Mapping of QTL for total spikelet number per spike on chromosome 2D in wheat using a high-density genetic map

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Abstract

Total spikelet number per spike (TSS) is one of the key components of grain yield in wheat. Chromosome (chr.) 2D contains numerous genes that control TSS. In this study, we evaluated 138 F₈ recombinant inbred lines (RILs) derived from an F₂ population of a synthetic hexaploid wheat line (SHW-L1) and a common wheat cultivar (Chuanmai 32) for TSS in six different environments. To identify quantitative trait loci (QTL) for TSS, we constructed an integrated high-density genetic map of chr. 2D containing two simple sequence repeats, 35 diversity array technology markers, and 143 single nucleotide polymorphisms. We identified three stable QTL for TSS that individually explained 9.7–19.2% of the phenotypic variation and predicted 23 putative candidate genes within the QTL mapping interval. Overall, our results provide insight into the genetic basis of TSS in synthetic hexaploid wheat that may be useful in breeding high-yielding wheat cultivars.

Keywords: recombinant inbred line, synthetic hexaploid wheat, quantitative trait locus, total spikelet number per spike.

Introduction

To feed the ever-growing population, improving the yield of wheat, one of the most important food crops globally, is becoming increasingly important (Rajaram, 2001; Godfray et al., 2010; Reynolds et al., 1996). Among the factors determining wheat yield, total spikelet number per spike (TSS) is considered one of the key factors, and previous studies have shown that spikelet number is closely related to grain number (Rawson, 1970) and determines where spikelets can set (Slafer and Andrade, 1993). As the basal units of inflorescences, spikelets are crucial for reproductive success and final yield (Cai et al., 2014).

TSS, as an important quantitative agronomic trait, is controlled by polygenes and influenced by the environment (Zhou et al., 2017). Understanding the genetic factors underlying variations in TSS without environmental interference is essential for the genetic improvement of wheat (Mackay, 2001; Wurschum, 2012). Previous genetic studies have revealed that chromosome (chr.) 2D is rich in genes that control spikelet number per spike in common wheat, and many quantitative trait loci (QTL), such as QSnm.cnau-2D.2 and QSnm.nau-2D, have been discovered on this chromosome (Ma et al., 2007; Zhai et al., 2016).

However, information about TSS-QTL on chr. 2D is still limited for synthetic hexaploid wheat (SHW), which contains a combination of genes from Aegilops tauschii and common wheat (Triticum aestivum), as well as novel functional genes (Mares and Mrva, 2008). Yu et al. (2014) identified a stable QTL (in the region wPt-6133-gpw4473) for TSS on chr. 2D in a population developed from a cross between SHW (SHW-L1) and the common wheat variety Chuanmai 32, using a genetic map containing simple sequence repeats (SSRs) and diversity arrays technology (DArT) markers. To accurately parse this QTL, we integrated the markers reported by Yu et al. (2014) with novel SNP markers into a new chr. 2D high-density genetic map and identified QTL for TSS. Our data might help to better understand the genetic basis of TSS in SHW and accelerate the development of new high-yielding wheat cultivars.

Materials and Methods

Plant material

A total of 138 F₈ recombinant inbred lines (RILs) derived from an F₂ SHW-L1/Chuanmai 32 population were used to construct an integrated linkage map for chr. 2D and detect QTL for TSS. SHW-L1 is an SHW derived from a cross between T. turgidum ssp. turgidum AS2255 (AABB)
and *A. tauschii* ssp. *tauschii* AS60 (DD) (Zhang et al., 2004), whereas Chuanmai 32 is a commercial hexaploid wheat cultivar grown in the southwest winter-wheat areas of China. Transgressing segregations for TSS have been previously observed in SHW-L1/Chuanmai RILs, and a total of 68 SSRs and 1794 DArT markers for important agronomic traits have been mapped (Yu et al., 2014).

**Field experiment and phenotyping**

All RILs and their parents were evaluated in a completely randomized block design with two replicates, at the experimental stations of Dujiang Weir (31°01’N and 103°32’W) in 2008, 2009, and 2010 (environments E1, E2, and E3, respectively), Guanghan (30°99’N and 104°25’W) in 2009 and 2010 (environments E4 and E5), and Wenjiang (30°36’N and 103°41’W) in 2011 (environment E6). Plants were sown in single 1.5-m rows with a 30-cm space between rows and a 10-cm space between individuals. Data for TSS were manually counted from 10 randomly selected guarded main spikes from each line in each environment (Yu et al., 2014).

