Mapping quantitative trait loci controlling agronomic traits in the spring wheat cross 
RL4452 × ‘AC Domain’

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Abstract: Relatively little is known about the genetic control of agronomic traits in common wheat (Triticum aestivum L.) compared with traits that follow Mendelian segregation patterns. A doubled-haploid population was generated from the cross RL4452 × ‘AC Domain’ to study the inheritance of the agronomic traits: plant height, time to maturity, lodging, grain yield, test weight, and 1000-grain weight. This cross includes the genetics of 2 western Canadian wheat marketing classes. Composite interval mapping was conducted with a microsatellite linkage map, incorporating 369 loci, and phenotypic data from multiple Manitoba environments. The plant height quantitative trait loci (QTLs), QHt.crc-4B and QHt.crc-4D, mapped to the expected locations of Rht-B1 and Rht-D1. These QTLs were responsible for most of the variation in plant height and were associated with other agronomic traits. An additional 25 agronomic QTLs were detected in the RL4452 × ‘AC Domain’ population beyond those associated with QHt.crc-4B and QHt.crc-4D. ‘AC Domain’ contributed 4 alleles for early maturity, including a major time to maturity QTL on 7D. RL4452 contributed 2 major alleles for increased grain yield at QYld.crc-2B and QYld.crc-4A, which are potential targets for marker-assisted selection. A key test weight QTL was detected on 3B and prominent 1000-grain weight QTLs were identified on 3D and 4A.

Key words: height, lodging, mapping, maturity, microsatellite markers, test weight, 1000-grain weight, Triticum aestivum, wheat, yield.

Introduction

Agronomic traits are among the most important and least understood traits of wheat. Understanding the genetic control of these traits is crucial for the sustained improvement of wheat. Grain yield, time to maturity, lodging resistance, and plant height are among the most important agronomic traits of wheat. Many genes affect these traits resulting in complex inheritance that has made genetic analysis difficult. Quantitative trait locus (QTL) analysis has facilitated the study of quantitative traits by allowing the identification of discrete chromosome segments controlling these traits (Lander
yield, test weight, and 1000-grain weight in the adapted plant height, time to maturity, lodging resistance, grain ada, which differ for agronomic and seed quality traits.

Previous genetic research has uncovered a number of genes affecting important agronomic traits. Numerous Rht (reduced height) genes affect plant height; however, only Rht-B1b (Rht1), Rht-D1b (Rht2), and Rht8c have been used extensively in agriculture (Borlaug 1968; Worland et al. 1998). Other important agronomic genes include the Ppd (response to photoperiod) genes, the Vrn (response to vernalization) genes, and the Eps (earliness per se) genes (McIntosh et al. 2003). Few QTL analysis studies have been undertaken to investigate the genetic control of agronomic traits in wheat. Börner et al. (2002) mapped QTLs for various agronomic traits in the International Triticeae Mapping Initiative (ITMI) population (Synthetic/Opata 85). Plant height and lodging resistance were studied in a wheat × spelt cross by Keller et al. (1999), while plant height was studied in the cross ‘Courtot’ × ‘Chinese Spring’ by Cadalen et al. (1998). Yield and domestication QTLs were identified in a Triticum dicocoides × Triticum durum cross (Peng et al. 2003). Most recently, Huang et al. (2004) reported QTLs for 7 agronomic traits in a winter wheat × synthetic wheat cross. Other studies have targeted specific chromosomes using recombinant inbred chromosome lines and recombinant substitution lines to map agronomic traits on chromosomes 3A (Campbell et al. 2003), 4A (Araki et al. 1999), and 5A (Kato et al. 1999, 2000). Plant height and time to flowering QTLs have also been reported in studies in which the main goal is to map disease resistance (Eriksen et al. 2003; Gervais et al. 2003; Schnurbusch et al. 2003; Somers et al. 2003a). In general, few whole-genome QTL analyses of agronomic traits have been conducted, particularly in elite North American wheat germplasm.

The objective of this study was to identify QTLs controlling plant height, time to maturity, lodging resistance, grain yield, test weight, and 1000-grain weight in the adapted spring wheat cross RL4452 × ‘AC Domain’. The experiment was designed to identify QTLs that were stable across environments. RL4452 and ‘AC Domain’ are representative of the genetics of 2 wheat marketing classes in western Canada, which differ for agronomic and seed quality traits.

Materials and methods

Plant materials

One hundred and eighty-two doubled haploid (DH) lines were generated from the cross RL4452 × ‘AC Domain’. ‘AC Domain’ and RL4452 are T. aestivum selections with spring growth habit. Doubled-haploid lines were generated by the maize pollination method (Pedak et al. 1997). ‘AC Domain’ is a widely grown cultivar registered in the Canada Western Red Spring (CQRS) marketing class in 1992 and is a prominent parent in western Canadian spring wheat breeding. RL4452 (‘Glenlea’ ×6’Kitt’) is an unregistered backcross derivative of the wheat cultivar ‘Glenlea’ that incorporates reduced plant height from Kitt. ‘Glenlea’ (Evans et al. 1972) is the quality standard for the Canada Western Extra Strong (CWES) marketing class. ‘Kitt’ is a semi-dwarf hard red spring wheat released by the University of Minnesota in 1975. ‘AC Domain’, RL4452, and ‘Glenlea’ were included as checks in all environments. The comparison between RL4452 and ‘Glenlea’ provided insight into the effect of the reduced plant height gene(s) on wheat traits.

