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Single nucleotide polymorphism markers linked to QTL for wheat yield traits

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Abstract Continuous improvement in grain yield is one of the major challenges for wheat (*Triticum aestivum* L.) breeding worldwide. This study characterized quantitative trait loci (QTL) underlying wheat grain yield and its components using a high-density genetic linkage map developed from a recombinant inbred line (RIL) population derived from 'Ning7840' × 'Clark'. The map consisted of 594 single nucleotide polymorphism and 404 simple sequence repeat markers covering a genetic distance of 4225.7 cM. The RIL population was evaluated for grain yield (GY), spike number per m^2 (SNPM), kernel number per spike (KNPS), and thousand-kernel weight (TKW) in three Oklahoma locations from 2001 to 2003. A total of 29 additive QTL (eight for GY, two for SNPM, five for KNPS, and 14 for TKW) were mapped on 13 chromosomes. Eight pairs of epistatic QTL were detected for different yield components: four for GY, two for KNPS, and two for TKW. Four additive QTL, including two for GY and two for KNPS, showed additive × environment interactions. QTL that were repeatable in multiple environments were identified for all traits except SNPM. Positive alleles were dispersed between the two parents for all traits, with 'Clark' contributing slightly more. Seven pleiotropic loci were co-localized for at least two traits. Interestingly, all co-localized loci overlapped for TKW, and four of them overlapped for GY. Thus, selecting QTL for TKW may simultaneously select for or against yield or other yield components in breeding.

Keywords Epistatic effects · QTL for yield traits · QTL × environment interaction · SNP · Triticum aestivum

Introduction

Attaining high grain yield (GY) in wheat (*Triticum aestivum* L.) is a primary objective of wheat breeding

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that is challenged by a patchwork understanding of its genetic determination and the omnipresence of genotype × environment interactions. GY can be dissected into three major components: number of spikes per unit area (NSPA), kernel number per spike (KNPS), and thousand-kernel weight (TKW). Many genes or quantitative trait loci (QTL) influence yield and its components (Cui et al. 2014). Interactions among and between QTL and the environment also modify the expression of the QTL in different genetic backgrounds (Barton and Keightley 2002; Walsh 2002). A QTL detected in one environment but not in others might indicate QTL × environment (QBE) interaction, but assessing the contribution of such interactions to phenotypic variation by simply comparing QTL detected in multiple environments is difficult. Goldringer et al. (1997) first estimated the additive and epistatic genetic variances for agronomic traits in a doubled haploid wheat population and demonstrated that GY and its components, as expected, showed either additive or additive plus epistatic effects. Significant epistasis and QBE interactions were identified subsequently for GY QTL (Kumar et al. 2007; Snape et al. 2007; Zhang et al. 2008; Reif et al. 2011; Patil et al. 2013). Thus, dissection of QTL effects and their interactions may facilitate better understanding of the genetic control of complex GY traits (Carlborg and Haley 2004).

Genetic linkage maps play a fundamental role in QTL identification by providing not only measurements of the relative effects of alleles in a mapped chromosomal region but also selectable DNA markers for breeders to manipulate traits through marker-assisted selection (MAS) (Torada et al. 2006). Several types of markers were used in QTL mapping of wheat agronomic traits (Li et al. 2007; Cuthbert et al. 2008; Wang et al. 2009; Mir et al. 2012; Cui et al. 2014). More recently, single nucleotide polymorphisms (SNP) were used to develop high-density genetic maps and QTL mapping in many crops (Malosetti et al. 2011; Shirasawa et al. 2012; Alam et al. 2014; Cui et al. 2014; Lee et al. 2014). SNP are the most common source of genetic variation among individuals of any species and the smallest unit of genetic variation, with virtually unlimited numbers (Deschamps and Campbell 2010). The availability of diverse SNP genotyping platforms facilitates genetic dissection, marker discovery, and genomic selection of complex crop traits (Collard and Mackill 2008; Jannink and Lorenz 2010). However, the highly repetitive nature of the hexaploid wheat genome has slowed progress in SNP discovery and detection. A few SNP markers are ready to be used for studying complex agronomic traits. Cavanagh et al. (2013) developed 9 K SNP assays and constructed the first high-density wheat consensus SNP map containing 7504 polymorphic loci. The SNP assay and map provide a powerful resource for further mapping of wheat traits of interest and for genomic research and genome-wide association studies in wheat.

