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ORIGINAL PAPER

Molecular detection of QTLs for agronomic and quality traits in a doubled haploid population derived from two Canadian wheats (*Triticum aestivum* L.)

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Abstract Development of high-yielding wheat varieties with good end-use quality has always been a major concern for wheat breeders. To genetically dissect quantitative trait loci (QTLs) for yield-related traits such as grain yield, plant height, maturity, lodging, test weight and thousand-grain weight, and for quality traits such as grain and flour protein content, gluten strength as evaluated by mixograph and SDS sedimentation volume, an F_1-derived doubled haploid (DH) population of 185 individuals was developed from a cross between a Canadian wheat variety ''AC Karma'' and a breeding line 87E03-S2B1. A genetic map was constructed based on 167 marker loci, consisting of 160 microsatellite loci, three HMW glutenin subunit loci: *Glu-A1*, *Glu-B1* and *Glu-D1*, and four STS-PCR markers. Data for investigated traits were collected from three to four environments in Manitoba, Canada. QTL analyses were performed using composite interval mapping. A total of 50 QTLs were detected, 24 for agronomic traits and 26 for quality-related traits. Many QTLs for correlated traits were mapped in the same genomic regions forming QTL clusters. The largest QTL clusters, consisting of up to nine QTLs, were found on chromosomes 1D and 4D. HMW glutenin subunits at *Glu-1* loci had the largest effect on breadmaking quality; however, other genomic regions also contributed genetically to breadmaking quality. QTLs detected in the present study are compared with other QTL analyses in wheat.

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Introduction

Bread wheat (*Triticum aestivum* L.) is one of the most important crops in the world. Development of high-yielding wheat varieties with good end-use quality is paramount in wheat breeding. Grain yield and agronomic traits related to yield such as plant height, maturity and thousand-grain weight, and quality traits such as protein content, composition and strength are generally controlled by multiple genes. These traits are often influenced by environmental factors and exhibit high genotype–environment interaction. The genetic basis for most of these traits is not well elucidated. Molecular markers such as RFLPs and microsatellites, and their maps, make it possible to dissect quantitative trait loci (QTLs) controlling yield-related traits and quality traits.

QTL analyses in wheat were hampered by using RFLP markers because they showed a low level of polymorphism in wheat, especially in narrow crosses between two cultivars (Chao et al. 1989). To identify QTLs using RFLP markers, wheat geneticists had to create mapping populations using crosses between an adapted variety and a wild species or a synthetic wheat line. For instance, Börner et al. (2002) identified QTLs for agronomically important traits using the International Triticeae Mapping Initiative (ITMI) population, which was developed from a cross between the bread wheat variety ''Opata'' and a synthetic line W-7984. Keller et al. (1999) used recombinant inbred lines

(RILs) originating from a cross between the Swiss winter wheat ''Forno'' and the Swiss winter spelt ''Oberkulmer'' (*T. spelta* L.) for QTL analysis of lodging resistance. Moreover, genetic mapping of QTLs for grain yield and its components on single chromosomes 3A (Shah et al. 1999; Campbell et al. 2003), 4A (Araki et al. 1999) and 5A (Kato et al. 2000) of wheat have been reported by using recombinant substitution lines and RFLP markers.

Microsatellite markers, also termed simple sequence repeats (SSRs), reveal a higher level of polymorphism than RFLP markers in wheat. Microsatellite markers, which are chromosome-specific and evenly distributed along chromosomes (Röder et al. 1998; Somers et al. 2004; Sourdille et al. 2004), are ideally suited for tagging resistance genes, for marker-assisted selection and to assess genetic diversity in wheat (for reviews see Huang and Röder 2004; Röder et al. 2004). A large number of wheat microsatellite markers currently available (Pestsova et al. 2000; Röder et al. 1998; Somers et al. 2004; Sourdille et al. 2004) make it feasible to detect and map QTLs in a wheat population, even from a cross between two wheat cultivars. Huang et al. (2003, 2004) applied microsatellite markers and the advanced backcross QTL (AB-QTL) approach for detecting and transferring valuable QTL alleles for agronomic traits from unadapted wild relatives into cultivated hexaploid wheat, whereas Prasad et al. (2003) identified QTLs for grain protein content in bread wheat using microsatellite markers.

The objectives of the present study were to: (1) construct a genetic map based on microsatellite markers, three HMW (high molecular weight) glutenin subunit gene loci (*Glu-A1*, *Glu-B1* and *Glu-D1*), and four STS-PCR markers using a doubled haploid (DH) population from the cross between two Canadian wheat lines; (2) determine the number of QTLs for six agronomic traits and eleven quality traits and map them to their genomic positions; (3) compare the QTLs with those detected in the previously reported studies.

Materials and methods

Plant materials and population development

A population of 414 DH lines was produced by hybridization with maize pollen of wheat F_1 hybrid plants from the cross between the Canadian white seed coat variety ''AC Karma'' (Canadian Prairie Spring wheat) and a breeding line 87E03-S2B1. The pedigree of ''AC Karma'' is HY-320*5/BW-553//HY-358(F2)/3/HY-358/7915-QX-76-B-2 and the pedigree of HY-358 is Glenlea/HY-320//HY-320/HY-402 (http://www.genbank.vurv.cz/wheat/pedigree/). The line 87E03-S2B1 was derived from the cross Glenlea/C7932 followed by seven backcrosses to the variety ''Glenlea'' (Canadian Western Extra Strong wheat). The line C7932 contributed the white seed coat colour alleles on homoeologous group 3 chromosomes. As a consequence, line 87E03-S2B1 is referred to as white Glenlea. The two parents of the mapping population were chosen because they have different HMW glutenin subunit composition, but very similar low molecular weight (LMW) glutenin and gliadin patterns. AC Karma has subunits 1, 7* + 9 and 2 + 12 at the *Glu-A1*, *Glu-B1* and *Glu-D1* loci, respectively, whereas the line 87E03-S2B1 has 2*, overexpressed 7 (H7) + 8 and 5 + 10. A subset of 185 DH lines of the original 414 lines was used in the present study.

Field trials

The field trials were conducted at three different locations in Manitoba, Canada in the years 1999 and 2000: Glenlea 1999, Portage La Praire 2000, Brandon 2000, and Glenlea 2000. A complete randomized block design was used for the field trials. The 185 DH lines were planted in a single replication at each location. In summer 1999, all lines were grown in single 1 m long rows and parental lines were grown in three-row plots each, whereas in summer 2000, all lines and parental lines were grown in 4 m long five-row plots. All trials were sprayed with the fungicide TILT (Syngenta Crop Protection) at anthesis to reduce potential infection by *Fusarium graminearum*.

Evaluation of agronomic traits

Grain yield and five agronomic traits related to yield were evaluated for each plot at three locations in the summer of 2000. Grain yield per plot (YLD) was evaluated based on the grain harvested from all plants in each plot. Test weight (TW) was measured in kilograms per hectolitre for each plot. Thousand-grain weight (TGW) was measured in grams as the average weight of two independent samples of 1,000 grains from each plot. Days to maturity (DTM) were evaluated as the number of days from seeding until 75% of the plants in the plots showed discoloured peduncles. Plant height (HT) was calculated as the average height of approximately ten stems in cm from the soil surface to the tip of the spike (awns excluded). Lodging (Ldg) was scored before harvest, using a scoring scale ranging from 1 (all plants in the plot upright) to 9 (all plants in the plot flat), depending on the degree of lodging.

Quality analyses

Clean grain (50 g) of each parental and a random subset of 124 DH lines from each year and location was used for quality analyses.

Grain and flour protein content

Grain protein content (GPC) was determined by near-infrared reflectance (NIR) (Approved Method 39-25, AACC 2000). Moisture content required for grain conditioning was determined simultaneously. Grain was tempered to 15% moisture in two steps (Approved Method 26-95, AACC 2000). Conditioned grain samples were milled with a Brabender Quadrumat laboratory mill (Brabender GmbH, Duisburg, Germany). Combustion nitrogen analysis (model FP-428, Leco Corp) was used to estimate total protein content of Brabender milled flour. Flour protein content (FPC) was obtained using a conversion factor of $N \times 5.7$ expressed on 14% moisture basis (mb).

