trait	Gene	LOD	R^2	Additive[a]	Positive allele	Increase[b] (%)	Environments observed/total
Yld	*Rht-B1b*	9.6	0.076	110.6 kg ha^{-1}	Superb	4.0	8/10
Yld	*B1*	19.2	0.186	178.4 kg ha^{-1}	Superb	6.0	9/10
Tgw	*Rht-B1b*	6.3	0.177	1.3 g	BW278	4.6	8/10
Tgw	*B1*	4.0	0.068	1.1 g	Superb	4.0	8/10
Asw	*Rht-B1b*	6.9	0.075	0.026 g	BW278	4.8	5/8
Asw	*B1*	12.2	0.123	0.039 g	Superb	6.2	7/8
Hi	*Rht-B1b*	14.2	0.118	0.016	Superb	4.9	6/8
Hi	*B1*	10.8	0.089	0.007	BW278	2.1	5/8
Sm2	*Rht-B1b*	19.4	0.172	43.0	Superb	6.3	8/8
Sm2	*B1*	8.4	0.083	31.7	BW278	4.6	4/8
Sns	*Rht-B1b*	3.1	0.052	1.0	BW278	5.3	6/8
Sns	*B1*	10.5	0.158	1.3	Superb	6.9	6/8
Gft	*Rht-B1b*	11.4	0.110	0.68 days	Superb	1.8	4/7
Gft	*B1*	12.3	0.121	0.69 days	Superb	2.0	6/7
Hdg	*Rht-B1b*	5.5	0.072	0.8 days	BW278	1.4	7/9
Hdg	*B1*	8.7	0.132	1.1 days	Superb	2.0	8/9
Mat	*Rht-B1b*	14.0	0.115	1.0 days	BW278	1.1	7/9
Mat	*B1*	9.2	0.078	0.7 days	Superb	0.8	7/9

[a] Additive effect of allele substitution

[b] Increasse (%) represents the improvement in the trait over the mean of the population

To be thorough and independently show the data adjustment was effective, the mapping population(178) was divided into eight subpopulations to remove the effects of *Rht-B1b* and *B1* including: short plants; tall plants; awned plants; awnless plants; short-awned; short-awnless; tall-awned; and tall-awnless and QTL analysis was completed for all traits on these subpopulations. When the results of the short and tall subsets were examined, a major effect was still observed from the *B1* locus for all traits ranging from $R^2 = 0.060$ for Asw to 0.295 for Yld. Similarly, when the results of the awned and awnless subsets were examined, a major effect was observed from the *Rht-B1b* locus ranging from $R^2 = 0.07$ for Hdg to 0.24 for Sm2. The subpopulations where both genes were fixed identified the same QTL that were detected for all traits when the mapping population(178) was analyzed and none of these QTL were coincident with *Rht-B1b* or *B1* (ie. effects were removed). These findings provided independant evidence that the data adjustment by the least squares ANOVA was successful in removing the major effects from the *Rht-B1b* and *B1* loci and permitted the identification of QTL for all traits in this study.

The phenotypic data indicated there was significant genetic variation for all traits in the Superb/BW278 population as well as considerable differences between the parents of the cross (Table 3). Transgressive segregants on both ends of the distribution were observed for all traits except Tgw and Asw in the mapping population(178). Estimates of broad sense heritability across environments and years were intermediate ($H^2 = 0.48$–0.58) for Yld, Hi, Sns, Gft, Hdg and Mat while the estimates for Tgw, Asw, and Sm2 were high ($H^2 = 0.77$–0.98). Correlations were calculated for all traits evaluated in the Superb/BW278 population (Table 4) and the association between yield and most of the yield components was highly significant ($P < 0.001$).

Genetic map

The genetic map was constructed with 268 microsatellite loci and spanned approximately 1,822 cM across 20 chromosomes. Chromosome 4A was monomorphic at all markers tested (data not shown). Figure 1 shows only the 13 chromosomes carrying QTL associated with yield and yield components and the *Rht-B1b* (Börner et al. 2002) and *B1* (Kato et al. 2000) loci.

Effect of *Rht-B1b* and *B1* genes

Superb alleles for reduced plant height and the presence of awns resulted in an increase in yield, most of the yield components, and agronomic traits. Exceptions to this were observed for Tgw and Asw at the *Rht-B1b* locus and Hi, Sm2, and Sns at the *B1* locus (Table 2). The LOD scores for yield and yield components ranged from 3.1 to 19.4 at the *Rht-B1b* locus and explained 5.2–17.7% of the variation in the mapping population. The LOD scores for yield and yield components at the *B1* locus in the mapping population ranged from 4.0 to 19.2 and explained 6.8–18.6% of the variation.