Agronomic traits

Data for 6 agronomic traits (Table 1) were collected at 3 Manitoba sites (Brandon, Glenlea, and Morden) in 1998, 1999, and 2000. The Brandon site was lost in 1999, giving a total of 8 site-years. Plant height, time to maturity, and lodging were measured in 8 site-years, grain yield in 7, and test weight and 1000-grain weight in 4 (Table 1). Please note that ‘Glenlea’ is the name of a cultivar and a location used in this study. Doubled-haploid lines were grown as yield plots following standard agronomic practices. The Brandon plots consisted of 4 rows that were 4-m long and spaced 22.9 cm apart. A plot at Glenlea consisted of 5 rows that were 4.3-m long and spaced 15.2 cm apart. The Morden plots consisted of 5 rows that were 4-m long and spaced 17.8 cm apart. A single randomized complete block was grown at each location in 1998 and 1999, while 2 blocks were grown at each location in 2000. Each replicate (i.e., block) had a unique randomization. Agronomic data were collected on 126 DH lines in 1998 and 1999, while agronomic data were collected on 168 DH lines (the original 126 DH lines plus 42 additional DH lines) in 2000. Consequently, phenotypic data was not collected on 14 DH lines used to calculate the genetic linkage map (182 – 168 = 14).

Analysis of variance (ANOVA) was conducted with the GLM procedure of SAS® 8.2 (SAS Institute Inc., Cary, North Carolina, USA) with replicates as a random effect and DH lines as a fixed effect. Heritability was calculated on an entry mean and per plot basis with the ANOVA mean squares and the expectations of mean squares. Doubled-haploid line means were calculated for the agronomic traits with the LSMEANS statement of the GLM procedure, which calculates least-square means. Missing data points were recorded in the 1998 and 1999 replicates for the 42 DH mapping lines that were only evaluated in the 2000 replicates. An overall mean dataset was generated by averaging agronomic trait data over all replicates. Year datasets were generated for 1998, 1999, and 2000 by averaging over replicates within a year. Site datasets were calculated for Brandon, Glenlea, and Morden by averaging over the replicates from 1998, 1999, and 2000 for each specific site. The 5 site-year datasets in 1998 and 1999 were based on a single replicate of data, while the 3 site-year datasets in 2000 were based on a mean of 2 replicates of data. Correlation analysis was used to investigate potential genetic relationships between the agronomic traits. Pearson’s correlation coefficients were estimated between the 6 agronomic traits with procedure CORR of SAS® using the DH line means from the overall mean dataset.

Genetic map construction and QTL analysis

Lyophilized seedling leaf tissue was used for DNA extraction with the Qiagen DNAeasy® 96 Plant Kit (Qiagen, Mississauga, Ontario). DNA was quantified by fluorimetry.
using Hoechst No. 33258 stain. A collection of approximately 700 microsatellite primer pairs were screened for polymorphism between ‘AC Domain’ and RL4452. PCR and the electrophoresis of microsatellite marker amplicons were conducted as described by McCartney et al. (2004). Primer sequences for GWM, GDM, WMC, and BARC microsatellite markers were obtained from Röder et al. (1998), Pestsova et al. (2000), the GrainGenes website (http://wheat.pw.usda.gov), and the USA Wheat and Barley Scab Initiative website (http://www.scabusa.org/pdfs/BARC_SSRs_011101.html), respectively. The map also includes 5 expressed sequence tags (ESTs) that were mapped on the basis of a single nucleotide polymorphism (SNP) between RL4452 and ‘AC Domain’. The ESTs are indicated by GeneBank accession number – nucleotide position of the site, year, and site-year datasets. Exceptions were considered if a QTL nearly met all of the declaration criteria and mapped in the same region as QTLs controlling other traits. Graphical chromosome maps were generated with the aid of MapChart 2.1 software (Voorrips 2002).

**Results**

**Linkage map**

The genetic linkage map consisted of 369 loci on 27 linkage groups, anchored to the 21 chromosomes of common wheat, and spanned 2793 cM. The 369 loci included 356 microsatellite loci from 306 primer pairs, 5 ESTs, and 8 genes (Fig. 1). The LMW glutelins Glu-A3, Glu-B3, and Glu-D3 mapped to homeologous positions on chromosomes 1AS, 1BS, and 1DS, whereas the HMW glutenin Glu-B1 was mapped in the same region as QTLs controlling other traits. Graphical chromosome maps were generated with the aid of MapChart 2.1 software (Voorrips 2002).
Considerable segregation was observed for the 6 agronomic traits evaluated in the RL4452 × ‘AC Domain’ DH population (Table 3). Plant height, time to maturity, test weight, and 1000-grain weight had high heritability estimates. Heritability estimates were low for grain yield and lodging on a per plot basis, but were substantially higher on an entry mean basis. RL4452 and ‘AC Domain’ had similar means for plant height, lodging, grain yield, test weight, and 1000-grain weight. These data and the sizeable segregation in the DH population suggested transgressive segregation for these traits. ‘AC Domain’ and RL4452 had time to maturity values near the minimum and maximum of the RL4452 × ‘AC Domain’ DH population suggesting that ‘AC Domain’ contributed most of the genetic variation for early maturity. RL4452 (‘Glenlea’ *6/’Kitt’) was approximately 17 cm shorter than ‘Glenlea’ averaged over all replicates (Table 3).

