Single-locus and two-locus QTL analyses to detect main effect and epistatic QTL for grain weight in bread wheat

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ABSTRACT

For the genome-wide genetic dissection of GW in bread wheat, a framework linkage map consisting of 294 loci (194 SSRs, 86 AFLP and 14 SAMPL) was prepared using an intervarietal RIL mapping population derived from Rye Selection111 × Chinese Spring. Using the genotypic data and data on GW of RILs collected over six environments (3 locations × 2 years), genome-wide single-locus QTL analysis (using inclusive composite interval mapping, ICIM) and two-locus QTL analysis (using QTL Network) were conducted to identify main effect QTL (M-QTL) and epistatic QTL (E-QTL). Single-locus QTL analysis identified 11 QTL (including four major and stable QTL), which contributed 4.37% to 82.0% to the phenotypic variation in GW in individual environments. Two locus QTL analysis resolved a total of 24 QTL, which included three M-QTL (also detected by single-locus analysis) and 21 E-QTL involved in digenic Q × Q interactions; no Q × E and Q × Q × E interactions were detected. The total PV due to all the M-QTL was 28.11%, while the PV due to all the E-QTL was 43.36%, which suggested that nearly three quarters (71.47%) of PV for GW was fixable. The molecular markers linked with QTL for high GW may prove useful in marker-assisted selection for the development of cultivars with high GW in bread wheat.

INTRODUCTION

Grain weight (GW) is one of the most important component traits contributing to grain yield1-2. GW also has high phenotypic stability and heritability with favorable effect on flour yield3. In the past, genetic dissection of GW in bread wheat has been carried out using classical genetic methods. However, only limited studies involving single marker analysis (SMA) and composite interval mapping (CIM) for QTL analysis for GW have been conducted in bread wheat4. The QTL analysis for GW was facilitated by utilizing either molecular maps of individual chromosome or for the whole genome5-8. However, there are hardly any reports for the construction of whole genome framework linkage map using a mapping population specially prepared for GW. Also there are no reports of two-locus QTL analysis for GW in wheat despite the fact that in many past studies the role of epistasis (QTL × QTL interaction) and QTL × environment interactions in genetic control of other important agronomic traits has been emphasized9-11.

In majority of QTL studies involving GW in bread wheat, QTL having main effects only were detected in the past thus leaving out many QTLs, which do not have any main effect but interact among themselves and with the environment. It has also been well recognized that the power of QTL discovery can be substantially improved by making provision for the detection and estimations of QQ epistatic interactions and the QE/QQE environmental interactions. In view of this, we constructed a framework linkage map and conducted QTL interval mapping for GW following both single-locus and two-locus QTL analyses to identify main effect QTL (M-QTL) and interacting QTL.

MATERIALS AND METHODS

Mapping population and its evaluation: A mapping population consisting of 92 recombinant inbred lines (RILs) derived from Chinese Spring (CS; low grain weight) × Rye Selection111 (RS; high grain weight) was used during the present study.

Preparation of whole genome framework linkage map: For the preparation of genome-wide framework linkage map, sets of 836 SSR (gwm, wmc, barc, cfd, cfa and pk series) mapped on 21 different wheat chromosomes9-17, 15 AFLP (E35 with 7 MseI primers and E36 with 8 MseI primers) and 14 SAMPL (2 SAMPL primers, S6 and S7 each in combination with 7 MseI primers) primers were tried on the two parental genotypes and polymorphic primers were used for genotyping the RILs. Genotyping data were used for construction of a genome-wide framework linkage map using MAPMAKER/EXP v 3.0, which contained 294 (194 SSRs, 86 AFLP and 14 SAMPL) loci.

QTL analysis: Single-locus QTL analysis involving detection of main effect QTL (M-QTL) was conducted following inclusive composite interval mapping (ICIM) using Windows QTL IciMapping v1.418. A LOD score of 2.5 was used for declaring the presence of a suggestive QTL. Threshold LOD scores for detection of definitive QTL were also calculated based on 1000-permutations19. A QTL was considered stable if it was detected in at least three of the seven sets of data (six environments + the pooled data).