We previously analyzed QTL for wheat yield traits in a wheat RIL population derived from 'Ning7840' × 'Clark' using simple sequence repeats (SSR) and amplified fragment length polymorphism (AFLP) markers (Marza et al. 2006). Because of low SSR density in the map and unusable AFLP markers for breeding selection, these markers have not been used in marker-assisted breeding for yield traits. In this study, we identified 2404 markers polymorphic between the parents using the wheat 9 K SNP chip. These SNP provide an opportunity to construct a high-density genetic map, thus enabling high-resolution QTL mapping and development of SNP markers for MAS in common wheat. The objectives of the study were to: (1) use the high-density SNP and SSR map to further characterize additive QTL, epistatic QTL, and QBE interactions for wheat yield traits, and (2) develop molecular markers closely linked to genes associated with traits of interest for future MAS.

Materials and methods

Plant materials and phenotypic data

A population of 127 F_{8-12} RILs was developed from the cross 'Ning7840' × 'Clark'. 'Ning7840' is a Chinese hard red facultative cultivar with pedigree (Avrora × Anhui 11) × Sumai 3. It was released for its resistance to rust pathogens (*Puccinia* spp.) and *Fusarium graminearum* (Bai et al. 1999). 'Clark', a soft red winter wheat cultivar developed at Purdue University, West Lafayette, IN, has good yield potential and high kernel weight (Ohm et al. 1988).

Yield traits were evaluated in field experiments in three crop years ending in 2001, 2002, and 2003. Briefly, the parents and RILs were grown at three Oklahoma locations (Stillwater, Lahoma and Altus)

using a replicates-in-sets design with three replications (Carver and Rayburn 1994). Plot size was 1.4 m^2, and wheat was planted at a density of 58 kg ha^{-1}. In brief, GY was measured by weighing all grain harvested from each plot; spike number per m^2 (SNPM) was calculated based on the number of spikes in two 50-cm row segments 23 cm apart; mean KNPS was calculated from 15 random spikes; and TKW was calculated from the weight of 200 random kernels at 11 % relative humidity, as previously described by Marza et al. (2006).

DNA extraction and marker analysis

Genomic DNA isolation from both parents and RILs, and PCR for SSR were conducted following previously described protocols (Zhang et al. 2010a). PCR products were separated by 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 with Infinium iSelect assays containing 9000 wheat SNP (Illumina Inc., San Diego, CA, USA). The assay was designed under International Wheat SNP Consortium protocols (Cavanagh et al. 2013). SNP genotype calling was performed using GenomeStudio v2011.1 software (Illumina Inc.). The genotyping assay was conducted at the USDA Small Grains Genotyping Laboratory at Fargo, ND.

Linkage map construction and QTL identification

To construct a linkage map, 'Ning7840' × 'Clark' RIL were screened with the 9000 SNP, and the 2404 segregating SNP in the population were used to construct an initial map. To simplify the map for QTL analysis, markers less than 1 cM apart in the initial map were removed, and the remaining 594 SNP and 413 polymorphic SSR markers were used for final map construction. The final map was constructed using the MAP function in QTL IciMapping 3.2 software (Wang et al. 2012) with a minimum LOD value of 5.0 and the Kosambi mapping function. Finally, 998 markers (594 SNP and 404 SSR) were mapped to 47 linkage groups representing all 21 wheat chromosomes. This map covering 4225.7 cM with an average marker interval of 4.2 cM was used to map the QTL for wheat yield traits.