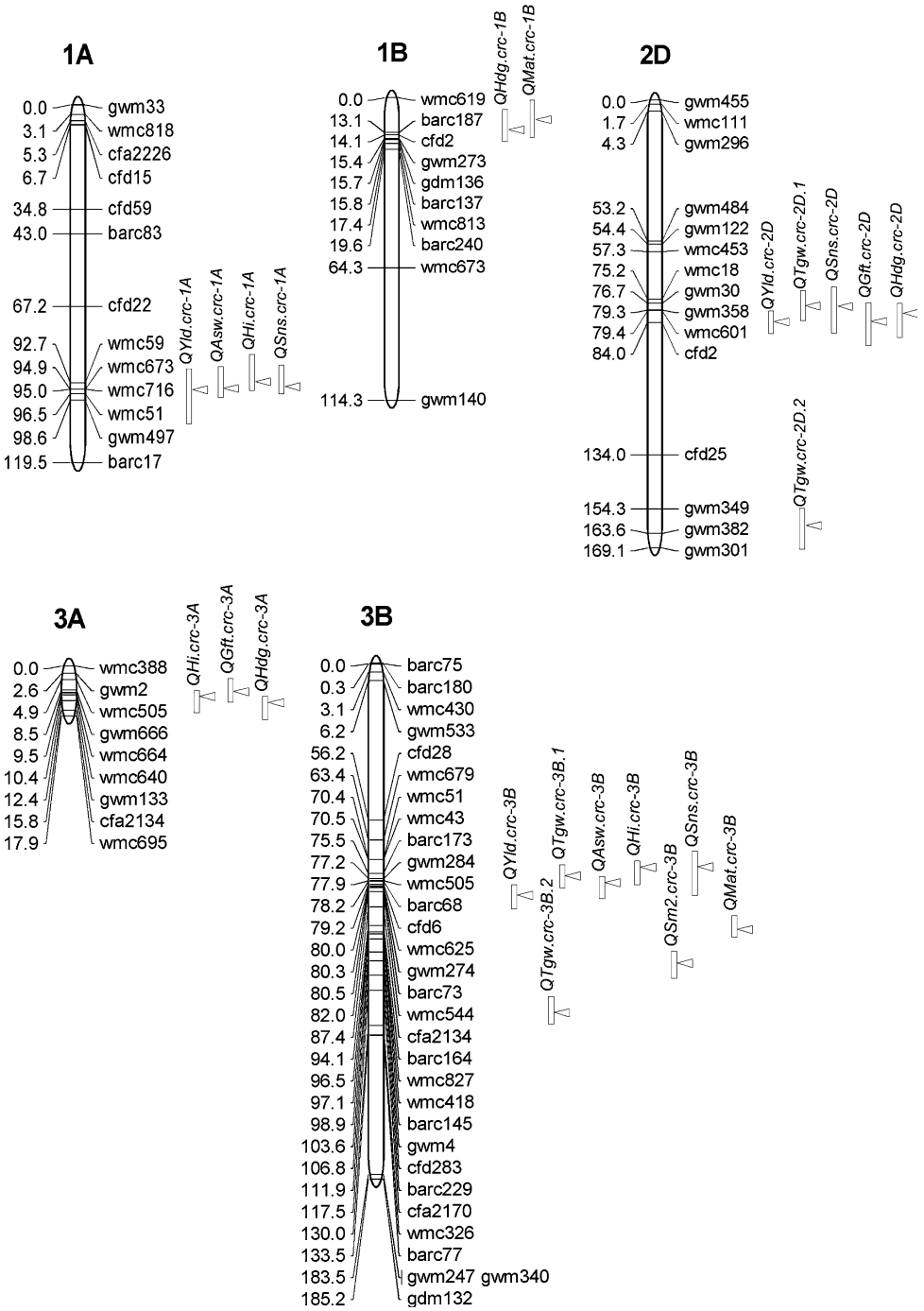

Fig. 1 Genetic linkage map of the 13 chromosomes and QTL for yield, yield components, and agronomic traits in the Superb/BW278 spring wheat cross. The QTL with *solid bars* on chromosomes 4B and 5A were detected in the mapping population. QTL indicated with *open bars* were detected in the mapping population(178) by accounting for the effects of the morphological genes controlling the presence/absence of awns, *B1,* and plant height, *Rht-B1b.* The LOD peak of each QTL is indicated by an *arrowhead* and the length of the bars indicate a 1.0 LOD drop in the QTL confidence interval. Map distances are indicated on the *left* of each chromosome in Kosambi centimorgan