Genotypic correlations were calculated between the DH line means for the agronomic traits measured on the RL4452 × ‘AC Domain’ population (Table 4). All possible correlations between plant height, lodging, grain yield, test weight, and 1000-grain weight were highly significant ($p < 0.001$). Time to maturity was not significantly correlated with plant height, lodging, or grain yield in this population. A significant positive correlation was identified between time to maturity and test weight, whereas a significant negative correlation was identified between time to maturity and 1000-grain weight.

Plant height QTLs

Composite interval mapping revealed 6 QTLs controlling plant height (Table 5, Fig. 1). The strongest height QTL was QHt.crc-4D on chromosome 4D. This QTL had a LOD score of 30.9 and an $R^2$ value of 47.5% based on the analysis of the overall mean dataset. The RL4452 allele reduced plant height by 10.9 cm relative to the ‘AC Domain’ allele (i.e., additive effect). The LOD score peak was in the Xwmc617–
interval (Fig. 1). The 2nd major QTL was \(QHt.crc-4B\), detected on chromosome 4B at \(Xgwm513\) with the peak LOD score of 7.7 (Table 5, Fig. 1). The ‘AC Domain’ allele reduced plant height by 4.0 cm relative to the RL4452 allele. The 4B and 4D plant height QTLs were detected in all datasets (i.e., the overall mean dataset, each site dataset, each year dataset, and each site-year dataset). In addition, prominent plant height QTLs were detected on chromosomes 2D (LOD = 4.2) and 5B (LOD = 6.1), while minor plant height QTLs were detected on 7A (LOD = 3.3) and 7B (LOD = 3.3).

**Time to maturity QTLs**

Four time to maturity QTLs were detected with composite interval mapping (Table 5, Fig. 1). The most significant QTL was \(QMat.crc-7D\), which had a LOD score of 17.5 at \(Xgwm130\) and explained 25.7% of the phenotypic variation in the overall mean dataset. \(QMat.crc-7D\) also had a LOD score >3 in 13 of the 14 site, year, and site-year datasets. The ‘AC Domain’ allele reduced time to maturity by 0.85 maturity units relative to the RL4452 allele. The other prominent time to maturity QTLs were mapped to chromosomes 4A and 4D. \(QMat.crc-4A\) (LOD = 6.1) overlapped a QTL for 1000-grain weight, and \(QMat.crc-4D\) (LOD = 5.1) was coincident with \(QHt.crc-4D\) (Fig. 1). A 4th QTL for time to maturity was detected on chromosome 3B near the centromere and was considered minor (LOD = 3.0). ‘AC Domain’ alleles reduced time to maturity at all 4 QTLs (Table 5). These data are consistent with ‘AC Domain’ reaching physiological maturity approximately 3 maturity units earlier than RL4452 (Table 3).

**Lodging QTLs**

Three QTLs were identified to control plant lodging (Table 5, Fig. 1). The 2 most significant QTLs were coincident with \(QHt.crc-4B\) and \(QHt.crc-4D\) (Fig. 1). For both chromosome regions, reduced plant height alleles coincided with reduced plant lodging. \(QLd.crc-4B\) and \(QLd.crc-4D\) had very similar LOD scores, \(R^2\) values, and magnitudes of additive effect, although the \(QHt.crc-4D\) had a larger impact on plant height than \(QHt.crc-4B\). The 3rd lodging resistance QTL, \(QLd.crc-3D\), was detected on chromosome 3D. The ‘AC Domain’ allele reduced plant lodging relative to the RL4452 allele.

**Grain yield QTLs**

The most significant of the 5 grain yield QTLs was \(QYld.crc-2B\) at the marker \(Xgwm257\) (Table 5, Fig. 1). The peak LOD score was 9.4 and explained 13.3% of the variation in grain yield in the overall mean dataset. \(QYld.crc-2B\) was detected in 6 of 12 site, year, and site-year datasets (LOD >3). Another prominent grain yield QTL was detected on chromosome 4A in the \(Xgwm397–Xwmc650\) interval. \(QYld.crc-4A\) was significant in 6 of 12 site, year, and site-year datasets (LOD >3). The RL4452 alleles, at the 2B and 4A yield QTLs, increased grain yield relative to the ‘AC Do-
main’ alleles. Less significant grain yield QTLs were detected on 2A, 3D, and 4D. The 3D and 4D yield QTLs were presented despite not meeting all of the criteria for declaration of a QTL. The 3D grain yield QTL was presented because it mapped to the same interval as a test weight QTL (Fig. 1), had a peak LOD score near 3 (2.5), and was significant in 3 of 12 site, year, and site-year datasets (LOD >3). The 4D yield QTL was presented because it mapped to the same interval as the major plant height QTL (Fig. 1), had a peak LOD near 3 (LOD = 2.8), and it was significant in 5 of 12 site, year, and site-year datasets (LOD >3). Increased grain yield was associated with increased plant height at the 4D locus.

