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Single nucleotide polymorphisms linked to quantitative trait loci for grain quality traits in wheat

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ABSTRACT

Wheat (*Triticum aestivum* L.) grain quality traits that are controlled by quantitative traits loci (QTL) define suitable growing areas and potential end-use products of a wheat cultivar. To dissect QTL for these traits including protein content (GPC); test weight (TW); single kernel characterization system (SKCS)-estimated kernel weight (SKW); kernel diameter (KD); kernel hardness measured by near-infrared reflectance spectroscopy (NIRS) hardness index (NHI); and SKCS-hardness index (SHI), a high-density genetic map with single nucleotide polymorphism (SNP) and simple sequence repeat (SSR) markers was developed using recombinant inbred lines (RILs) derived from Ning7840 × Clark. The RILs were evaluated for these quality traits in seven Oklahoma environments from 2001 to 2003. A total of 41 QTL with additive effects on different traits were mapped on most wheat chromosomes, excluding 1A, 2A, 3D, 4D, 6D, and 7B. Seven chromosome regions showed either tightly linked QTL or QTL with pleiotropic effects on two to four traits. Ten pairs of QTL showed additive × additive effects (AA), four QTL were involved in additive × environment (AE) effects, and one was involved in AAE effects. Two to eleven QTL for each of the six traits and 139 tightly linked markers to these QTL were identified. The findings shed light on the inheritance of wheat grain quality traits and provide DNA markers for manipulating these important traits to improve quality of new wheat cultivars.

1. Introduction

Grain protein content (GPC), test weight (volumetric grain weight, TW), kernel weight (KW), kernel size (KS), and kernel hardness (KH) are important grain quality traits in bread wheat (*Triticum aestivum* L.). Quantitative trait locus (QTL) analysis for GPC has been extensively studied and a large number of QTL were reported to cover all 21 wheat chromosomes

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[1,2,3,4,5,6,7,8,9,10,11]. Previous studies detected many QTL for TW located on almost all 21 wheat chromosomes except for 6D [3,5,8,12,13,14,15,16]. KW is an important component of not only grain yield but also flour yield. Many studies on QTL for KW have been performed and QTL were detected on all chromosomes except 3D and 6D [8,11,14,15,16,17,18,19,20,21,22,23]. The uniformity of KS or its distribution allows for a more efficient milling and quality control. Different QTL were detected in diverse germplasm lines when different methods were used to assess KS. QTL for KS, which is conditioned by genes independently of those for kernel length and width, were mapped to 16 wheat chromosomes excluding 3A, 3D, 4D, 6D, and 7D [14,20,23,24,25,26,27,28]. Pleiotropic QTL were also identified for KS and kernel weight on chromosomes 2A, 5D, 6A [14] and 2B, 2D, 4B, 5B [20]. KH is an important quality trait of bread wheat (*Triticum aestivum* L.) and determines wheat classification and end-use properties. Previous studies indicated that QTL with large effects on KH were co-located with the *Ha* locus on chromosome 5DS [2,4,13,24,29]. In addition, a number of QTL that affect wheat KH have been identified in different mapping populations and covered all 21 wheat chromosomes except for 3D and 6A [6,9,30,31,32,33,34].

Although QTL on the 21 chromosomes have been identified for grain quality traits in wheat germplasm, epistatic effects among them have not been well documented despite the importance in understanding the genetic basis of complex traits. Also, environments often influence expression of grain quality traits and genotype × environment interaction significantly contributes to phenotypic variations of such traits. Sun et al. [19] used a Ning7840 × Clark recombinant inbred line (RIL) population to construct a SSR and AFLP-based map and identified 25 QTL for quality factors, but they did not consider epistatic effects and QTL × environment interactions. Besides, single nucleotide polymorphisms (SNPs) are the most common polymorphism among individuals of any species with virtually unlimited numbers and constitute the basis of most genetic variation between individuals [35]. The availability of diverse SNP genotyping platforms facilitates genetic dissection, marker discovery and genomic selection of traits in crop plants [36]. In the present study, we used a high-density, SNP and SSR genetic map developed for the Ning7840 × Clark RIL population to identify new additive QTL for wheat grain quality traits and SNP markers closely linked to the QTL, and evaluated interaction effects between QTL and between QTL and environments.