When the interval mapping population was analyzed, significant effects were also observed at the *Rht-B1b* and *B1* loci explaining 6.0 and 16.4% of the variation in yield at the *Rht-B1b* and *B1* loci, respectively (data not shown). The phenotypic data for grain yield in the interval mapping population was also adjusted using the results of a least squares ANOVA. The interval mapping population size was reduced from 216 to 193 DH lines since plant height for 16 lines was intermediate and could not be categorically determined as well the presence/absence of awns data was missing for 7 DH lines. This population is hereafter referred to as the interval mapping population(193). The mapping population and interval mapping population were combined to determine the effects of *Rht-B1b* and *B1* loci on grain. The *Rht-B1b* locus explained 6.7% of the variation for yield while the *B1* locus explained 15.3% of the variation for yield. A yield increase of 3.4% over the population mean for genotypes carrying the Superb *Rht-B1b* allele was observed while a 6.4% increase in yield was observed over the population mean for genotypes carrying

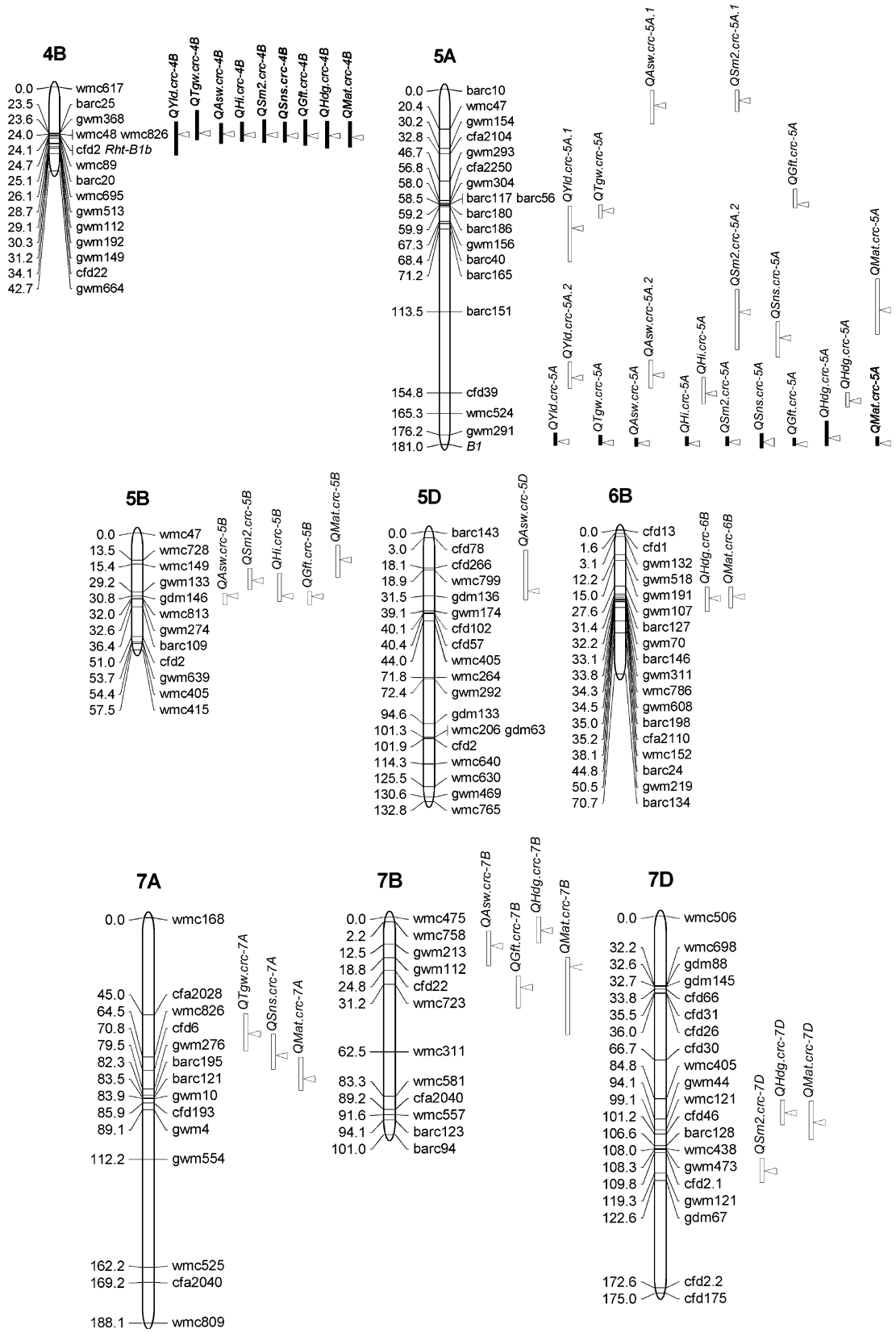

Fig. 1 continued

Table 3 Mean and range of the adjusted BLUP trait values across all environments for the nine yield, yield components, and agronomic traits measured on the Superb/BW278 mapping population(178)

