Relationship between QTL for grain shape, grain weight, test weight, milling yield, and plant height in the spring wheat cross RL4452/‘AC Domain’

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Abstract

Kernel morphology characteristics of wheat are complex and quantitatively inherited. A doubled haploid (DH) population of the cross RL4452/‘AC Domain’ was used to study the genetic basis of seed shape. Quantitative trait loci (QTL) analyses were conducted on a total of 18 traits: 14 grain shape traits, flour yield (Fyd), and three agronomic traits (Plant height [Plht], 1000 Grain weight [Gwt], Test weight [Twt]), using data from trial locations at Glenlea, Brandon, and Morden in Manitoba, Canada, between 1999 and 2004. Kernel shape was studied through digital image analysis with an Acurum® grain analyzer. Plht, Gwt, Twt, Fyd, and grain shape QTL were correlated with each other and QTL analysis revealed that QTL for these traits often mapped to the same genetic locations. The most significant QTL for the grain shape traits were located on chromosomes 4B and 4D, each accounting for up to 24.4% and 53.3% of the total phenotypic variation, respectively. In addition, the most significant QTL for Plht, Gwt, and Twt were all detected on chromosome 4D at the Rht-D1 locus. Rht-D1b decreased Plht, Gwt, Twt, and kernel width relative to the Rht-D1a allele. A narrow genetic interval on chromosome 4B contained significant QTL for grain shape, Gwt, and Plht. The ‘AC Domain’ allele reduced Plht, Gwt, kernel length and width traits, but had no detectable effect on Twt. The data indicated that this variation was inconsistent with segregation at Rht-B1. Numerous QTL were identified that control these traits in this population.

Introduction

Wheat (Triticum aestivum L.) is an allohexaploid species (2n = 6x = 42) comprised of A, B, and D sub-genomes totalling ~17 Gbp. Along with other important cereal crops, it has been subject to artificial selection for increased grain size since the early stages of its cultivation [1]. Size
and shape of wheat kernels affect kernel weight and test weight [2], besides also influencing milling yields and grain protein content [3]. Both milling yields and grain protein content traits are distinct and independent of each other [4].

Grain or kernel size of wheat is most often described by grain-length and grain-width parameters. Although QTL for grain size and/or grain shape have been identified on almost all wheat chromosomes [2, 4–10], only a few of the underlying genes influencing grain size or shape have been cloned. The grain size locus TaGS-D1 on chromosome 7DS, associated with grain length and grain weight is an ortholog of the OsGs3 gene located on chromosome 3 of rice [11, 12]. A second locus TaGw2, controlling grain width and grain weight is located on chromosome 6A of wheat [13], and is an ortholog of the GW2 locus controlling grain weight on chromosome 2 of rice [14]. Besides the two grain weight loci, another locus for grain weight TaCKX6-D1 on chromosome 3D of wheat was cloned [15], and is an ortholog of OsCKX2 located on chromosome 1 of rice [16]. On rice chromosome 5, grain size and grain width loci GS5 [17] and GW5 [18, 19] have been cloned and functionally characterized.

Semi-dwarf wheat varieties were first released in the US in 1961 (‘Gaines’), and later in Mexico in 1962 (‘Pitic 62’, ‘Penjamo 62’), and in 1964 (‘Sonora 64’, ‘Lerma Rojo 64’, ‘Super X’, ‘Siete Cerros’). All the above varieties contained either one or two of the dwarfing/reduced height genes (Rht1, Rht2) derived from the Japanese winter wheat variety Norin 10 [20, 21]. These two gibberellic acid-insensitive genes Rht1 (Rht-B1) and Rht2 (Rht-D1) [22, 23] located on chromosomes 4B and 4D, respectively [24, 25], have been studied extensively. In addition, their wild type and mutant alleles have also been cloned [26]. The same RL4452/‘AC Domain’ DH population used in this study identified Plht QTL near the expected locations of Rht-B1 and Rht-D1 on chromosomes 4B and 4D, respectively [27]. Several other studies have investigated relationships between Rht genes and yield/yield components: [28–33]. Pleiotrophic effects of Rht genotype on coleoptile length, early vigour, and dry matter partitioning [34–36] and on grain shape (Rht8) [37] have also been reported.

Our objectives were to: a) identify significant grain morphology and agronomic trait QTL (Plht, Gwt, Twt, Fyd), and b) determine their interrelationships.

Materials and methods

Plant material

A total of 193 DH progeny genotypes derived from a cross between Canadian spring wheats RL4452/‘AC Domain’ were used in the construction of a genetic linkage map. ‘AC Domain’ was a widely grown cultivar, which was registered in the Canada Western Red Spring (CWRS) marketing class in 1992 [38]. ‘AC Domain’ has the pedigree BW83/ND585 (alternatively, ND499/RL4137//ND585). It is a prominent parent in western Canadian spring wheat breeding because of its excellent pre-harvest sprouting resistance [39]. RL4452 (pedigree: ‘Glenlea’6//‘Kitt’) is an unregistered backcross derivative of the wheat cultivar ‘Glenlea’ with the dwarfing gene Rht-D1b introgressed from Kitt. ‘Glenlea’ [40] was 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. QTL mapping was carried out using 183 DH progeny genotypes for which trait data was available.

Grain shape traits

An Acurum® grain analyzer was used to evaluate 14 grain shape traits on the RL4452/‘AC Domain’ DH population (Table 1). Details regarding the Acurum® grain analyzer were outlined in US Patent 7,218,775 B2, “Method and apparatus for identifying and quantifying characteristics of seeds and other small objects” [41]. The Acurum system consists of image
capture of the sample (i.e. grain) and neural network analysis. Both average and standard deviation values for grain shape traits were calculated. A plot-wise analysis of grain traits with the Acurum® grain analyzer permitted calculation of average values (for all of the grains per plot) that were used for detecting QTL. Standard deviation values for grain shape were included to study variability in grain size and/or shape within grain samples (i.e. possibly from tillers or fertile tertiary florets).

Plant height, grain weight, test weight, and flour yield (Plht, Gwt, Twt and Fyd)

Data on Plht was obtained from field trials at Glenlea (1998, 1999, and 2000) and Morden (1998, 1999, and 2000) in Manitoba, Canada. Gwt and Twt measurement were carried out using grain harvested from trials at Glenlea (1999 and 2000) and Morden (1999 and 2000) as described in McCartney et al. (2005). LS means for Gwt and Twt were used for QTL detection. Similarly, data for Fyd was collected and previously reported in McCartney et al. (2006). Grain samples were milled into straight-grade flour with a Buhler laboratory automatic-pneumatic mill (Model 202, Buhler AG, Uzwil, Switzerland) after tempering to 16.5% moisture. Flour yield was calculated based on total recovered products.

Statistical analyses of trait data

Analysis of variance (ANOVA) was conducted with the GLM procedure of SAS® 9.3 (SAS Institute Inc., Cary, North Carolina, USA) with environments, replicates, and genotypes as random effects. Heritability was calculated on an entry mean and per plot basis with the ANOVA mean squares and the expectations of mean squares. Genotype line means were calculated for the agronomic traits with the LSMEANS statement of the MIXED procedure, which calculates least-square means. In this case, genotypes were considered fixed effects, while with environments and replicates were random effects. An overall mean dataset was generated for all traits by averaging trait data over all replicates. Correlation analysis was used to investigate potential genetic relationships between the traits. Pearson’s correlation coefficients were estimated between the agronomic, milling, and seed shape traits with procedure CORR of SAS® using the DH line means from the overall mean dataset.

Table 1. Grain shape traits measured on wheat grain samples with the Acurum® grain analyzer.

| Abbreviation | Trait Description |
|--------------|------------------|
| AMaL         | Axis Major Length Length of major axis |
| AML          | Axis Minor Length Length of minor axis |
| Area         | Grain area       |
| ArPe         | Area/Perimeter Ratio of grain area/perimeter |
| Asym         | Asymmetry        |
| DMax         | Diameter Max Maximum diameter of the grain |
| DMen         | Mean Diameter Mean diameter of the grain |
| DMin         | Diameter Min Minimum diameter of the grain |
| Per          | Perimeter        |
| Rect         | Rectangularity Measurement of how closely a grain resembles a rectangle; a ratio of an object to its minimum bounding rectangle |
| Rndn         | Roundness       |
| Sphr         | Sphericity      |
| SzLn         | Size-Length Maximum length of the grain |
| SzWd         | Size-Width Maximum width of the grain |

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**Linkage mapping and QTL analyses**

Linkage and QTL mapping procedures for this experiment have been previously detailed [39]. In brief, an initial of 12,351 polymorphic markers (SSR, SNP, Diversity Arrays Technology [DArT], and ESTs) of an Illumina wheat 90K Infinium Custom beadchip [42] were screened on 193 DH progeny of the RL4452/'AC Domain' population. A total of 12,202 informative markers were used for linkage mapping with MapDisto [43]. Linkage groups were identified using a minimum LOD score of 4, and a maximum recombination fraction of 0.25. Recombination fractions were converted into centiMorgan (cM) map distances using the Kosambi mapping function. The RL4452/'AC Domain' linkage map is reported in S1 Table. More than one linkage group was obtained for chromosomes 1B, 2B, 3D, 5A, 5D, 6D, 7B, and 7D. For instance, there were two linkage groups for chromosome 1B. Linkage group 1B.1 consisted of the short arm and most of the long arm, and linkage group 1B.2 consisted of the distal end of the long arm.

The most informative marker per linkage bin was utilized for QTL analyses (i.e. 1,055 markers were retained). QTL IciMapping software version 4.1.0.0 was used to test for additive effect and epistatic QTL from multi-year trial datasets using inclusive composite interval mapping (ICIM) [44]. Additive effect QTL were detected by ICIM (QIC module) with a walk speed of 0.1 cM. LOD thresholds were based on 1,000 permutations. The confidence interval was determined by one LOD drop-off, which approximates a 96.8% confidence interval [45]. Epistatic QTL were identified via a two-dimensional scan for mapping digenic epistasis using ICIM-epistasis (QICE module) with default LOD scores of 5.0, coupled with walk speeds of 2 cM. QTL were deemed significant if For agronomic and milling traits, QTL were reported when the peak LOD score exceeded the significance threshold determined by the permutation analyses in two or more environments. For seed shape traits, QTL were reported when the peak LOD score exceeded the significance threshold determined by permutation in a minimum of three combinations of shape traits by environment (Glenlea 2000, Brandon 2004, or meaned over both years). The phenotypic variation explained due to respective QTL was derived from marker-trait regression ($r^2$) values.

**Physical locations of SNP markers**

The physical locations of SNP markers were obtained with a BLASTN search against the IWGSC Chinese Spring RefSeq v1.0 database (https://urgi.versailles.inra.fr/blast_iwgsc/blast.php). The best BLAST hit for a SNP marker was reported for the chromosome to which it mapped in the RL4452/'AC Domain' DH population. The BLAST hits are reported in S1 Table.

**Results**

Descriptive statistics of the seed shape, agronomic, and milling traits analyzed in the RL4452/'AC Domain' DH population are presented in S2 Table. Seed shape traits had high heritability estimates. The traits based upon mean seed shape parameters had heritabilities on a per plot basis ranging from 0.82 to 0.88, which was comparable to per plot heritability for test weight but exceeded the per plot heritability of plant height, grain weight, and flour yield.

Correlation analysis revealed the interrelationship between the traits assessed in the RL4452/'AC Domain' DH population (S3 Table). All seed shape traits were correlated with Gwt, with some being strongly correlated with Gwt ($r > 0.9$). Gwt was strongly positively correlated with kernel width (AmiL_M, DMin_M, SzWd_M), which also included mean seed diameter (DMen_M). There were also strong positive correlations between Gwt and seed area (Area_M), and Gwt and seed area-perimeter ratio (ArPe_M). Gwt was also highly correlated with Gwt.
with seed length (AmaL_M, DMax_M, SzLn_M), but less so relative to kernel width. Plht and Twt were positively correlated with kernel width, but were not significantly correlated with kernel length. Flour yield (Fyd) was not strongly correlated with any trait, although statistically significant correlations were identified. Fyd was most strongly correlated with Sphericity (Sphr; r = -0.328). Rectangularity (Rect) had a strong positive correlation with Sphericity (Sphr; r = 0.986), and a strong negative correlation with Roundness (Rndn; r = -0.993). Kernel Area (Area_M) was correlated with all traits, except Rndn and Sphr. Kernel Perimeter (Per_M) was correlated with all traits, except Twt, Rect, and Rndn. Seed area-perimeter ratio (ArPe_M) was correlated with all traits to a certain degree.

Additive effect QTL for agronomic traits (Plht, Gwt, Twt) and flour yield (Fyd) are reported in Table 2, while additive effect QTL for kernel shape traits are outlined in Table 3. Agronomic trait QTL were detected on chromosomes 4B and 4D (Plht), 2B, 3B, 3D, 4A, 4B, 4D, 6B (Gwt), 1D, 2A, 2B, 2D, 3B, 3D, 4D, 7A (Twt), and 1B, 3B, 3D, 4B, 7D (Fyd). The most significant agronomic trait QTL QPlht.crc-4D, QGwt.crc-4D, and QTwt.crc-4D were all detected on chromosome 4D. Another notable QTL region was detected on chromosome 4B at 54 cM. This region affected Plht, Gwt, Fyd, and numerous grain shape parameters. The most significant QTL for Fyd were QFyd.crc-3B and QFyd.crc-7D on chromosomes 3B and 7D, respectively. QTL for kernel morphology traits were identified on 16 of the 21 wheat chromosomes. The most significant QTL (explaining the highest % phenotypic variation) for grain shape traits were identified on chromosomes 4B and 4D near the corresponding plant height (Plht) QTL.

ICIM-epistasis (QICE module) identified a small number of epistatic QTL, which are reported in S4 Table. For seed shape traits, epistatic QTL were detected for Area, ArPe, DMen, DMin, Rect, SzWd, variability of Area, variability of AmiL, and variability of DMen. Epistatic QTL were also detected for Plht, Gwt, Twt, and Fyd. The epistatic interaction between chromosome 1D at 38 cM and chromosome 6B at 84 cM was detected more consistently than the others. This epistatic interaction involved Gwt, Area, ArPe, and DMen, which intuitively should be correlated. Interestingly, additive effect QTL were not detected on chromosome 1D at 38 cM or chromosome 6B at 84 cM using the QIC module for any trait. The remaining epistatic interactions were not consistently identified in different seed shape traits and/or between different datasets (i.e. environments).

Chromosome 1A
QTL for ArPe (QArPe.crc-1A), DMen (QDMen.crc-1A), DMin (QDMin.crc-1A), Per (QPer.crc-1A), SzLn (QSzLn.crc-1A), and SzWd (QSzWd.crc-1A) had LOD peaks from 0 to 23.5 cM. These QTL had relatively low LOD scores and were mainly detected in the Glenlea 2000 dataset. The ‘AC Domain’ allele decreased each of these seed shape traits. No other QTL for other traits (Gwt, Twt, Fyd) were identified on this chromosome.

Chromosome 1B
A flour yield QTL QFyd.crc-1B mapped to linkage group 1B.1 with LOD peaks at 81.7 and 92.1 cM, while three marginally significant seed shape QTL had LOD peaks nearby (QDMen.crc-1B, QArea(var).crc-1B, QArPe(var).crc-1B). The ‘AC Domain’ allele decreased Fyd in the region.