Test weight QTLs

Ten QTLs were identified for test weight (Table 5, Fig. 1). The most significant test weight QTLs were detected on chromosomes 3B and 4D. The test weight and time to maturity QTLs on chromosome 3B were coincident (Fig. 1). QTwt.crc-3B had a LOD score of 15.4 and explained 12.1% of the test weight variation in the overall mean dataset. The RL4452 allele at QTwt.crc-3B increased test weight. QTwt.crc-4D was located in the same interval as QHt.crc-4D (Fig. 1). QTwt.crc-4D had a LOD score of 11.6 and explained 17.4% of the test weight variation in the overall mean dataset. The ‘AC Domain’ allele at QTwt.crc-4D increased test weight. Other significant test weight QTLs were located on chromosomes 1B, 1D, 2D, 3D, and 5D. QTwt.crc-3D overlapped a minor QTL for grain yield (Fig. 1). The 1B, 1D, 2D, and 5D test weight QTLs mapped to chromosome regions that did not affect the other agronomic traits evaluated in the RL4452 × ‘AC Domain’ cross. The 3 test weight QTLs on chromosomes 2B, 6B, and 7D did not meet all criteria for being declared a QTL, but their LOD scores were above 2 in the overall mean dataset and above LOD 3 in at least 4 of the 8 site, year, and site-year datasets (Table 5).

1000-grain weight QTLs

Six QTLs were detected for 1000-grain weight (Table 5, Fig. 1). The 2 most significant 1000-grain weight QTLs were coincident with the plant height QTLs on chromosomes 4B and 4D. QGwt.crc-4B explained 11.9% of the variation in 1000-grain weight, while QGwt.crc-4D explained 31.8% of the variation in 1000-grain weight. For both of these QTL regions, increased plant height correlated with increased 1000-grain weight. The 1000-grain weight QTL on 2A, 3D, 4A, and 6D had similar magnitudes of additive effect. QGwt.crc-2A was declared a 1000-grain weight QTL because it was significant in 5 of 8 site, year, and site-year datasets (LOD >3); however, the maximum LOD score was 2.6 in the overall mean dataset. ‘AC Domain’ alleles decreased 1000-grain weight at QGwt.crc-2A, QGwt.crc-3D, and QGwt.crc-4D, but increased 1000-grain weight at QGwt.crc-4A. QGwt.crc-2A overlapped a grain yield QTL, QGwt.crc-3D overlapped a lodging QTL, QGwt.crc-4A over-
lapped a time to maturity QTL, and \( Q_{G wt.crc-6D} \) was not associated with other agronomic traits.

**Discussion**

Two major plant height QTLs, \( Q_{H t.crc-4B} \) and \( Q_{H t.crc-4D} \), mapped to the expected locations for \( Rht-B1 \) and \( Rht-D1 \), respectively (Gale et al. 1995; Sourdille et al. 1998). ‘Norin 10’, the source of \( Rht-B1b \) and \( Rht-D1b \) in wheat breeding programs (Gale and Youssefian 1985), is present in the pedigrees of both ‘AC Domain’ and RL4452. This strongly suggests that the major plant height QTLs on 4B and 4D are \( Rht-B1 \) and \( Rht-D1 \). If this is the case, the ‘AC Domain’ allele of \( Rht-B1 \) remains undetermined based on our data. ‘AC Domain’ had the tall allele at the \( Rht-B1 \) locus in the cross ‘AC Domain’ × ‘Haruyutaka’ (Kato et al. 2001). ‘Haruyutaka’ was reported to carry \( Rht-B1b \) (\( Rht1 \)) based on response to gibberellic acid, final culm length in a field test, and crosses to tester lines (Yamada 1990). The ‘AC Domain’ allele of \( Rht-B1 \) could be a weaker dwarfing allele similar to \( Rht-B1d \) from ‘Saitama 27’ (Worland and Petrovic 1988). The RL4452 reduced height allele on chromosome 4D is likely \( Rht-D1b \) given its widespread deployment and the pedigree of RL4452. \( Q_{H t.crc-4B} \) and \( Q_{H t.crc-4D} \) were coincident with numerous agronomic QTLs, possibly explaining much of the correlation detected between these traits. \( Q_{H t.crc-4D} \) explained the most variation in plant height in the RL4452 × ‘AC Domain’ population. Reduced height at \( Q_{H t.crc-4D} \) was significantly associated with decreased lodging, decreased grain yield, decreased test weight, decreased 1000-grain weight, and increased time to maturity. The comparison of the RL4452 (Glenlea *6/Kitt’) and ‘Glenlea’ agronomic trait data provided additional evidence of this relationship. The extent of the difference between RL4452 and ‘Glenlea’ for each trait was comparable to the estimated additive effect of the 4D QTLs based on the QTL analysis. In addition, reduced height at \( Q_{H t.crc-4B} \) was significantly associated with decreased lodging and decreased 1000-grain weight. These findings are generally consistent with the effect of dwarfing alleles at \( Rht-B1 \) and \( Rht-D1 \) in
other studies, with regard to time to maturity, lodging, test weight, and 1000-grain weight (Gale and Yousefian 1985; Brandle and Knott 1986; Ehdaie and Waines 1996; Singh et al. 2001).