Trait	Parents		DH population			Heritability[a]
	Superb	BW278	Mean	Min	Max	
Yld	3756.7	3178.8	3348.1	2291.1	4285.8	0.48
Tgw	39.0	24.6	28.4	20.0	36.4	0.77
Asw	0.730	0.311	0.530	0.253	0.723	0.97
Hi	0.360	0.321	0.333	0.233	0.406	0.50
Sm2	637.0	817.8	682.3	445.3	972.6	0.98
Sns	18.7	12.6	18.7	8.3	25.3	0.58
Gft	33.7	32.5	33.6	29.8	36.3	0.52
Hdg	51.9	54.3	53.3	46.8	57.8	0.49
Mat	86.8	87.3	87.8	80.8	93.3	0.48

[a] Heritability was estimated from the variance components for the 186 DH lines of the Superb/BW278 mapping population ($H^2 = \sigma^2_g/\sigma^2_g + \sigma^2_{ge/e} + \sigma^2_{e/re}$)

Table 4 Correlations coefficients of adjusted BLUP trait values across all environments between yield, yield components, and agronomic traits measured on the Superb/BW278 mapping population(178)

Trait	Yld	Tgw	Asw	Hi	Sm2	Sns	Gft	Mat
Tgw	0.30***							
Asw	0.62***	0.50***						
Hi	0.59***	0.14NS	0.68***					
Sm2	−0.05NS	−0.49***	−0.61***	0.08NS				
Sns	0.60***	−0.08NS	0.82***	0.66***	−0.35***			
Gft	−0.16**	0.01NS	−0.10*	0.11NS	0.04NS	−0.01NS		
Hdg	−0.39***	−0.06NS	−0.30***	−0.44***	0.04NS	−0.38***	0.03NS	
Mat	−0.23**	−0.11NS	−0.34***	−0.31***	0.23***	−0.30***	−0.04NS	0.69***

*, **, *** Significant at $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively, and *NS* not significant

the Superb *B1* allele. Comparable results are shown in Table 2 for the mapping population.

QTL mapping

QTL analysis of the mapping population(178) detected 53 repeatable QTL across environments for grain yield, yield components and the agronomic traits that were not coincident with either *Rht-B1b* or *B1* (Table 5; Fig. 1). Five QTL were identified on four chromosomes, 1A, 2D, 3B and 5A, for grain yield with each QTL explaining between 4.1 and 20.4% of the variation. LOD scores for the observed yield QTL ranged from 3.7 to 12.6 while the mean increase in yield of the genotypes carrying the positive allele ranged from 5.3 to 10.1% over the population mean. These five QTL were also measured in the interval mapping population(193) with LOD scores between 3.1 and 9.9 and accounted for 3.9–17.4% of the variation observed. The DH lines from the mapping population(178) and interval mapping population(193) were combined for QTL analysis. The same five yield QTL on chromosomes 1A, 2D, 3B, and 5A, were observed. LOD scores for yield in the combined populations ranged between 3.1 and 9.9 while each QTL explained between 3.5 and 20.4% of the variation (data not shown).

Superb alleles were associated with an increase in yield at four QTL identified on chromosomes 2D, 3B, and 5A while BW278 was the positive allele at the yield QTL on chromosome 1A (Fig. 1; Table 5). The allele present at each of the yield QTL was determined for the top ten highest yielding lines in the entire population (Table 6). Eight of the ten highest yielding lines had Superb alleles at the four QTL on chromosomes 2D, 3B, and 5A and BW278 alleles were observed at the yield QTL on chromosome 1A. The other two lines had BW278 alleles instead of Superb at the QTL on chromosome 3B (Table 6).

For the yield components examined in this study, six QTL were detected for Tgw and five QTL were detected for Sm2 and Sns (Table 5; Fig. 1). The LOD scores for the yield component QTL ranged between 3.3 and 10.3 with each QTL explaining between 2.7 and 16.0% of the variation. Seven QTL were identified for Asw and five QTL were observed for Hi that explained between 3.0 and 20.9% of the observed variation. Seven, eight, and five QTL were detected for Hdg, Mat, and Gft, respectively (Table 5; Fig. 1).