Chromosome 1D
On chromosome 1D, the most statistically significant QTL peaks for grain shape traits (QAMaL.crc-1D, QAsym.crc-1D, QDMax.crc-1D, QPer.crc-1D, QSzLn.crc-1D, QAsym(var).crc-1D) were located within a 23 cM interval (79.3–102.3 cM). These QTL were located near a Twt
Table 2. Inclusive Composite Interval Mapping (QIC) of Plant height (Plht), Grain weight (Gwt), Test weight (Twt), and Flour yield (Fyd) QTL identified in the RL4452/'AC Domain' DH population grown in replicated multi-year trials.

| QTL Trait name | Chr | Peak (cM) | CI (cM) | LOD r² (%) | Add | Left marker | Right marker | LOD threshold (α 0.05) |
|---------------|-----|-----------|---------|------------|-----|-------------|--------------|----------------------|
| Plant Height (Plht) | | | | | | | | |
| QPlht.crc-4B Ht_MOR99 | 4B | 52.9 | 52.4–53.5 | 6.7 | 9.9 | -2.9 | Tdurum_contig5562_441 | TA003708-0300 | 3.11 |
| QPlht.crc-4B Ht_GLE99 | 4B | 54.2 | 52.9–54.2 | 6.0 | 6.2 | -2.5 | BS00066282_51 | wmc657 | 3.18 |
| QPlht.crc-4B Ht_GLE98 | 4B | 54.3 | 54.2–55.5 | 13.1 | 15.6 | -3.6 | wmc657 | Excalibur_c21727_851 | 3.06 |
| QPlht.crc-4B Ht_avg | 4B | 54.8 | 54.2–55.8 | 15.3 | 14.4 | -2.9 | wmc657 | Excalibur_c21727_851 | 3.19 |
| QPlht.crc-4B Ht_BRA98 | 4B | 54.8 | 54.2–55.7 | 7.5 | 10.4 | -2.9 | wmc657 | Excalibur_c21727_851 | 3.08 |
| QPlht.crc-4B Ht_BRA00 | 4B | 54.8 | 54.2–55.7 | 11.9 | 13.9 | -2.7 | wmc657 | Excalibur_c21727_851 | 3.07 |
| QPlht.crc-4B Ht_GLE00 | 4B | 54.8 | 54.2–55.9 | 7.6 | 8.8 | -2.3 | wmc657 | Excalibur_c21727_851 | 3.10 |
| QPlht.crc-4B Ht_MOR00 | 4B | 54.8 | 54.2–55.9 | 8.5 | 11.1 | -2.4 | wmc657 | Excalibur_c21727_851 | 3.16 |
| QPlht.crc-4B Ht_MOR98 | 4B | 55.9 | 54.8–58.6 | 5.5 | 13.3 | -4.1 | Excalibur_c21727_851 | RAC875_rep_c98992_464 | 3.20 |
| QPlht.crc-4D Ht_MOR99 | 4D | 32.8 | 28.9–36.2 | 24.0 | 51.0 | 6.6 | wmc617c | wMAS000002 | 3.11 |
| QPlht.crc-4D Ht_MOR98 | 4D | 33.4 | 25.9–37.2 | 10.0 | 26.8 | 5.8 | wmc617c | wMAS000002 | 3.20 |
| QPlht.crc-4D Ht_avg | 4D | 34.2 | 32.1–36.1 | 38.3 | 58.6 | 5.8 | wmc617c | wMAS000002 | 3.19 |
| QPlht.crc-4D Ht_BRA98 | 4D | 34.2 | 31.4–36.4 | 25.4 | 50.7 | 6.3 | wmc617c | wMAS000002 | 3.08 |
| QPlht.crc-4D Ht_GLE99 | 4D | 34.2 | 32.0–37.1 | 32.8 | 57.9 | 7.6 | wmc617c | wMAS000002 | 3.18 |
| QPlht.crc-4D Ht_BRA00 | 4D | 34.2 | 32.5–35.9 | 29.5 | 44.5 | 4.9 | wmc617c | wMAS000002 | 3.07 |
| QPlht.crc-4D Ht_GLE00 | 4D | 34.2 | 32.4–35.7 | 30.4 | 49.7 | 4.9 | wmc617c | wMAS000002 | 3.10 |
| QPlht.crc-4D Ht_MOR00 | 4D | 34.3 | 32.7–37.2 | 26.5 | 45.5 | 4.9 | wMAS000002 | wmc48b | 3.16 |
| QPlht.crc-4D Ht_GLE98 | 4D | 35.2 | 32.7–39.0 | 28.2 | 46.8 | 6.3 | wMAS000002 | wmc48b | 3.06 |
| Grain Weight (Gwt) | | | | | | | | |
| QGwt.crc-2B.1 Gwt_GLE00 | 2B.1 | 55.4 | 54.8–56.5 | 4.2 | 4.8 | -0.7 | RAC875_c31358_214 | Tdurum_contig42153_4272 | 3.05 |
| QGwt.crc-2B.1 Gwt_BRA04 | 2B.1 | 65.3 | 64.4–66.0 | 8.5 | 5.6 | -1.1 | wsnp_Ex_c21092_30220702 | Excalibur_c6502_397 | 3.14 |
| QGwt.crc-2B.1 Gwt_avg | 2B.1 | 67.9 | 67.2–69.5 | 4.6 | 6.7 | -0.9 | RFL_Config914_2723 | BS00030497_51 | 3.28 |
| QGwt.crc-2B.2 Gwt_MOR00 | 2B.2 | 80 | 78.6–81.0 | 10.8 | 9.6 | -0.9 | RFL_Config1953_583 | wsnp_CAP11_c114_140053 | 3.15 |
| QGwt.crc-2B.2 Gwt_MOR99 | 2B.2 | 86.8 | 84.0–87.8 | 7.2 | 7.9 | -1.2 | Tdurum_contig26542_281 | wsnp_Ex_rep_c105551_89940311 | 3.09 |
| QGwt.crc-2B.2 Gwt_GLE00 | 2B.2 | 94.9 | 92.9–96.0 | 3.2 | 3.6 | -0.6 | wmc500b | wsnp_Ex_c9729_16071358 | 3.05 |
| QGwt.crc-3B Gwt_GLE99 | 3B | 0 | 0–0.6 | 8.3 | 8.2 | -1.3 | Tdurum_contig50954_1393 | Kukri_c15654_309 | 3.11 |

(Continued)
| QTL      | Trait name         | Chr | Peak (cM) | CI (cM) | LOD | r² (%) | Add (%) | Left marker              | Right marker              | LOD threshold (α₀.₀₅) |
|----------|--------------------|-----|-----------|---------|-----|--------|---------|--------------------------|--------------------------|-----------------------|
| QGwt.crc-3B | Gwt_GLE00 | 3B | 0         | 0–0.6   | 6.3 | 7.5    | -0.9    | Tdurum_contig50954_1393  | Kukri_c15654_309        | 3.05                  |
| QGwt.crc-3D | Gwt_MOR99 | 3D.2 | 4.9      | 3.6–5.3 | 5.8 | 6.2    | -1.1   | tplb0029j24_2118         | wsnp_Ex_rep_c101732_87042471 | 3.09                  |
| QGwt.crc-3D | Gwt_GLE99 | 3D.2 | 5.3      | 4.1–5.9 | 4.5 | 4.2    | -0.9   | wsnp_Ex_rep_c101732_87042471 | Kukri_c8913_385         | 3.11                  |
| QGwt.crc-3D | Gwt_GLE00 | 3D.2 | 20.9     | 12.4–33.8 | 4.2 | 6.2    | -0.8   | BobWhite_c23305_1192     | wmc552                   | 3.05                  |
| QGwt.crc-4A | Gwt_avg | 4A | 90.1     | 89.5–92.8 | 3.4 | 4.9    | 0.8    | Excalibur_c4325_1150     | RAC875_c59673_500        | 3.28                  |
| QGwt.crc-4A | Gwt_MOR99 | 4A | 90.1     | 89.5–92.7 | 6.6 | 7.2    | 1.2    | Excalibur_c4325_1150     | RAC875_c59673_500        | 3.09                  |
| QGwt.crc-4A | Gwt_MOR00 | 4A | 90.1     | 89.5–92.4 | 6.4 | 5.3    | 0.6    | Excalibur_c4325_1150     | RAC875_c59673_500        | 3.15                  |
| QGwt.crc-4A | Gwt_BRA04 | 4A | 90.1     | 89.5–92.8 | 6.3 | 4.0    | 1.0    | Excalibur_c4325_1150     | RAC875_c59673_500        | 3.14                  |
| QGwt.crc-4B | Gwt_MOR00 | 4B | 51.4     | 51.3–52.4 | 15.8 | 15.1   | -1.1   | BS00105308_51            | Tdurum_contig29989_132   | 3.15                  |
| QGwt.crc-4B | Gwt_MOR99 | 4B | 51.9     | 51.3–52.4 | 12.2 | 14.9   | -1.7   | Tdurum_contig29989_132   | Tdurum_contig5562_441    | 3.09                  |
| QGwt.crc-4B | Gwt_avg | 4B | 52.4     | 51.8–52.9 | 8.9  | 14.0   | -1.3   | Tdurum_contig29989_132   | Tdurum_contig5562_441    | 3.28                  |
| QGwt.crc-4B | Gwt_GLE00 | 4B | 52.4     | 51.8–52.9 | 6.3  | 7.4    | -0.9   | Tdurum_contig29989_132   | Tdurum_contig5562_441    | 3.05                  |
| QGwt.crc-4B | Gwt_BRA04 | 4B | 52.4     | 51.9–52.9 | 21.8 | 17.4   | -2.0   | Tdurum_contig29989_132   | Tdurum_contig5562_441    | 3.14                  |
| QGwt.crc-4B | Gwt_GLE99 | 4B | 52.5     | 52.4–53.4 | 7.8  | 7.5    | -1.2   | Tdurum_contig5562_441    | TA003708-0300            | 3.11                  |
| QGwt.crc-4B | Gwt_avg | 4B | 31.8     | 27.3–34.3 | 16.5 | 31.1   | 2.0    | wmc617c                  | wMAS0000002             | 3.28                  |
| QGwt.crc-4B | Gwt_MOR99 | 4B | 33.3     | 28.2–37.4 | 19.5 | 27.9   | 2.3    | wmc617c                  | wMAS0000002             | 3.09                  |
| QGwt.crc-4B | Gwt_GLE99 | 4B | 34.2     | 30.2–36.5 | 29.4 | 45.0   | 3.0    | wmc617c                  | wMAS0000002             | 3.11                  |
| QGwt.crc-4B | Gwt_GLE00 | 4B | 34.2     | 31.0–38.3 | 19.7 | 28.4   | 1.7    | wmc617c                  | wMAS0000002             | 3.05                  |
| QGwt.crc-4B | Gwt_MOR00 | 4B | 34.2     | 31.3–37.1 | 25.9 | 28.8   | 1.5    | wmc617c                  | wMAS0000002             | 3.15                  |
| QGwt.crc-4B | Gwt_BRA04 | 4B | 34.2     | 31.4–35.9 | 34.6 | 33.4   | 2.8    | wmc617c                  | wMAS0000002             | 3.14                  |
| QGwt.crc-6B | Gwt_BRA04 | 6B | 139.4    | 135.7–142.1 | 5.1  | 3.4    | 0.9    | RAC875_c6813_168         | BS00049082_51           | 3.14                  |
| QGwt.crc-6B | Gwt_GLE99 | 6B | 159.1    | 158.6–159.1 | 3.2  | 2.9    | 0.8    | Tdurum_contig68258_1773  | Kukri_c30924_203        | 3.11                  |

Test weight (Twt)

| QTwt.crc-1D | Twt_MOR99 | 1D | 96.9     | 96.1–97.5 | 9.8  | 11.3   | -0.8   | IAAV724                  | gpw0360                  | 3.06                  |
| QTwt.crc-1D | Twt_MOR00 | 1D | 111      | 97.7–124.9 | 4.7  | 6.0    | -0.6   | gpw0360                  | BS00022188_51           | 3.03                  |
| QTwt.crc-1D | Twt_BRA04 | 1D | 112.3    | 103.0–123.2 | 6.2  | 5.9    | -0.8   | gpw0360                  | BS00022188_51           | 3.15                  |
| QTL        | Trait name* | Chr | Peak (cM) | CI (cM) | LOD | r² (%) | Add* | Left marker                  | Right marker                  | LOD threshold (α₀.₀₅) |
|------------|-------------|-----|-----------|---------|-----|--------|------|-----------------------------|-------------------------------|------------------------|
| QTwt.crc-1D | Twt_GLE00   | 1D  | 117.3     | 104.1–117.2 | 6.2 | 7.0   | -0.7 | gpw0360                     | BS00022188_51               | 3.02                   |
| QTwt.crc-2A | Twt_GLE00   | 2A  | 89.6      | 88.9–92.2  | 3.4 | 3.3   | -0.5 | Kukri_rep_c68300_216         | RAC875_c9523_328             | 3.02                   |
| QTwt.crc-2A | Twt_MOR00   | 2A  | 89.6      | 88.9–92.2  | 3.2 | 3.3   | -0.5 | Kukri_rep_c68300_216         | RAC875_c9523_328             | 3.03                   |
| QTwt.crc-2B | Twt_MOR00   | 2B  | 27.6      | 26.4–36.0  | 5.5 | 6.0   | -0.6 | gpw5229                      | Excalibur_c40567_1893       | 3.03                   |
| QTwt.crc-2B | Twt_BRA04   | 2B  | 33.4      | 27.9–36.8  | 14.2| 12.2  | -1.1 | gpw5229                      | Excalibur_c40567_1893       | 3.15                   |
| QTwt.crc-2B | Twt_GLE00   | 2B  | 89.6      | 88.9–92.2  | 3.2 | 3.3   | -0.5 | Kukri_rep_c68300_216         | RAC875_c9523_328             | 3.03                   |
| QTwt.crc-2B | Twt_MOR00   | 2B  | 89.6      | 88.9–92.2  | 3.2 | 3.3   | -0.5 | Kukri_rep_c68300_216         | RAC875_c9523_328             | 3.03                   |
| QTwt.crc-2D | Twt_BRA04   | 2D  | 88.9      | 87.3–92.6  | 3.4 | 2.5   | 0.5  | gpw5256                      | Kukri_c92104_87              | 3.15                   |
| QTwt.crc-2D | Twt_MOR99   | 2D  | 102.7     | 100.9–104.3| 3.1 | 3.1   | 0.4  | wspn_Ku_c498_1036380         | Kukri_c52608_142             | 3.06                   |
| QTwt.crc-3B | Twt_BRA04   | 3B  | 60.1      | 58.8–61.2  | 11.5| 9.3   | -1.0 | Kasp3B(Exome)_3              | wspn_Ku_c18538_27857915     | 3.15                   |
| QTwt.crc-3B | Twt_GLE99   | 3B  | 70.4      | 70.1–72.9  | 7.3 | 15.3  | -1.0 | Tdurum_contig27495_111       | Kasp3B(survey)_17            | 3.08                   |
| QTwt.crc-3B | Twt_MOR99   | 3B  | 70.8      | 70.1–73.1  | 13.8| 17.0  | -1.0 | Kasp3B(survey)_17            | wspn_Ex_c16378_24870688     | 3.06                   |
| QTwt.crc-3B | Twt_GLE00   | 3B  | 72.1      | 70.2–73.1  | 13.7| 15.4  | -1.0 | Kasp3B(survey)_17            | wspn_Ex_c16378_24870688     | 3.02                   |
| QTwt.crc-3B | Twt_MOR00   | 3B  | 72.7      | 70.8–73.1  | 12.7| 15.1  | -1.0 | Kasp3B(survey)_17            | wspn_Ex_c16378_24870688     | 3.03                   |
| QTwt.crc-3B | Twt_GLE00   | 3B  | 77.1      | 66.5–77.7  | 5.1 | 5.1   | -0.6 | barc270                      | RAC875_c5606_501             | 3.02                   |
| QTwt.crc-3B | Twt_MOR00   | 3B  | 77.1      | 67.0–77.7  | 3.8 | 4.0   | -0.5 | barc270                      | RAC875_c5606_501             | 3.03                   |
| QTwt.crc-3B | Twt_MOR99   | 3B  | 77.7      | 77.1–82.5  | 5.4 | 5.6   | -0.6 | RAC875_c5606_501             | CAP7_c4219_359              | 3.06                   |
| QTwt.crc-4D | Twt_MOR99   | 4D  | 34.2      | 31.1–38.2  | 17.0| 22.3  | 1.2  | wmc617c                      | wMAS0000002                  | 3.06                   |
| QTwt.crc-4D | Twt_GLE00   | 4D  | 35        | 32.2–38.8  | 19.2| 24.0  | 1.2  | wMAS000002                   | wmc48b                       | 3.02                   |
| QTwt.crc-4D | Twt_GLE99   | 4D  | 35.4      | 28.7–41.4  | 8.8 | 19.8  | 1.2  | wMAS000002                   | wmc48b                       | 3.08                   |
| QTwt.crc-4D | Twt_MOR00   | 4D  | 36.4      | 32.7–41.2  | 16.8| 22.5  | 1.2  | wMAS000002                   | wmc48b                       | 3.03                   |
| QTwt.crc-4D | Twt_BRA04   | 4D  | 36.7      | 34.4–40.3  | 28.8| 31.0  | 1.8  | wMAS000002                   | wmc48b                       | 3.15                   |
| QTwt.crc-7A | Twt_MOR99   | 7A  | 84.1      | 83.5–85.2  | 5.2 | 5.4   | 0.6  | Kukri_c53682_85              | BS00103846_51               | 3.06                   |
| QTwt.crc-7A | Twt_GLE00   | 7A  | 84.1      | 83.5–85.2  | 3.3 | 3.2   | 0.5  | Kukri_c53682_85              | BS00103846_51               | 3.02                   |

**Flour yield (Fyd)**

| QFyd.crc-1B | Fyd_99     | 1B  | 81.7      | 81.1–88.1  | 3.8 | 6.1   | -0.6 | BS001110231_51               | gwm274a                     | 3.14                   |
| QFyd.crc-1B | Fyd_avg    | 1B  | 92.1      | 90.9–93.0  | 5.1 | 6.0   | -0.4 | Excalibur_c37496_271         | wPt-2257                    | 3.07                   |

(Continued)
QTL with LOD peaks located between 96.9 and 117.3 cM. No Gwt QTL was identified on chromosome 1D. Based on the additive effects of these QTL (Tables 2 and 3), the ‘AC Domain’ allele increased kernel length, Asym, and Per, and decreased Twt. The changes in kernel shape as a result of variation in this region of chromosome 1D appear to affect packing efficiency of kernels (i.e. test weight).

Chromosome 2A
QTL analysis identified a Twt QTL on chromosome 2A with LOD peaks at 89.6 cM with the ‘AC Domain’ allele decreasing Twt. No other QTL were identified in this genomic region.

