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Conditional QTL mapping of three yield components in common wheat (*Triticum aestivum* L.)

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ABSTRACT

Spike number per m^2 (SN), kernel number per spike (KNPS) and thousand-kernel weight (TKW) are the three main components determining wheat (*Triticum aestivum* L.) yield. To evaluate the relationships among them a doubled haploid (DH) population consisting of 168 lines grown at three locations for three years was analyzed by unconditional and conditional QTL mapping. Thirty-three unconditional QTL and fifty-nine conditional QTL were detected. Among them, two QTL (*QSN-DH-2B* and *QSN-DH-3A-1.1*) improved SN, with no effect on KNPS. *QKNPS-DH-2B-2.1* improved KNPS, with no effect on SN. *QKNPS-DH-1A-1.1*, *QKNPS-DH-2D-1.1* and *QKNPS-DH-6A* improved KNPS, with no effect on SN or TKW. *QKNPS-DH-6B* was associated with increased SN and TKW. In addition, *QTKW-DH-4B*, *QTKW-DH-5B* and *QTKW-DH-7B* increased TKW without decreasing KNPS. These results provide useful information for marker assisted selection (MAS) and improvement in wheat yield.

1. Introduction

Common wheat (*Triticum aestivum* L.) is one of the most important crops worldwide. Its yield is significantly correlated with spike number per m^2 (SN), kernel number per spike (KNPS) and thousand-kernel weight (TKW). In wheat-breeding and agronomic studies the relationships of the three components are frequently investigated. Understanding the genetics is crucial for improving yield. Quantitative trait loci (QTL) analysis can dissect and characterize the genetic complexity of yield traits produce a better understanding of the genetic architecture of yield components. Researchers have conducted unconditional QTL analyses on KNPS [1–4], SN [1–3,5] and TKW

[3–8] in different genetic backgrounds and different environments. However, all tree traits are controlled by multiple genes and are affected by environment as well as genetic background. Previous unconditional QTL studies did not always provide an overall true expression of accumulated effects of QTL. Consequently, this method may not be suitable for analysing interactions among QTL or genes controlling related traits [1,3,4].

Zhu [9] developed conditional analysis methods that are capable of excluding the contribution of a causal trait to variation of the resultant trait. The remaining variation in the resultant trait is defined as conditional variation, or net variation, which indicates the effects of genes that are independent of the causal trait [10]. Therefore, this method

can also define the genetic relationships among different traits at the QTL level. To date, this method has been used not only to study the dynamic behaviour of developmental traits but also the effects of conditional variation in the resultant trait on multiple related traits in rice [10–11], wheat [12–16], maize and rapeseed [17]. In wheat, many cause–effect conditional QTL, such as protein content with yield and yield-related traits [15], flour components with sedimentation volume [18], TKW with kernel length and kernel width [19]. These results indicate that conditional QTL analysis of related traits is helpful for revealing the genetic relationships of closely related individual QTL and for clarifying the positive or negative genetic relationships of two traits at the level of a single QTL or gene [9,20].

Some studies indicated that the conditional QTL method could also detect more QTL than the traditional QTL mapping method, especially with regard to the identification of important QTL/genes that increase one trait without affecting others. For instance, Guo et al. [21] investigated the relationship between yield and number of tillers per plant, grains per panicle and TKW using a population of 241 recombinant inbred lines (F_9 RILs) derived from the elite hybrid rice cross 'Zhenshan 97' × 'Minghui 63' by unconditional and conditional QTL mapping methods. Similarly Yu and Chen [22] identified 36 QTL for water logging tolerance in ITMI wheat population and 10 QTL in an SHW-L1 × Chuanmai 32 (SC) population, and dissected the genetic relationships between QTL for total dry weight index and its components. Zhang [19] conducted a QTL analysis of kernel weight and provided a better understanding of the relationships between yield-contributing traits at the QTL level. These results provided a theoretical basis for application in marker-assisted selection (MAS) for grain yield improvement in wheat.