Table 5 Summary of QTL detected in the Superb/BW278 mapping population(178) for yield, yield components, and agronomic traits based on adjusted BLUP trait values across all environments

QTL (LOD threshold[a])	Marker	Allele size (bp)		LOD	R^2	Additive[b]	Positive allele	% Increase[c]	Environments observed/total
		Superb	BW278						
Yld (3.00)									
QYld.crc-1A	wmc716	137	165	6.1	0.066	219.9 kg ha^{-1}	BW278	6.6	7/10
QYld.crc-2D	cfd2	231	229	3.7	0.042	178.4 kg ha^{-1}	Superb	5.3	8/10
QYld.crc-3B	wmc544	126	Null	4.5	0.041	197.6 kg ha^{-1}	Superb	5.9	5/10
QYld.crc-5A.1	gwm156	336	339	5.1	0.050	197.8 kg ha^{-1}	Superb	5.9	9/10
QYld.crc-5A.2	cfd39	190	171	12.6	0.204	340.2 kg ha^{-1}	Superb	10.1	9/10
Tgw (3.30)									
QTgw.crc-2D.1	wmc601	223	211	5.1	0.047	1.3 g	Superb	4.6	9/10
QTgw.crc-2D.2	gwm382	85	Null	5.6	0.055	1.4 g	Superb	4.9	9/10
QTgw.crc-3B.1	gwm284	116	122	7.5	0.076	1.8 g	Superb	6.3	10/10
QTgw.crc-3B.2	cfa2170	153	158	5.0	0.047	1.4 g	Superb	4.9	10/10
QTgw.crc-5A	barc186	196	211	10.2	0.107	2.1 g	Superb	7.4	9/10
QTgw.crc-7A	wmc826	262	258	3.5	0.050	1.5 g	Superb	5.3	8/10
Asw (3.18)									
QAsw.crc-1A	wmc716	137	165	7.0	0.067	0.051 g	BW278	9.7	4/8
QAsw.crc-3B	cfd6	Null	323	7.9	0.096	0.063 g	Superb	11.9	8/8
QAsw.crc-5A.1	barc10	299	Null	6.0	0.080	0.055 g	Superb	10.4	7/8
QAsw.crc-5A.2	cfd39	190	171	12.5	0.209	0.091 g	Superb	17.1	7/8
QAsw.crc-5B	wmc813	247	243	4.4	0.058	0.046 g	Superb	8.7	6/8
QAsw.crc-5D	gdm136	160	169	3.0	0.029	0.029 g	Superb	5.5	4/8
QAsw.crc-7B	gwm213	Null	117	3.1	0.030	0.032 g	Superb	6.0	4/8
Hi (3.08)									
QHi.crc-1A	wmc673	Null	124	8.9	0.081	0.019	BW278	5.7	5/8
QHi.crc-3A	gwm666	101	99	7.8	0.070	0.017	Superb	5.1	5/8
QHi.crc-3B	barc173	Null	348	5.0	0.042	0.015	Superb	4.5	4/8
QHi.crc-5A	cfd39	190	171	12.1	0.119	0.028	Superb	8.4	6/8
QHi.crc-5B	gdm146	178	208	9.9	0.112	0.022	Superb	6.6	5/8
Sm2 (3.01)									
QSm2.crc-3B	cfd283	Null	268	10.3	0.102	69.1	BW278	10.0	6/8
QSm2.crc-5A.1	barc10	299	Null	6.2	0.079	55.3	BW278	8.8	4/8
QSm2.crc-5A.2	barc151	224	237	4.6	0.049	41.7	BW278	6.6	4/8
QSm2.crc-5B	gwm133	191	150	3.3	0.027	34.9	BW278	5.6	5/8
QSm2.crc-7D	gwm121	326	324	6.5	0.060	47.5	Superb	7.0	5/8
Sns (3.03)									
QSns.crc-1A	wmc673	Null	124	6.8	0.071	1.7	BW278	9.0	5/8
QSns.crc-2D	wmc601	223	211	5.1	0.054	1.7	BW278	9.0	5/8
QSns.crc-3B	barc173	Null	348	4.3	0.042	1.3	Superb	7.0	4/8
QSns.crc-5A	cfd39	190	171	8.6	0.160	2.4	Superb	12.8	7/8
QSns.crc-7A	wmc826	262	258	7.4	0.076	1.7	BW278	9.0	5/8
Gft (3.11)									
QGft.crc-2D	cfd2	231	229	3.4	0.039	0.70 days	Superb	2.0	5/7
QGft.crc-3A	gwm666	101	99	4.8	0.053	0.79 days	BW278	2.3	5/7
QGft.crc-5A	barc180	192	203	4.6	0.051	0.77 days	BW278	2.2	5/7
QGft.crc-5B	gdm146	178	208	4.9	0.054	0.81 days	Superb	2.3	5/7
QGft.crc-7B	wmc723	209	197	6.3	0.072	1.01 days	Superb	2.9	6/7