Chromosome 2B
Three QTL clusters were present on chromosome 2B (linkage group 2B.1). QTL for grain width (QAMiL.crc-2B.1, QDMin.crc-2B.1, QSzWd.crc-2B.1) and ArPe (QArPe.crc-2B.1) were approximately located at 37 cM, which is the location of QTwt.crc-2B at 33 cM. The ‘AC Domain’ allele reduced Twt and grain width (Tables 2 and 3). This same region resulted in variability in Rect and Rndn. In addition, grain roundness QTL (QRect.crc-2B, QRndn.crc-2B, QSphr.crc-2B), kernel width (QAMiL.crc-2B.2, QDMin.crc-2B.2, QSzWd.crc-2B.2), and ArPe (QArPe.crc-2B.2) were located at 66 cM, which was also the location of QGwt.crc-2B.1. The ‘AC Domain’ allele decreased Gwt, Rect, Sphr, AMiL, DMin, SzWd, and ArPe, but increased Rndn. Finally, QTL for grain size (QArea.crc-2B) and mean kernel diameter (QDMen.crc-2B.3)

Table 2. (Continued)

| QTL     | Trait namea | Chr | Peak (cM) | CI (cM)b | LOD | r² (%) | Addc | Left marker | Right marker | LOD threshold (α₀.05) |
|---------|-------------|-----|-----------|----------|-----|--------|------|-------------|---------------|----------------------|
| QFyd.crc-3B | Fyd_00      | 3B  | 62.9      | 61.8–63.9| 9.7 | 17.5   | 0.7  | wsnp_Ku_c18538_27857915 | wsnp_Ex_c4769_8510104 | 3.12                 |
| QFyd.crc-3B | Fyd_avg     | 3B  | 65.1      | 64.6–65.6| 11.9| 15.2   | 0.6  | Kukri_c4310_489         | TA002966-0294       | 3.07                 |
| QFyd.crc-3B | Fyd_99      | 3B  | 65.1      | 64.5–65.6| 4.5 | 7.3    | 0.6  | Kukri_c4310_489         | TA002966-0294       | 3.14                 |
| QFyd.crc-3D | Fyd_avg     | 3D.2| 77.2      | 77.1–82.0| 4.9 | 5.7    | -0.4 | RAC875_c5606_501        | CAP7_c4219_359      | 3.07                 |
| QFyd.crc-3D | Fyd_00      | 3D.2| 77.7      | 76.9–78.7| 3.3 | 5.4    | -0.4 | RAC875_c5606_501        | CAP7_c4219_359      | 3.12                 |
| QFyd.crc-4B | Fyd_avg     | 4B  | 53        | 52.4–53.5| 3.9 | 4.5    | -0.3 | TA003708-0300           | BS00066282_51       | 3.07                 |
| QFyd.crc-4B | Fyd_00      | 4B  | 54.2      | 53.5–54.8| 3.1 | 5.0    | -0.4 | BS00066282_51           | wmc657              | 3.12                 |
| QFyd.crc-7D | Fyd_avg     | 7D.2| 13.8      | 13.7–14.3| 16.3| 21.7   | 0.7  | wsnp_Ra_c6894_11980338  | Excalibur_c22419_460| 3.07                 |
| QFyd.crc-7D | Fyd_99      | 7D.2| 15        | 13.7–18.9| 11.3| 20.7   | 1.0  | Excalibur_c22419_460   | wsnp_CAP8_rep_c9647_4198594 | 3.14                |
| QFyd.crc-7D | Fyd_00      | 7D.2| 23.9      | 22.0–28.1| 8.7 | 16.0   | 0.6  | wsnp_CAP8_rep_c9647_4198594 | Kukri_c35508_426    | 3.12                 |
| QFyd.crc-7D | Fyd_98      | 7D.2| 43.3      | 42.4–44.6| 3.9 | 13.1   | 0.7  | Ku_c26916_669          | wsnp_Ex_c11813_18968198 | 3.11                |

a BRA = Brandon, GLE = Glenlea, MOR = Morden, 98 = 1998, 99 = 1999, 00 = 2000, 04 = 2004.
b Confidence interval determined by one LOD drop-off.
c Additive effect of allele substitution. The units are those of the respective trait. A positive sign indicated that the ‘AC Domain’ allele increased the respective quantitative trait, and vice-versa.
Table 3. Inclusive Composite Interval Mapping (QIC) of QTL for 14 grain shape traits in the RL4452/‘AC Domain’ DH population from replicated trials.

| QTL Trait namea | Trait nameb | Chr | Peak (cM) | CI (cM)b | LOD | r² (%) | Addc | Left marker | Right marker | LOD threshold (α 0.05) |
|-----------------|-------------|-----|-----------|----------|------|--------|-------|-------------|--------------|-------------------|
| QDMen.cr-1A     | DMenG00A    | 1A  | 0         | 0–5.3    | 4.41 | 3.7    | -0.445| Tdurum_contig42405_197 | Tdurum_contig46413_779 | 3.0               |
| QPer.cr-1A      | Per2YRA     | 1A  | 0         | 0–5.9    | 3.98 | 4.9    | -2.0269 | Tdurum_contig42405_197 | Tdurum_contig46413_779 | 3.0               |
| QSzLn.cr-1A     | SzLn2YRA    | 1A  | 0.3       | 0–7.8    | 4.92 | 5.3    | -0.9539| Tdurum_contig42405_197 | Tdurum_contig46413_779 | 3.1               |
| QArPe.cr-1A     | ArPeG00A    | 1A  | 1.9       | 0–8.8    | 4.86 | 3.8    | -0.1095| Tdurum_contig42405_197 | Tdurum_contig46413_779 | 3.1               |
| QDMin.cr-1A     | DMinG00A    | 1A  | 1.9       | 0–9.5    | 3.32 | 2.3    | -0.315 | Tdurum_contig42405_197 | Tdurum_contig46413_779 | 3.1               |
| QArPe.cr-1A     | ArPe2YRA    | 1A  | 23.5      | 22.9–28.2| 3.37 | 2.2    | -0.0859| Excalibur_c3941_537 | RAC875_c14926_589 | 3.1               |
| QSzLn.cr-1A     | SzLn2YRA    | 1A  | 23.5      | 22.9–27.1| 3.46 | 2.4    | -0.3309| Excalibur_c3941_537 | RAC875_c14926_589 | 3.1               |
| QArPe.cr-1A     | ArPeG00S    | 1B.1| 57.7      | 55.0–58.8| 3.46 | 7.4    | -0.0237| wsnp_Ra_c4296_7819 | RAC875_c8849_134 | 3.0               |
| QArea.cr-1A     | AreaG00S    | 1B.1| 65.6      | 65.0–66.9| 3.10 | 2.4    | -0.4475| RAC875_c16391_426 | IAAV724 | 3.1               |
| QDMen.cr-1B     | DMenB04A    | 1B.1| 66.9      | 65.5–67.4| 3.35 | 3.7    | 0.7464 | Excalibur_c33661_412 | BS00038418_51 | 3.1               |
| QAMaL.cr-1D     | AMaLG00A    | 1D  | 79.3      | 77.9–80.3| 4.35 | 5.2    | 0.9503 | Excalibur_c33661_412 | BS00038418_51 | 3.1               |
| QMax.cr-1D      | DMaxG00A    | 1D  | 79.3      | 77.9–80.3| 4.35 | 5.2    | 0.9503 | Excalibur_c33661_412 | BS00038418_51 | 3.1               |
| QSzLn.cr-1D     | SzLnG00A    | 1D  | 79.3      | 77.9–80.3| 5.12 | 5.5    | 0.97   | Excalibur_c33661_412 | BS00038418_51 | 3.1               |
| QPer.cr-1D      | Per2YRA     | 1D  | 80.3–90.5 | 80.3–90.5| 4.85 | 5.6    | 2.1005 | BS00038418_51 | IAAV724 | 3.1               |
| QArea.cr-1D     | AreaG00S    | 1D  | 80.3–90.5 | 80.3–90.5| 5.11 | 7.1    | 1.0973 | BS00038418_51 | IAAV724 | 3.1               |
| QAMaL.cr-1D     | AMaLB04A    | 1D  | 96.1–107.1| 96.1–107.1| 4.03 | 5.4    | 1.6713 | IAAV724 | gpw0360 | 3.0               |
| QAMaL.cr-1D     | AMaLB04A    | 1D  | 96.1–107.1| 96.1–107.1| 3.97 | 4.1    | 0.8513 | IAAV724 | gpw0360 | 3.1               |
| QMax.cr-1D      | DMaxG00A    | 1D  | 96.1–107.4| 96.1–107.4| 5.04 | 5.3    | 0.9635 | gpw0360 | BS00022188_51 | 3.2               |
| QMax.cr-1D      | DMaxB04A    | 1D  | 96.1–107.4| 96.1–107.4| 3.71 | 4.9    | 0.9605 | gpw0360 | BS00022188_51 | 3.1               |
| QSzLn.cr-1D     | SzLnB04A    | 1D  | 96.1–108.0| 96.1–108.0| 3.74 | 5.0    | 0.9711 | gpw0360 | BS00022188_51 | 3.0               |
| QAMaL.cr-1D     | AMaL2YRA    | 1D  | 96.1–107.4| 96.1–107.4| 5.34 | 5.3    | 0.9239 | gpw0360 | BS00022188_51 | 3.1               |
| QAsym.cr-1D     | AsymG00A    | 1D  | 96.1–111.2| 96.1–111.2| 5.49 | 6.4    | 1.8218 | gpw0360 | BS00022188_51 | 3.1               |
| QAsym.cr-1D     | Asym2YRS    | 1D  | 96.1–113.7| 96.1–113.7| 4.59 | 6.8    | 0.4098 | gpw0360 | BS00022188_51 | 3.1               |
| QPer.cr-1D      | Per2YRA     | 1D  | 96.1–109.8| 96.1–109.8| 3.83 | 4.1    | 1.9833 | gpw0360 | BS00022188_51 | 3.1               |
| QAsym.cr-1D     | Asym2YRA    | 1D  | 96.1–110.7| 96.1–110.7| 6.24 | 7.1    | 1.9083 | gpw0360 | BS00022188_51 | 3.0               |

(Continued)
| QTL                 | Trait name* | Chr | Peak (cM)   | CI (cM)  | LOD | $r^2$ (%) | Add*   | Left marker | Right marker | LOD threshold ($\alpha=0.05$) |
|---------------------|-------------|-----|-------------|----------|-----|-----------|--------|-------------|--------------|--------------------------------|
| QAsym (var).crc-1D  | AsymB04S    | 1D  | 102.3       | 96.1–119.1| 3.33| 2.0       | 0.3884 | gpw0360     | BS00022188_S1| 3.1                                      |
| QAMiLcrc-2B.1       | AMiLG00A    | 2B:1| 36.2        | 31.0–36.8| 6.97| 4.8       | -0.4397| gpw5229     | Excalibur_c40567_1893| 3.1                                      |
| QArPe_crc-2B.1      | ArPe2YRA    | 2B:1| 36.2        | 30.6–36.8| 6.50| 4.4       | -0.1211| gpw5229     | Excalibur_c40567_1893| 3.1                                      |
| QArPe_crc-2B.1      | ArPeG00A    | 2B:1| 36.2        | 31.8–36.8| 6.42| 4.8       | -0.1225| gpw5229     | Excalibur_c40567_1893| 3.1                                      |
| QDMen_crc-2B.1      | DMenG00A    | 2B:1| 36.2        | 28.3–36.8| 4.11| 3.5       | -0.4282| gpw5229     | Excalibur_c40567_1893| 3.0                                      |
| QDMin_crc-2B.1      | DMinG00A    | 2B:1| 36.2        | 28.4–36.8| 6.29| 4.1       | -0.4216| gpw5229     | Excalibur_c40567_1893| 3.1                                      |
| QRRec_crc-2B.1      | Rec2YRS     | 2B:1| 36.2        | 31.9–36.8| 6.34| 6.6       | 0.0017 | gpw5229     | Excalibur_c40567_1893| 3.0                                      |
| QRRec_crc-2B.1      | RecB04S     | 2B:1| 36.2        | 32.7–36.8| 7.71| 8.6       | 0.0022 | gpw5229     | Excalibur_c40567_1893| 3.2                                      |
| QRndn_crc-2B.1      | Rndn2YRS    | 2B:1| 36.2        | 28.2–36.8| 3.20| 4.1       | 0.0023 | gpw5229     | Excalibur_c40567_1893| 3.1                                      |
| QRndn_crc-2B.1      | RndnB04S    | 2B:1| 36.2        | 30.7–36.8| 5.05| 6.7       | 0.0035 | gpw5229     | Excalibur_c40567_1893| 3.1                                      |
| QSzWd_crc-2B.1      | SzWdG00A    | 2B:1| 36.2        | 31.3–36.8| 6.52| 5.0       | -0.4394| gpw5229     | Excalibur_c40567_1893| 3.0                                      |
| QSzWd_crc-2B.1      | SzWdB04A    | 2B:1| 36.2        | 31.7–36.8| 14.09| 9.7      | -0.8567| gpw5229     | Excalibur_c40567_1893| 3.1                                      |
| QSzWd_crc-2B.1      | SzWd2YRA    | 2B:1| 37.4        | 36.7–41.2| 7.13| 5.3       | -0.4846| wsnp_Exp_rep_c68623_67474885| GENE-1999_98| 3.1                                      |
| QAMiL_crc-2B.1      | AMiL2YRA    | 2B:1| 38.2        | 36.7–41.5| 6.38| 3.9       | -0.4388| wsnp_Exp_rep_c68623_67474885| GENE-1999_98| 3.1                                      |
| QAMiL_crc-2B.1      | AMiLB04A    | 2B:1| 38.6        | 36.7–41.1| 14.53| 11.9      | -0.9161| wsnp_Exp_rep_c68623_67474885| GENE-1999_98| 3.0                                      |
| QDMin_crc-2B.1      | DMinB04A    | 2B:1| 39.0        | 36.7–41.2| 16.11| 11.6      | -0.9374| wPt-8404    | Tdurum_contig54704_176| 3.1                                      |
| QRRec_crc-2B.1      | Rec2YRS     | 2B:1| 61.4        | 58.8–63.1| 8.25| 13.9      | -0.0035| wsnp_Ku_c12721_20478606| Tdurum_contig54704_176| 3.0                                      |
| QRndn_crc-2B.1      | Rndn2YRA    | 2B:1| 61.6        | 58.8–63.1| 8.53| 15.0      | 0.0113 | wsnp_Ku_c12721_20478606| Tdurum_contig54704_176| 3.1                                      |
| QSphr_crc-2B.1      | Sphr2YRA    | 2B:1| 61.9        | 58.9–63.1| 7.68| 12.4      | -0.0063| wsnp_Ku_c12721_20478606| Tdurum_contig54704_176| 3.0                                      |
| QArPe_crc-2B.2      | ArPeB04A    | 2B:1| 63.2        | 60.2–64.4| 9.04| 7.4       | -0.1876| Tdurum_contig54704_176| wsnp_Exp_c21092_30220702| 3.0                                      |
| QDMen_crc-2B.2      | DMenB04A    | 2B:1| 63.2        | 60.0–64.4| 6.13| 5.0       | -0.64  | Tdurum_contig54704_176| wsnp_Exp_c21092_30220702| 3.0                                      |
| QRRec_crc-2B.2      | RecG00S     | 2B:1| 63.2        | 59.2–64.4| 4.74| 6.2       | 0.0016 | Tdurum_contig54704_176| wsnp_Exp_c21092_30220702| 3.1                                      |
| QRRec_crc-2B.2      | RecB04A     | 2B:1| 63.6        | 63.2–64.4| 8.80| 12.3      | -0.0045| Tdurum_contig54704_176| wsnp_Exp_c21092_30220702| 3.1                                      |
| QSphr_crc-2B.2      | SphrB04A    | 2B:1| 63.9        | 63.2–64.4| 8.80| 11.9      | -0.0085| Tdurum_contig54704_176| wsnp_Exp_c21092_30220702| 3.2                                      |
| QRRec_crc-2B.2      | RecG00A     | 2B:1| 64.4        | 63.2–64.4| 11.11| 15.6      | -0.0039| Tdurum_contig54704_176| wsnp_Exp_c21092_30220702| 3.2                                      |
| QRndn_crc-2B.2      | RndnG00A    | 2B:1| 64.4        | 59.8–64.4| 5.55| 7.5       | 0.0088 | Tdurum_contig54704_176| wsnp_Exp_c21092_30220702| 3.2                                      |