**Statistical analysis**

To estimate random effects, a best linear unbiased prediction (BLUP) mixed model was used to obtain BLUP-TSS values (Piepho et al., 2008). The BLUP for the phenotypic value of plant $Y_i$ was calculated as follows: $Y_i = X_i f + a_i + e_i$, where $f$ is a vector of fixed effects, $X_i$ is an incidence vector, $e_i$ is the environmental deviation, and $a_i$ is the phenotypic value (Goddard, 1992). An analysis of variance (ANOVA) was performed using SAS 9.1.3 (SAS Institute, Cary, NC, USA) to estimate the effects of genotype on TSS. The estimated broad-sense heritability of TSS was calculated as follows: $h^2 = \sigma^2_g / (\sigma^2_g + \sigma^2_e / r)$, where $\sigma^2_g$ is the genetic variance, $\sigma^2_e$ is the residual variance, and $r$ is the number of replicates per genotype.

**Construction of a genetic map for chr. 2D**

A total of 13 SSRs, 93 DArT markers, and 2306 SNPs reported in previous studies (Yu et al., 2014; Yang, 2016) were used to construct a genetic map for chr. 2D. After the removal of redundant markers that were located on the same loci (Yang, 2016), the genetic map consisted of 13 SSRs, 86 DArT markers, and 244 SNPs. The remaining markers were assigned to linkage groups using Joinmap 4.0 (Van Ooijen, 2006) with a recombination frequency of 0.25–0.05. The final genetic distances were obtained using the Kosambi mapping function (Kosambi, 2016).

**QTL mapping**

QTL screening was conducted using interval mapping (IM) in MapQTL 6.0 (Van Ooijen, 2009). Logarithm of odds (LOD) threshold values for IM were determined based on 1000 permutations to declare significant QTL at $p<0.05$, whereas QTL with LOD values <3.0 were excluded to ensure the authenticity and reliability of the reported QTL. QTL that explained more than 10% of variation in TSS were considered as major QTL.

**Prediction of candidate genes**

To predict candidate/flanking genes, the interval flanking marker sequence was aligned via a BLAST search against the International Wheat Genome Sequencing Consortium and EnsemblPlants databases to determine the position with the highest identity and detect genes within the closed interval. To predict the function of the candidate genes, we conducted Gene Ontology (GO) annotation and Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway enrichment analysis at $p<0.05$, using *Arabidopsis thaliana* as a background species, in KOBAS 3.0.

**Results**

**TSS variation in RILs**

The results of the mean phenotypic performance and BLUP values for the TSS of RILs and their parents in the six environments are presented in Table 1. The ANOVA and heritability ($h^2$) values are presented in Table 2. Variation among the RILs was high, with a coefficient of variation ranging from 9.53% in E1 to 14.39% in E6. Distributions were continuous across all environments (Figure 1), and, thus, the RILs were suitable for analyzing QTL for TSS.

### Table 1 - The mean phenotypic performance for TSS of the recombinant inbred lines (RILs) and their parents in six environments.

| Environments | Parent Population | Min | Max | Mean | SD | CV (%) |
|--------------|-------------------|-----|-----|------|----|--------|
| E1           | SHW-L1 Chuanmai 32| 16.80 | 27.20 | 22.12 | 2.11 | 9.53   |
| E2           |               | 15.00 | 26.40 | 20.27 | 2.28 | 11.24  |
| E3           |               | 13.60 | 27.20 | 19.86 | 2.35 | 12.07  |
| E4           |               | 12.71 | 24.00 | 18.31 | 2.63 | 13.57  |
| E5           |               | 14.00 | 28.00 | 19.36 | 2.63 | 13.57  |
| E6           |               | 13.33 | 26.20 | 18.67 | 2.69 | 14.39  |
| BLUP         |               | 15.49 | 23.85 | 19.78 | 1.67 | 8.46   |
Construction of genetic linkage map for chr. 2D

Different types of molecular markers were used to construct a genetic map for chr. 2D. At a maximum recombination frequency score of 0.4 and a minimum LOD score of 1.00, 180 markers were assigned to two different linkage groups (LG) that covered 207.33 cM, with a mean interval distance of 1.15 cM between the markers; however, the other 163 markers remained unassigned. LG 1 consisted of two SSRs, 35 DArT markers, and 90 SNPs, whereas LG 2 consisted of 53 SNPs.

Stable QTL for TSS

Three QTL for TSS (QTSS.sicau-2D.1, QTSS.sicau-2D.2, and QTSS.sicau-2D.3) with significant effects in at least four environments were identified on chr. 2D. The existence and stability of the QTL were confirmed by BLUP values. The three major QTL individually explained 9.7–19.2% of the phenotypic variation (Table 3, Figure 2), and the additive effects of QTL showed that the positive alleles (i.e., those related to a high number of TSS) on chr. 2D originated from SHW-L1. Of these, QTSS.sicau-2D.1 was detected in all environments, except E5, whereas
Figure 2 - Chromosomal locations of quantitative trait loci for TSS and associated markers in the SHW-L1/Chuanmai 32 recombinant inbred line (RIL) population under 6 environments. The black bar points to the LOD peak of QTL.