The results of this study suggested that the ‘AC Domain’ reduced height allele at \( QHt.crc-4B \) is more suitable for western Canadian growing conditions than the RL4452 reduced height allele at \( QHt.crc-4D \). Both genes reduced lodging to a similar degree since the magnitude of the additive effect was very similar for \( QLd.crc-4B \) and \( QLd.crc-4D \). However, the \( R^2 \) value was higher for \( QHt.crc-4D \). Reduced height at \( QHt.crc-4D \) was associated with adverse changes in the agronomic traits to a greater degree than \( QHt.crc-4B \). Reduced height at \( QHt.crc-4D \) was also associated with reduced test weight and increased time to maturity, whereas \( QHt.crc-4B \) had no significant effect on test weight or time to maturity. Reduced height at \( QHt.crc-4D \) also reduced 1000-grain weight to a greater extent than reduced height at \( QHt.crc-4B \). The association of the reduced height allele at \( QHt.crc-4D \) and reduced grain yield has particularly important implications for western Canadian wheat breeding efforts. \( QYld.crc-4D \) was significant in environments that tended to have less precipitation between April and August than the other environments (www.climate.weatheroffice.ec.gc.ca). These dry environments had precipitation levels similar to the precipitation normals for these sites. The wet environments (mainly the Glenlea site-years) had above normal precipitation. This suggested that the grain yield of wheats with reduced height at \( QHt.crc-4D \) would be inferior under drought conditions in western Canada.

MacKey (1973) reported that reduced plant height and shoot weight were related to reduced root depth and root weight in a greenhouse test involving spring and winter lines isogenic for ‘Norin 10’ and ‘Tom Thumb’ dwarfing genes. \( QHt.crc-5B \) was the most prominent height QTL after \( QHt.crc-4B \) and \( QHt.crc-4D \). Whereas \( QHt.crc-4B \) and \( QHt.crc-4D \) were coincident with lodging resistance QTLs, \( QHt.crc-5B \) was not associated with lodging resistance (or the other agronomic traits). This was intriguing because \( QHt.crc-4B \) and \( QHt.crc-5B \) had similar estimated effects on plant height in the overall mean dataset and, therefore, would be expected to have similar effects on lodging. This discrepancy likely resulted from the inconsistent detection of
QHt.crc-5B relative to QHt.crc-4B. QHt.crc-4B was significant in every dataset, whereas QHt.crc-5B was significant in less than half of the datasets. The effect of QHt.crc-5B was likely overestimated in the overall mean dataset. QHt.crc-2D was more consistently expressed over environments than QHt.crc-5B, but it too was not significantly associated with lodging. These data suggest that these minor plant height QTLs may have little or no effect on lodging in the field. QHt.crc-5B did not map near the plant height QTLs reported by Schnurbusch et al. (2003), but may correspond to the
lodging resistance QTLs reported in Keller et al. (1999). The minor height QTLs QHt.crc-2D was not located near Rht8 or Ppd-D1 (Korzun et al. 1998; Pestsova and Röder 2002), but may correspond to the peduncle length QTL, QPdl.ipk-2D (Börner et al. 2002). QHt.crc-7A and QHt.crc-7B appear to be coincident with previously reported plant height QTLs (Cadalen et al. 1998; Keller et al. 1999; Schnurbusch et al. 2003), based on comparison of RFLP and microsatellite maps (Cadalen et al. 1998; Röder et al. 1998).

The largest QTL affecting time to maturity was located on the distal end of 7DS in the RL4452 × ‘AC Domain’ population. QMat.crc-7D was weakly linked to QTwt.crc-7D, such that recombinants should be obtainable if desired to meet specific breeding targets. ‘AC Domain’ had the early maturity and increased test weight alleles. QMat.crc-7D mapped to a similar region as a QTL for ear emergence time, QEet.ipk-7D, that was mapped in the Synthetic × ‘Opata’ (ITMI) population (Börner et al. 2002), suggesting that these QTLs may be the same. Interestingly, QEet.ipk-7D mapped near the adult plant leaf rust resistance gene Lr34 (Nelson et al. 1995, 1997) and QTLs for leaf rust and powdery mildew resistance (Börner et al. 2002). Other studies have detected associations between Lr34 and leaf tip necrosis, decreased yield and yield components in fungicide-protected plots, and increased yield and yield components in nonprotected plots (Drijepondt et al. 1990; Singh 1992; Singh and Huerta-Espino 1997). The RL4452 × ‘AC Domain’ population was not evaluated for adult plant leaf rust resistance and probably does not segregate for Lr34, because it is present in ‘AC Domain’ (Liu and Kolmer 1997) and ‘Glenlea’ (Dyck et al. 1985). The RL4452 × ‘AC Domain’ 7D map was truncated on the short arm, because the parents were monomorphic at microsatellite loci in that region. This information suggested that Lr34 may be located distal to Xgwm130, just off the short arm of the RL4452 × ‘AC Domain’ 7D map. This location is consistent with the mapping of Lr34 near Xgwm130 in the cross ‘Fukuho-komugi’ × Oligoculum (Suenaga et al. 2003), ‘AC Domain’ carries the favourable allele combination of Lr34 and early maturity allele at QMat.crc-7D, which is desirable for western Canadian wheat production.