QTL mapping was performed by QTL IciMapping 3.2 (Wang et al. 2012) using the inclusive composite interval mapping of additive (ICIM-ADD) and two-locus epistatic QTL (ICIM-EPI) modules. Additive QTL were detected using a 1.0 cM step in scanning. The probability used in stepwise regression was 0.001. Significant LOD thresholds were determined for each dataset by 1000 permutations. Type I error to determine the LOD threshold from permutation tests was 0.05. Epistatic QTL were detected using a step of 5 cM in scanning, a probability of 0.0001 in stepwise regression, and a LOD threshold of 5.0 to claim significant epistatic QTL. QTL names were designated following standard nomenclature. For an example, a QTL for GY on 5AS was named *QGy.hwwgr-5AS,* where *hwwgr* refers to USDA Hard Winter Wheat Genetics Research Unit in Manhattan, KS, USA.

QTL × environment interactions were detected using the multi-environment trials (MET) module, and additive × environment (AE) effects and epistasis × environment (AAE) effects were identified using ICIM-ADD and ICIM-EPI modules in QTL IciMapping software. AE and AAE interactions were detected using a 1.0 cM step 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).

Results

QTL for wheat yield traits

QTL mapping identified 29 putative QTL with additive effects for GY and yield components across environments, with 8, 2, 5, and 14 additive QTLs for GY, SNPM, KNPS and TKW, respectively (Table 1; Fig. 1). Among them, 15 (52 %) were in the A genome, 8 (27 %) were in the B genome, and 6 (21 %) were in the D genome. The number of additive QTL from homoeologous groups 1–7 were 2, 3, 2, 3, 6, 7 and 6, respectively. A total of 130 markers (SNP and SSR) showed tight linkage to these QTL, and the distances between markers and QTLs ranged from 0.8 to 18.2 cM. Most of these markers are useful candidates for MAS of linked QTL.

For GY, eight additive QTL were detected on seven chromosomes, with five positive alleles on chromosomes 1BS, 5AL, 6AL, 7AL, and 7DS contributed by

Table 1 Details of QTL detected for grain yield and yield components in seven Oklahoma environments from 2001 to 2003