Mixograph

A multichannel, computer-based, 10-g mixograph was used to test dough physical properties (Pon et al. 1989). Brabender milled flour (10 g) was mixed with 6.2 ml (62% absorption) of distilled water. Torque was recorded and data were analyzed electronically. Eight parameters from mixograph curves were obtained: peak height of mean curve (PKH); mixing development time (MDT); energy to peak (ETP); first minute slope (FMS); peak bandwidth (PBW); slope after peak (SAP); total energy (TEG); bandwidth energy (BWE).

SDS sedimentation volume

Whole grain flour obtained using the Udy cyclone mill (UDY Corporation, Fort Collins, USA) was used for the SDS sedimentation test. For each sample, 2.5 g of ground whole meal was analyzed using lactic acid (85%, v/v) and sodium dodecyl sulfate (12%, v/v) in standard 25×200-mm cylinder tubes (Approved Method 56-70, AACC 2000). Sedimentation volume (SV, ml) was recorded.

Statistical analysis of phenotypic trait data

Using general linear model (GLM) procedure of Statistical Analysis System (SAS) v8.2 (SAS Institute Inc., Cary, NC, USA), analysis of variance (ANOVA) was performed to determine the significance of differences among the genotypes of the population and among the locations (environments). Pearson's correlation coefficients between traits were calculated using the procedure CORR of SAS. Heritability (H^2) and confidence intervals (CI) were calculated using the GLM procedure of SAS according to Knapp et al. (1985). Formula for estimating H^2 is

$$\hat{H}^2 = 1 - M_2/M_1$$

where M_1 and M_2 are mean square for genotype and genotype × enviroment, respectively. In this study, replications $r = 1$, it was not possible to estimate genotype × enviroment interaction variance. Mean square for residual error is used as M_2.

Exact confidence limits for H^2 are

$$1-\alpha = P\{1-[(M_1/M_2)F_{1-\alpha/2:df_2,df_1}]^{-1} \leq H^2 \leq 1-[(M_1/M_2)F_{\alpha/2:df_2,df_1}]^{-1}\}$$

where $\alpha = 0.10$, and df_1 and df_2 are degree of freedom for genotype and genotype × enviroment, respectively.

Protein extraction, SDS-PAGE and PCR amplification of STS markers

Protein extraction, SDS-PAGE, and PCR amplification of STS markers for all three HMW glutenin coding regions were described by Lukow et al. (1992) and Radovanovic and Cloutier (2003). A co-dominant PCR marker for the allele encoding HMW glutenin subunit Ax2*, a dominant and a co-dominant marker for the allele encoding the over-expressed HMW glutenin subunit Bx7, and a dominant marker for the allele encoding HMW glutenin subunit Dx5 developed by Radovanovic and Cloutier (2003) were designated as STS-Ax2*, STS-Bx7.1, STS-Bx7.2 and STS-Dx5, respectively.

Microsatellite marker analyses and construction of genetic map

Total genomic DNA was extracted from leaf tissue of individual plants including the two parents ''AC Karma'' and 87E03-S2B1, and each of 185 DH lines using the DNeasy 96 Plant Kit (Qiagen, Missisauga, ON, Canada). Microsatellite polymorphism was determined using parental DNA. Primer sequences for gwm, gdm, wmc, and barc microsatellite markers were available from Röder et al. (1998), Pestsova et al. (2000), the Graingenes website (http://www.wheat.pw.usda.gov/ggpages/SSR/WMC/), and the US wheat and barley scab initiative website (http://www.scabusa.org/pdfs/BARC_SSRs_011101.html), respectively. The poly-

morphic microsatellite markers, three HMW-GS loci, *Glu-A1*, *Glu-B1* and *Glu-D1*, and four STS-PCR markers were used for constructing the genetic map that was subsequently used for QTL analysis.

Raw data for microsatellite fragments were collected using M13 tailing and fluorescent capillary electrophoresis on an ABI3100 Genetic Analyser (Applied Biosystems, Foster City, CA USA) (Schuelke 2000). The polymerase chain reactions (PCR) were performed according to Somers et al. (2004) with slight modifications. PCR contained 45 ng genomic DNA as template, 1× PCR buffer, 1.5 mM $MgCl_2$, 0.8 mM dNTPs, 2 pmol reverse primer, 0.2 pmol forward primer, 1.8 pmol M13 primer (CACGACGTTGTAAAACGAC) fluorescently labeled with 6-FAM, HEX or NED (Applied Biosystems), 0.5 U *Taq* DNA polymerase in a total volume of 10 µl. The PCR reactions were carried out in a DNA engine PTC-200 thermocycler (MJ Research Inc., Incline Village, NV, USA). After 2 min denaturation at 93°C, 31 cycles were performed with 1 min at 94°C (0.5°C/s to 49 or 58°C), 50 s at 49 or 58°C (depending on the individual microsatellite marker), (0.5°C/s to 72°C), 1 min at 72°C (0.5°C/s to 94°C) and a final extension step of 5 min at 72°C before cooling to 4°C. The internal size standard for the ABI3100 was Genescan-500 Rox (Applied Biosystems). Data collected by fluorescent capillary electrophoresis were converted to a gel-like image with Genographer (available at http://www.hordeum.oscs.montana.edu/genographer).

The genetic map was constructed with MAPMAKER/Exp version 3.0b (Lander et al. 1987). The commands ''group'' with LOD scores ≥ 3.0, ''try'', ''compare'' and ''ripple'' were used to develop the linkage map. Unlinked groups were oriented and placed to the same chromosome based on the microsatellite consensus map (Somers et al. 2004). The Kosambi mapping function (Kosambi 1944) was used to convert recombination fractions into centiMorgans (cM) as map distances.

QTL analysis

The positions and effects of QTLs averaged over all the environments (means) were determined by composite interval mapping (CIM) using QTL Cartographer v. 2.0 (Wang et al. 2004). CIM (Zeng 1994; Basten et al. 2001) combines interval mapping with multiple regression. The statistical model is defined as

$$Y = x^*b^* + z^*d^* + XB + E$$

where Y is a vector of trait values. b^* and d^* are the additive and dominance effects of the putative QTL being tested. x^* and z^* are indicator variable vectors specifying the probabilities of an individual being in different genotypes for the putative QTL constructed by flanking makers. B is the vector of effects of other selected markers fitted in the model. X is the marker information matrix for those selected markers. E is the error vector (Basten et al. 2001).

Model 6 was used for CIM. In this model, a window size and the number of markers to control the genetic background are the two parameters used. CIM fits parameters for a target QTL in one interval while simultaneously fitting partial regression coefficients for background markers to account for variance caused by non-target QTL. For model 6, a window size of 10 cM was used for adding markers during the forward stepwise regression and for deleting markers during the backward elimination step. Five marker cofactors with a 2 cM window were used to control background effects (Basten et al. 2001; Wang et al. 2004). The significant threshold for detection of QTLs was calculated based on 1,000 permutation tests at $P \leq 0.05$ (Churchill and Doerge 1994; Doerge and Churchill 1996), with an average likelihood ratio of 13.7, corresponding to a LOD score of 2.97. We decide to use a LOD score ≥ 2.9 to declare a QTL in the present study.

The proportion of observed phenotypic variance explained by a QTL was estimated as the coefficient of determination (R^2) using maximum likelihood for CIM (Basten et al. 2001).

The trait will have a variance s^2. Under the null hypothesis ($b^* = 0$ and $d^* = 0$)

$$H_0 : Y = XB + E$$

the sample variance of the residuals will be s_0^2. For a given alternative model, say

$$H_1 : Y = x^*b^* + z^*d^* + XB + E$$

the variance of the residuals would be s_1^2. R^2 is estimated by

$$R^2 = \left(s_0^2 - s_1^2\right)/s^2.$$

If confidence intervals of three and more QTLs for different traits are overlapped in a chromosomal region, these QTLs are considered as a QTL cluster.

Results

Means and heritability of agronomic and quality traits, and ANOVA for genotypes and environments

Mean values of traits for the parents ''AC Karma'' and 87E03-S2B1, and for the DH lines over environments are shown in Table 1. Large differences between the parents were observed for all quality traits and for several agronomic traits such as TGW and plant height, whereas small differences between the two parents were found for grain yield, lodging, test weight and days to maturity. The wide range of variation of the investigated traits (Table 1) and the normal phenotypic distributions (data not shown) indicated transgressive segregations, suggesting polygenic inheritance of the traits.