Table 2 - Analysis of variance (ANOVA) and the heritability ($h^2$) values.

| Degrees of Freedom (DF) | Type III SS | Mean Square | F Value | Significance | Heritability ($h^2$) |
|-------------------------|-------------|-------------|---------|--------------|---------------------|
| E                       | 2           | 785.34      | 392.67  | 19.04        | Significant at $p<0.01$ |
| G                       | 2           | 278.75      | 139.38  | 6.95         | **Significant at $p<0.01$ |
| E*G                     | 2           | 2646.17     | 1223.08 | 61.19        | ***Significant at $p<0.001$ |

Table 3 - Quantitative trait loci (QTL) for TSS identified in the SHW-L1/Chuanmai 32 recombinant inbred line (RIL) population under 6 environments.

| QTL | Environments | Marker interval | Nearest Flanking marker | Max LOD | Combined LOD | % Expl. | Source |
|-----|--------------|-----------------|-------------------------|---------|--------------|---------|--------|
| QTSS.sicau-2D.1 | E1, E2, E3, E6, BLUP | AX98481433-AX1035711066 | AX110571866 | 3.31-6.48 | 25.17 | 9.7-19.2 | SHW-L1 |
| QTSS.sicau-2D.2 | E1, E2, E3, E6, BLUP | AX10650508-AX94497721 | AX10650508 | 4.17-6.22 | 22.67 | 17.78 | SHW-L1 |
| QTSS.sicau-2D.3 | E1, E2, E3, E6, BLUP | AX94497721 | AX94497721 | 3.21-6.49 | 17.78 | 10-14.3 | SHW-L1 |
QTSS.sicau-2D.2 and QTSS.sicau-2D.3 were found in four environments (E1–3 and E6).

Putative candidate genes in QTL intervals

A total of 23 putative candidate genes associated with TSS were identified (Table S1). Two genes were predicted in the QTSS.sicau-2D.1 interval (IWGSC_ref_V1_chr2D chr2D:9346330-9579108), 19 in the QTSS.sicau-2D.2 interval (IWGSC_ref_V1_chr2D chr2D:38222754-43976070), and two in the QTSS.sicau-2D.3 interval (IWGSC_ref_V1_chr2D chr2D:77381440-78089285). Of these, five genes, LECRK42, AT2G34930, PME21, COBL7, and PIP5K4, regulate flower development, and three, CRK8, RPPL1, and AT4G29780, are related to spikelet number differentiation. KEGG pathway enrichment analysis showed that PIP5K4 is involved in inositol phosphate metabolism, phosphatidylinositol signaling system, and endocytosis; PME21 and PME53 are involved in starch and sucrose metabolism and pentose and glucuronate interconversions; and AT2G07689 and ATP1 are involved in oxidative phosphorylation.

Discussion

In the present study, by using an integrated high-density genetic map, three major QTL for TSS were detected on chr. 2DS (short arm of chr. 2D). Among them, QTSS.sicau-2D.2 was located in the marker interval wPt6133–gpw4473, which might correspond to that reported by Yu et al. (2014) in the same marker interval (Figure 3). Notably, using the integrated high-density genetic map for chr. 2D, we managed to decrease the marker interval range from 15.6 cM to 1.04 cM, which is a substantial improvement over that obtained in previous studies, and two additional QTL were detected. Similarly, by high-density consensus map, Marone et al. (2012) increased the map density from 11.8 cM per marker (as obtained by Nachit et al., 2001) to 1.6 cM per marker, and Sourdille et al. (2003) confirmed previously detected QTL and identified three novel ones, suggesting that good coverage of chromosome is important for QTL detection. Therefore, this study provides a strategy for identifying QTL, which combines new molecular data with phenotypic data and enables possible detection of previously overlooked QTL.
For chr. 2D, previous studies have identified numerous putative QTL (Li et al., 2002; Sourdille et al., 2003; Quarrie et al., 2006; Cui et al., 2012; Liu et al., 2014; Zhai et al., 2016; Zhou et al., 2017). Ma et al. (2007) reported two QTL for TSS in the marker intervals Xwmc181.1-Xaf12d (near IWGSC_ref_V1_chr2D chr2D: 647432804-647432824) and Xaf12-Xcfd239 (near IWGSC_ref_V1_chr2D chr2D: 647432804-647432824); Cui et al. (2012) also reported two QTL for TSS in the marker intervals Xcfd267 (near IWGSC_ref_V1_chr2D chr2D: 647432804-647432824) and Xaf12 (near IWGSC_ref_V1_chr2D chr2D: 647432804-647432824). Comparison with data in the IWGSC database revealed that these above-mentioned QTL were found on chr. 2DL (long arm of chr.2D). The three QTL we detected were located on chr. 2DS; so, we paid more attention to the QTL previously detected on chr. 2DS. Li et al. (2002) reported a QTL for TSS in the marker interval Xbcd611–Xgwm484 (IWGSC_ref_V1_chr2D chr2D: 34894502-48174393) on chr. 2DS; by comparison, this marker interval is different from those of QTSS.sicau-2D.1 (IWGSC_ref_V1_chr2D chr2D: 9346330-9579108) and QTSS.sicau-2D.3 (IWGSC_ref_V1_chr2D chr2D: 77381440-78089285), but contains QTSS.sicau-2D.2 (IWGSC_ref_V1_chr2D chr2D: 3822754-43976070). Zhou et al. (2017) also reported two QTL for TSS on chr. 2DS: QTsn.czm-2D.2 was located in the marker interval XPpd_D1-2DS_5382880_5243 (IWGSC_ref_V1_chr2D chr2D: 29716047-67557838) that contains QTSS.sicau-2D.2, while the other QTL, named QTsn.czm-2D.1 (IWGSC_ref_V1_chr2D chr2D: 9346330-9579108) was different from QTSS.sicau-2D.1 and QTSS.sicau-2D.3. Therefore, QTSS.sicau-2D.1 and QTSS.sicau-2D.3 are probably novel QTL that can be used for further fine mapping and genetic analysis.