In the present study the relationships among three major yield components were examined at the QTL/gene level using a DH population planted in different years and locations according to both unconditional and conditional QTL mapping methods. The aims were to 1) identify QTL for the three grain components conditioned on other traits, 2) analyse the relationships among the three grain components at the QTL/gene level, and 3) determine the important QTL regions controlling three yield components.

2. Materials and methods

2.1. Plant materials

A doubled haploid (DH) population consisting of 168 lines produced from a cross between Chinese wheat cultivars Huapei 3 and Yumai 57 was used in this study. Huapei 3 is an elite variety with large panicles, large grains and medium number of spike-bearing tillers [23]. Yumai 57 has medium–large panicles, a large number of spike-bearing tillers, and can be cultivated under a wide range of environmental conditions [24]. Huapei 3 and Yumai 57 were released in 2006 [23] and 2003 [24], respectively.

2.2. Field trials

The parental lines, together with the DH population, were evaluated at three locations: Tai'an (36°57′ N, 116°36′ E), Jinan

(36°71′ N, 117°09′ E) and Jiyuan (112°36′ E, 35°05′ N), and five environments: Tai'an in 2010–2011 (E1), Jinan in 2011–2012 (E2), Tai'an in 2011–2012 (E3), Jiyuan in 2011–2012 (E4), and Jinan in 2012–2013.

All entries were planted in two replications at each location in randomized complete block designs in October 2010. At Tai'an all DH lines and parents were grown 2 m plots of four rows spaced 26 cm apart. The same materials were planted in four row plots of 2.7 m and 20 cm roe spacing, four row plots of 3 m and 25 cm roe spacing, and three row plots of 2.6 m and 20.0 cm row spacing, respectively, at Tai'an, Jinan and Jiyuan. The lines and parents were evaluated in four-row 3 m plots with row spacing of 25 cm apart at Jinan in October 2012. The population density at the different locations and environments was approximately 1.8 million per hectare. Field management was in accordance with local agronomic practices.

Data for SN and KNPS were recorded at maturity from 10 randomly selected plants grown in the central rows of each plot before harvesting. TKW was measured from the same plants harvested from central rows of each plot.

2.3. Genetic linkage map

The genetic linkage map contained 323 markers (including 284 simple sequence repeat (SSR) loci, 37 expressed sequence tag (EST) loci, one inter-simple sequence repeat (ISSR) locus, and one high-molecular-weight glutenin subunit locus). These linked markers formed 24 linkage groups over 21 chromosomes [25].

2.4. Data analysis and QTL mapping

Simple correlation coefficients were calculated using SPSS version 19.0 software (SPSS, Chicago, USA). Unconditional QTL for SN, KNPS and TKW were detected using the inclusive composite interval mapping function of QTL IciMapping 3.2 software (Beijing, China) with stepwise regression and simultaneous consideration of all marker information (http://www.isbreeding.net/). The 'Deletion' command was used to delete missing phenotypic data.

Data on conditional phenotypic values $y_{hk(T1/T2)}$ were obtained from QGA Station 1.0 (http://ibi.zju.edu.cn/software/Qga/index.htm) [9], where T1/T2 means for trait 1 conditioned on trait 2 (for example, SN|TKW = SN conditioned on TKW). Conditional QTL mapping was conducted using QTL IciMapping 3.2 software. For all QTL, the mapping parameters of each step and the probability of the stepwise regression were set at 1.0 cM and 0.001, respectively, for each mapping method. The threshold LOD scores were calculated using 1000 permutations, with a type I error of 0.05. The QTL LOD values below 2.5 were ignored to increase the accuracy and reliability of QTL detection.

3. Results

3.1. Phenotypic variation and correlation

The means, standard deviation, maximum, and minimum values of SN, KNPS and TKW were calculated for all five environments (Table 1). Strong transgressive segregations for all three traits indicated control by multiple genes.