(Continued)
| QTL      | Trait name*   | Chr | Peak (cM) | CI (cM) | LOD  | r²  | Add* | Left marker                      | Right marker                      | LOD threshold (α=0.05) |
|----------|---------------|-----|-----------|--------|------|-----|------|----------------------------------|----------------------------------|------------------------|
| QRndn.crc-2B | RndnB04A     | 2B.1 | 64.4 63.2–64.4 | 9.63 11.9 | 0.0136 | Tdurum_contig54704_176 | wsnp_Ex_c21092_30220702      | 3.0                  |
| QPhr.crc-2B | SphrG00A     | 2B.1 | 64.4 63.2–64.4 | 6.76 9.8  | -0.0054 | Tdurum_contig54704_176 | wsnp_Ex_c21092_30220702      | 3.1                  |
| QAMiL.crc-2B.2 | AMiL2YRA   | 2B.1 | 70.0 69.5–70.6 | 5.11 3.0 | -0.3877 | BS00030497_51 | Tdurum_contig62852_538      | 3.1                  |
| QArPe.crc-2B.2 | ArPe2YRA   | 2B.1 | 70.0 69.5–70.6 | 5.22 3.4  | -0.1075 | BS00030497_51 | Tdurum_contig62852_538      | 3.1                  |
| QSzWd.crc-2B.2 | SzWdG00A   | 2B.1 | 70.0 69.5–70.6 | 4.45 3.2  | -0.375  | BS00030497_51 | Tdurum_contig62852_538      | 3.1                  |
| QAMiL.crc-2B.2 | AMiLG00A   | 2B.1 | 70.1 69.5–70.6 | 7.22 5.0   | -0.4483 | Tdurum_contig62852_538 | RAC875_c55059_202  | 3.1                  |
| QDMn.crc-2B.2 | DMinG00A    | 2B.1 | 70.1 69.5–70.6 | 10.74 9.7 | -0.695  | Tdurum_contig62852_538 | RAC875_c55059_202  | 2.9                  |
| QDMn.crc-2B.2 | DMinG00A    | 2B.1 | 70.1 69.5–70.6 | 8.29 5.6  | -0.4908 | Tdurum_contig62852_538 | RAC875_c55059_202  | 3.1                  |
| QSzWd.crc-2B.2 | SzWdG00A   | 2B.1 | 70.1 69.5–70.6 | 4.61 3.4  | -0.3647 | Tdurum_contig62852_538 | RAC875_c55059_202  | 3.0                  |
| QArPe.crc-2B.2 | ArPeG00A   | 2B.1 | 80.1 78.6–81.0 | 7.55 5.7  | -0.1342 | RFL_Context1953_583 | wsnp_CAP11_c114_140053 | 3.1                  |
| QArea.crc-2B | Area2YRA     | 2B.1 | 87.9 86.7–90.6 | 5.08 5.3  | -0.06369 | Tdurum_contig62852_538 | RAC875_c55059_202  | 3.0                  |
| QArea.crc-2B | AreaG00A     | 2B.1 | 90.6 87.8–91.7 | 5.26 5.5  | -0.56430 | Tdurum_contig62852_538 | RAC875_c55059_202  | 3.1                  |
| QRect.crc-2D | RectG00A     | 2D   | 82.1 79.9–83.8 | 4.35 5.7 | 0.0023 | gpw0163  | BobWhite_c39793_88  | 3.2                  |
| QRndn.crc-2D | RndnG00A     | 2D   | 87.5 86.6–88.8 | 7.51 10.5 | -0.0104 | wPt-6847  | gpw5256  | 3.2                  |
| QRndn.crc-2D | RndnG00A     | 2D   | 87.9 86.6–88.8 | 4.57 7.5  | -0.008  | wPt-6847  | gpw5256  | 3.1                  |
| QRect.crc-2D | Rect2YRA     | 2D   | 88.0 86.6–88.8 | 4.52 7.1  | 0.0025 | wPt-6847  | gpw5256  | 3.0                  |
| QPhr.crc-2D | SphrG00A     | 2D   | 88.0 86.6–88.8 | 4.38 6.3  | 0.0043 | wPt-6847  | gpw5256  | 3.1                  |
| QPhr.crc-2D | SphrB04A     | 2D   | 88.0 86.6–88.8 | 3.24 4.2  | 0.005  | wPt-6847  | gpw5256  | 3.2                  |
| QPhr.crc-2D | Sphr2YRA     | 2D   | 88.1 86.6–88.8 | 4.94 7.6 | 0.0049 | wPt-6847  | gpw5256  | 3.0                  |
| QAMiL (var).crc-2D | AMiL2YRS | 2D   | 101.6 100.3–102.6 | 4.05 6.1  | 0.0767 | IACX14755 | wsnp_Ku_c498_1036380 | 3.2                   |
| QAMiL (var).crc-2D | AMiLB04S | 2D   | 101.7 100.3–102.6 | 3.69 8.1  | 0.1051 | IACX14755 | wsnp_Ku_c498_1036380 | 3.1                   |

(Continued)
| QTL                  | Trait name* | Chr | Peak (cM) | CI (cM)* | LOD  | r²  | Add*  | Left marker | Right marker | LOD threshold (α0.05) |
|----------------------|-------------|-----|-----------|----------|------|-----|-------|-------------|--------------|----------------------|
| QDMin (var).crc-2D   | DMinB04S    | 2D  | 101.9     | 100.9–104.3 | 3.27 | 6.4 | 0.0976 | IACX14755   | wsnp_Ku_c498_1036380 | 3.1                  |
| QSzWd (var).crc-2D   | SzWdB04S    | 2D  | 101.9     | 100.3–102.6 | 3.33 | 6.6 | 0.0954 | IACX14755   | wsnp_Ku_c498_1036380 | 3.2                  |
| QSphr(var).crc-3A    | Sphr2YRS    | 3A  | 65.9      | 64.6–68.3   | 5.01 | 12.6| 0.0013 | Excalibur_c2578_1966 | wsnp_Ku_rep_c71761_71496470 | 3.0                  |
| QSphr(var).crc-3A    | SphrB04S    | 3A  | 65.9      | 64.6–68.9   | 4.08 | 10.5| 0.0016 | Excalibur_c2578_1966 | wsnp_Ku_rep_c71761_71496470 | 3.0                  |
| QSphr(var).crc-3A    | SphrG00S    | 3A  | 65.9      | 64.6–67.9   | 5.40 | 13.7| 0.0012 | Excalibur_c2578_1966 | wsnp_Ku_rep_c71761_71496470 | 3.2                  |
| QSzWd(crc-3B         | SzWd2YRA    | 3B  | 0.1       | 0–0.6    | 3.13 | 2.2 | -0.3152 | Tdurum_contig50954_1393 | Kukri_c15654_309 | 3.1                  |
| QArPe(crc-3B         | ArPe2YRA    | 3B  | 0.2       | 0–0.6    | 5.87 | 4.0 | -0.1165 | Tdurum_contig50954_1393 | Kukri_c15654_309 | 3.1                  |
| QPer(var).crc-3B     | PerG00A     | 3B  | 0.2       | 0–0.6    | 4.77 | 5.4 | -2.0615 | Tdurum_contig50954_1393 | Kukri_c15654_309 | 3.1                  |
| QAMiL(crc-3B         | AMil2YRA    | 3B  | 0.3       | 0–0.6    | 4.85 | 3.0 | -0.3836 | Tdurum_contig50954_1393 | Kukri_c15645_309 | 3.1                  |
| QAMiL(crc-3B         | AMilG00A    | 3B  | 0.3       | 0–0.6    | 6.82 | 6.2 | -0.5011 | Tdurum_contig50954_1393 | Kukri_c15654_309 | 3.1                  |
| QArea(crc-3B         | AreaG00A    | 3B  | 0.3       | 0–0.6    | 6.25 | 6.8 | -62.9258 | Tdurum_contig50954_1393 | Kukri_c15654_309 | 3.1                  |
| QArPe(crc-3B         | ArPeG00A    | 3B  | 0.3       | 0–0.6    | 5.56 | 4.2 | -0.1146 | Tdurum_contig50954_1393 | Kukri_c15654_309 | 3.1                  |
| QDMen(crc-3B         | DMenG00A    | 3B  | 0.3       | 0–0.6    | 6.66 | 9.2 | 2.1778 | TA001464-0572 | BS000078127_51 | 3.0                  |
| QAMiL(crc-3B         | AMilG00A    | 3B  | 0.3       | 0–0.6    | 4.47 | 3.3 | -0.3772 | Tdurum_contig50954_1393 | Kukri_c15654_309 | 3.1                  |
| QSzWd(crc-3B         | SzWdG00A    | 3B  | 0.3       | 0–0.6    | 7.03 | 5.5 | -0.464  | Tdurum_contig50954_1393 | Kukri_c15654_309 | 3.0                  |
| QAsym(crc-3B         | AsymB04A    | 3B  | 65.6      | 65.1–66.2 | 6.66 | 9.2 | 2.1778 | TA001464-0572 | BS000078127_51 | 3.0                  |
| QArea(var).crc-3B    | Area2YRS    | 3B  | 65.7      | 65.1–66.2 | 3.83 | 6.3 | 11.7414 | BS000078127_51 | TA001464-0572 | 3.0                  |
| QArea(var).crc-3B    | AreaG00S    | 3B  | 65.7      | 65.1–66.2 | 5.17 | 8.4 | 13.4493 | BS000078127_51 | TA001464-0572 | 3.0                  |
| QAsym(crc-3B         | Asym2YRA    | 3B  | 65.7      | 65.1–66.2 | 10.96 | 11.8 | 2.4649 | BS000078127_51 | TA001464-0572 | 3.0                  |
| QAsym(crc-3B         | AsymG00A    | 3B  | 65.7      | 65.1–66.2 | 9.11 | 10.5 | 2.3461 | BS000078127_51 | TA001464-0572 | 3.1                  |
| QAsym(var).crc-3B    | AsymB04S    | 3B  | 68.4      | 67.3–69.0  | 8.51 | 4.8 | 0.6076 | Excalibur_c73633_120 | wsnp_Ex_rep_c69664_68618163 | 3.1                  |
| QPer(var).crc-3B     | PerG00S     | 3B  | 68.4      | 67.3–69.0  | 3.35 | 6.9 | 0.3687 | Excalibur_c73633_120 | wsnp_Ex_rep_c69664_68618163 | 3.1                  |
| QAsym(var).crc-3B    | Asym2YRS    | 3B  | 70.2      | 70.1–70.7  | 7.88 | 11.5 | 0.5337 | Tdurum_contig27495_111 | Kasp3B(survey)_17 | 3.1                  |
| QDMen(var).crc-3B    | DMenG00S    | 3B  | 70.2      | 70.1–70.7  | 4.82 | 10.0 | 0.117  | Tdurum_contig27495_111 | Kasp3B(survey)_17 | 3.2                  |
| QAsym(var).crc-3B    | AsymG00S    | 3B  | 72.5      | 70.1–73.1  | 8.41 | 17.1 | 0.6415 | Kasp3B(survey)_17 | wsnp_Ex_c146378_24870688 | 3.1                  |
| QAMiL(var).crc-3B    | AMilG00S    | 3B  | 74.5      | 73.1–77.9  | 4.34 | 13.4 | 0.099  | wsnp_Ex_c37115_44930934 | wsnp_Ex_c18915_27811736 | 3.1                  |

(Continued)
| QTL        | Trait name* | Chr | Peak (cM) | CI (cM) | LOD  | \( r^2 \) (%) | Add* | Left marker | Right marker | LOD threshold (\( \alpha = 0.05 \)) |
|------------|-------------|-----|-----------|---------|------|--------------|------|-------------|-------------|-------------------------------------|
| QArPe(var).crc-3B | ArPeG00 3B | 74.5 | 73.1–78.0 | 4.34   | 9.3  | 0.0266       |      | wsnp_Ex_c37115_44930934 | wsnp_Ex_c18915_27811736 | 3.0                                  |
| QDMin(var).crc-3B  | DMinG00 3B | 74.5 | 73.1–77.5 | 4.66   | 14.7 | 0.1055       |      | wsnp_Ex_c37115_44930934 | wsnp_Ex_c18915_27811736 | 3.0                                  |
| QSzWd(var).crc-3B  | SzWdG00 3B | 74.5 | 73.1–77.8 | 4.62   | 14.0 | 0.1038       |      | wsnp_Ex_c37115_44930934 | wsnp_Ex_c18915_27811736 | 3.0                                  |
| QArPe.crc-3D     | ArPe2YRA 3D.2 | 2.3  | 0.5–3.7   | 3.39   | 2.2  | -0.0855      |      | wsnp_Ra_c17636_26538543 | gwm191a 3.1                          |
| QAMiL.crc-3D     | AMiL00A 3D.2 | 14.1 | 12.4–25.8 | 5.33   | 3.6  | -0.3799      |      | BobWhite_c23305_1192    | wmc552 3.1                          |
| QSzWd.crc-3D     | SzWdG00 3D.2 | 14.1 | 12.4–27.4 | 4.52   | 3.3  | -0.3605      |      | BobWhite_c23305_1192    | wmc552 3.0                          |
| QDMin.crc-3D     | DMinG00 3D.2 | 15.7 | 12.4–29.3 | 6.56   | 4.5  | -0.4407      |      | BobWhite_c23305_1192    | wmc552 3.1                          |
| QArPe.crc-3D     | ArPeG00 3D.2 | 21.1 | 14.0–32.4 | 3.45   | 4.4  | -50.6042     |      | BobWhite_c23305_1192    | wmc552 3.1                          |
| QArea.crc-3D     | AreaG00 3D.2 | 22.4 | 12.4–22.4 | 7.20   | 8.3  | -0.659       |      | BobWhite_c23305_1192    | wmc552 3.0                          |
| QDMen.crc-3D     | DMenG00 3D.2 | 24.8 | 14.0–35.4 | 4.38   | 7.9  | -1.1569      |      | BobWhite_c23305_1192    | wmc552 3.1                          |
| QSzLn.crc-3D     | SzLnG00 3D.2 | 35.0 | 20.4–48.9 | 4.09   | 5.8  | -0.3973      |      | BobWhite_c23305_1192    | wmc552 3.1                          |
| QArPe.crc-3D     | ArPeG00 3D.2 | 35.5 | 24.0–48.3 | 5.19   | 8.1  | -2.5149      |      | BobWhite_c23305_1192    | wmc552 3.1                          |
| QAMaL.crc-3D     | AMaL2YRA 3D.2 | 78.5 | 77.7–84.0 | 4.24   | 4.0  | -0.8077      |      | CAP7_c4219_359          | wsnp_Ex_c12369_19730765 3.1         |
| QDMax.crc-3D     | DMaxG00 3D.2 | 80.4 | 77.7–84.5 | 4.07   | 5.1  | -0.9385      |      | CAP7_c4219_359          | wsnp_Ex_c12369_19730765 3.1         |
| QDMax.crc-3D     | DMax2YRA 3D.2 | 80.7 | 77.7–84.3 | 3.73   | 4.0  | -0.8408      |      | CAP7_c4219_359          | wsnp_Ex_c12369_19730765 3.2         |
| QAMaL.crc-3D     | AMaL00A 3D.2 | 81.0 | 77.7–84.5 | 5.39   | 6.3  | -0.9763      |      | CAP7_c4219_359          | wsnp_Ex_c12369_19730765 3.1         |
| QAMaL.crc-3D     | AMaLB04 3D.2 | 82.8 | 77.7–84.7 | 3.55   | 3.7  | -0.8024      |      | CAP7_c4219_359          | wsnp_Ex_c12369_19730765 3.1         |
| QSzLn.cell-4A.1  | SzLn2YRA 4A | 37.4 | 36.6–38.3 | 7.54   | 8.4  | 1.2002       |      | wsnp_Ex_c5492_9691241   | wsnp_Ex_rep_c66706_65037564 3.1     |
| QAMaL.crc-4A.1   | AMaL2YRA 4A | 37.7 | 36.6–38.3 | 9.53   | 9.8  | 1.2573       |      | wsnp_Ex_c5492_9691241   | wsnp_Ex_rep_c66706_65037564 3.1     |
| QAMaL.crc-4A.1   | AMaL00A 4A | 37.7 | 36.6–38.3 | 7.18   | 8.2  | 1.1231       |      | wsnp_Ex_c5492_9691241   | wsnp_Ex_rep_c66706_65037564 3.1     |
| QAMaL.crc-4A.1   | AMaLB04 4A | 37.7 | 36.6–38.3 | 9.51   | 10.7 | 1.3735       |      | wsnp_Ex_c5492_9691241   | wsnp_Ex_rep_c66706_65037564 3.1     |
| QSym.crc-4A.1    | AsymYRA 4A | 37.7 | 36.6–38.3 | 4.14   | 4.1  | 1.449        |      | wsnp_Ex_c5492_9691241   | wsnp_Ex_rep_c66706_65037564 3.0     |
| QSym.crc-4A.1    | AsymB04 4A | 37.7 | 36.6–38.3 | 5.18   | 7.0  | 1.9068       |      | wsnp_Ex_c5492_9691241   | wsnp_Ex_rep_c66706_65037564 3.0     |
| QDMax.crc-4A.1   | DMax2YRA 4A | 37.7 | 36.6–38.3 | 7.73   | 8.4  | 1.2189       |      | wsnp_Ex_c5492_9691241   | wsnp_Ex_rep_c66706_65037564 3.2     |
| QDMax.crc-4A.1   | DMaxG00 4A | 37.7 | 36.6–38.3 | 7.57   | 9.5  | 1.2824       |      | wsnp_Ex_c5492_9691241   | wsnp_Ex_rep_c66706_65037564 3.1     |