In wheat, the development of polymorphism markers based on QTL is an effective method for molecular-assisted breeding (Roussel et al., 2005); so, the three QTL for TSS identified in this study may be used for the breeding of high yield wheat varieties. Furthermore, the results revealed that SHW-L1 contributed positively to all the three major loci. Hence, future breeding programs can use the QTL-associated markers to fully exploit the genetic potential of QTL in increasing SHW-L1 production.

A total of 23 A. thaliana gene homologs were predicted in the three QTL intervals. The results of GO annotation suggest that seven candidate genes deserve our attention; these are: LECRK42, AT2G34930, PME21, COBL7, PIP5K4 (located in the QTSS.sicau-2D.2 intervals), CRK8 (located in the QTSS.sicau-2D.3 intervals), and RPPL1 (located in the QTSS.sicau-2D.1 intervals). Among them, LECRK42, PME21, and PIP5K4 play critical roles in pollen and pollen tube development (Sousa et al., 2008; Wan et al., 2008; Oo et al., 2014); AT2G34930 encodes cell wall proteins in the apoplastic fluids of rosettes (Boudart et al., 2005); and COBL7 influences the development and function of the gynoecium (Scutt et al., 2003). Pollen and flower development is closely related to flowering time, and flowering time genes affect ear differentiation, including TSS (Jiang et al., 1982). Moreover, differentiation of TSS indicates a switch from vegetative to reproductive development (Li, 1976). Interestingly, CRK8 is involved in reproductive signal transduction (Zhao et al., 2011), and RPPL1, which interacts with GRF2, plays crucial roles in controlling growth and development in plants (Gökirmak et al., 2015; Ghorbel et al., 2017). For all these reasons, the seven candidate genes located in the three QTL intervals were considered to be closely related to TSS, which validates the accuracy of our results, provides reference for future map-based cloning experiments, and helps to better understand the genetic mechanism of spikelet growth and development in wheat.

Conclusions

In this study, we provided a strategy of identifying QTL by combining new molecular data with phenotypic data, and identified two novel QTL for TSS. A total of seven candidate genes associated with TSS were predicted. Overall, our data provides insight into the genetic basis of TSS, which might accelerate the development of high-yielding wheat cultivars.

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

MD conducted data analysis and drafted the manuscript; FW performed the analysis of genotyping data and partially drafted the manuscript; WZ, JL, YuL and XY participated in the design of the study; YZ...
coordinated the study and helped to draft the manuscript; YaL designed and coordinated this study and revised the manuscript; All authors have read and approved the final manuscript.

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Internet Resources
International Wheat Genome Sequencing Consortium (IWGSC) database, https://urgi.versailles.inra.fr/blast_iwgsc/blast.php/ (April 21, 2018)
Ensembl Plants database, http://plants.ensembl.org/hmmer/index.html/ (April 21, 2018)
KOBASE 3.0 database, http://kobas.cbi.pku.edu.cn/ (April 21, 2018)

Supplementary material
The following online material is available for this article:
Table S1 - SNPs and candidate genes significantly associated with Total spikelet number per spike (TSS) QTL.

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