Estimates of heritability of the traits varied much from trait to trait. Two agronomic traits grain yield and lodging, and two quality traits peak bandwidth and bandwidth energy were estimated to have low heritability. The other agronomic and quality traits had high heritability estimates (Table 1).

The mean square (MS) of ANOVA-GLM for the genotypes and environments was calculated (data not shown). Significant differences among genotypes of DH lines were found for all 17 investigated traits ($P < 0.01$). But significant differences among environments were also observed for all traits ($P < 0.01$), indicating that these traits were influenced by environmental factors.

Correlations between traits

The correlation coefficients between six agronomic traits and between eleven quality traits were calculated, respectively. Grain yield (YLD) showed a significant positive correlation with TW and TGW, but a negative correlation with days to maturity (DTM). There was a significant positive correlation between TW and TGW and plant height (HT). Positive correlations were also found between DTM and HT and lodging (LDG), and between HT and LDG.

Grain protein content (GPC) was highly correlated with flour protein content (FPC). Both GPC and FPC showed a positive correlation with SDS sedimentation volume (SV) and most mixograph parameters except mixing development time (MDT) and energy to peak (ETP). The strongest correlation ($r = 0.943$) was observed between MDT and ETP. Negative correlations were found between YLD and GPC ($r = –0.043$), and between YLD and FPC ($r = –0.115$), but were not significant.

Construction of genetic map

Four hundred and eighty-nine microsatellite markers were evaluated for polymorphism between the two parents ''AC Karma'' and 87E03-S2B1. A total of 191

Table 1 Means, range, heritability (H^2) and confidence intervals (CI) of traits investigated for the AC Karma/87E03-S2B1 DH lines and parental lines

Trait	Parental lines		DH lines				
	AC Karma	87E03-S2B1	Mean	SD	Range	H^2	CI for H^2
Grain yield (t/ha)	3.04	3.22	2.61	0.42	1.17–3.52	0.37	0.22[a]–0.49[b]
Test weight (kg/hl)	72.7	74.7	72.2	3.02	61.3–77.3	0.91	0.89–0.93
Thousand-grain weight (g)	29.0	39.0	31.2	3.92	21.7–41.0	0.92	0.91–0.94
Plant height (cm)	87	102	91.0	9.2	69.0–109.0	0.92	0.91–0.94
Days to maturity (day)	93	94	95.3	2.85	89.0–102.0	0.76	0.71–0.81
Lodging	4	6	4.7	1.2	2.3–8.0	0.41	0.28–0.53
Grain protein content (%)	12.9	14.0	13.58	0.60	12.25–15.13	0.81	0.76–0.85
Flour protein content (14% mb)	12.0	13.4	13.0	0.67	11.4–15.2	0.79	0.73–0.84
Mixing development time (min)	2.2	5.4	3.45	1.21	1.55–6.30	0.89	0.86–0.91
Peak height (cm)	0.12	0.17	0.15	0.02	0.11–0.20	0.74	0.67–0.80
Energy to peak (N m)	11.8	37.4	21.57	6.81	9.78–38.70	0.89	0.86–0.91
First minute slope (Nm/min)	0.064	0.076	0.074	0.016	0.03–0.11	0.75	0.68–0.81
Peak bandwidth (N m)	0.067	0.089	0.094	0.012	0.06–0.14	0.46	0.31–0.58
Slope after peak (N m/min)	0.014	0.007	0.013	0.005	0.0–0.03	0.74	0.67–0.80
Total energy (N m)	55.57	79.43	65.64	7.66	49.80–86.58	0.68	0.60–0.75
Bandwidth energy (N m)	36.59	48.50	41.49	5.56	29.60–55.18	0.45	0.31–0.58
SDS sedimentation volume (ml)	61.0	76.0	62.05	5.75	47.75–78.0	0.84	0.80–0.88

[a]The lower 90% confidence limit for heritability

[b]The upper 90% confidence limit for heritability

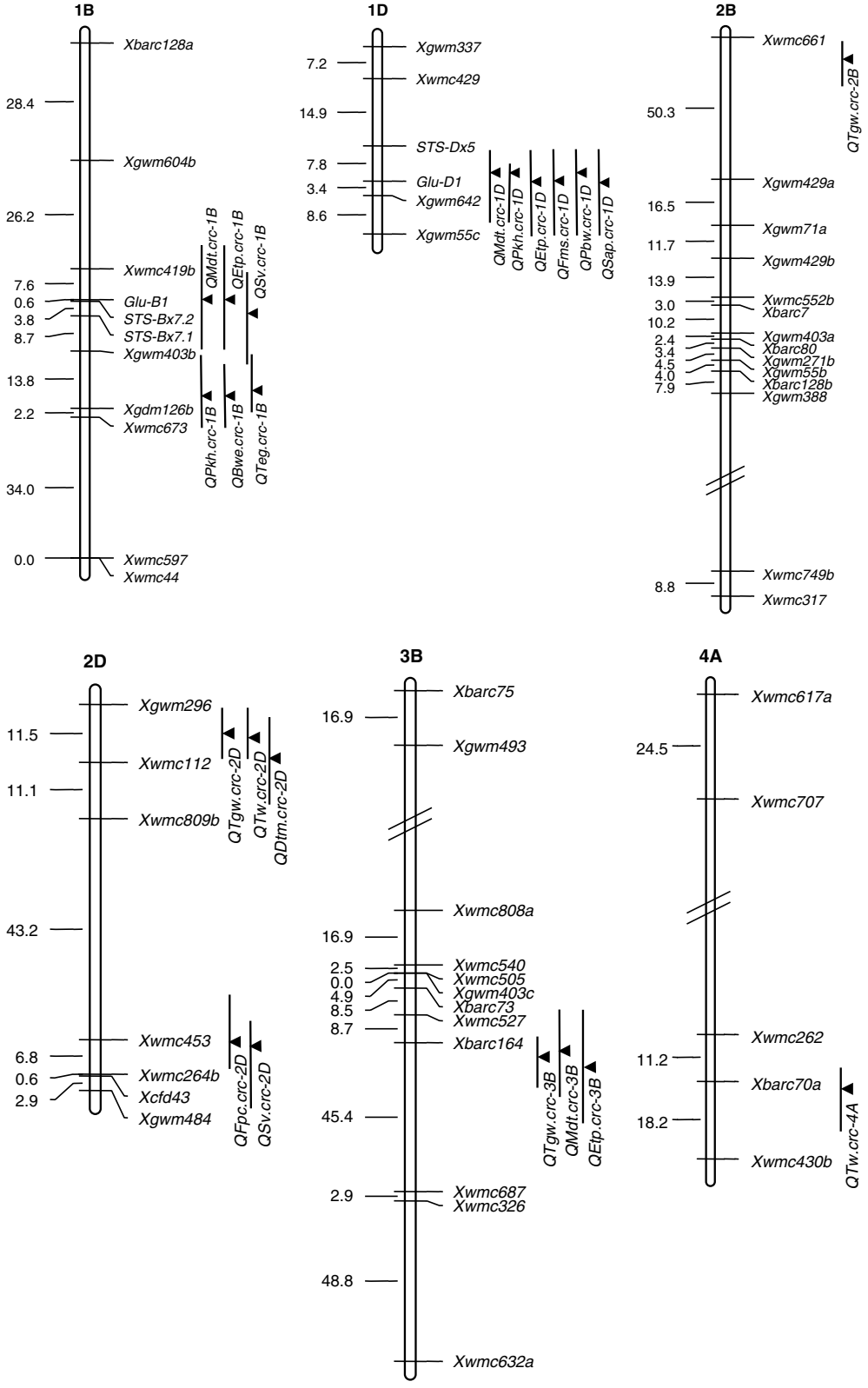

Fig. 1 Fifty QTLs for agronomic traits and quality parameters on the genetic map of the 185 AC Karma/87E03-S2B1 F_1-derived DH lines. Mapped markers are indicated on the *right* and their corresponding genetic distances (cM) are indicated on the *left*. QTL confidence interval with a LOD score ≥ 3 is indicated by a *vertical bar*, whereas LOD max is pointed by a *triangle*. Gaps in the genetic map were indicated with *hatched lines*