Table 5 continued

QTL (LOD threshold[a])	Marker	Allele size (bp)		LOD	R^2	Additive[b]	Positive allele	% Increase[c]	Environments observed/total
		Superb	BW278						
Hdg (3.09)									
QHdg.crc-1B	barc187	258	253	5.2	0.045	0.8 days	BW278	1.4	5/9
QHdg.crc-2D	wmc601	223	211	8.2	0.070	1.0 days	BW278	1.7	6/9
QHdg.crc-3A	gwm133	Null	87	10.6	0.095	1.1 days	Superb	2.0	7/9
QHdg.crc-5A	cfd39	190	171	13.7	0.146	1.4 days	Superb	2.6	9/9
QHdg.crc-6B	barc146	132	128	8.5	0.073	1.0 days	Superb	1.7	9/9
QHdg.crc-7B	wmc758	225	233	3.3	0.031	0.6 days	Superb	1.1	5/9
QHdg.crc-7D	cfd46	185	182	5.9	0.058	0.9 days	Superb	1.6	5/9
Mat (2.50)									
QMat.crc-1B	barc187	258	253	3.2	0.028	0.8 days	BW278	0.9	4/9
QMat.crc-3B	wmc827	222	208	5.1	0.045	1.0 days	Superb	1.1	4/9
QMat.crc-5A	barc151	224	237	5.8	0.055	1.2 days	BW278	1.3	7/9
QMat.crc-5B	wmc149	175	178	11.6	0.118	1.7 days	Superb	1.8	8/9
QMat.crc-6B	barc146	132	128	14.9	0.168	2.0 days	Superb	2.2	8/9
QMat.crc-7A	gwm276	83	132	2.6	0.028	0.8 days	BW278	0.9	4/9
QMat.crc-7B	cfd22	237	239	9.5	0.119	1.6 days	Superb	1.8	4/9
QMat.crc-7D	gwm44	175	181	3.6	0.035	0.9 days	Superb	1.0	4/9
Yld[d]									
QYld.crc-1A	wmc716	137	165	5.1	0.059	187.92 kg ha^{-1}	BW278	5.5	n/a
QYld.crc-2D	cfd2	231	229	3.1	0.039	138.43 kg ha^{-1}	Superb	4.0	n/a
QYld.crc-3B	wmc544	126	Null	3.5	0.044	157.13 kg ha^{-1}	Superb	4.6	n/a
QYld.crc-5A.1	gwm156	336	339	4.2	0.048	168.63 kg ha^{-1}	Superb	4.9	n/a
QYld.crc-5A.2	cfd39	190	171	9.9	0.174	317.42 kg ha^{-1}	Superb	9.3	n/a

[a] LOD thresholds were estimated in QTL Cartographer v2.0 using 1000 permutations

[b] Additive effect of allele substitution

[c] Increase (%) represents the improvement in the trait over the mean of the population

[d] Yld QTL detected in the combined mapping population(178) + interval mapping population(193) using interval mapping

Table 6 Alleles present at the five yield QTL of the top ten yielding DH lines based on BLUP trait values across all environments in the Superb/BW278 mapping population

DH Line	Yield (kg ha^{-1})	*QYld.crc-1A* (BW278)[a]	*QYld.crc-2D* (Superb)	*QYld.crc-3B* (Superb)	*QYld.crc-5A.1* (Superb)	*QYld.crc-5A.2* (Superb)	*B1* (Superb)	Rht-B1b (Superb)	%Increase[b]
A75	4285.75	BW278	Superb	Superb	Superb	Superb	BW278	Superb	28.0
B73	4268.27	BW278	Superb	Superb	Superb	Superb	Superb	Superb	27.5
B143	4102.58	BW278	Superb	Superb	Superb	Superb	BW278	Superb	22.5
A45	4101.37	BW278	Superb	Superb	Superb	Superb	BW278	Superb	22.5
B66	4018.45	BW278	Superb	BW278	Superb	Superb	Superb	Superb	20.0
A44	3959.73	BW278	Superb	Superb	Superb	Superb	Superb	Superb	18.3
B99	3942.19	BW278	Superb	Superb	Superb	Superb	BW278	Superb	17.7
B139	3918.55	BW278	Superb	Superb	Superb	Superb	BW278	Superb	17.0
B25	3914.69	BW278	Superb	Superb	Superb	Superb	Superb	Superb	16.9
B28	3913.75	BW278	Superb	BW278	Superb	Superb	Superb	Superb	16.9

[a] Allele associated with increased yield at each identified QTL

[b] Increase (%) represents the improvement in yield over the mean of the population

Discussion

The present study discovers QTL controlling yield, yield components, and agronomic traits in a spring wheat DH population. Unlike other studies, the traits examined were evaluated in disease free conditions to accurately assess the yield potential of each line in the DH population. In similar studies conducted by Börner et al. (2002), Marza et al. (2005) and Kuchel et al. (2007) the RIL and DH populations were affected by leaf rust, yellow rust, stripe rust, FHB, powdery mildew, and barley yellow dwarf virus. The occurrence of these diseases facilitated identification of QTL for disease resistance in each population, however, the yield potential of each line was likely compromised and the estimates for the yield and yield component QTL detected in these studies may have been affected.