QTL	Env.[a]	Position	Marker interval	Interval distance (cM)	LOD[b]	PVE %[c]	ADD[d]	Associated markers
Grain yield (GY, kg ha^{-1})								
QGy.hwwgr-5AL	ST01	34	*IWA649–IWA7509*	9.6	8.3	24.7	317.9	*IWA649, IWA7509, IWA648, IWA3335*
QGy.hwwgr-7AL	AL03	192	*Xbarc108–IWA6207*	4.4	5.6	21.1	343.1	*Xbarc108, IWA6207, IWA5860, IWA5844, IWA1524, IWA208, IWA6208*
QGy.hwwgr-5AS	AL03	151	*IWA3365–Xgwm154*	1.3	4.4	16.2	−300.4	*Xgwm154, IWA3365, IWA5614*
	AL02	126	*Xbarc180–Xwmc150.3*	2.3	5	14.5	−213.2	*Xbarc180, Xwmc150.3*
QGy.hwwgr-1BS	ST03	23	*Xbarc152–Xgwm339.2*	4.0	4.2	14.3	205	*Xbarc152, Xgwm339.2*
QGy.hwwgr-7DS	ST03	125	*IWA6623–IWA235*	1.3	3.9	12.6	191	*IWA6623, IWA235, IWA5391*
QGy.hwwgr-6AL	AL02	73	*Xbarc3–Xgwm132.1*	13.8	3.8	12.5	198.1	*Xbarc3, Xgwm132.1*
	ST01	59	*IWA731–IWA5075*	1.6	4.5	11.1	209.7	*IWA731, IWA5075, IWA5466, IWA4147, IWA3525, IWA1956, IWA7295*
QGy.hwwgr-4AL	LA03	105	*IWA6035–Xwmc258*	11.4	4.5	11.7	−271.8	*Xwmc258, IWA6035*
QGy.hwwgr-2DS	LA03	36	*Xwmc25.1–Xgwm296.2*	5.5	4.1	10.5	−257	*Xwmc25.1, Xgwm296.2*
Spike number per m^2 (SNPM, = no. m^{-2})								
QSnpm.hwwgr-5DL	ST02	0	*Xgwm212–Xcfd30*	10.7	6.6	21.4	−46.2	*Xgwm212, Xcfd30*
QSnpm.hwwgr-6BL	ST01	94	*Xcfa2110–IWA7628*	4.2	4.6	14.1	29	*Xcfa2110, IWA7628, IWA3460, IWA451, IWA450, IWA5346*
Kernel number per spike (KNPS, no. Spike^{-1})								
QKnps.hwwgr-7AL	ST01	94	*IWA7406–IWA6670*	4.0	8.0	21.9	2.5	*IWA7406, IWA6670, IWA7407*
	ST02	97	*IWA6670–IWA6535*	2.5	8.0	19.9	1.9	*IWA6670, IWA6535, IWA5913, IWA4196, IWA7409*
	ST03	96	*IWA6670–IWA6535*	2.5	6.4	18.2	1.9	*IWA6670, IWA6535, IWA5913, IWA4196, IWA7409*
	LA03	96	*IWA6670–IWA6535*	2.5	3.5	12.9	1.4	*IWA6670, IWA6535, IWA5913, IWA4196, IWA7409*
QKnps.hwwgr-4BS	ST02	49	*Xbarc20–Xwmc48*	0.9	6.3	14.5	−1.6	*Xbarc20, Xwmc48*
	ST03	37	*IWA4662–IWA482*	11.0	4.3	14.0	−1.6	*IWA4662, IWA482*
	AL02	40	*IWA4662–IWA482*	11.0	5.1	12.5	−2.3	*IWA4662, IWA482*
QKnps.hwwgr-3BS	AL02	27	*Xwmc674.1–Xgwm533*	3.5	4.8	11.4	−2.2	*Xwmc674.1, Xgwm533*
QKnps.hwwgr-5AL	ST03	41	*IWA7509–IWA6988*	0.8	3.9	10.3	−1.4	*IWA7509, IWA6988, IWA2642, IWA6082, IWA2645, IWA2641*
	ST01	42	*IWA6988–Xcfa2149.1*	1.3	3.9	9.8	−1.7	*Xcfa2149.1, IWA6988, IWA6082, IWA2645, IWA2641, IWA564*
QKnps.hwwgr-6AL	AL03	59	*IWA731–IWA5075*	1.6	4.1	9.7	2.0	*IWA731, IWA5075, IWA5466, IWA4147, IWA3525, IWA1956, IWA7295*