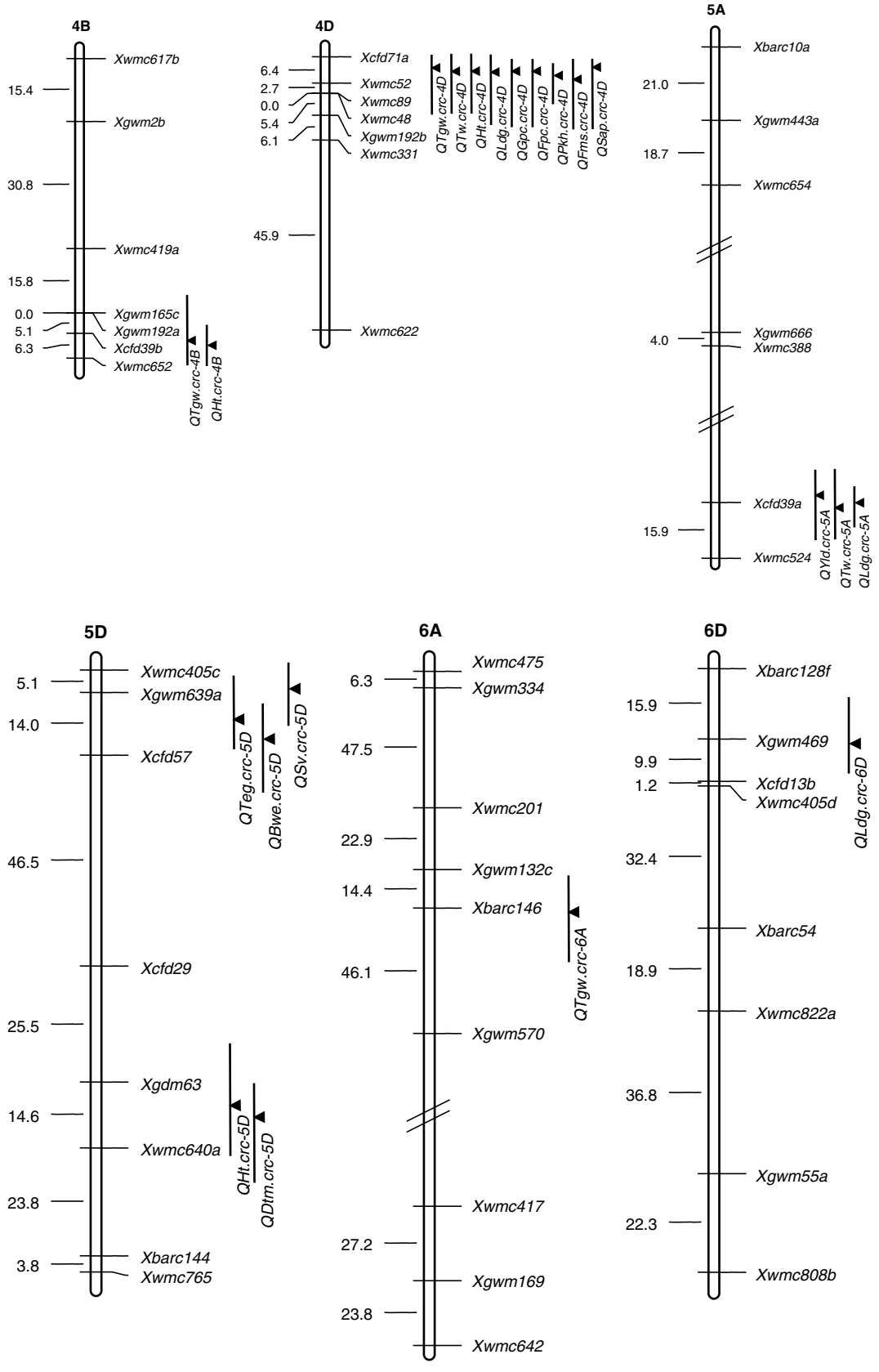

Fig. 1 continued

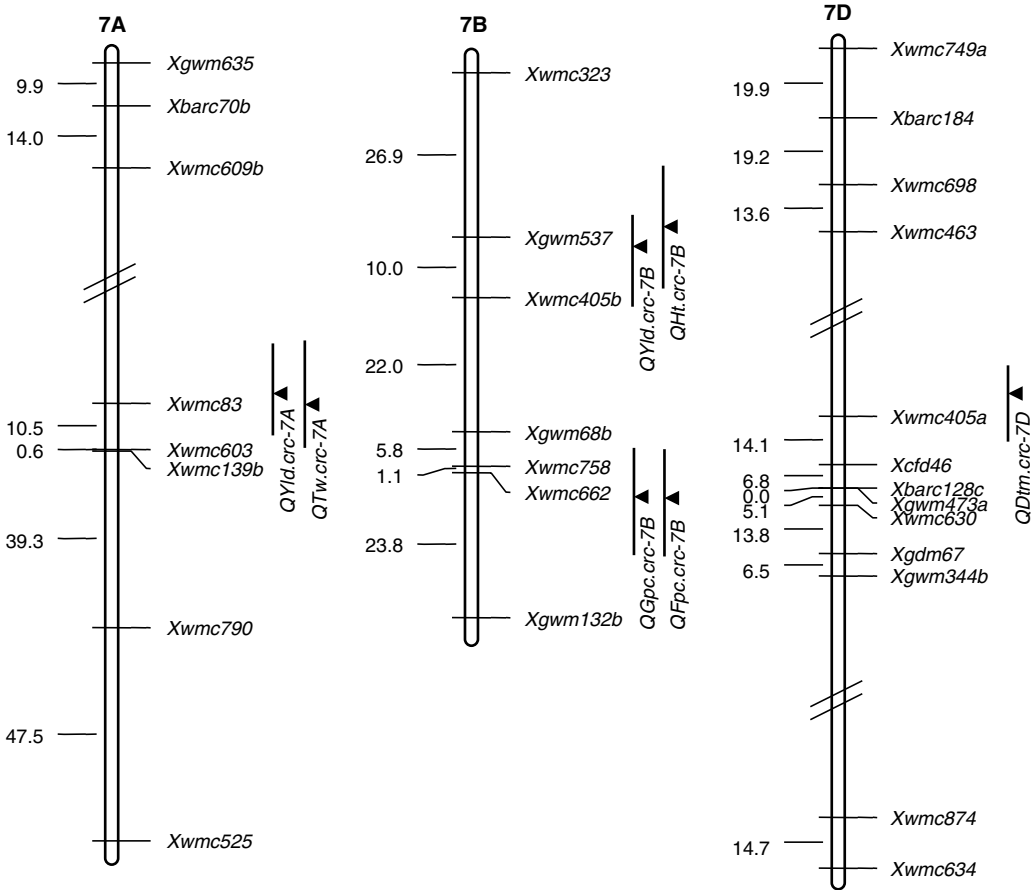

Fig. 1 continued

(39.0 %) microsatellite markers were polymorphic. In total, 173 loci, consisting of 166 microsatellite loci, three HMW glutenin subunit gene loci *Glu-A1*, *Glu-B1* and *Glu-D1*, and four STS-PCR markers were used to genotype 185 DH lines. In all, 167 loci were mapped to 21 wheat chromosomes (Fig. 1) and six microsatellite loci (*Xbarc128d*, *Xgwm271a*, *Xgwm473b*, *Xwmc488b*, *Xwmc139a* and *Xwmc822b*) remained unlinked. The STS marker STS-Ax2* co-segregated with *Glu-A1*. Both STS-Bx7.1 and STS-Bx7.2 were tightly linked to *Glu-B1* with genetic distances of 0.6 and 4.4 cM, respectively. STS-Dx5 was mapped 7.8 cM proximal from *Glu-D1*. The genetic map spanned 2403.9 cM with an average marker distance of 14.4 cM. The marker numbers in the three genomes A, B and D were 51, 65 and 51, respectively. The marker orders were consistent with the microsatellite maps published by Röder et al. (1998) and Somers et al. (2004).