(Continued)
| QTL     | Trait name* | Chr | Peak (cM) | CI (cM) | LOD  | $r^2$ (%) | Add* | Left marker  | Right marker  | LOD threshold ($\alpha = 0.05$) |
|---------|-------------|-----|-----------|---------|------|-----------|------|--------------|---------------|-------------------------------|
| QDMax.crc-4A.1 | DMaxB04A | 4A  | 37.7 | 36.6–38.3 | 8.82 | 12.5 | 1.5386 | wsnp_Ex_c5492_9691241 | wsnp_Ex_rep_c66706_65037564 | 3.1 |
| QPer.crc-4A.1 | PerG00A | 4A  | 37.7 | 36.6–38.3 | 5.72 | 6.5  | 2.2612 | wsnp_Ex_c5492_9691241 | wsnp_Ex_rep_c66706_65037564 | 3.1 |
| QPer.crc-4A.1 | PerB04A | 4A  | 37.7 | 36.6–38.3 | 6.94 | 6.9  | 2.5781 | wsnp_Ex_c5492_9691241 | wsnp_Ex_rep_c66706_65037564 | 3.1 |
| QSzLn.crc-4A.1 | SzLnG00A | 4A  | 37.7 | 36.6–38.3 | 6.34 | 8.3  | 1.1953 | wsnp_Ex_c5492_9691241 | wsnp_Ex_rep_c66706_65037564 | 3.1 |
| QSzLn.crc-4A.1 | SzLnB04A | 4A  | 37.7 | 36.6–38.3 | 8.75 | 12.4 | 1.5407 | wsnp_Ex_c5492_9691241 | wsnp_Ex_rep_c66706_65037564 | 3.0 |
| QRect.crc-4A | RectG00A | 4A  | 38.8 | 38.2–39.4 | 4.80 | 6.3  | -0.0025 | wsnp_Ku_c13640_21686670 | wsnp_Ex_c829_1621908 | 3.2 |
| QRect.crc-4A | RectYRA  | 4A  | 39.3 | 38.8–40.9 | 5.66 | 8.8  | -0.0028 | wsnp_Ex_c829_1621908 | Kukri_rep_c69389_1215 | 3.0 |
| QRect.crc-4A | RectB04A | 4A  | 39.3 | 38.8–40.9 | 5.11 | 6.7  | -0.0034 | wsnp_Ex_c829_1621908 | Kukri_rep_c69389_1215 | 3.1 |
| QRndn.crc-4A | RndnYRA  | 4A  | 39.3 | 38.8–40.9 | 4.80 | 7.7  | 0.0081 | wsnp_Ex_c829_1621908 | Kukri_rep_c69389_1215 | 3.1 |
| QRndn.crc-4A | RndnB04A | 4A  | 39.3 | 38.8–40.9 | 4.43 | 5.1  | 0.009  | wsnp_Ex_c829_1621908 | Kukri_rep_c69389_1215 | 3.0 |
| QSphr.crc-4A | SphrYRA  | 4A  | 39.3 | 38.8–40.9 | 5.83 | 8.8  | -0.0054 | wsnp_Ex_c829_1621908 | Kukri_rep_c69389_1215 | 3.0 |
| QSphr.crc-4A | SphrG00A | 4A  | 39.3 | 38.8–40.9 | 4.54 | 6.4  | -0.0044 | wsnp_Ex_c829_1621908 | Kukri_rep_c69389_1215 | 3.1 |
| QSphr.crc-4A | SphrB04A | 4A  | 39.3 | 38.8–40.9 | 5.17 | 6.6  | -0.0064 | wsnp_Ex_c829_1621908 | Kukri_rep_c69389_1215 | 3.2 |
| QAMiL.crc-4A.1 | AMiLG00A | 4A  | 61.6 | 60.3–62.6 | 4.06 | 2.7  | -0.3287 | RAC875_c25124_182 | wsnp_Ku_c4924_8816643 | 3.1 |
| QDMin.crc-4A.1 | DMinG00A | 4A  | 61.6 | 60.3–62.6 | 5.86 | 3.8  | -0.4053 | RAC875_c25124_182 | wsnp_Ku_c4924_8816643 | 3.1 |
| QArea(var).crc-4A.1 | AreaG00S | 4A  | 63.8 | 63.2–65.9 | 4.76 | 7.7  | 12.8161 | Tdurum_contig13489_292 | wsnp_JD_c38619_27992279 | 3.0 |
| QArPe(var).crc-4A | ArPeG00S | 4A  | 63.8 | 63.2–65.9 | 4.12 | 8.8  | 0.0258 | Tdurum_contig13489_292 | wsnp_JD_c38619_27992279 | 3.0 |
| QDMen(var).crc-4A.1 | DMenG00S | 4A  | 63.8 | 63.2–65.9 | 3.88 | 8.1  | 0.1051 | Tdurum_contig13489_292 | wsnp_JD_c38619_27992279 | 3.2 |
| QAMaL(var).crc-4A.1 | AMaLB04S | 4A  | 82.6 | 81.9–83.5 | 4.30 | 8.5  | 0.2175 | RAC875_c88582_131 | Excalibur_c74397_238 | 3.0 |
| QAMaL(var).crc-4A.1 | AMaLB2YRS | 4A  | 83.5 | 82.4–84.1 | 4.42 | 9.0  | 0.1885 | RAC875_c88582_131 | Excalibur_c74397_238 | 3.1 |
| QAMaL.crc-4A.2 | AMaLB2YRA | 4A  | 86.3 | 85.2–89.3 | 5.24 | 5.1  | 0.8999 | RAC875_c7016_2039 | Excalibur_c4325_1150 | 3.1 |
| QAMaL.crc-4A.2 | AMaLB04A | 4A  | 86.3 | 86.2–90.1 | 7.09 | 7.7  | 1.1555 | RAC875_c7016_2039 | Excalibur_c4325_1150 | 3.1 |
| QAsym.crc-4A.2 | AsymG00A | 4A  | 86.3 | 85.2–89.5 | 5.15 | 5.6  | 1.7105 | RAC875_c7016_2039 | Excalibur_c4325_1150 | 3.1 |
| QDMax.crc-4A.2 | DMax2YRA | 4A  | 86.3 | 85.2–89.5 | 6.00 | 6.4  | 1.0552 | RAC875_c7016_2039 | Excalibur_c4325_1150 | 3.2 |
| QAsym(var).crc-4A | AsymYRA  | 4A  | 87.4 | 86.2–90.1 | 4.10 | 5.8  | 0.3782 | RAC875_c7016_2039 | Excalibur_c4325_1150 | 3.1 |

(Continued)
| QTL        | Trait name* | Chr | Peak (cM) | CI (cM) | LOD | r² (%) | Add* | Left marker | Right marker | LOD threshold (0.05) |
|------------|-------------|-----|-----------|---------|-----|--------|------|-------------|--------------|---------------------|
| QPer.crc-4A.2 | PerB04A     | 4A   | 87.7      | 86.2–90.1 | 8.63 | 8.9   | 2.9068 | RAC875_c7016_2039 | Excalibur_c4325_1150 | 3.1                |
| QArea.crc-4A | AreaG00A    | 4A   | 89.6      | 86.2–90.1 | 3.71 | 3.8   | 46.7029 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QDMax.crc-4A.2 | DMaxB04A  | 4A   | 89.6      | 89.5–92.7 | 5.73 | 7.8   | 1.2042 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QDMin.crc-4A.2 | DMin2YRA  | 4A   | 89.6      | 86.2–90.1 | 3.25 | 2.6   | 0.3624 | Excalibur_c4325_1150 | RAC875_c59673_500 | 2.9                |
| QSzLn.crc-4A.2 | SzLnB04A  | 4A   | 89.6      | 89.5–92.7 | 5.69 | 7.7   | 1.2068 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.0                |
| QAMiL.crc-4A.2 | AMiL2YRA  | 4A   | 90.1      | 89.5–93.3 | 3.83 | 2.2   | 0.3329 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QAMiL.crc-4A.2 | AMiLG00A   | 4A   | 90.1      | 89.5–92.1 | 8.25 | 5.8   | 0.4827 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QArea.crc-4A | Area2YRA    | 4A   | 90.1      | 86.2–90.1 | 6.60 | 7.0   | 69.0294 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.0                |
| QArea.crc-4A | AreaB04A    | 4A   | 90.1      | 86.2–90.1 | 6.50 | 6.4   | 76.291  | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.0                |
| QArea(var).crc-4A.2 | Area2YRS  | 4A   | 90.1      | 89.5–92.7 | 5.34 | 9.0   | 14.0057 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.0                |
| QArPe.crc-4A | ArPe2YRA    | 4A   | 90.1      | 89.5–92.7 | 7.76 | 5.3   | 0.1335 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QArPe.crc-4A | ArPeG00A    | 4A   | 90.1      | 89.5–92.5 | 4.78 | 3.5   | 0.1046 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QAsym(var).crc-4A.2 | AsymB04S   | 4A   | 90.1      | 89.5–90.1 | 29.63 | 22.9 | 1.321  | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QDMen.crc-4A.2 | DMen2YRA   | 4A   | 90.1      | 86.3–90.1 | 5.54 | 5.6   | 0.5782 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QDMen.crc-4A.2 | DMenG00A   | 4A   | 90.1      | 89.5–92.3 | 6.55 | 5.7   | 0.5497 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.0                |
| QDMen.crc-4A.2 | DMenB04A   | 4A   | 90.1      | 89.5–93.0 | 8.22 | 6.9   | 0.753  | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.0                |
| QDMen.crc-4A.2 | DMenG00A   | 4A   | 90.1      | 89.5–91.9 | 10.04 | 6.9   | 0.5473 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QPer.crc-4A.2 | Per2YRA     | 4A   | 90.1      | 86.2–90.1 | 7.87 | 10.3  | 2.918  | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.0                |
| QSzLn.crc-4A.2 | SzLn2YRA   | 4A   | 90.1      | 86.2–90.1 | 4.83 | 5.1   | 0.9367 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QSzWd.crc-4A.2 | SzWd2YRA   | 4A   | 90.1      | 86.2–90.1 | 4.28 | 3.0   | 0.3672 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.1                |
| QSzWd.crc-4A.2 | SzWdG00A   | 4A   | 90.1      | 89.5–93.4 | 3.56 | 2.6   | 0.3179 | Excalibur_c4325_1150 | RAC875_c59673_500 | 3.0                |
| QAMaL(var).crc-4A | AMaL2YRA  | 4A   | 90.2      | 89.5–94.4 | 4.15 | 8.5   | 0.1867 | RAC875_c59673_500 | RFL_Contig4334_379 | 3.1                |
| QArea(var).crc-4A.2 | AreaB04S   | 4A   | 90.2      | 89.5–92.6 | 8.60 | 13.3  | 21.4436 | RAC875_c59673_500 | RFL_Contig4334_379 | 3.0                |
| QArPe.crc-4A | ArPeB04A    | 4A   | 90.2      | 89.5–94.0 | 5.73 | 4.5   | 0.1462 | RAC875_c59673_500 | RFL_Contig4334_379 | 3.0                |
| QDMen(var).crc-4A.2 | DMenB04S  | 4A   | 90.2      | 89.5–93.6 | 3.37 | 7.2   | 0.1098 | RAC875_c59673_500 | RFL_Contig4334_379 | 3.1                |

(Continued)
| QTL                  | Trait name*                  | Chr | Peak (cM) | CI (cM) | LOD  | r²   | Add* | Left marker                  | Right marker                  | LOD threshold (α0.05) |
|---------------------|------------------------------|-----|-----------|---------|------|------|------|-------------------------------|-------------------------------|----------------------|
| QPer(var).crc-4A    | Per2YRS                      | 4A  | 90.2      | 89.5–93.4 | 4.79 | 9.3  | 0.428 | RAC875_c59673_500             | RFL_Ccontig4334_379          | 3.0                  |
| QPer(var).crc-4A    | PerG00S                      | 4A  | 90.2      | 89.5–94.3 | 3.56 | 7.3  | 0.3799 | RAC875_c59673_500             | RFL_Ccontig4334_379          | 3.1                  |
| QPer(var).crc-4A    | PerB04S                      | 4A  | 90.2      | 89.5–93.2 | 4.35 | 8.8  | 0.4581 | RAC875_c59673_500             | RFL_Ccontig4334_379          | 3.0                  |
| QSphecrc-4B         | SphrG00A                     | 4B  | 38.4      | 33.2–42.8 | 7.32 | 11.3 | 0.0058 | BS00022431_51                 | GENE-3024_59                 | 3.1                  |
| QRect crc-4B        | Rect2YRA                     | 4B  | 39.2      | 32.1–42.8 | 5.37 | 8.6  | 0.0028 | BS00022431_51                 | GENE-3024_59                 | 3.0                  |
| QRndn crc-4B        | RndnG00A                     | 4B  | 39.4      | 34.1–42.3 | 8.02 | 11.9 | -0.0112 | BS00022431_51                 | GENE-3024_59                 | 3.2                  |
| QAMaL crc-4B        | AMaLB04A                     | 4B  | 43.3      | 40.0–43.3 | 12.97| 15.2 | -1.6474 | Excalibur_rep_c113261_400    | GENE-3024_59                 | 3.1                  |
| QAsym crc-4B        | AsymB04A                     | 4B  | 43.3      | 39.0–43.3 | 10.01| 14.5 | -2.7553 | Excalibur_rep_c113261_400    | GENE-3024_59                 | 3.0                  |
| QDMax crc-4B        | DMaxB04A                     | 4B  | 51.3      | 50.7–51.8 | 14.04| 15.9 | -2.8586 | Tdurum_contig57516_269     | BS00105308_51                | 3.0                  |
| QAMaL crc-4B        | AMaL2YRA                     | 4B  | 52.4      | 51.8–52.9 | 16.04| 18.1 | -1.7029 | Tdurum_contig29989_132     | Tdurum_contig5562_441       | 3.1                  |
| QArea crc-4B        | AreaB04A                     | 4B  | 52.4      | 51.9–52.9 | 15.18| 16.9 | -124.204 | Tdurum_contig29989_132   | Tdurum_contig5562_441       | 3.0                  |
| QArPe(var).crc-4B   | ArPe2YRS                     | 4B  | 52.4      | 51.8–52.9 | 5.89 | 13.9 | -0.0291 | Tdurum_contig29989_132     | Tdurum_contig5562_441       | 3.1                  |
| QDMax crc-4B        | DMaxB04A                     | 4B  | 52.4      | 51.8–52.9 | 11.05| 16.2 | -1.7438 | Tdurum_contig29989_132     | Tdurum_contig5562_441       | 3.1                  |
| QDMen(var).crc-4B   | DMen2YRS                     | 4B  | 52.4      | 51.8–52.9 | 6.82 | 15.9 | -0.1314 | Tdurum_contig29989_132     | Tdurum_contig5562_441       | 3.1                  |
| QDMen(var).crc-4B   | DMenG00S                     | 4B  | 52.4      | 51.8–52.9 | 5.56 | 11.8 | -0.1274 | Tdurum_contig29989_132     | Tdurum_contig5562_441       | 3.2                  |
| QPer crc-4B         | PerB04A                      | 4B  | 52.4      | 51.8–52.9 | 15.25| 17.2 | -4.0413 | Tdurum_contig29989_132     | Tdurum_contig5562_441       | 3.1                  |
| QSZL crc-4B         | SZL2YRA                      | 4B  | 52.4      | 51.8–52.9 | 10.97| 16.1 | -1.7467 | Tdurum_contig29989_132     | Tdurum_contig5562_441       | 3.0                  |
| QAMaL crc-4B        | AMaLG00A                     | 4B  | 52.5      | 52.4–53.5 | 15.12| 19.4 | -1.7161 | Tdurum_contig5562_441       | TA003078-0300               | 3.1                  |
| QArea crc-4B        | Area2YRA                     | 4B  | 52.5      | 52.4–53.5 | 15.85| 19.0 | -114.4186 | Tdurum_contig5562_441     | TA003078-0300               | 3.0                  |
| QAsym crc-4B        | AsymG00A                     | 4B  | 52.5      | 52.4–53.5 | 13.04| 24.4 | -23.0986 | Tdurum_contig5562_441     | TA003078-0300               | 3.0                  |

(Continued)
### Table 3. (Continued)

| QTL                        | Trait name* | Chr | CI (cM) | LOD  | r²  | Add* | Left marker | Right marker | LOD threshold (α=0.05) |
|----------------------------|-------------|-----|---------|------|-----|------|-------------|--------------|------------------------|
| QAsym (var).crc-4B         | AsymG00S    | 4B  | 52.5    | 52.4–53.5 | 9.11 | 18.7 | -0.6711     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QDMax.crc-4B               | DMaxG00A    | 4B  | 52.5    | 52.4–53.5 | 13.99 | 19.1 | -1.8178     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QDMax (var).crc-4B         | DMax2YRS    | 4B  | 52.5    | 51.8–52.9 | 6.32  | 13.3 | -0.2212     | Tdurum_contig5562_441 | TA003708-0300          | 3.0                    |
| QDMax (var).crc-4B         | DMaxB04S    | 4B  | 52.5    | 51.8–52.9 | 4.14  | 9.1  | -0.2171     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QDMin.crc-4B               | DMin2YRA    | 4B  | 52.5    | 51.8–52.9 | 13.91 | 15.8 | -0.9733     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QDMin.crc-4B               | DMin2YRA    | 4B  | 52.5    | 51.8–52.9 | 5.48  | 4.6  | -0.4794     | Tdurum_contig5562_441 | TA003708-0300          | 2.9                    |
| QPer.crc-4B                | Per2YRA     | 4B  | 52.5    | 52.4–53.5 | 16.36 | 23.9 | -4.4629     | Tdurum_contig5562_441 | TA003708-0300          | 3.0                    |
| QPer(var).crc-4B           | PerG00S     | 4B  | 52.5    | 52.4–53.5 | 6.56  | 14.1 | -0.5268     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QSzLn(var).crc-4B          | SzLn2YRS    | 4B  | 52.5    | 51.8–52.9 | 6.23  | 12.9 | -0.2214     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QSzLn(var).crc-4B          | SzLnB04S    | 4B  | 52.5    | 51.8–52.9 | 4.13  | 9.2  | -0.2181     | Tdurum_contig5562_441 | TA003708-0300          | 3.0                    |
| QSzWd.crc-4B               | SzWdB04A    | 4B  | 52.5    | 51.8–52.9 | 10.16 | 6.6  | -0.709      | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QAMaL (var).crc-4B         | AMaL2YRS    | 4B  | 52.9    | 51.8–52.9 | 6.68  | 14.0 | -0.2359     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QAMaL (var).crc-4B         | AMaLG00S    | 4B  | 52.9    | 52.4–53.5 | 6.61  | 14.0 | -0.2402     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QAMiL.crc-4B               | AMiLG00A    | 4B  | 52.9    | 51.8–52.9 | 8.41  | 5.9  | -0.4881     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QArPe.crc-4B               | ArPeG00A    | 4B  | 52.9    | 51.8–52.9 | 13.21 | 10.8 | -0.1846     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QArPe.crc-4B               | ArPeB04A    | 4B  | 52.9    | 51.9–52.9 | 12.75 | 11.0 | -0.2295     | Tdurum_contig5562_441 | TA003708-0300          | 3.0                    |
| QAsym (var).crc-4B         | Asym2YRS    | 4B  | 52.9    | 51.8–52.9 | 12.54 | 19.6 | -0.6993     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QDMax (var).crc-4B         | DMaxG00S    | 4B  | 52.9    | 52.4–53.5 | 8.49  | 0.5  | -0.2571     | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QDMin.crc-4B               | DMin2YRA    | 4B  | 52.9    | 51.8–52.9 | 15.11 | 13.9 | -1.0724     | Tdurum_contig5562_441 | TA003708-0300          | 3.0                    |
| QSzLn(var).crc-4B          | SzLnG00S    | 4B  | 52.9    | 52.4–53.5 | 8.41  | 0.5  | -0.257      | Tdurum_contig5562_441 | TA003708-0300          | 3.1                    |
| QSzWd.crc-4B               | SzWdG00A    | 4B  | 52.9    | 51.8–52.9 | 10.36 | 8.3  | -0.5679     | Tdurum_contig5562_441 | TA003708-0300          | 3.0                    |
| QArea(var).crc-4B          | AreaB04S    | 4B  | 52.9    | 52.4–53.5 | 10.50 | 16.7 | -24.0438    | TA003708-0300          | BS00066282_51          | 3.0                    |
| QPer(var).crc-4B           | Per2YRS     | 4B  | 52.9    | 52.4–53.5 | 7.42  | 15.0 | -0.5432     | TA003708-0300          | BS00066282_51          | 3.0                    |
| QAMiL.crc-4B               | AMiL2YRA    | 4B  | 52.9    | 52.9–53.5 | 18.31 | 13.0 | -0.8057     | TA003708-0300          | BS00066282_51          | 3.1                    |
| QArea.crc-4B               | AreaG00A    | 4B  | 52.9    | 52.4–53.5 | 14.08 | 16.4 | -97.877     | TA003708-0300          | BS00066282_51          | 3.1                    |
| QArea (var).crc-4B         | AreaG00S    | 4B  | 52.9    | 52.4–53.5 | 12.09 | 21.6 | -21.5565    | TA003708-0300          | BS00066282_51          | 3.0                    |