Table 1 continued

QTL	Env.[a]	Position	Marker interval	Interval distance (cM)	LOD[b]	PVE %[c]	ADD[d]	Associated markers
Thousand kernel weight (TKW, g)								
QTkw.hwwgr-2DL	ST01	16	*IWA5252–Xgwm539*	10.4	11.8	19.2	−1.5	*Xgwm539, IWA5252*
QTkw.hwwgr-2AL	LA03	15	*Xgwm312–IWA6090*	15.2	4.7	15.1	1.2	*Xgwm312, IWA6090, IWA6089, IWA5574, IWA5449, IWA5409, IWA3718, IWA3199, IWA6270*
QTkw.hwwgr-7AL.1	LA03	69	*IWA7325–IWA4626*	7.7	4.4	14.8	−1.2	*IWA7325, IWA4626, IWA4483, IWA4187, IWA7884*
	AL02	95	*IWA7406–IWA6670*	4.0	12.0	13.6	−1.3	*IWA7406, IWA6670, IWA7407*
	ST03	90	*Xgwm332–IWA7406*	7.7	5.0	13.0	−1.2	*Xgwm332, IWA7406, IWA7407*
	ST02	99	*IWA6535–IWA1424*	18.2	4.4	11.1	−1.2	*IWA6535, IWA1424, IWA6261, IWA5852, IWA1726, IWA1725*
	ST01	98	*IWA6670–IWA6535*	2.5	7.7	10.9	−1.2	*IWA6670, IWA6535, IWA5913, IWA4196, IWA7409*
QTkw.hwwgr-4BS	ST02	36	*IWA4662–IWA482*	11.0	4.7	14.4	1.3	*IWA4662, IWA482*
QTkw.hwwgr-6AL.1	LA03	54	*IWA233–IWA5239*	5.8	3.6	11.2	−1.1	*IWA233, IWA5239, IWA5238, IWA1875, IWA1874, IWA1873, IWA1276, IWA1049, IWA1048, IWA902, IWA6311*
QTkw.hwwgr-6AL.2	ST01	93	*IWA2367–IWA7431*	4.4	6.9	9.8	−1.1	*IWA2367, IWA7431*
	AL02	100	*IWA7431–Xwmc807*	3.0	4.8	4.6	−0.7	*Xwmc807, IWA7431*
QTkw.hwwgr-6BL.1	ST03	212	*IWA6140–IWA3268*	1.7	4.1	9.5	−1.0	*IWA6140, IWA3268, IWA5204, IWA5605, IWA5606*
QTkw.hwwgr-7AL.2	ST02	37	*IWA2929–IWA7184*	3.0	3.6	9.4	−1.1	*IWA2929, IWA7184, Xwmc346, IWA2675, IWA1223, IWA865, IWA4594, IWA4595, IWA2905*
	ST01	32	*Xcfa2040–IWA4177*	1.7	4.1	5.4	−0.8	*Xcfa2040, IWA4177, Xcfa2040.2, IWA8057, IWA7728, IWA4434, IWA4363, IWA4176, IWA4173*
QTkw.hwwgr-5AS	ST01	128	*Xgwm293.3–Xwmc96.1*	2.2	4.9	6.5	−0.9	*Xgwm293.3, Xwmc96.1*
QTkw.hwwgr-1BS	AL02	30	*Xgwm339.2–Xbarc185*	3.9	6.2	6.1	0.9	*Xgwm339.2, Xbarc185, Xbarc184*
QTkw.hwwgr-5AL	AL02	41	*IWA7509–IWA6988*	0.8	5.2	4.8	0.8	*IWA7509, IWA6988, IWA2642, IWA6082, IWA2645, IWA2641*
QTkw.hwwgr-6BL.2	AL02	80	*Xcfd47.1–Xbarc216.3*	12.4	4.1	4.5	−0.7	*Xcfd47.1, Xbarc216.3*

Table 1 continued

QTL	Env.[a]	Position	Marker interval	Interval distance (cM)	LOD[b]	PVE %[c]	ADD[d]	Associated markers
QTkw.hwwgr-3DL	AL02	6	*IWA5230–Xgwm383.1*	6.7	4.3	4.2	0.7	*Xgwm383.1, IWA5230*
QTkw.hwwgr-7DS	AL02	0	*Xwmc150–Xgwm121*	2.2	3.9	3.6	0.7	*Xwmc150, Xgwm121*

[a] Environments ST01, ST02, ST03, LA02, LA03, AL02, AL03, phenotype data from Stillwater 2001, Stillwater 2002, Stillwater 2003, Lahoma 2002, Lahoma 2003, Altus 2002, and Altus 2003, respectively

[b] Peak LOD value

[c] Percentage of phenotypic variance explained by the QTL

[d] A positive additive effect indicates that the 'Ning7840' allele increased the phenotypic value, whereas a negative value indicates that the 'Ning7840' allele decreased the phenotypic value