Table 3. Mean, range, and heritabilities of the 6 agronomic traits in the RL4452 × ‘AC Domain’ doubled haploid (DH) population.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Check means</th>
<th>DH population</th>
<th>DH lines tested</th>
<th>Heritability</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>'AC</td>
<td>RL4452</td>
<td>'Glenlea'</td>
<td>1998</td>
</tr>
<tr>
<td>Plant height</td>
<td>88.7</td>
<td>84.7</td>
<td>101.5</td>
<td>86.2</td>
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<tr>
<td>Time to maturity</td>
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<td>4.42</td>
<td>4.27</td>
<td>2.68</td>
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<td>2.00</td>
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<td>2.95</td>
<td>3.05</td>
<td>2.71</td>
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<td>Test weight</td>
<td>77.2</td>
<td>75.4</td>
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<td>74.1</td>
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<td>1000-grain weight</td>
<td>29.9</td>
<td>33.6</td>
<td>36.7</td>
<td>31.1</td>
</tr>
</tbody>
</table>

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tion between yield and test weight attributable to loci on chromosomes 2B and 4D. The minor positive correlation between yield and 1000-grain weight can be attributed to the combined effects of loci on 2A and 4D, which cancelled each other out to a certain degree. The grain yield and 1000-grain weight QTLs on 4D resulted in a positive correlation, whereas the QTL on 2A gave a negative correlation. The moderate positive correlation between test weight and 1000-grain weight were attributed to the test weight and 1000-grain weight QTLs on 4D based on this QTL analysis. *QYld.crc-2A*, *QYld.crc-2B*, and *QYld.crc-4A* were not associated with time to maturity in this cross. Correlations have been reported between later maturing genotypes and increased grain yield, but these correlations are not detected in