(Continued)
| QTL      | Trait name* | Chr | Peak (cM) | CI (cM)* | LOD  | $r^2$ (%) | Add* | Left marker   | Right marker  | LOD threshold (α 0.05) |
|----------|-------------|-----|-----------|----------|-------|-----------|------|---------------|---------------|----------------------|
| QArPe.crc-4B | ArPe2YRA  | 4B  | 53.5      | 52.4–53.5 | 16.88 | 13.0      | -0.2092 | TA003708-0300 | BS00066282_51 | 3.1                           |
| QArPe(var).crc-4B | ArPeG00S | 4B  | 53.5      | 52.9–54.1 | 4.98  | 10.8      | -0.0286 | TA003708-0300 | BS00066282_51 | 3.0                           |
| QDMen.crc-4B | DMenG00A  | 4B  | 53.5      | 52.4–53.5 | 16.35 | 16.3      | -0.9274 | TA003708-0300 | BS00066282_51 | 3.0                           |
| QDMin.crc-4B | DMinB04A  | 4B  | 53.5      | 52.9–54.2 | 9.31  | 6.1       | -0.6804 | TA003708-0300 | BS00066282_51 | 3.1                           |
| QPer.crc-4B | PerG00A   | 4B  | 53.5      | 53.0–53.5 | 15.70 | 20.5      | -3.9994 | TA003708-0300 | BS00066282_51 | 3.1                           |
| QSzWd.crc-4B | SzWd2YRA  | 4B  | 53.5      | 52.4–53.5 | 11.77 | 9.2       | -0.6402 | TA003708-0300 | BS00066282_51 | 3.1                           |
| QDMin.crc-4B | DMinG00A  | 4B  | 53.6      | 52.9–54.2 | 8.42  | 5.7       | -0.4961 | BS00066282_51 | wmc657         | 3.1                           |
| QAMiL.crc-4B | AMiLB04A  | 4B  | 53.8      | 52.9–54.2 | 7.43  | 5.5       | -0.6257 | BS00066282_51 | wmc657         | 3.0                           |
| QAMiL(var).crc-4B | AMi2YRS | 4B  | 54.1      | 53.5–54.8 | 6.25  | 9.1       | -0.0942 | BS00066282_51 | wmc657         | 3.2                           |
| QDMin(var).crc-4B | DMin2YRS | 4B  | 54.1      | 53.5–54.8 | 6.05  | 10.5      | -0.0997 | BS00066282_51 | wmc657         | 3.0                           |
| QAMaL(var).crc-4B | AMaLB04S | 4B  | 54.2      | 53.5–54.8 | 4.20  | 8.3       | -0.2155 | BS00066282_51 | wmc657         | 3.0                           |
| QAMiL(var).crc-4B | AMiLB04S | 4B  | 54.2      | 53.5–54.8 | 3.39  | 6.7       | -0.0965 | BS00066282_51 | wmc657         | 3.1                           |
| QArPe(var).crc-4B | ArPeB04S | 4B  | 54.2      | 53.5–54.8 | 4.97  | 11.1      | -0.0327 | BS00066282_51 | wmc657         | 3.0                           |
| QAsym(var).crc-4B | AsymB04S | 4B  | 54.2      | 53.5–54.8 | 10.73 | 6.3       | -0.6943 | BS00066282_51 | wmc657         | 3.1                           |
| QDMen(var).crc-4B | DMenB04S | 4B  | 54.2      | 53.5–54.8 | 5.55  | 12.2      | -0.1433 | BS00066282_51 | wmc657         | 3.1                           |
| QDMin(var).crc-4B | DMinB04S | 4B  | 54.2      | 53.5–54.8 | 4.88  | 8.9       | -0.1158 | BS00066282_51 | wmc657         | 3.1                           |
| QPer(var).crc-4B | PerB04S   | 4B  | 54.2      | 53.5–54.8 | 4.93  | 10.0      | -0.4902 | BS00066282_51 | wmc657         | 3.0                           |
| QSzWd(var).crc-4B | SzWd2YRS | 4B  | 54.2      | 53.5–54.8 | 4.58  | 9.4       | -0.0862 | BS00066282_51 | wmc657         | 3.1                           |
| QSzWd(var).crc-4B | SzWB04S   | 4B  | 54.2      | 53.5–54.8 | 4.73  | 8.9       | -0.111  | BS00066282_51 | wmc657         | 3.2                           |
| QAMiL.crc-4D  | AMi2YRA   | 4D  | 34.2      | 32.5–35.9 | 42.07 | 43.3      | 1.4647  | wmc617c       | wMAS000002     | 3.1                           |
| QAMiL.crc-4D  | AMiLG00A  | 4D  | 34.2      | 31.9–37.5 | 33.42 | 34.1      | 1.17    | wmc617c       | wMAS000002     | 3.1                           |
| QAMiL.crc-4D  | AMiLB04A  | 4D  | 34.2      | 31.9–36.8 | 36.68 | 41.5      | 1.7134  | wmc617c       | wMAS000002     | 3.0                           |
| QArea.crc-4D  | AreaG00A  | 4D  | 34.2      | 27.5–38.7 | 11.89 | 13.5      | 88.5    | wmc617c       | wMAS000002     | 3.1                           |
| QArPe.crc-4D  | ArPe2YRA  | 4D  | 34.2      | 32.2–36.3 | 34.59 | 35.1      | 0.3431  | wmc617c       | wMAS000002     | 3.1                           |
| QArPe.crc-4D  | ArPeB04A  | 4D  | 34.2      | 31.9–36.3 | 30.82 | 34.8      | 0.4067  | wmc617c       | wMAS000002     | 3.0                           |
| QDMen.crc-4D  | DMenB04A  | 4D  | 34.2      | 31.7–36.9 | 24.08 | 25.4      | 1.4441  | wmc617c       | wMAS000002     | 3.0                           |

(Continued)
| QTL          | Trait name        | Chr | Peak (cM) | CI (cM)  | LOD  | $r^2$ (%) | Add* | Left marker | Right marker | LOD threshold (α0.05) |
|--------------|-------------------|-----|-----------|----------|------|-----------|------|-------------|--------------|---------------------|
| QDMin.crc-4D | DMinB04A          | 4D  | 34.2      | 32.1–37.3| 41.12| 43.3      | 1.8107| wmc617c     | wMAS000002   | 3.1                 |
| QPer.crc-4D  | PerB04A           | 4D  | 34.2      | 29.0–38.2| 8.54 | 8.7       | 2.8765| wmc617c     | wMAS000002   | 3.1                 |
| QSzWd.crc-4D | SzWd2YRA          | 4D  | 34.2      | 32.7–36.8| 38.08| 44.8      | 1.4058| wmc617c     | wMAS000002   | 3.1                 |
| QSzWd.crc-4D | SzWdB04A          | 4D  | 34.2      | 32.2–36.7| 41.49| 43.1      | 1.8076| wmc617c     | wMAS000002   | 3.1                 |
| QArea.crc-4D | AreaB04A          | 4D  | 34.3      | 31.5–38.0| 19.07| 22.5      | 142.9027| wMAS000002  | wmc48b       | 3.0                 |
| QArPe.crc-4D | ArPeG00A          | 4D  | 34.3      | 32.3–38.5| 27.96| 28.4      | 0.299 | wMAS000002  | wmc48b       | 3.1                 |
| QDMen.crc-4D | DMenG00A          | 4D  | 34.3      | 31.3–39.3| 16.34| 16.5      | 0.9301 | wMAS000002  | wmc48b       | 3.0                 |
| QSzWd.crc-4D | SzWdG00A          | 4D  | 34.3      | 32.4–37.5| 32.81| 36.9      | 1.1957 | wMAS000002  | wmc48b       | 3.0                 |
| QArea.crc-4D | Area2YRA          | 4D  | 34.6      | 31.7–39.6| 14.87| 17.9      | 110.5507| wMAS000002  | wmc48b       | 3.0                 |
| QRect.crc-4D | RectG00A          | 4D  | 35.3      | 30.6–40.8| 11.86| 17.8      | 0.0041 | wMAS000002  | wmc48b       | 3.2                 |
| QDMin.crc-4D | DMin2YRA          | 4D  | 35.4      | 32.9–38.9| 34.88| 45.7      | 1.509  | wMAS000002  | wmc48b       | 2.9                 |
| QRect(var).crc-4D | Rect2YRS       | 4D  | 35.4      | 33.8–39.1| 33.91| 53.3      | -0.0049| wMAS000002  | wmc48b       | 3.0                 |
| QRndn.crc-4D | RndnG00A          | 4D  | 35.4      | 31.4–40.8| 11.40| 17.5      | -0.0134| wMAS000002  | wmc48b       | 3.2                 |
| QSphr.crc-4D | SphrG00A          | 4D  | 35.4      | 31.2–40.8| 10.77| 17.5      | 0.0071 | wMAS000002  | wmc48b       | 3.1                 |
| QDMen.crc-4D | DMen2YRA          | 4D  | 35.6      | 32.1–40.0| 19.92| 25.5      | 1.2353 | wMAS000002  | wmc48b       | 3.1                 |
| QSphr.crc-4D | Sphr2YRA          | 4D  | 35.7      | 31.9–40.5| 16.44| 30.1      | 0.0098 | wMAS000002  | wmc48b       | 3.0                 |
| QRect.crc-4D | Rect2YRA          | 4D  | 36.0      | 30.9–40.9| 15.27| 28.6      | 0.0051 | wMAS000002  | wmc48b       | 3.0                 |
| QRect(var).crc-4D | RectB04S       | 4D  | 36.0      | 34.2–39.9| 31.88| 51.0      | -0.0053| wMAS000002  | wmc48b       | 3.2                 |
| QRndn.crc-4D | Rndn2YRA          | 4D  | 36.1      | 31.0–41.5| 13.84| 26.5      | -0.015 | wMAS000002  | wmc48b       | 3.1                 |
| QRect(var).crc-4D | RectG00S       | 4D  | 37.2      | 34.3–42.0| 25.22| 45.2      | -0.0042| wMAS000002  | wmc48b       | 3.1                 |
| QRndn.crc-4D | RndnB04A          | 4D  | 37.7      | 34.4–41.9| 24.11| 38.8      | -0.0246| wMAS000002  | wmc48b       | 3.0                 |
| QRect(var).crc-4D | RectG00S       | 4D  | 37.9      | 34.5–43.6| 17.92| 35.3      | -0.006 | wMAS000002  | wmc48b       | 3.0                 |
| QRect.crc-4D | RectB04A          | 4D  | 38.1      | 34.7–42.6| 21.43| 37.3      | 0.0079 | wMAS000002  | wmc48b       | 3.1                 |
| QSphr.crc-4D | SphrB04A          | 4D  | 38.3      | 34.9–42.8| 22.99| 39.3      | 0.0154 | wMAS000002  | wmc48b       | 3.2                 |
| QRndn(var).crc-4D | Rndn2YRS      | 4D  | 39.3      | 35.6–43.9| 24.34| 45.0      | -0.0075| wMAS000002  | wmc48b       | 3.1                 |

(Continued)
| QTL       | Trait name* | Chr | Peak (cM) | CI (cM) | LOD  | $r^2$ (%) | Add* | Left marker | Right marker | LOD threshold ($\alpha=0.05$) |
|-----------|-------------|-----|-----------|---------|------|-----------|------|-------------|--------------|-----------------------------|
| QRndn(var).crc-4D | crc-4D RndnB04S | 4D | 39.9 | 36.0–44.4 | 23.49 | 43.3 | -0.009 | wMAS000002 | wmc48b | 3.1 |
| QRandn.crc-4D.2 | RndnG00A | 4D | 51.8 | 49.9–54.2 | 8.08 | 11.4 | -0.0108 | wmc48b | wsnp_BE444858D_Ta_1_1 | 3.2 |
| QSphr.crc-4D.2 | SphrG00A | 4D | 51.9 | 49.9–54.6 | 8.98 | 13.5 | 0.0063 | wsnp_BE444858D_Ta_1_1 | wsnp_Ex_c42133_48794975 | 3.1 |
| QAsym (var).crc-4D.2 | AsymB04S | 4D | 53.3 | 49.9–54.6 | 5.43 | 3.0 | -0.4792 | wsnp_BE444858D_Ta_1_1 | wsnp_Ex_c42133_48794975 | 3.1 |
| QRect.crc-4D.2 | RectG00A | 4D | 54.4 | 49.9–54.6 | 7.42 | 10.0 | 0.0031 | wsnp_BE444858D_Ta_1_1 | wsnp_Ex_c42133_48794975 | 3.2 |
| QAMiL.crc-5B.1 | AMiLB04A | 5B | 56.2 | 55.5–57.2 | 9.97 | 7.6 | 0.7347 | wsnp_Ex_rep_c66696_65023462 | wsnp_RFL_Contig4_565_5399994 | 3.0 |
| QDMin.crc-5B.1 | DMinB04A | 5B | 56.5 | 55.5–57.2 | 10.03 | 6.6 | 0.7086 | wsnp_Ex_rep_c66696_65023462 | wsnp_RFL_Contig4_5399994 | 3.1 |
| QAMiL.crc-5B.1 | AMiL2YRA | 5B | 57.7 | 57.2–59.3 | 5.33 | 3.2 | 0.3963 | BS00110635_51 | TA004924-0669 | 3.1 |
| QDMin.crc-5B.1 | DMin2YRA | 5B | 57.8 | 57.2–59.3 | 4.92 | 4.9 | 0.5422 | TA004924-0669 | wsnp_Ku_c17875_27051169 | 3.1 |
| QAMiL.crc-5B.1 | AMiL2YRA | 5B | 57.7 | 57.2–59.3 | 3.52 | 2.9 | 0.3776 | TA004924-0669 | wsnp_Ku_c17875_27051169 | 2.9 |
| QArPe.crc-5B.1 | ArPe2YRA | 5B | 59.0 | 57.7–59.9 | 4.13 | 2.9 | 0.3608 | TA004924-0669 | wsnp_Ku_c17875_27051169 | 3.1 |
| QArea.crc-5B | Area2YRA | 5B | 59.3 | 57.7–59.3 | 4.93 | 5.1 | 0.8311 | TA004924-0669 | wsnp_Ku_c17875_27051169 | 3.0 |
| QArea.crc-5B | AreaB04A | 5B | 59.3 | 57.2–59.3 | 8.79 | 8.9 | 0.9434 | TA004924-0669 | wsnp_Ku_c17875_27051169 | 3.0 |
| QArPe.crc-5B.1 | ArPeB04A | 5B | 59.4 | 57.7–59.9 | 11.18 | 9.5 | 0.3119 | TA004924-0669 | wsnp_Ku_c17875_27051169 | 3.0 |
| QDMen.crc-5B | DMen2YRA | 5B | 59.4 | 57.2–59.3 | 12.06 | 10.7 | 0.9362 | wsnp_Ku_c17875_27051169 | wsnp_Ex_c24933_34187952 | 3.0 |
| QPer.crc-5B | PerB04A | 5B | 59.4 | 57.7–59.9 | 5.15 | 5.0 | 2.1802 | wsnp_Ku_c17875_27051169 | wsnp_Ex_c24933_34187952 | 3.1 |
| QSzWd.crc-5B.1 | SzWdB04A | 5B | 59.4 | 57.7–59.9 | 10.84 | 7.1 | 0.7336 | wsnp_Ku_c17875_27051169 | wsnp_Ex_c24933_34187952 | 3.1 |
| QArPe.crc-5B.2 | ArPeG00A | 5B | 130.3 | 127.0–132.5 | 3.56 | 2.7 | 0.0917 | tPt-3144 | wsnp_BE446509B_Ta_2_6 | 3.1 |
| QDMin.crc-5B.2 | DMinG00A | 5B | 131.7 | 127.0–132.5 | 3.08 | 2.0 | 0.2918 | tPt-3144 | wsnp_BE446509B_Ta_2_6 | 3.1 |
| QSzWd.crc-5B.2 | SzWdG00A | 5B | 131.9 | 127.0–132.5 | 3.50 | 2.6 | 0.3167 | tPt-3144 | wsnp_BE446509B_Ta_2_6 | 3.0 |
| QAMiL.crc-5B.2 | AMiLB04A | 5B | 139.7 | 139.0–144.0 | 3.80 | 2.7 | 0.4339 | Excalibur_c92555_283 | tplb0051n17_791 | 3.0 |
| QDMin.crc-5B.2 | DMinB04A | 5B | 139.7 | 139.0–144.0 | 4.29 | 2.6 | 0.4458 | Excalibur_c92555_283 | tplb0051n17_791 | 3.1 |
| QSzWd.crc-5B.2 | SzWdB04A | 5B | 139.7 | 139.0–144.0 | 5.53 | 3.4 | 0.5057 | Excalibur_c92555_283 | tplb0051n17_791 | 3.1 |
| QRect(var).crc-5B | RectB04S | 5B | 157.0 | 154.0–162.3 | 3.41 | 3.9 | -0.0015 | wsnp_JD_c12221_12509984 | RAC875_c17841_242 | 3.2 |