QTLs detection

QTLs detected by CIM are listed in Table 2, and their map positions are shown in Fig. 1. A total of 50 QTLs were identified, ranging from 1 to 6 QTLs for each trait. They were mapped to 19 chromosomal locations with 1–9 QTLs per cluster, the largest cluster being in the *Xcfd71a–Xwmc52* interval of chromosome 4D. The confidence intervals are indicated on the map.

Grain yield

Three QTLs, located on chromosomes 5A, 7A and 7B, had an effect on grain yield. These three QTLs accounted for 8.1 to 11.0% of the phenotypic variation with the effect attributed to the ''AC Karma'' alleles for increased grain yield. Two QTLs, namely *QYld.crc-7A* and *QYld.crc-7B*, were mapped in homoeologous positions.

Plant height

Four QTLs significantly influenced plant height and mapped to four chromosomes. For all the QTLs, the 87E03-S2B1 alleles increased plant height. The phenotypic variation explained by individual QTLs ranged from 4.1 to 29.2%.

Lodging

Three QTLs were identified for plant lodging, with phenotypic variance ranging from 6.4 to 10.9%. For two of them, *QLdg.crc-5A* and *QLdg.crc-6D*, the ''AC Karma'' alleles increased plant lodging. For *QLdg.crc-4D*, the 87E03-S2B1 allele increased plant lodging.

Test weight

Five QTLs were associated with test weight. For the QTLs located on chromosomes 4A and 4D, the 87E03-S2B1 allele increased test weight, whereas for the QTLs on 2D, 5A, and 7A, the ''AC Karma'' allele increased test weight. The QTLs on chromosomes 4A and 4D were not in homoeologous position. The phenotypic variation explained by these individual QTLs ranged from 5.1 to 13.1%.

Thousand-grain weight

Six QTLs, distributed on six chromosomes, were significantly associated with TGW. For three of six QTLs, the 87E03-S2B1 allele increased TGW. The largest portion of the total phenotypic variation (R^2 = 26.3%) was explained by *QTgw.crc-4D* with an additive effect of up to a 2.0 g increase from the 87E03-S2B1 allele (Table 2).

Days to maturity

Three QTLs were detected for days to maturity, *QDtm.crc-2D*, *QDtm.crc-5D* and *QDtm.crc-7D*. These three QTLs explained 5.0, 6.8 and 31.6% of the phenotypic variance, respectively. For all three QTLs, the 87E03-S2B1 allele delayed maturity.

Grain and flour protein content

Two genomic regions were simultaneously associated with grain protein content and flour protein content. This is consistent with the significant positive correlation between GPC and FPC. Two QTLs explained 12.6 and 32.7% of the phenotypic variation. At the two QTL loci, the 87E03-S2B1 alleles caused significant increase in protein content. QTL on chromosome 2D was detected only for flour protein content. For this QTL, the ''AC Karma'' allele increased protein content.

Mixograph parameters

Three QTLs on chromosomes 1B, 1D and 3B were detected for MDT. *QMdt.crc-1D* associated with *Glu-D1* had the largest effect from 87E03-S2B1 with LOD = 26.8 and explained 55.9% of the phenotypic variance. The third QTL on chromosomes 3B had relatively smaller effect.

Three QTLs were detected for PKH, explaining from 13.5 to 20.5% of the phenotypic variance with a corresponding LOD of 3.3–8.5. The QTL *QPkh.crc-1D* had the largest effect and was identified from an ''AC Karma'' allele. For the other two QTLs, the 87E03-S2B1 alleles increased PKH.

Three QTLs on chromosomes 1B, 1D and 3B were associated with ETP. For all three QTLs, the 87E03-S2B1 alleles increased ETP. The *QEtp.crc-1D* associated with *Glu-D1* had the largest effect with LOD = 23.8 and explained 49.9% of the phenotypic variance.

FMS was associated with two genomic regions where QTLs were identified. For one QTL *QFms.crc-1D*, the ''AC Karma'' allele increased FMS, whereas for another QTL on chromosome 4D, the 87E03-S2B1 allele increased FMS. The phenotypic variance explained by the two QTLs was 14.5 and 27.2%, respectively.

Only one QTL was found for PBW on chromosome 1D. The QTL *QPbw.crc-1D* had an effect from ''AC Karma'', explaining 14.84% of the variance with a LOD score of 5.5.

Two QTLs were detected for SAP. For QTL on chromosome 1D, the AC Karma allele contributed to SAP. Another QTL mapped on chromosome 4D increased SAP from the 87E03-S2B1 allele. Two QTLs explained 13.1 and 38.6% of the phenotypic variance, respectively.

Two QTLs, on chromosomes 1B and 5D, influenced TEG, but the QTL on chromosome 1B was not associated with *Glu-B1*. These two QTLs each explained more than 14% of the phenotypic variance. For both QTLs, the 87E03-S2B1 allele increased TEG.

Two QTLs associated with BWE mapped on chromosomes 1B and 5D. For these two QTLs, the 87E03-S2B1 allele showed an increasing effect on BWE. Two QTLs explained 10.9% for *QBwe.crc-5D* and 15.7% for *QBwe.crc-1B* of the phenotypic variance, respectively.

SDS sedimentation volume

Three QTLs were identified for SDS-SV. These individual QTLs explained 8.8–14.9% of the phenotypic variance with a LOD of 3.7–5.9. For two QTLs, the 87E03-S2B1 alleles increased SDS-SV, while for the QTL *QSv.crc-2D*, the alleles from ''AC Karma'' increased SDS-SV.

Table 2 QTLs for agronomic and quality traits detected in the AC Karma/87E03-S2B1 F_1-derived doubled haploid population

Trait	QTL	Closest marker	LOD[a]	R^2 (%) [a]	Additive effect [b]
Grain yield	*QYld.crc-5A* [c]	*Xcfd39a*	4.7	11.0	-1.40
	QYld.crc-7A	*Xwmc83*	3.1	8.1	-1.54
	QYld.crc-7B	*Xgwm537*	2.9	8.8	-1.25
Plant height	*QHt.crc-4B*	*Xwmc652*	2.9	4.1	1.93
	QHt.crc-4D	*Xwmc52*	14.0	29.2	4.96
	QHt.crc-5D	*Xwmc640a*	5.4	8.5	2.74
	QHt.crc-7B	*Xgwm537*	3.8	7.7	2.55
Lodging	*QLdg.crc-4D*	*Xwmc52*	3.3	6.4	0.29
	QLdg.crc-5A	*Xcfd39a*	5.1	10.9	-0.52
	QLdg.crc-6D	*Xgwm469*	3.2	6.7	-0.30
Test weight	*QTw.crc-2D*	*Xwmc112*	3.0	5.1	-0.70
	QTw.crc-4A	*Xbarc70a*	3.5	5.4	0.71
	QTw.crc-4D	*Xwmc52*	7.8	13.1	1.10
	QTw.crc-5A	*Xcfd39a*	4.7	8.5	-0.88
	QTw.crc-7A	*Xwmc83*	6.0	10.6	-0.99
Thousand-grain weight	*QTgw.crc-2B*	*Xwmc661*	3.1	6.6	-1.01
	QTgw.crc-2D	*Xwmc112*	6.5	9.2	-1.20
	QTgw.crc-3B	*Xbarc164*	3.1	3.7	-0.76
	QTgw.crc-4B	*Xcfd39b*	4.6	6.1	0.98
	QTgw.crc-4D	*Xcfd71a*	10.9	26.3	2.00
	QTgw.crc-6A	*Xbarc146*	7.3	13.9	1.46
Days to maturity	*QDtm.crc-2D*	*Xwmc112*	2.9	5.0	0.66
	QDtm.crc-5D	*Xwmc640a*	3.2	6.8	0.76
	QDtm.crc-7D	*Xwmc405a*	6.7	31.6	1.62
Grain protein content	*QGpc.crc-4D*	*Xwmc52*	8.3	32.7	0.36
	QGpc.crc-7B	*Xwmc662*	4.5	12.6	0.21
Flour protein content	*QFpc.crc-2D*	*Xwmc453*	3.1	6.6	-0.21
	QFpc.crc-4D	*Xwmc52*	7.2	28.6	0.44
	QFpc.crc-7B	*Xwmc662*	6.3	16.5	0.34
Mixing development time	*QMdt.crc-1B*	*Glu-B1*	12.6	14.9	0.47
	QMdt.crc-1D	*Glu-D1*	26.8	55.9	0.93
	QMdt.crc-3B	*Xbarc164*	5.4	6.0	0.31
Peak height	*QPkh.crc-1B*	*Xgdm126b*	6.5	14.8	0.008
	QPkh.crc-1D	*Glu-D1*	8.5	20.5	-0.009
	QPkh.crc-4D	*Xwmc52*	3.3	13.5	0.007
Energy to peak	*QEtp.crc-1B*	*Glu-B1*	15.1	20.9	3.19
	QEtp.crc-1D	*Glu-D1*	23.8	49.9	4.97
	QEtp.crc-3B	*Xbarc164*	5.0	6.1	1.72
First minute slope	*QFms.crc-1D*	*Glu-D1*	11.7	27.2	-0.009
	QFms.crc-4D	*Xwmc52*	4.3	14.5	0.006
Peak bandwidth	*QPbw.crc-1D*	*Glu-D1*	5.5	14.8	-0.005
Slope after peak	*QSap.crc-1D*	*Glu-D1*	16.6	38.6	-0.003
	QSap.crc-4D	*Xcfd71a*	3.8	13.1	0.002
Total energy	*QTeg.crc-1B*	*Xgdm126b*	5.6	14.9	3.22
	QTeg.crc-5D	*Xcfd57*	4.7	14.1	2.89
Bandwidth energy	*QBwe.crc-1B*	*Xgdm126b*	4.9	14.8	2.14
	QBwe.crc-5D	*Xcfd57*	2.9	7.4	1.55
SDS sedimentation volume	*QSv.crc-1B*	*STS-Bx7.2*	5.9	14.9	2.15
	QSv.crc-2D	*Xwmc453*	3.7	14.2	-2.19
	QSv.crc-5D	*Xgwm639a*	3.7	8.8	1.71