<table>
<thead>
<tr>
<th>QTL</th>
<th>Marker or interval</th>
<th>LODa</th>
<th>R² x 100 (%)b</th>
<th>Additivec</th>
<th>Significant datasetsc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>QHt.crc-2D</em></td>
<td>BE497718–260</td>
<td>4.2</td>
<td>3.4</td>
<td>2.88 cm</td>
<td>99, 00, B, G98, G99, M99, B00</td>
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<td><em>QHt.crc-4B</em></td>
<td>Xgwm513</td>
<td>7.7</td>
<td>6.4</td>
<td>4.04 cm</td>
<td>98, 99, 00, B, G, M, B98, G98, M98, G99, M99, B00, G00, M00</td>
</tr>
<tr>
<td><em>QHt.crc-4D</em></td>
<td>Xwmc617–Xwmc48</td>
<td>30.9</td>
<td>47.5</td>
<td>–10.92 cm</td>
<td>98, 99, 00, B, G, M, B98, G98, M98, G99, M99, B00, G00, M00</td>
</tr>
<tr>
<td><em>QHt.crc-5B</em></td>
<td>Xwmc640</td>
<td>6.1</td>
<td>5.0</td>
<td>4.80 cm</td>
<td>98, G, M, B00, G00</td>
</tr>
<tr>
<td><em>QHt.crc-7A</em></td>
<td>Xwmc139</td>
<td>3.3</td>
<td>2.6</td>
<td>2.50 cm</td>
<td>B, M, B00, G00</td>
</tr>
<tr>
<td><em>QHt.crc-7B</em></td>
<td>Xgwm333</td>
<td>3.3</td>
<td>2.6</td>
<td>–2.51 cm</td>
<td>98, M, G98, G99</td>
</tr>
<tr>
<td>Time to Maturity</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>QMat.crc-3B</em></td>
<td>Xwmc231</td>
<td>3.0</td>
<td>3.4</td>
<td>0.32 units</td>
<td>98, 00, M00</td>
</tr>
<tr>
<td><em>QMat.crc-4A</em></td>
<td>Wx-B1</td>
<td>6.1</td>
<td>8.5</td>
<td>0.50 units</td>
<td>98, 00, G, G98, M99, G00, M00</td>
</tr>
<tr>
<td><em>QMat.crc-4D</em></td>
<td>Xwmc617–Xwmc48</td>
<td>5.1</td>
<td>8.4</td>
<td>0.49 units</td>
<td>00, B, M, M99, B00, M00</td>
</tr>
<tr>
<td><em>QMat.crc-7D</em></td>
<td>Xgwm130</td>
<td>17.5</td>
<td>25.7</td>
<td>0.85 units</td>
<td>98, 99, 00, B, G, M, B98, G98, G99, M99, B00, G00, M00</td>
</tr>
<tr>
<td>Lodging</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>QLd.crc-3D</em></td>
<td>Xgwm191</td>
<td>3.7</td>
<td>4.4</td>
<td>0.55 units</td>
<td>00, M, M00</td>
</tr>
<tr>
<td><em>QLd.crc-4B</em></td>
<td>Xwmc826–Xwmc238</td>
<td>7.8</td>
<td>9.9</td>
<td>0.51 units</td>
<td>00, B, M, B98, B00, M00</td>
</tr>
<tr>
<td><em>QLd.crc-4D</em></td>
<td>Xwmc617–Xwmc48</td>
<td>7.8</td>
<td>13.6</td>
<td>–0.59 units</td>
<td>99, 00, G, M, M98, G99, G00, M00</td>
</tr>
<tr>
<td>Grain yield</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>QYld.crc-2A</em></td>
<td>Xgwm339</td>
<td>3.0</td>
<td>4.0</td>
<td>–0.10 t/ha</td>
<td>00, G, B00, G00</td>
</tr>
<tr>
<td><em>QYld.crc-2B</em></td>
<td>Xgwm257</td>
<td>9.4</td>
<td>13.3</td>
<td>0.18 t/ha</td>
<td>00, G, M99, B00, G00, M00</td>
</tr>
<tr>
<td><em>QYld.crc-3D</em></td>
<td>Xbarc71</td>
<td>2.5</td>
<td>3.7</td>
<td>0.09 t/ha</td>
<td>00, B, B00</td>
</tr>
<tr>
<td><em>QYld.crc-4A</em></td>
<td>Xgwm397–Xwmc650</td>
<td>4.4</td>
<td>6.3</td>
<td>0.12 t/ha</td>
<td>00, B, G, B98, B00, G00</td>
</tr>
<tr>
<td><em>QYld.crc-4D</em></td>
<td>Xwmc617–Xwmc48</td>
<td>2.8</td>
<td>4.8</td>
<td>–0.10 t/ha</td>
<td>00, B, M, B00, M00</td>
</tr>
<tr>
<td>Test weight</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>QTwt.crc-1B</em></td>
<td>Xgwm374.1</td>
<td>3.9</td>
<td>3.7</td>
<td>1.01 kg/hL</td>
<td>00, G, M, G00</td>
</tr>
<tr>
<td><em>QTwt.crc-1D</em></td>
<td>Xgdm126</td>
<td>5.8</td>
<td>6.0</td>
<td>1.26 kg/hL</td>
<td>00, G, M, G00, M00</td>
</tr>
<tr>
<td><em>QTwt.crc-2B</em></td>
<td>Xbarc183</td>
<td>2.3</td>
<td>2.1</td>
<td>0.92 kg/hL</td>
<td>G, G99, G00, M00</td>
</tr>
<tr>
<td><em>QTwt.crc-2D</em></td>
<td>Xgwm349–Xbarc59</td>
<td>5.2</td>
<td>5.4</td>
<td>–1.34 kg/hL</td>
<td>99, 00, G, G99, M99</td>
</tr>
<tr>
<td><em>QTwt.crc-3B</em></td>
<td>Xwmc625–Xbarc164</td>
<td>15.4</td>
<td>12.1</td>
<td>1.77 kg/hL</td>
<td>99, 00, G, M, G99, M99, G00, M00</td>
</tr>
<tr>
<td><em>QTwt.crc-3D</em></td>
<td>Xbarc71</td>
<td>5.2</td>
<td>5.5</td>
<td>1.22 kg/hL</td>
<td>99, 00, G, M, M99, G00</td>
</tr>
<tr>
<td><em>QTwt.crc-4D</em></td>
<td>Xwmc617–Xwmc48</td>
<td>11.6</td>
<td>17.4</td>
<td>–2.13 kg/hL</td>
<td>99, 00, G, M, G99, M99, G00, M00</td>
</tr>
<tr>
<td><em>QTwt.crc-5D</em></td>
<td>Xgdm63–Xwmc765</td>
<td>5.3</td>
<td>7.1</td>
<td>–1.40 kg/hL</td>
<td>99, G, M99</td>
</tr>
<tr>
<td><em>QTwt.crc-6B</em></td>
<td>Xwmc104–Xwmc494</td>
<td>2.7</td>
<td>2.9</td>
<td>–0.92 kg/hL</td>
<td>00, M99, G00, M00</td>
</tr>
<tr>
<td><em>QTwt.crc-7D</em></td>
<td>Xwmc488</td>
<td>2.5</td>
<td>2.4</td>
<td>–0.87 kg/hL</td>
<td>99, 00, M, G99, M00</td>
</tr>
<tr>
<td>1000-grain weight</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>QGwt.crc-2A</em></td>
<td>Xgwm558–Xgwm294</td>
<td>2.6</td>
<td>3.0</td>
<td>1.22 g</td>
<td>99, M, G99, M99, M00</td>
</tr>
<tr>
<td><em>QGwt.crc-3D</em></td>
<td>Xgwm341–Xwmc552</td>
<td>4.3</td>
<td>6.0</td>
<td>1.67 g</td>
<td>99, 00, G, M, M99, G00, M00</td>
</tr>
<tr>
<td><em>QGwt.crc-4A</em></td>
<td>Xgwm494–Xgwm162</td>
<td>6.7</td>
<td>7.6</td>
<td>–1.86 g</td>
<td>00, G, M99, M99, M00</td>
</tr>
<tr>
<td><em>QGwt.crc-4B</em></td>
<td>Xwmc238</td>
<td>11.6</td>
<td>11.9</td>
<td>2.30 g</td>
<td>99, 00, G, M, G99, M99, G00, M00</td>
</tr>
<tr>
<td><em>QGwt.crc-4D</em></td>
<td>Xwmc617–Xwmc48</td>
<td>20.9</td>
<td>31.8</td>
<td>–3.85 g</td>
<td>99, 00, G, M, G99, M99, G00, M00</td>
</tr>
<tr>
<td><em>QGwt.crc-6D</em></td>
<td>Xgwm325–Xgwm55</td>
<td>3.9</td>
<td>3.6</td>
<td>1.25 g</td>
<td>99, 00, G, M, G99, G00</td>
</tr>
</tbody>
</table>