2. Materials and methods

2.1. Plant materials and phenotypic data collection

A population of 127 $F_{10–12}$ RILs was developed from the cross Ning7840 × Clark by single-seed descent. Ning7840 (Avrora/Anhui 11//Sumai 3) is a Chinese hard red wheat breeding line. It has relatively low yield potential, but a high level of resistance to various rust pathogens and *Fusarium graminearum* [37]. Clark is a soft winter wheat cultivar released from Purdue University, IN, with good yield potential [38].

Phenotypic data were collected from field experiments at three Oklahoma locations, Stillwater (ST), Lahoma (LA) and Altus (AL) in three crop years ending in 2001, 2002, and 2003, respectively. The RILs along with the parents were measured for six grain quality traits including GPC, TW, single kernel characterization system (SKCS)-estimated kernel weight (SKW), kernel diameter (KD), SKCS-grain hardness index (SHI), and near-infrared reflectance spectroscopy (NIR)-estimated grain hardness index (NHI). Experiments were conducted in seven combinations of years and locations: Stillwater 2001 to 2003 (ST01 to ST03), Lahoma 2002 and 2003 (LA02 and LA03), and AL02 and AL03 (Altus 2002 and 2003). The RILs were arranged in a replicates-in-sets design with three replicates and a plot size of 1.4 m^2 planted at a density of 58 kg ha^{-1}. The phenotypic data for GPC, TW, SKW, KD, SHI, and NHI were collected as previously described [19].

2.2. DNA extraction and marker analysis

Genomic DNA isolation from both the parents and RILs and PCR for SSR were conducted following previously described protocols [39]. PCR fragments were separated with an ABI PRISM 3730 DNA Analyzer (Applied Biosystems, Foster City, CA, USA) and scored using GeneMarker version 1.6 (Soft Genetics LLC, State College, PA, USA).

SNP genotyping was performed using Infinium iSelect SNP genotyping assays containing 9000 wheat SNPs developed by Illumina Inc. (San Diego, CA, USA). The assay was designed under protocols of the International Wheat SNP Consortium [40]. SNP call was performed using GenomeStudio v2011.1 software (Illumina Inc.). The genotyping assay was conducted at the USDA Small Grains Genotyping Laboratory at Fargo, ND.

2.3. QTL identification

A linkage map for QTL mapping of grain quality traits was reported previously [41]. This map consisted of 998 markers (594 SNPs and 404 SSRs) in 47 linkage groups that corresponded to all 21 wheat chromosomes and covered 4225.7cM of total genetic distance. This final map was used to map the QTL for grain quality traits. QTL mapping was performed using inclusive composite interval mapping of additive (ICIM-ADD) and epistatic QTL (ICIM-EPI) functionalities in the software QTL IciMapping version 3.2 [42]. Additive QTL were detected using 1.0cM steps. The significance probability was set at 0.001 for stepwise regression. Significant LOD thresholds were determined for each dataset by 1000 permutations. Type I error to determine the LOD thresholds from permutation tests was set at $P < 0.05$. Epistatic QTL were detected using a scanning step of 5.0cM, a probability of 0.0001 in stepwise regression, and a LOD threshold of 5.0 to claim significance.

QTL × environment interactions were detected using the Multi-Environment Trials (MET) functionality. Additive × environment (AE) effects and additive × additive × environment (AAE) effects were identified using ICIM-ADD and ICIM-EPI functionalities in the software QTL IciMapping [42]. AE and AAE interactions were detected using 1.0cM steps in scanning, a probability of 0.001 for stepwise regression, and a LOD threshold of 2.5 for claiming significant QTL in each dataset. Significant AE interactions were claimed at $P < 0.05$ (LOD = 3.8) and significant AAE interactions were claimed at $P < 0.001$ (LOD = 10.2).