[a]Values calculated from the overall mean

[b]Positive value are associated with an increasing effect from 87E03-S2B1 alleles and negative value are associated with an increasing effect from AC Karma alleles

[c]Nomenclature for QTLs in wheat: the *Q* for QTLs should be followed by a trait designator, a period, a laboratory designator, a hyphen (-) and the symbol for the chromosome in which the QTL is located

Distribution of the detected QTLs

Of 50 QTLs detected in the present study, the highest number of QTLs was found in the D genome, with 27 QTLs (54%); 7 (14%) and 16 (32%) QTLs were found in genomes A and B, respectively (Table 2; Fig. 1). The number of QTLs from homoeologous groups 1 to 7 were 12 (24%), 6 (12%), 3 (6%), 12 (24%), 8 (16%),

2 (4%) and 7 (14%), respectively. Except for chromosomes 1A, 2A, 3A, 3D, 5B and 6B, these QTLs were distributed on the other 15 chromosomes. Eight QTL clusters were observed on seven chromosomes 1B, 1D, 2D, 3B, 4D, 5A and 5D (Fig. 1), of which two QTL clusters with three QTLs each were found on chromosome 1B. The largest QTL cluster consisting of nine QTLs was found on chromosome 4D, followed by QTL cluster on chromosome 1D with six QTLs.

Discussion

In the present study, we detected 50 QTLs for six agronomic traits and eleven quality-related parameters using a DH population derived from a cross between a Canadian wheat variety and an adapted breeding line in combination with composite interval mapping (CIM).

QTLs for agronomic traits

Three QTLs for grain yield were identified. The ''AC Karma'' alleles were associated with a positive effect on grain yield for all three QTLs. No QTLs for grain yield were detected to have a positive effect from 87E03-S2B1 (Table 2), even though its yield was slightly higher than that of ''AC Karma'' (Table 1). 87E03-S2B1 (White Glenlea) was developed for the Manitoba environment, while ''AC Karma'' was developed in the brown and dark brown soil zones of the Central Prairies. The yield test indicated that ''AC Karma'' possesses potential to increase grain yield in the Eastern Prairies (Knox et al. 1995). ''Glenlea'' is present in the pedigree of ''AC Karma'' and the yield-increasing QTL alleles from 87E03-S2B1 (White Glenlea) may not be segregating in this population. Another possible explanation could be that the yield-increasing alleles are identical between the two lines. The three yield-QTLs were mapped on chromosomes 5A, 7A and 7B, respectively (Table 2; Fig. 1). Yield-QTLs on chromosomes 5A and 7A were also coincident with the QTLs for test weight. Kato et al. (2000) mapped a yield QTL in the similar location on chromosome 5AL.

Four QTLs for plant height were mapped to chromosomes 4BL, 4DS, 5DL and 7BS. The height-QTL on chromosome 7BS was found at the same location as the QTL for grain yield (Fig. 1). For this location, the 87E03-S2B1 allele increased plant height, but decreased grain yield (Table 2). Twenty-one *Rht* (reduced plant height) genes have been identified to date (McIntosh et al. 1998), of which two GA-insensitive semi-dwarfing genes *Rht-B1b* (*Rht1*) *Rht-D1b* (*Rht2*) have been successfully used in wheat breeding programs worldwide and are located on chromosomes 4B and 4D, respectively. The ''AC Karma'' alleles at locus *QHt.crc-4D* that decreased plant height corresponded to the presence of *Rht-D1b* (R DePauw, personal communication; Knox et al. 1995). But the QTL on the long arm of chromosome 4B was not linked to *Rht-B1b* (*Rht1*), which is located on the short arm of chromosome 4B. Height QTLs mapped in the similar locations of chromosomes 4B and 4D were also presented by Cadalen et al. (1998) and McCartney et al. (2005). The QTLs controlling plant height identified on chromosomes 1AS, 1BL and 7AL found by Cadalen et al. (1998) and Börner et al. (2002) were not detected in the present study.

In general, an increase in plant height can result in increased lodging severity. This was confirmed by the results that lodging was significantly correlated with plant height, and one of three QTLs for lodging coincided with a plant height QTL. This QTL was located on chromosome 4DS (Table 2; Fig. 1). For QTLs, *QLdg.crc-5A* and *QLdg.crc-6D*, the 87E03-S2B1 allele decreased lodging severity. Keller et al. (1999) identified nine QTLs for lodging, of which five QTLs were coincident with QTLs for plant height. Only QTL *QLdg.crc-5A* detected in this study was in a similar position to a QTL for lodging on chromosome 5AL identified by Keller et al. (1999). This QTL was associated with the yield QTL, *QYld.crc-5A*. In this genomic region, the ''AC Karma'' allele increased lodging severity and also increased grain yield. It appears that the heavy grains lead to increased lodging severity.

Of five QTLs detected for test weight, two QTLs on chromosomes 5A and 7A were coincident with QTLs for grain yield, and one QTL on chromosome 4DS was located in the same position as the QTL for plant height (Fig. 1). This is consistent with the result that test weight was significantly correlated with plant height. *QTw.crc-7A* was located in a similar position to a QTL for test weight on chromosome 7AS detected by Elouafi and Nachit (2004) in a durum wheat population.

The QTLs for TGW were detected on chromosomes 4BL and 4DS, and were mapped in the same genomic regions as the QTLs for plant height (Fig. 1). Four TGW QTLs on chromosomes 2D, 4B, 4D and 6A were stable across all environments (data not shown) making them good candidates for marker-assisted selection. At two QTL loci on chromosomes 2D and 4D, increased TGW was associated with increased TW making these QTLs good candidates to assist in the development of large and densely filled seeds. The

QTL, *QTgw.crc-4D* on chromosome 4DS was in a comparable location to the QTL *QTgw.ipk-4D* (Huang et al. 2003).

QDtm.crc-2D was located in a similar position to the photoperiodic insensitivity gene *Ppd-D1* on the short arm of chromosome 2D (Pestsova and Röder 2002), and was associated with TW and TGW. At this locus, delayed maturity was related with decreased TW and TGW. *QDtm.crc-5D* was in the same location as the QTL for plant height and delayed maturity was associated with increased plant height (Table 2; Fig. 1). The QTL *QDtm.crc-7D* was in a similar location to the QTL for ear emergence time *QEet.ipk-7D* (Huang et al. 2004).