(Continued)
Table 3. (Continued)

| QTL                | Trait name* | Chr | Peak (cM) | CI (cM) | LOD | $r^2$ (%) | Add* | Left marker | Right marker | LOD threshold ($\alpha=0.05$) |
|---------------------|-------------|-----|-----------|---------|-----|-----------|------|-------------|--------------|-------------------------------|
| QRect(var). crc-5B  | Rect2YRS    | 5B  | 164.1     | 162.2– 164.1 | 3.55 | 3.6     | -0.0013 | Kukri_c3070_72 | Tdurum_contig43552_666     | 3.0                           |
| QAMaL crc-5D       | AMaLB04A    | SD.2 | 55.8      | 52.3– 65.6 | 7.06 | 8.5     | -1.218 | gdm63       | BS00088592_51          | 3.1                           |
| QPer crc-5D        | PerB04A     | SD.2 | 56.1      | 47.2– 71.3  | 3.77 | 4.0     | -1.9431 | gdm63       | BS00088592_51          | 3.1                           |
| QAsym crc-5D       | AsymB04A    | SD.2 | 58.7      | 52.3– 72.7  | 4.35 | 6.8     | -1.8617 | gdm63       | BS00088592_51          | 3.0                           |
| QAsym crc-5D       | Asym2YRA    | SD.2 | 61.6      | 49.0– 77.4  | 3.95 | 4.6     | -1.5365 | gdm63       | BS00088592_51          | 3.0                           |
| QDMax crc-5D       | DMax2YRA    | SD.2 | 63.5      | 50.9– 77.5  | 4.34 | 5.6     | -0.9869 | gdm63       | BS00088592_51          | 3.2                           |
| QAMaL crc-5D       | AMaLB04A    | SD.2 | 81.7      | 81.0– 82.6  | 3.80 | 3.6     | -0.761  | wsnp_Ku_c46270_53 | Excalibur_c20024_806     | 3.1                           |
| QAMaL crc-5D       | AMaLB04A    | SD.2 | 88.8      | 87.5– 88.8  | 4.46 | 6.5     | -13.9761 | wsnp_Ex_c5185_9189 | Lr1                       | 3.0                           |
| QAMaL crc-6B       | DMen2YRA    | 6B  | 138.3     | 134.4– 142.1 | 3.32 | 3.4     | 0.4556 | Kukri_c16404_100 | RAC875_c6813_168        | 3.1                           |
| QAMaL crc-6B       | Area2YRA    | 6B  | 138.4     | 134.4– 142.1 | 3.71 | 3.8     | 51.0205 | RAC875_c6813_168 | BS00049082_51          | 3.0                           |
| QAMaL crc-6B       | ArPe2YRA    | 6B  | 139.0     | 135.4– 142.1 | 3.97 | 2.7     | 0.0954 | RAC875_c6813_168 | BS00049082_51          | 3.1                           |
| QAMaL crc-6B       | ArPe2YRA    | 6B  | 139.0     | 135.4– 142.1 | 4.41 | 3.5     | 0.1299 | RAC875_c6813_168 | BS00049082_51          | 3.0                           |
| QAMaL crc-6B       | DMenB04A    | 6B  | 139.2     | 135.6– 142.1 | 5.30 | 4.5     | 0.608  | RAC875_c6813_168 | BS00049082_51          | 3.0                           |
| QAMaL crc-6B       | Area2YRA    | 6B  | 139.4     | 134.5– 142.1 | 4.51 | 4.6     | 64.4603 | RAC875_c6813_168 | BS00049082_51          | 3.0                           |
| QAMaL crc-6B       | PerB04A     | 6B  | 139.6     | 133.3– 142.1 | 4.78 | 4.9     | 2.1552 | RAC875_c6813_168 | BS00049082_51          | 3.1                           |
| QAMaL crc-6B       | AsymB04S    | 6D.1 | 53.7      | 52.0– 55.1  | 4.34 | 2.3     | -0.4217 | Ku_c13130_1319 | BS00047195_51          | 3.1                           |
| QDMax crc-6D       | DMaxB04A    | 6D.1 | 53.8      | 52.0– 55.1  | 4.04 | 5.4     | -1.0099 | Ku_c13130_1319 | BS00047195_51          | 3.1                           |
| QAMaL crc-6D       | AMaLB04A    | 6D.1 | 53.9      | 52.0– 55.1  | 9.02 | 9.2     | -1.2132 | BS00047195_51 | D_GDRF1KQ02FFPXT_243   | 3.1                           |
| QAMaL crc-6D       | AMiLG00A    | 6D.1 | 64.8      | 64.2– 65.5  | 6.95 | 4.8     | -0.4392 | RAC875_c18002_58  | Excalibur_c37749_45436366 | 3.1                           |
| QAMaL crc-6D       | ArPe2YRA    | 6D.1 | 64.8      | 64.2– 66.1  | 3.63 | 2.3     | -0.0888 | RAC875_c18002_58  | Excalibur_c37749_45436366 | 3.1                           |
| QAMaL crc-6D       | ArPe2YRA    | 6D.1 | 64.8      | 64.2– 65.4  | 6.84 | 5.1     | -0.1268 | RAC875_c18002_58  | Excalibur_c37749_45436366 | 3.1                           |
| QAMaL crc-6D       | ArPe2YRA    | 6D.1 | 64.8      | 64.2– 66.3  | 3.47 | 2.5     | -0.3291 | RAC875_c18002_58  | Excalibur_c37749_45436366 | 3.1                           |
| QAMaL crc-6D       | ArPe2YRA    | 6D.1 | 64.8      | 64.2– 65.5  | 6.94 | 5.3     | -0.4547 | RAC875_c18002_58  | Excalibur_c37749_45436366 | 3.0                           |
| QAMaL crc-6D       | Area2YRA    | 6D.1 | 64.9      | 64.8– 66.2  | 8.94 | 9.5     | -74.2415 | wsnp_Ex_c37749_45436366 | barc273                  | 3.1                           |

(Continued)
Table 3. (Continued)

| QTL            | Trait name* | Chr | Peak (cM) | CI (cM) | LOD | $r^2$ (%) | Add$^c$ | Left marker | Right marker | LOD threshold ($\alpha$0.05) |
|----------------|-------------|-----|-----------|--------|-----|----------|------|-------------|--------------|---------------------------|
| QDMen.crc-6D   | DMenG00A    | 6D.1 | 64.9      | 64.8–65.9 | 7.29 | 6.2      | -0.5715 | wsnp_Ex_c37749_45436366 | barc273       | 3.0                        |
| QDMin.crc-6D   | DMinG00A    | 6D.1 | 64.9      | 64.8–65.7  | 6.98 | 4.4      | -0.4352 | wsnp_Ex_c37749_45436366 | barc273       | 3.1                        |
| QArea.crc-6D   | Area2YRA    | 6D.1 | 65.7      | 64.8–68.6  | 4.76 | 5.2      | -0.59586 | wsnp_Ex_c37749_45436366 | barc273       | 3.0                        |
| QDMen.crc-6D   | DMen2YRA    | 6D.1 | 65.7      | 64.8–68.9  | 4.46 | 4.7      | -0.5298 | wsnp_Ex_c37749_45436366 | barc273       | 3.1                        |
| QAsym.crc-6D   | AsymG00A    | 6D.1 | 65.8      | 64.8–68.9  | 7.84 | 9.1      | -2.1758 | wsnp_Ex_c37749_45436366 | barc273       | 3.1                        |
| QDMin.crc-6D   | DMin2YRA    | 6D.1 | 65.8      | 64.8–68.9  | 3.62 | 3.1      | -0.39   | wsnp_Ex_c37749_45436366 | barc273       | 2.9                        |
| QAMil.(var).crc-6D | AMil2YRS | 6D.1 | 66.0      | 64.8–68.9  | 3.53 | 5.4      | -0.072  | wsnp_Ex_c37749_45436366 | barc273       | 3.2                        |
| QArea.crc-6D   | AreaB04A    | 6D.1 | 66.0      | 64.8–68.9  | 3.05 | 3.0      | -52.3209 | wsnp_Ex_c37749_45436366 | barc273       | 3.0                        |
| QDMin.(var).crc-6D | DMin2YRS | 6D.1 | 66.0      | 64.8–68.9  | 3.10 | 5.6      | -0.0727 | wsnp_Ex_c37749_45436366 | barc273       | 3.0                        |
| QPer.crc-6D    | Per2YRA     | 6D.1 | 66.1      | 64.8–68.9  | 3.54 | 4.5      | -1.9293 | wsnp_Ex_c37749_45436366 | barc273       | 3.0                        |
| QSzWd.(var).crc-6D | SzWd2YRS | 6D.1 | 66.2      | 64.9–68.9  | 3.42 | 7.2      | -0.0752 | wsnp_Ex_c37749_45436366 | barc273       | 3.1                        |
| QPer.crc-6D    | PerB04A     | 6D.1 | 66.3      | 65.1–68.4  | 5.14 | 5.1      | -2.1925 | wsnp_Ex_c37749_45436366 | barc273       | 3.1                        |
| QAMaL.(var).crc-6D | AMaL2YRS  | 6D.1 | 66.4      | 65.1–68.7  | 4.86 | 5.1      | -0.9457 | barc273       | BS00021881_51 | 3.1                        |
| QArea(var).crc-6D | Area2YRS  | 6D.1 | 66.4      | 65.3–68.5  | 3.63 | 6.0      | -11.394 | barc273       | BS00021881_51 | 3.0                        |
| QAsym.(var).crc-6D | Asym2YRA  | 6D.1 | 66.4      | 65.3–68.4  | 8.13 | 8.5      | -2.0773 | barc273       | BS00021881_51 | 3.0                        |
| QAsym.(var).crc-6D | AsymB04A  | 6D.1 | 66.4      | 65.3–68.7  | 5.66 | 7.7      | -1.9888 | barc273       | BS00021881_51 | 3.0                        |
| QAsym.(var).crc-6D | Asym2YRS  | 6D.1 | 66.4      | 65.0–68.8  | 3.32 | 4.6      | -0.3368 | barc273       | BS00021881_51 | 3.1                        |
| QDMax.crc-6D   | DMax2YRA    | 6D.1 | 66.4      | 65.1–68.8  | 6.99 | 7.6      | -1.147  | barc273       | BS00021881_51 | 3.2                        |
| QDMax.crc-6D   | DMaxG00A    | 6D.1 | 66.4      | 65.4–68.5  | 7.42 | 9.3      | -1.2619 | barc273       | BS00021881_51 | 3.1                        |
| QAMaL.(var).crc-6D | AMaLG00A | 6D.1 | 66.5      | 65.3–68.6  | 7.52 | 8.7      | -1.1501 | barc273       | BS00021881_51 | 3.1                        |
| QPer.crc-6D    | PerG00A     | 6D.1 | 66.6      | 65.0–68.9  | 5.97 | 6.9      | -2.3155 | barc273       | BS00021881_51 | 3.1                        |
| QSzLn.crc-6D   | SzLn2YRA    | 6D.1 | 66.7      | 65.3–68.9  | 5.21 | 5.7      | -0.9848 | barc273       | BS00021881_51 | 3.1                        |
| QSzLn.crc-6D   | SzLnG00A    | 6D.1 | 66.9      | 65.1–68.9  | 4.59 | 6.1      | -1.0146 | barc273       | BS00021881_51 | 3.1                        |
| QDMax.crc-7A   | DMaxB04A    | 7A   | 139.4     | 138.3–140.5| 3.37 | 4.4      | -0.916  | Excalibur_c8066_791   | wsnp_Ex_c9476_15710162 | 3.1                        |
| QPer.crc-7A    | Per2YRA     | 7A   | 139.4     | 138.3–140.5| 3.14 | 3.8      | -1.7931 | Excalibur_c8066_791   | wsnp_Ex_c9476_15710162 | 3.0                        |
| QPer.crc-7A    | PerG00A     | 7A   | 139.4     | 138.3–140.5| 4.13 | 4.6      | -1.9008 | Excalibur_c8066_791   | wsnp_Ex_c9476_15710162 | 3.1                        |
| QSzLn.crc-7A   | SzLn2YRA    | 7A   | 139.4     | 138.3–140.5| 4.00 | 4.2      | -0.8525 | Excalibur_c8066_791   | wsnp_Ex_c9476_15710162 | 3.1                        |

(Continued)
was located at approximately 91 cM, which was near the location of another grain weight QTL, QGwt.crc-2B.2 at 87 cM. The ‘AC Domain’ allele decreased Gwt, grain area, and mean kernel diameter.

**Chromosome 2D**

QTL for grain shape traits Rect, Rndn, and Sphr (QRect.crc-2D, QRndnd.crc-2D, and QSphr.crc-2D) were identified at approximately 87 cM. QTL for variation in kernel width mapped nearby at 102 cM. A Twt QTL (QTwt.crc-2D) was also identified at 88.9 cM (Brandon 2004 dataset) and at 102.7 cM (Morden 1999 dataset).

**Chromosome 3A**

A strong QTL for variability in Sphericity (Sphr) was consistently detected at 65.9 cM. The ‘AC Domain’ allele increased variability in this trait. No other QTL were detected on chromosome 3A.

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**Table 3. (Continued)**

| QTL       | Trait name* | Chr | Peak (cM) | CI (cM)b | LOD  | r²  | Addc  | Left marker            | Right marker            | LOD threshold (0.05) |
|-----------|-------------|-----|-----------|----------|-------|-----|-------|------------------------|------------------------|---------------------|
| QSzLn.crc-7A | SzLnG00A    | 7A  | 139.4     | 138.3–140.5 | 4.82  | 6.2 | -1.0314 | Excalibur_c8066_791   | wsnp_Ex_c9476_1571062  | 3.1                 |
| QSzLn.crc-7A | SzLnB04A    | 7A  | 139.4     | 138.3–140.5 | 3.41  | 4.5 | -0.9274 | Excalibur_c8066_791   | wsnp_Ex_c9476_1571062  | 3.0                 |
| QAMaL.crc-7A | AMaLB04A    | 7A  | 154.7     | 153.5–156.8 | 4.46  | 4.7 | -0.9134 | wmc809               | BS00009886_51          | 3.1                 |
| QAsym.crc-7A | Asym2YRA    | 7A  | 154.7     | 153.5–156.8 | 5.12  | 5.1 | -1.6306 | wmc809               | BS00009886_51          | 3.0                 |
| QAsym.crc-7A | AsymB04A    | 7A  | 154.7     | 153.5–156.8 | 3.11  | 4.1 | -1.4637 | wmc809               | BS00009886_51          | 3.0                 |
| QDMax.crc-7A | DMax2YRA    | 7A  | 154.7     | 153.6–156.8 | 6.93  | 7.5 | -1.1542 | wmc809               | BS00009886_51          | 3.2                 |
| QPer.crc-7A | PerB04A     | 7A  | 154.7     | 153.5–156.8 | 3.41  | 3.2 | -1.7728 | wmc809               | BS00009886_51          | 3.1                 |
| QAMaL.crc-7A | AMaL2YRA    | 7A  | 154.8     | 153.8–156.8 | 7.85  | 7.9 | -1.1332 | BS00009886_51        | BS00068055_51          | 3.1                 |
| QArea.crc-7A | AreaG00A    | 7A  | 155.0     | 153.5–156.8 | 3.21  | 3.2 | -43.8849 | BS00009886_51        | BS00068055_51          | 3.1                 |
| QDMax.crc-7A | DMaxG00A    | 7A  | 155.4     | 153.7–156.8 | 5.36  | 6.5 | -1.073  | BS00009886_51        | BS00068055_51          | 3.1                 |
| QAMaL.crc-7A | AMaLG00A    | 7A  | 156.4     | 153.7–156.8 | 6.04  | 6.8 | -1.0352 | BS00009886_51        | BS00068055_51          | 3.1                 |
| QAsym.crc-7A | AsymG00A    | 7A  | 157.3     | 156.7–157.3 | 3.52  | 3.8 | -1.4281 | BS00068055_51        | Excalibur_c3476_691    | 3.1                 |
| QSphr.crc-7A | SphrG00A    | 7A  | 157.3     | 156.7–157.3 | 3.09  | 4.3 | 0.0036  | BS00068055_51        | Excalibur_c3476_691    | 3.1                 |

*a Trait, environment (G00 = Glenlea 2000, B04 = Brandon 2004), statistic (A = average, S = standard deviation, var = variance/variability). e.g. AMaLG00A is the average Major Axis Length in Glenlea 2000.

b Confidence interval determined by one LOD drop-off.