*Values calculated from the overall mean dataset.

Additive effect of allele substitution. The units are those of the respective trait. A positive sign indicated that the RL4452 allele increased the respective quantitative trait, and vice-versa.

Datasets where the LOD score >3.
all experiments (Knott and Gebeeyehou 1987). Our data suggested that yield improvements can be made independent of time to maturity, and with relatively minor changes in test weight and 1000-grain weight.

Previous studies have identified important agronomic genes on chromosome 4A (Araki et al. 1999; Börner et al. 2002). Our data agreed with these findings. QMat.crc-4A mapped to the Wx-B1 locus, which was the location of a QTL for ear emergence time in a population of single-chromosome recombinant substitution lines derived from ‘Chinese Spring’ and ‘Kanto107’ (Araki et al. 1999). QMat.crc-4A was the 2nd largest time to maturity QTL in the RL4452 × ‘AC Domain’ population. The Wx-B1 locus may not have a direct effect on ear emergence time or time to maturity. In Araki et al. (1999), the early ear emergence was in coupling with the null allele from ‘Kanto107’, whereas early maturity was in coupling with a variant allele from ‘AC Domain’ in the present study. The ‘AC Domain’ variant Wx-B1 allele could be Wx-B1e, because they have similar SDS-PAGE profiles (Yamamori and Quynh 2000). Also nearby was QGwt.crc-4A, which was the largest 1000-grain weight QTL in this study other than the 1000-grain weight QTL linked or pleiotropic with QHt.crc-4B and QHt.crc-4D. Börner et al. (2002) identified QTL controlling ear length, ear emergence time, grain number, grain weight/ ear, height, and waxiness in this region in the ITMI population. The 2nd largest grain yield QTL was also located on chromosome 4A in the RL4452 × ‘AC Domain’ population, although about 40 cM from QGwt.crc-4A, QMat.crc-4A, and Wx-B1.

Kernel shape and size are key components of kernel visual distinguishability (KVD), which is the basis by which western Canadian wheat cultivars are segregated into marketing classes at the grain elevator. Breeding lines must meet the KVD requirements to be registered as cultivars in a particular marketing class. The cross RL4452 × ‘AC Domain’ involves 2 marketing classes and segregates for kernel shape and size. Kernel shape is expected to be related to test weight, since the kernel shape will alter the packing efficiency of a given weight of kernels into a given volume. The kernel size is expected to be proportional to the 1000-grain weight. Therefore, the test weight and 1000-grain weight QTLs detected in this cross may directly influence the registration of western Canadian wheat cultivars. Reduced height at QHt.crc-4B and QHt.crc-4D were associated with reduced 1000-grain weight, while reduced height at QHt.crc-4D was also associated with reduced test weight. These linkage or pleiotropic effects could limit the deployment of the reduced height alleles at QHt.crc-4B and QHt.crc-4D in certain western Canadian market classes. For instance, RL4452 (‘Glenlea’ *6’Kitt’) does not meet the seed shape requirements of the Canadian Western Extra Strong (CWES) market class that was founded by ‘Glenlea’, because it does not have adequate grain filling. The poor grain filling of RL4452 is most likely due to reduced height at QHt.crc-4D. However, the right combination of test weight and 1000-kernel weight QTLs could overcome these KVD problems. This study identified numerous test weight and 1000-kernel weight QTLs that could be useful in this regard. Clearly, there is a need to understand the genetic relationship between kernel shape, kernel size, test weight, 1000-kernel weight, and KVD to facilitate western Canadian wheat breeding efforts.

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