QTLs for quality-related traits

Bread wheat quality can be defined in many ways. The fabrication of bread with its appealing qualities of volume, texture and taste will ultimately dictate the fate of the wheat varieties in their intended markets. As a consequence, breeders have very specific targets of quality for each class of wheat. Grain and flour protein contents have a major impact on the end product.

Grain protein content is considered a quantitative trait controlled by several genes distributed throughout the entire genome in tetraploid (Blanco et al. 2002; Joppa et al. 1997; Khan et al. 2000; Mesfin et al. 1999) and hexaploid wheats (Börner et al. 2002; Groos et al. 2003; Prasad et al. 2003). Two genomic regions were associated with both grain and flour protein contents (Table 2), of which, one coincided with QTLs for HT, TW and TGW on chromosome 4DS and mapped in the same location as the QTL identified by Groos et al. (2003). *QGpc.crc-7B* and *QFpc.crc-7B* may be allelic to *QPro.mgb-7B* identified in a RIL population of tetraploid wheats (Blanco et al. 2002). *QFpc.crc-2D* was located in a comparable position to QTL for protein content detected by Börner et al. (2002) and Prasad et al. (2003). QTLs for protein content mapped on chromosomes 2AS, 2BL, 3DS, 4AL, 6BL, 7AS and 7DS by Prasad et al. (2003) were not detected in this DH population. No QTLs were identified to be associated with the *Glu-3* loci encoding LMW glutenin subunits and the loci *Gli-1* and *Gli-2* encoding gliadins. This can be explained by the fact that there are few allelic variations between the two parental lines at the loci *Glu-3*, *Gli-1* and *Gli-2* (Radovanovic et al. 2002). Although allelic variations existed at all *Glu-1* loci between the parents, HMW glutenins only represent 6–10% of total protein fraction (Payne 1987). This is consistent with the result of Radovanovic et al. (2002) who reported that grain protein concentration was not significantly affected by HMW glutenin composition.

Among the 18 QTLs identified for eight mixograph parameters, six QTLs for MDT, PKH, ETP, FMS, PBW and SAP, and three QTLs for MDT, ETP and SV were found to be associated with *Glu-D1* and *Glu-B1*, respectively (Table 2; Fig. 1). No QTLs associated with *Glu-A1* were detected. Long MDT combined with large ETP is indicative of strong gluten. For two QTLs, *QMdt.crc-1D* and *QEtp.crc-1D*, subunits 5 + 10 at the *Glu-D1* locus in 87E03-S2B1 contributed the positive effects and explained 55.9 and 49.9% of the phenotypic variance, respectively. This result supports the results of Hsam et al. (2001) who reported that the HMW-GS 5 + 10 of wild goatgrass (*Aegilops tauschii* Coss.), donor of the D-genome of bread wheat, is responsible for good breadmaking properties. For the other four QTLs, *QPkh.crc-1D*, *QFms.crc-1D, QPbw.crc-1D* and *QSap.crc-1D*, subunits 2+12 in ''AC Karma'' showed positive effects, meaning that doughs from lines with these subunits develop faster (FMS), have a higher peak (PKH) and a higher peak bandwidth (PBW), but also a faster dough degradation after peak (SAP) compared to lines with 5 + 10 *Glu-D1* HMW-GS. Similar results were reported by Radovanovic et al. (2002). MDT, ETP and BWE are indicators used by breeders to select breeding lines with strength potential. For two QTLs, *QMdt.crc-1B* and *QEtp.crc-1B*, the *Glu-B1* alleles of 87E03-S2B1 had positive effects. *QBwe.crc-1B* identified on chromosome 1B was not coincident with *Glu-B1*. In total, eleven QTLs for eight mixograph parameters were found to be associated with genomic regions other than *Glu-1* loci and were mapped in one case in the same position as the QTL for protein content. This indicates that breadmaking quality is affected by protein content and although HMW glutenin subunits have the largest effect on most quality parameters measured herein, other genomic regions of bread wheat also contribute genetically to wheat quality.

Similarly, only one of three QTLs for SDS-SV, *QSv.crc-1B*, was associated with the HMW locus *Glu-B1*, for which the 87E03-S2B1 allele contributed the positive effect. Of the remaining two QTLs, one QTL was in the same position as the QTL for flour protein content on chromosome 2D, and another QTL were mapped on chromosome 5D. The QTL *QSv.crc-5D* was coincident with QTLs for TEG and BWE. These QTLs may be located near the grain *Hardness* (*Ha*) locus on the short arm of chromosome 5D (Huang and Röder 2005). The QTLs for SDS-SV on chromosomes 3AS, 3BL, 5AL, 6AL and 7BS identified in durum wheat by Blanco et al. (1998) were not detected in this study.

Clustering of the detected QTLs

Using a DH population in combination with composite interval mapping, a total of 50 QTLs for agronomic and quality-related traits were detected in the present study. These QTLs were distributed on 15 of the 21 chromosomes; exceptions being chromosomes 1A, 2A, 3A, 3D, 5B and 6B. Thirty-four QTLs formed 8 clusters on seven chromosomes 1B (2), 1D, 2D, 3B, 4D, 5A and 5D (Fig. 1). In wheat, qualitatively inherited genes are often located in the gene-rich regions with hot spots of recombination (Gill et al. 1996; Faris et al. 2000; Sandu et al. 2001). Like single genes, these QTLs mapped in the same genomic regions forming clusters (Fig. 1). Similarly, Peng et al. (2003) analysed QTLs for agronomic traits in an F_2 population of durum wheats and discovered seven QTL clusters on four chromosomes, namely 1B, 2A, 3A and 5A. The first two large QTL clusters in this study were found on chromosomes 1D and 4D (Fig. 1). Two clusters consist of 6 and 9 QTLs, respectively. At the major QTL locus on chromosome 4DS, the 87E03-S2B1 alleles increased HT, TW, TGW, GPC, FPC, PKH, FMS and SAP, but decreased lodging resistance (Table 5). This finding is consistent with the positive correlations observed between pairs of these traits. Similar results for agronomic traits were also reported in bread wheat by McCartney et al. (2005). Pleiotropy is another possible explanation for the ''QTL clusters'', especially the clusters on chromosomes 1D, 4D and 5D. In order to further clarify pleiotropic or close linkage effects of these traits, it is necessary to increase the population size and saturate the target genomic regions by adding more molecular markers.

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References

American Association of Cereal Chemists (2000) Approved Methods of the AACC, 10th edn St. Paul. Methods 26-95A, 39-25, and 56-70

Araki E, Miura H, Sawada S (1999) Identification of genetic loci affecting amylose content and agronomic traits on chromosome 4A of wheat. Theor Appl Genet 98:977–984

Basten CJ, Weir BS, Zeng Z-B (2001) QTL Cartographer, version 1.15. Department of Statistics, North Carolina State University, Raleigh

Blanco A, Bellomo MP, Lotti C, Maniglio T, Pasqualone A, Simeone R, Troccoli A, Di Fonzo N (1998). Genetic mapping of sedimentation volume across environments using recombinant inbred lines of durum wheat. Plant Breed 117:413–417

Blanco A, Pasqualone A, Troccoli A, Di Fonzo N, Simeone R (2002) Detection of grain protein content QTLs across environments in tetraploid wheats. Plant Mol Biol 48:615–623

Börner A, Schumann E, Fürste A, Cöster H, Leithold B, Röder MS, Weber WE (2002) Mapping of quantitative trait loci for agronomic important characters in hexaploid wheat (*Triticum aestivum* L.). Theor Appl Genet 105:921–936

Cadalen T, Sourdille P, Charmet G, Tixier MH, Gay G, Boeuf C, Bernard S, Leroy P, Bernard M (1998) Molecular markers linked to genes affecting plant height in wheat using a doubled-haploid population. Theor Appl Genet 96:933–940

Campbell BT, Baenziger PS, Gill KS, Eskridge KM, Budak H, Erayman M, Dweikat I, Yen Y (2003) Identification of QTLs and environmental interactions associated with agronomic traits on chromosome 3A of wheat. Crop Sci 43:1493–1505