There are very few reports of QTL controlling grain yield, yield components, and agronomic traits covering the whole genome of hexaploid wheat. QTL shown to be associated with grain yield across multiple environments and/or years are less common. Previous yield QTL studies have evaluated crosses between synthetic wheat (Börner et al. 2002; Huang et al. 2003, 2004; Kumar et al. 2007), Chinese × American wheat (Marza et al. 2005), Canadian wheat (Huang et al. 2006) and Australian cultivars (Kuchel et al. 2007) in order to map the effects of yield QTL. The DH population evaluated in this study was suitable to identify and estimate the effects of QTL for yield, yield components, and agronomic traits since it was derived from a cross between locally bred, adapted (i.e. acceptable maturity) lines differing in yield. The performance of the parents as well as the range of values observed for the DH population indicated there was substantial genetic variation for all traits evaluated (Table 3).

In the Superb/BW278 DH population, two morphological genes, *Rht-B1b* and *B1*, segregated and had significant effects on all traits evaluated in this study (Table 2). *Rht-B1b* maps to 4BS and is a gibberellic acid insensitive dwarfing gene derived from "Norin10" (Gale and Youssefian 1985). The source of the *Rht-B1b* allele in Superb is from the parental Grandin and was confirmed by PCR (Ellis et al. 2002). These findings are supported by Kato et al. (2000) where AC Domain had tall alleles at the *Rht-B1b* locus in the cross AC Domain/Haruyutaka.

Significant increases in Yld, Sm2, Sns and significant decreases in grain weight and plant biomass have been observed in semidwarf wheats (Law et al. 1978; Gale and Youssefian 1985; Brandle and Knott 1986; Uddin and Marshall 1989; Allan 1986; Kuchel et al. 2007). Chapman et al. (2007) compared the grain yield of six near isogenic pairs of semidwarf and tall spring wheat lines and reported the average yield advantage of the semidwarf lines was 6%. The current study also observed an increase in Yld and Sm2 as well as a decrease in kernel weight associated with the dwarfing alleles at *Rht-B1*. Knott (1986) observed that semidwarf alleles were associated with earliness as was observed in this study (Table 2).

In other studies, the presence of awns increased Yld and grain weight (Goulden and Neatby 1929; Atkins and Norris 1955; Patterson et al. 1962; Weyhrich et al. 1994). The current study also observed significant increases in Yld and kernel weight when awns were present (Table 2). McNeal et al. (1969) reported a yield increase of nearly 7% at one location in awned wheat lines compared to awnless. This result is similar to the 6% yield increase over all site-years observed in this study and is in agreement with data reported by Suneson and Ramage (1962) and with the response predicted by Grundbacher (1963). Grain yield differences between awned and awnletted lines of hard red spring wheat were inconsistent among locations in Canada; however, kernel weight of the awned lines was significantly higher at all locations (Knott 1986). In contrast, McKenzie (1972) observed lower yields and kernel weights of awned spring wheat when compared with awnless spring wheats in southern Alberta. McNeal et al. (1969) reported an awned population took significantly longer to head than the awnless populations at all locations evaluated. The current study observed time to heading increased 1 day in the awned DH lines and maturity was 0.7 days earlier than the awnless DH lines. Knott (1986) also observed awned lines were earlier to head and mature than awnletted lines.

The present study identified five major grain yield QTL on four chromosomes and in all instances the grain yield QTL were consistent across the environments evaluated and coincident with QTL for at least one yield component. Significant correlations were observed between grain yield and most of the yield components suggesting pleiotropy and/or coincidence with these QTL. The yield components, Asw and Sns, were most frequently associated with the grain yield QTL while Sm2 was the least coincident yield component. This was consistent with the highly significant correlations observed between Yld, Asw, and Sns and no observed correlation between Yld and Sm2 (Table 4). Quarrie et al. (2005) also observed similar relationships between Yld, Sns, and Sm2 in a cross between Chinese Spring and an experimental breeding line. Huang et al. (2003, 2004) did not observe any positive correlations between yield and its components and in most cases, the QTL identified for yield and yield components mapped independently. In other studies, significant correlations and coincident QTL were observed between grain yield and the evaluated yield components (Kato et al. 2000; Börner et al. 2002; Quarrie et al. 2005; Huang et al. 2006; Kuchel et al. 2007; Kumar et al. 2007).