Two-locus QTL analysis was performed using the software QTLNetwork version 2.0, which allowed estimation of positions and effects of M-QTL, E-QTL and those involved in QE or QQE interactions. The QTL for GW were designated following standard
nomenclature for QTL as recommended for wheat and as used in our earlier study. 

RESULTS AND DISCUSSION

In bread wheat, yield component traits including GW have been only sparingly subjected to QTL analysis. The data on GW recorded on RILs gave a good fit to normal distribution; a significant RILs (GW) × environment interaction was reported earlier. The significant and positive rank correlations of GW of RILs in paired environments and high estimates of heritability suggested predictable g × e interaction as reported in earlier studies also.

A summary of the results of QTL analysis for GW carried out following single-locus and two-locus analyses is presented in Table 1. It may be noted that of the 11 QTL, one each on chromosomes 1A, 1B, 5A and 6A, were stable and explained >20% PV. One of the major and stable QTL on chromosome 1B (QGw.ccsu-1B.1; LOD value =10.7-32.0) detected in four of the seven environments explained maximum PV (26.0-82.0%) in individual environments (Figure 1). This QTL may prove beneficial for marker assisted breeding for improvement of GW in bread wheat and is also a good candidate for QTL cloning to understand the genetic basis of GW in bread wheat. Chromosomes 1A, 1B, 5A and 6A, which carried each a major and stable QTL, were also reported to carry QTL for GW in earlier studies.

<table>
<thead>
<tr>
<th>Method of QTL analysis</th>
<th>No of QTL Identified</th>
<th>Chromosome</th>
<th>LOD range/ P value</th>
<th>Range of PVE (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single-locus</td>
<td>11</td>
<td>1A, 1B, 4B, 7D, 1D, 2B, 5A, 6A, 7A</td>
<td>3.95 - 32.00</td>
<td>4.37- 82.00</td>
</tr>
<tr>
<td>Two-locus (M-QTL)</td>
<td>3</td>
<td>1A, 7D</td>
<td>P &lt;0.05</td>
<td>5.91 - 14.5</td>
</tr>
<tr>
<td>Two-locus (E-QTL)</td>
<td>21</td>
<td>1D, 2A, 2B, 2D, 3A, 3B, 3D, 5D, 6A, 6B, 6D, 7D</td>
<td>P &lt;0.05</td>
<td>0.40 - 11.37</td>
</tr>
</tbody>
</table>

Figure 1. A QTL IciMapping v 1.4 plot for chromosome 1B obtained following inclusive composite interval mapping (ICIM) for GW in bread wheat. Marker designations are given at the bottom of the horizontal line.

Table 1: A summary of different methods of QTL analyses for GW in bread wheat.
during the present study. The identification of two QTL in addition to a QTL on 1A earlier identified by us signifies the importance of genome-wide QTL analysis in bread wheat. The QTL on 7D detected following both single and two-locus analyses (see below) during the present study appeared to be the same as reported earlier. This QTL was later fine mapped and explained up to 84 % PV in GW.

During the two-locus analysis, the total PV due to all the M-QTL was 28.11%, while the PV due to all the E-QTL was 43.36%. This suggested that nearly three quarters (71.47%) of PV for GW is fixable, suggesting the importance of both the M-QTL and E-QTL for GW in bread wheat. The negative effect of the M-QTL suggested that the superior QTL allele for GW are derived from the inferior parent, which may also be exploited for improving GW in bread wheat through MAS. Also as much as 28.53% PV for GW still remained unexplained and can be attributed either to higher order interactions or environmental variation. The presence of these higher order interactions has been documented in earlier studies. The possibility that some of the QTL explaining genetic variation in GW escaped detection can not be ruled out.

From the above, we conclude that the polygenic genetic control of GW in bread wheat involving only a few major QTL and many QTL with minor effects limit the chances of success for improvement of GW in bread wheat through classical methods of plant breeding. Hence, use of molecular markers linked with high GW may be used in marker-assisted selection to accelerate development of cultivars with high GW in bread wheat.

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