Chao S, Sharp PJ, Worland AJ, Warham EJ, Koebner RMD, Gale MD (1989) RFLP-based genetic maps of wheat homoeologous group 7 chromosomes. Theor Appl Genet 78:495–504

Churchill GA, Doerge RW (1994) Empirical threshold values for quantitative trait mapping. Genetics 138:963–971

Doerge RW, Churchill GA (1996) Permutatuion tests for multiple loci affecting a quantitative character. Genetics 142:285–294

Elouafi I, Nachit MM (2004) A genetic linkage map of the Durum × *Triticum dicoccoides* backcross population based on SSRs and AFLP markers, and QTL analysis for milling traits. Theor Appl Genet 108:401–413

Faris JD, Haen KM, Gill BS (2000) Saturation mapping of a gene-rich recombination hot spot region in wheat. Genetics 154:823–835

Gill KS, Gill BS, Endo TR, Taylor T (1996) Identification and high-density mapping of gene-rich regions in chromosome group 1 of wheat. Genetics 144:1883–1891

Groos C, Robert N, Bervas E, Charmet G (2003) Genetic analysis of grain protein-content, grain yield and thousand-kernel weight in bread wheat. Theor Appl Genet 106:1032–1040

Hsam SLK, Kieffer R, Zeller FJ (2001) Significance of *Aegilops tauschii* glutenin genes on breadmaking properties of wheat. Cereal Chem 78:521–525

Huang XQ, Röder MS (2004) Molecular mapping of powdery mildew resistance genes in wheat: a review. Euphytica 137:203–223

Huang XQ, Röder MS (2005) Development of SNP assays for genotyping of the puroindoline b gene for grain hardness in wheat using Pyrosequencing. J Agric Food Chem 53:2070–2075

Huang XQ, Cöster H, Ganal MW, Röder MS (2003) Advanced backcross QTL analysis for the identification of quantitative trait loci alleles from wild relatives of wheat (*Triticum aestivum* L.). Theor Appl Genet 106:1379–1389

Huang XQ, Kempf H, Ganal MW, Röder MS (2004) Advanced backcross QTL analysis in progenies derived from a cross between a German elite winter wheat variety and a synthetic wheat (*Triticum aestivum* L.). Theor Appl Genet 109:933–943

Joppa LR, Du C, Hart GE, Hareland GA (1997) Mapping gene(s) for grain protein in tetraploid wheat (*Triticum turgidum* L.) using a population of recombinant inbred chromosome lines. Crop Sci 37:1586–1589

Kato K, Miura H, Sawada S (2000) Mapping QTLs controlling grain yield and its components on chromosome 5A of wheat. Theor Appl Genet 101:1114–1121

Keller M, Karutz Ch, Schmid JE, Stamp P, Winzeler M, Keller B, Messmer MM (1999) Quantitative trait loci for lodging resistance in a segregating wheat × spelt population. Theor Appl Genet 98:1171–1182

Khan IA, Procunier JD, Humphreys DG, Tranquilli G, Schlatter AR, Marcucci-Poltri S, Frohberg R, Dubcovsky J (2000) Development of PCR-based markers for a high grain protein content gene from *Triticum turgidum* ssp. dicoccoides transferred to bread wheat. Crop Sci 40:518–524

Knapp SJ, Stroup WW, Ross WM (1985) Exact convidence intervals for heritability on a progeny mean basis. Crop Sci 25:192–194

Knox RE, De Pauw RM, McCaig TN, Clarke JM, McLeod JG, Fernandez MR (1995) AC Karma white spring wheat. Can J Plant Sci 75: 899–901

Kosambi DD (1944) The estimation of map distances from recombination values. Ann Eugen 12:172–175

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Lukow OM, Forsyth SA, Payne PI (1992) Over-production of HMW glutenin subunits coded on chromosome 1B in common wheat, *Triticum aestivum*. J Genet Breed 46:187–192

McCartney CA, Somers DJ, Humphreys DG, Lukow O, Ames N, Noll J, Cloutier S, McCallum BD (2005) Mapping quantitative trait loci controlling agronomic traits in the spring wheat cross RL4452 × 'AC Domain'. Genome 48:870–883

McIntosh RA, Hart GE, Devos KM, Gale MD, Rogers WJ (1998) Catalogue of gene symbols for wheat. In: Slinkard AE (ed) Proceedings of the 9th International Wheat Genet Symp, vol 5. University Extension Press, University of Saskatchewan, Canada

Mesfin A, Frohberg RC, Anderson JA (1999) RFLP markers associated with high grain protein from *Triticum turgidum* L. var. *dicoccoides* introgressed into hard red spring wheat. Crop Sci 39:508–513

Payne PI (1987) Genetics of wheat strorage proteins and the effect of allelic variation on breadmaking quality. Annu Rev Plant Physiol 38:141–153

Peng JH, Ronin Y, Fahima T, Röder MS, Li YC, Nevo E, Korol A (2003) Domestication quantitative trait loci in *Triticum dicoccoides*, the progenitor of wheat. Proc Natl Acad Sci USA 100:2489–2494

Pestsova E, Röder MS (2002) Microsatellite analysis of wheat chromosome 2D allows the reconstruction of chromosomal inheritance in pedigrees of breeding programmes. Theor Appl Genet 106:84–91

Pestsova E, Ganal MW, Röder MS (2000) Isolation and mapping of microsatellite markers specific for the D genome of bread wheat. Genome 43:689–697

Pon CR, Lukow OM, Buckley DJ (1989) A multichannel, computer-based system for analysing dough rheology. J Texture Stud 19:343–360

Prasad M, Kumar N, Kulwal PL, Röder MS, Balyan HS, Dhaliwal HS, Gupta PK (2003) QTL analysis for grain protein content using SSR markers and validation studies using NILs in bread wheat. Theor Appl Genet 106:659–667

Radovanovic N, Cloutier S (2003) Gene-assisted selection for high molecular weight glutenin subunits in wheat doubled haploid breeding programs. Mol Breed 12:51–59

Radovanovic N, Cloutier S, Brown D, Humphreys DG, Lukow OM (2002) Genetic variance for gluten strength contributed by high molecular weight glutenin proteins. Cereal Chem 79:843–849

Röder MS, Korzun V, Wendehake K, Plaschke J, Tixier MH, Leroy P, Ganal MW (1998) A microsatellite map of wheat. Genetics 149:2007–2023

Röder MS, Huang XQ, Ganal MW (2004) Wheat microsatellites in plant breeding—potential and implications. In: Lörz H, Wenzel G (eds) Biotechnology in agriculture and forestry, vol 55, molecular marker systems in plant breeding and crop improvement. Springer, Berlin Heidelberg New York, pp 255–266

Sandhu D, Champoux JA, Bondareva SN, Gill KS (2001) Identification and physical localization of useful genes and markers to a major gene-rich region on wheat group 1S chromosomes. Genetics 157:1735–1747

Schuelke M. (2000) An economic method for the fluorescent labelling of PCR fragments. Nat Biotechnol 18:233–234

Shah MM, Gill KS, Baenziger PS, Yen Y, Kaeppler SM, Ariyarathne HM (1999) Molecular mapping of loci for agronomic traits on chromosome 3A of bread wheat. Crop Sci 39:1728–1732

Somers DJ, Isaac P, Edwards K (2004) A high-density microsatellite consensus map for bread wheat (*Triticum aestivum* L.). Theor Appl Genet 109:1105–1114

Sourdille P, Singh S, Cadalen T, Brown-Guedira GL, Gay G, Qi L, Gill BS, Dufour P, Murigneux A, Bernard M (2004) Microsatellite-based deletion bin system for the establishment of genetic–physical map relationships in wheat (*Triticum aestivum* L.). Funct Integr Genomics 4:12–25

Wang S, Basten CJ, Zeng Z-B (2004) Windows QTL Cartographer 2.0. Department of Statistics, North Carolina State University, Raleigh (http://www.statgen.ncsu.edu/qtlcart/WQTLCart.htm)

Zeng Z-B (1994) Precision mapping of quantitative trait loci. Genetics 136:1457–1468