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

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Chromosome 3B
Two QTL regions were detected on chromosome 3B. The first region, located at 0.0–0.3 cM, affected Gwt and seed shape traits (Area, Per, ArPe, AMiL, DMen, DMin, and SzWd). The ‘AC Domain’ allele decreased Gwt and the seed shape traits. In the second QTL region on chromosome 3B, QTL for grain shape (QAsym.crc-3B), Twt (QTwt.crc-3B), and Fyd (QFyd.crc-3B) were identified within a 14.4 cM region (60.1–74.5 cM). This genetic interval also contained a KASP marker Kasp3B (survey)_17, which was developed from a survey sequence SNP associated with pre-harvest sprouting resistance (PHS) on chromosome 3B [39]. QTwt.crc-3B has been previously reported [27], and was flanked by SSR markers wmc625 and barc164, located at 61.9 and 69.0 cM, respectively [39]. Similarly, QFyd.crc-3B mapped to wmc446 [46] and is located at position 61.9 cM on chromosome 3B [39]. A positive additive effect for Asym on 3B could be interpreted as the ‘AC Domain’ allele contributing to grain shape asymmetry (Asym), which in turn might have resulted in the reduction in Twt and increased Fyd associated with this region. QTL for variability in Area, Per, ArPe, Asym, AMiL, DMen, DMin, SzWd were detected in this region with the ‘AC Domain’ increasing variability in these traits.

Chromosome 3D
On linkage group 3D.2, QTL for grain shape (numerous QTL), Twt (QTwt.crc-3D), Gwt (QGwt.crc-3D), and Fyd (QFyd.crc-3D) were detected in two main regions. Twt, Fyd, Amal, and DMax QTL had LOD peaks within a 5.1 cM interval (77.1–82.8 cM), in which the ‘AC Domain’ allele decreased each of these traits. The Gwt QTL mapped to a different location with QTL peaks ranging 4.9–20.9 cM. QTL for Area, Per, ArPe, Asym, AMiL, DMen, DMin, SzLn, and SzWd also mapped to this same general region with LOD peaks ranging between 2.3 and 35.5 cM. Again, the ‘AC Domain’ allele decreased each of these traits.

Chromosome 4A
Numerous QTL were detected on chromosome 4A. A Gwt QTL was detected at 90.1 cM along with QTL for Amal, AMil, Area, ArPe, Asym, DMax, DMen, DMin, Per, SzLn, and SzWd, and variability in Amal, Area, Asym, DMen, and Per. The ‘AC Domain’ allele increased each of these traits. Grain shape QTL were detected at 38 cM for the traits Amal, Amil, DMax, Per, Rect, Rndn, Sphr, and SzLn. The ‘AC Domain allele’ increase Amal, Asym, DMax, Per, Rndn, and SzLn, but decreased Rect and Sphr. At 63 cM, QTL for Amil and DMin, and variation in Area, ArPe, and DMen were detected in the Glenlea 2000 dataset. The QTL located at 38 and 63 cM had no detectable effect on Gwt, Twt, or Fyd.

Chromosome 4B
On chromosome 4B, a 4.5 cM interval (51.4–55.9 cM) coincided with the LOD peak locations of a major QTL for Plht (QPlht.crc-4B), Gwt (QGwt.crc-4B), and Fyd (QFyd.crc-4B) (Fig 1). In addition, a significant QTL was detected in this region of chromosome 4B for each of the 14 seed shape traits, and for variability in Amal, AMil, Area, ArPe, Asym, DMax, DMen, DMin, Per, SzLn, and SzWd. When considering 1 LOD drop-off confidence intervals for these QTL, this narrow genetic region corresponds to a very large ~601 Mbp physical region in the IWGSC Chinese Spring RefSeq v1.0 (S1 Table). The interval includes the centromere and appears to be an area of low recombination. The HighConfidenceGenesv1.0 track in JBrowse indicates that 2,979 high confidence genes are present in this interval. The diagnostic SNP marker wMAS000001 for the Rht-B1 locus (http://www.cerealsdb.uk.net/cerealgenomics/CerealsDB/kasp_download.php?) was tested on the RL4452/‘AC Domain’ population to
determine if Rht-B1 was responsible for this QTL region, but the marker was monomorphic in the population. In the IWGSC Chinese Spring RefSeq v1.0 sequence, Rht-B1 is physically located between 30,861,382 to 30,863,247 bp (around 40 cM on the 4B linkage map in this cross). The 'AC Domain' allele reduced Plht, Gwt, Fyd, etc.(Tables 2 and 3).

Chromosome 4D

On chromosome 4D, a 4.9 cM genomic region (31.8–36.7 cM) coincided with the LOD peaks of QTL for Plht (QPlht.crc-4D), Gwt (QGwt.crc-4D), and Twt (QTwt.crc-4D). Also in the same region with QTL peaks ranging from 34.2–39.9 cM were QTL for Amil, Area, ArPe, DMen, DMin, Per, Rect, Rndn, Sphr, and SzWd, and QTL for variability in Rect and Rndn. The diagnostic SNP marker wMAS000002 for the Rht-D1 locus mapped to 34.2 cM, which is the predicted location for all of these QTL. The 'AC Domain' allele increased Plht, Gwt, Twt, grain length, grain width, grain area, etc. (Tables 2 and 3).

Chromosome 5B

QTL for grain width, Area, Per, and ArPe were detected at approximately 59 cM on chromosome 5B. In addition, a second QTL for grain width was detected at 131 cM based upon the Glenlea 2000 dataset, and at 140 cM based upon the Morden 2004 dataset. A QTL for

Fig 1. Plht, Gwt, Twt, Fyd, and the most significant seed shape QTL (LOD peaks > 10), and their 1 LOD drop-off confidence intervals, identified in the RL4452/'AC Domain' DH population on (A) chromosome 4B within a 6.5 cM region (in gray) and (B) chromosome 4D within a 14.2 cM region (in gray).

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variability in Rect was identified at 161 cM. The ‘AC Domain’ alleles increased grain width in these two QTL regions. Interestingly, there were no QTL for Gwt, Twt, or Fyd detected on chromosome 5B.

**Chromosome 5D**
A cluster of QTL affecting AMaL (QAMaLcrc-5D), Asym (QAsymcrc-5D), DMax (QDMaxcrc-5D), Per (QPercrc-5D), SzLn (QSzLncrc-5D), and variability in Area (QArea(var)rcrc-5D) were identified on linkage group 5D.2 with LOD peaks from 55.8 to 88.8 cM. The ‘AC Domain’ allele decreased each of these traits. No other QTL were detected on chromosome 5D.

**Chromosome 6B**
A Gwt QTL (QGwttcrc-6B) was detected on chromosome 6B with LOD peaks located at 139.4 and 159.1 cM. QTL for Area (QArccrc-6B), ArPe (QArPercrc-6B), DMen (QDMencrc-6B), and Per (QPercrc-6B) were also identified at 139 cM. In this region, the ‘AC Domain allele’ increased Gwt and the four seed shape traits.

**Chromosome 6D**
QTL for a number of grain shape traits had LOD peaks mainly located within a 2.1 cM interval (64.8–66.9 cM) on linkage group 6D.1. However in four instances, the LOD peaks for the same traits were located at 54 cM. The ‘AC Domain’ allele decreased grain length (AMaL, DMax, SzLn), grain width (AMiL, DMin, SzWd), Per, Asym, and Area. No QTL for Gwt, Twt, or Fyd were detected in this region.

**Chromosome 7A**
QTL peaks for grain shape (QAMaLcrc-7A, QAreacrc-7A, QAsymcrc-7A, QDMaxcrc-7A, QPercrc-7A, QSphrcrc-7A, QSzLncrc-7A) were identified in a 17.9 cM interval (139.4–157.3 cM), while a Twt QTL (QTwtcrc-7A) was located at 84.1 cM. Since these QTL regions were not closely linked, it is assumed that one QTL predominantly affects Twt and the other seed shape (i.e. at least two genes control this variability). For QTwtcrc-7A, the ‘AC Domain’ allele increased test weight. For the grain shape QTL region, the ‘AC Domain’ allele reduced grain length, Area, Asym, Per, and Sphr. No Gwt or Fyd QTL were identified on 7A.

**Chromosome 7D**
The major flour yield QTL QFydrcrc-7D was not coincident with QTL for Gwt, Twt, or seed shape, but was coincident with a major maturity QTL QMeltcrc-7D previously identified in this population [27]. QFydrcrc-7D was a broad QTL with the main peak located at 16.2 cM and secondary peaks located at 31.9 and 43.1 cM based on interval mapping (IM-ADD, S1 Fig). Based on these data, it is possible that QFydrcrc-7D is the result of two or more linked genes. Interestingly, the maturity QTL QMeltcrc-7D has a single peak at 19.6 cM and no secondary peaks (S1 Fig). No seed shape QTL were identified on chromosome 7D.

**Discussion**
The objectives of our study were to identify significant grain shape and agronomic trait QTL, and determine their interrelationships. SNPs from a wheat 90K Infinium Custom Beadchip were previously used to generate a high density linkage map of a RL4452/‘AC Domain’ DH population [39], which in turn was used to identify QTL for the above traits. QTL were identified on chromosomes 1A, 1B, 1D, 2B, 2D, 3A, 3B, 3D, 4A, 4B, 4D, 5B, 5D, 6B, 6D, 7A (grain...
shape); 4B, 4D (Plht); 2B, 3B, 3D, 4A, 4B, 4D, 6B (Gwt); 1D, 2A, 2B, 2D, 3B, 3D, 4D, 7A (Twt); and 1B, 3B, 3D, 4B, 7D (Fyd). The most significant QTL for grain shape, Plht, and Gwt were detected on chromosomes 4B and 4D. The most significant Twt QTL were identified on 3B and 4D. The most significant Fyd was located on chromosome 7D, but another important Fyd QTL coincided with the Twt QTL on chromosome 3B.

A major QTL for grain shape, Gwt, Fyd, and Plht mapped to a narrow genetic region on chromosome 4B, which corresponds to the centromere and a very large portion of the chromosome. ‘AC Domain’ alleles contributed to a reduction in Plht, Gwt, Fyd, and grain size, in addition to negative additive effect values for grain shape traits. The same Gwt QTL was identified on 4B, and is associated with SSR marker wmc238 [27], located at 51.9 cM. In our study, wmc238 was located 0.5 cM from Tdurum_contig5562_441, positioned at 52.4 cM on chromosome 4B [39]. Further, the Plht QTL of both studies mapped essentially to the same position based upon the linked SSR marker gwm513 that co-segregates with TA003708-0300. Markers gwm513 and TA003708-0300 were 0.6 cM apart from the grain shape and Gwt QTL peak SNP marker Tdurum_contig5562_441 of our study. Therefore, all SNP and SSR markers within this narrow region on 4B may be useful for MAS of grain size, Gwt, and Plht traits in germplasm and breeding material. QPlht crc-4B, QGwt crc-4B, QFyd crc-4B, and the many seed shape QTL in this region overlap with the ‘QTL region 15’ in the cross ND705/PI 414566, which affects Twt, Gwt, kernel area, and kernel length [10]. The grain shape, Fyd, and Gwt QTL in the RL4452/‘AC Domain’ are likely the result of pleiotropy of the reduced plant height ‘AC Domain’ allele at QPlht crc-4B.

The plant height QTL QPlht crc-4B was previously believed to be the result of segregation at the Rht-B1 locus [27]. However, the improved SNP-based linkage map revealed that QPlht crc-4B mapped proximal of the expected location of Rht-B1 (possibly on 4BL), which could not be resolved based on the older SSR map [27]. It is important to note that the RL4452/‘AC Domain’ mapping population was also monomorphic for the KASP marker wMAS000001, a diagnostic marker for Rht-B1. Rht-B1 is also physically located outside the confidence interval for these QTL. QPlht crc-4B and the other linked/pleiotropic QTL must not be the result of segregation at the Rht-B1 locus. Based upon the BLAST locations of the SNP markers in the 4B linkage map and 1 LOD drop-off confidence intervals for these QTL, this region contains 2,979 high confidence genes in the IWGSC Chinese Spring RefSeq v1.0. Additional research is needed to identify candidate genes responsible for these QTL.

The genetic interval on chromosome 4D flanked by SSR markers wmc617 and wmc48 was found to carry the most significant QTL for seed shape, Plht, Gwt, and Twt. Rht-D1 mapped to this centre of this region as indicated by the diagnostic SNP marker wMAS000002, a diagnostic marker for Rht-D1. Rht-D1 is also physically located outside the confidence interval for these QTL. QPlht crc-4B and the other linked/pleiotropic QTL must not be the result of segregation at the Rht-D1 locus. Based upon the BLAST locations of the SNP markers in the 4B linkage map and 1 LOD drop-off confidence intervals for these QTL, this region contains 2,979 high confidence genes in the IWGSC Chinese Spring RefSeq v1.0. Additional research is needed to identify candidate genes responsible for these QTL.

The genetic interval on chromosome 4A was particularly interesting in this population. Three QTL regions were identified in this study affecting seed size and shape. QTL for grain length (AMaL, DMax, SzLn), Per, Rect, and Sphr mapped to 38 cM on chromosome 4A. These QTL were supported by the identification of the same QTL region (Twt, Gwt, kernel area) in the cross ND705/PI 414566 (Twt, Gwt, kernel area) [10] and in Synthetic/Opata (vertical perimeter) [7]. QTL for grain width (AMiL, DMin) and variability for kernel parameters within samples were detected at 63 cM. Likewise, a QTL for length-width ratio (QKLWR ndsu 4A 1) was detected in the same region [10]. Finally, a QTL for grain weight QGwt crc-4A mapped to 90 cM along with
numerous grain shape parameters in the RL4452/'AC Domain' population. This was also supported by a second length-width ratio QTL (QKLWR.ndsu.4A.2) in the ND705/PI 414566 population [10]. Surprisingly, there were no QTL for Twt detected on chromosome 4A in the RL4452/'AC Domain' population.

Another interesting locus in the RL4452/'AC Domain' population is located on chromosome 7D (linkage group 7D.2). The most important Fyd QTL QFyd.crc-7D mapped to a large interval with predicted locations at 14.4, 23.8, and 43.3 cM based on ICIM. Interval mapping showed multiple peaks in each environment (S1 Fig). Also in this region is a major, days to maturity QTL at 19.6 cM [27, 39], which did not have any secondary peaks (S1 Fig). The presence of multiple peaks for Fyd suggested that multiple genes controlling the trait could be located in this region. One of the genes affecting Fyd could be the maturity QTL itself. It was hypothesized that this maturity QTL was responsible for a falling number QTL in this region since the parental allele contributing the beneficial additive effect varied between growing environments [39]. Presumably the weather conditions affecting pre-harvest sprouting (i.e. rain and high humidity) varied in different growing seasons. In addition, QFyd.crc-7D overlaps with QTGW.ndsu.7D, QTW.ndsu.7D, QKW.ndsu.7D, and QKLWR.ndsu.7D [10]. Additional research is needed to clarify the genetic control of these traits at this point in the genome.

A number of other QTL detected in the RL4452/'AC Domain' population were also in common with grain shape and size QTL detected in the cross ND705/PI 414566 [10]. QFyd.crc-1B overlaps with QTL region 2 (QKW.ndsu.1B, QLWR.ndsu.1B.2) [10]. The QTL QTwt.crc-2D, QRndn.crc-2D, and QSphr.crc-2D likely overlap with the QTL QTGW.ndsu.2D.1 and QKLWR.ndsu.2D.1. QGwt.crc-3D likely overlaps with the thousand kernel weight QTL QTKW.ndsu.3D and the kernel area QTL QKA.ndsu.3D. Grain width QTL (QDMin.crc-5B and QSzWd.crc-5B) overlapped with kernel area and length QTL. Grain length (AMaL, DMax, SzLn), Asym, and Per QTL of our study mapped to approximately 149 cM on the 7A linkage group, which is consistent with QTL for Gwt, kernel length, width, and area [10]. Similarities between QTL on chromosomes 4A, 4B, and 7D in these two populations have already been discussed in the preceding paragraphs. These similarities likely result from shared parentage. ‘AC Domain’ has the pedigree ND499/RL4137//ND585. ND499, ND585, and ND705 are all wheat lines developed by North Dakota State University, so ‘AC Domain’ and ND705 are likely to share many of the same alleles. In addition, the kernel shapes of ‘AC Domain’ and ND705 are similar (short plump kernels), while the kernels of RL4452 and PI 414566 are relatively longer.

Conclusions

This study identified significant QTL for grain morphology, plant height, grain weight, test weight, and flour yield. Previous QTL studies to identify grain shape have utilized SSRs, DArTs, and other PCR-based markers in segregating populations. In deploying a combination of wheat 90K Infinium SNPs and landmark SSRs, we have been successful in enhancing the marker density on the RL4452/'AC Domain' linkage map, and in defining QTL relative to this improved genetic map and the Chinese Spring pseudomolecules. The association between Plht, Gwt, Twt, Fyd, and grain shape QTL confirmed past findings. Genetic analysis of kernel image analysis showed promise, and uncovered additional variation for Gwt, Twt, and Fyd. The per plot heritability estimates were higher for the grain shape traits than Gwt and Fyd, and grain shape QTL were identified that were not associated with Gwt, Twt, and Fyd. Our results should also provide a consensus on the location of linked SNPs and landmark SSRs across maps, which in turn might enable validation of these grain shape QTL in other populations. SNP markers associated with the above traits might also be useful for MAS, and in the identification of candidate genes from rice or other monocots.
Supporting information

S1 Fig. Interval mapping LOD scans for flour yield (Fyd) and time to maturity (Mat) on linkage group 7D.2. Mat data was described previously [27].

S1 Table. The RL4452/AC Domain’ linkage map constructed with 193 DH lines tested with 12,202 DNA markers (11,283 SNPs and 919 PCR-based markers).

S2 Table. Descriptive statistics and heritability estimates of the traits evaluated on the RL4452/AC Domain’ DH population.

S3 Table. Correlation analysis of agronomic, milling, and seed shape traits in the RL4452/AC Domain’ DH population.

S4 Table. Digenic epistatic QTL identified in the RL4452/AC Domain’ DH population by Inclusive Composite Interval Mapping (QICE module) for agronomic, milling, and seed shape traits.

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