In previous studies, grain yield QTL are reported on all chromosomes with the exception of chromosomes 3D and

5D (Börner et al. 2002; Huang et al. 2003; 2004, 2006; Marza et al. 2005; McCartney et al. 2005; Quarrie et al. 2005; Kuchel et al. 2007; Kumar et al. 2007). Most of these studies have identified a large number of grain yield QTL however, the majority of these QTL were only detected in a single environment. When a QTL was detected in more than one environment, variation in the magnitude of its effects was typically observed (Huang et al. 2003, 2004; Kumar et al. 2007; Kuchel et al. 2007).

The most significant QTL identified for grain yield in the current study was located on chromosome 5AL proximal to *B1* (Fig. 1). Chromosome 5A is known to carry a number of major genes affecting productivity and adaptability and several QTL studies have reported the most repeatable Yld QTL are located on chromosome 5AL in a similar position to *QYld.crc-5A.2* (Kato et al. 2000; Huang et al. 2004; Marza et al. 2005; Quarrie et al. 2005). The presence the Superb allele at *QYld.crc-5A.2* increased yield, Asw, Hi, Sns and decreased Sm2 suggesting the increase in yield contributed by *QYld.crc-5A.2* is the result of an increased number of heavier seeds spike^{-1} being produced on fewer spikes m^{-2} (Table 5). Quarrie et al. (2005) also observed this Yld QTL was coincident with Sm2, Sns, and Tgw.

There were 17 recombinants identified as being awnless (BW278 allele) and carrying Superb alleles at *QYld.crc-5A.2*. These recombinants had an average yield of 3,585 kg ha^{-1} with yields ranging between 2,792 and 4,285 kg ha^{-1} compared to the yield of Superb at 3,756.7 kg ha^{-1}. These recombinants show that the *B1* locus and *QYld.crc-5A.2* were independent loci and the recombinants are useful to develop awnless, high yielding cultivars of spring wheat. The *QYld.crc-3B* interval is approximately 70 cM from the recently mapped *Fhb1* gene conferring *Fusarium* resistance on the distal end of chromosome 3B (Cuthbert et al. 2006). Given the large distance between these loci, potential yield penalties associated with *Fhb1* derived from exotic sources would be avoided by selection of recombinants with *QYld.crc-3B*.

The presence of Superb alleles at *QYld.crc-3B* was associated with an increase in Tgw, Asw, Hi, and Sns and a decrease in Sm2 suggesting that the increase in grain yield at *QYld.crc-3B* is the result of an increased number of heavier seeds being produced on fewer spikes (Table 5). A grain yield QTL on chromosome 3B was observed in one of the RIL populations evaluated by Kumar et al. (2007) only in one environment with no coincident yield components QTL observed. *QYld.crc-3B* was the weakest of the five grain yield QTL identified in the current study and would likely not be a target for MAS in spring wheat breeding programs.

Yield was also significantly correlated with the agronomic traits: Hdg, Mat, and Gft however, the correlations were very low and would have little biological significance (Table 4). QTL for Hdg, Mat and Gft were coincident with a maximum of two of the five YLD QTL and never with *QYld.crc-1A* (Table 5; Fig. 1). A limited number of QTL studies have evaluated agronomic traits such as Hdg, Mat, and Gft and there are no consistent relationships between these traits and Yld (Börner et al. 2002; Marza et al. 2005). Photoperiod, vernalization, and "earliness per se" are groups of major genes known to control Hdg in hexaploid wheat (Shah et al. 1999). "Earliness per se" genes are known to map to groups 2 and 4, and to chromosomes 3A, 6B, and 7B (Shah et al. 1999). Four of the seven QTL identified for Hdg in the current study map to these same chromosomes and were coincident with QTL for Mat.

Superb alleles were associated with increased yield at four of the five identified grain yield QTL. Superb carries a Grandin allele at these four yield QTL whereas the Sumai 3 allele from BW278 was responsible for increasing yield at *QYld.crc.1A*. Sumai 3 is an adapted Chinese spring wheat cultivar with known resistance genes for Fusarium head blight (Bai et al. 1999) that has been widely used in spring wheat breeding programs. This finding suggests that there is a deficiency in Superb for grain yield at *QYld.crc-1A*.

Traditionally, breeding high yielding spring wheat cultivars has been accomplished by making direct selections for grain yield. Since yield is a complex trait with low heritability, early generation selection has generally not been effective and breeders usually maintain large breeding population for a number of generations before selecting for grain yield. In the current study, the grain yield QTL were coincident with an increase in at least one yield component suggesting selecting for a yield component could efficiently increase grain yield. High heritabilities were also observed for the yield components (Table 3). The results of the analysis indicated the potential improvement marker assisted selection could make in yield and yield components with the identified QTL. With future validation work, the identified grain yield and yield components QTL should allow marker assisted breeding strategies to be developed and implemented in spring wheat breeding programs.

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