'Ning7840' and three on chromosomes 2DS, 4AL, and 5AS contributed by 'Clark' (Table 1). Among them, *QGy.hwwgr-5AS* from 'Clark' and *QGy.hwwgr-6AL* from 'Ning7840' were significant in two environments, whereas the other QTL were each identified in only one environment. These QTL accounted for 10.5–24.7 % of the phenotypic variation, with LOD values ranging from 3.8 to 8.3. In the interval *IWA649–IWA7509*, *QGy.hwwgr-5AL* had the largest effect on GY, accounting for 24.7 % of the phenotypic variance. *QGy.hwwgr-7AL* was located between *Xbarc108* and *IWA6207* and explained 21.1 % of the phenotypic variation in GY. *QGy.hwwgr-1BS* peaked in the *Xbarc152–Xgwm339.2* interval, accounting for 14.3 % of the variation in GY. *QGy.hwwgr-7DS* peaked in marker interval *IWA6623–IWA235* and explained 12.6 % of the phenotypic variation. *QGy.hwwgr-6AL*, in interval *IWA731–Xgwm132.1*, explained about 12 % of the phenotypic variation in two environments. Among the positive QTL alleles contributed by 'Clark', *QGy.hwwgr-5AS* was mapped between markers *Xbarc180* and *Xgwm154* on chromosome 5A and explained 14.5 and 16.2 % of the phenotypic variation in two environments. *QGy.hwwgr-4AL* was detected in the interval *IWA6035-Xwmc258* on chromosome 4A and explained 11.7 % of the phenotypic variation. *QGy.hwwgr-2DS* was located between loci *Xwmc25.1* and *Xgwm296.2* and explained 10.5 % of the phenotypic variation in one location.

For SNPM, two QTL were detected on chromosomes 5DL in 2001 and 6BL in 2002, at Stillwater. *QSnpm.hwwgr-5DL* peaked in marker interval *Xgwm212–Xcfd30*, with the 'Clark' allele providing increased spikes/m^2. This QTL accounted for 21.4 % of the phenotypic variance. *QSnpm.hwwgr-6BL* was positioned between markers *Xcfa2110* and *IWA7628* with the positive allele from 'Ning7840', and accounted for 14.1 % of the phenotypic variance.

Five QTL were identified for KNPS, with two positive alleles on chromosomes 6AL and 7AL contributed by 'Ning7840' and positive alleles on chromosomes 3BS, 4BS, and 5AL contributed by 'Clark'. *QKnps.hwwgr-7AL* between *IWA7406* and *IWA6535* showed the largest effect on KNPS, accounting for 12.9–21.9 % of the phenotypic variation in four environments (2001–2003 in Stillwater and 2003 in Lahoma). The second QTL, *QKnps.hwwgr-4BS* between *IWA4662* and *Xbarc20*, explained

12.5–14.5 % of the phenotypic variation in three environments. *QKnps.hwwgr-5AL,* in the interval *IWA7509–Xcfa2149.1,* explained 9.8 and 10.3 % of the phenotypic variation in two environments. Two other QTL, *QKnps.hwwgr-3BS* and *QKnps.hwwgr-6AL*, were detected in a single environment and accounted for 11.4 and 9.7 % of phenotypic variation, respectively.

Fourteen additive QTL for TKW were detected on chromosomes 1BS, 2AL, 2DL, 3DL, 4BS, 5AS, 5AL, 6AL, 6BL, 7AL, and 7DS and explained from 3.6 to 19.2 % of the phenotypic variation. 'Clark' contributed the positive alleles at most of the loci (*QTkw.hwwgr-2DL*, *QTkw.hwwgr-5AS*, *QTkw.hwwgr-6AL.1*, *QTkw.hwwgr-6AL.2*, *QTkw.hwwgr-6BL.1*, *QTkw.hwwgr-6BL.2*, *QTkw.hwwgr-7AL.1,* and *QTkw.hwwgr-7AL.2*), with three of them significant in multiple environments. *QTkw.hwwgr-7AL.1* in interval *IWA7325–IWA1424* was identified across five environments and accounted for 10.9–14.8 % of the phenotypic variation. Both *QTkw.hwwgr-6AL.2* and *QTkw.hwwgr-7AL.2* were significant in two environments. *QTkw.hwwgr-6AL.2* located between *IWA2367* and *Xwmc807* explained 4.6 and 9.8 % of the phenotypic variation, and *QTkw.hwwgr-7AL.2* located between *Xcfa2040* and *IWA7184* explained 5.4 and 9.4 % of the phenotypic variance in TKW. *QTkw.hwwgr-2DL* in the interval *IWA5252–Xgwm539* showed the largest effect on TKW, explaining 19.2 % of the phenotypic variation. Six 'Ning7840' alleles, *QTkw.hwwgr-1BS, QTkw.hwwgr-2AL, QTkw.hwwgr-3DL, QTkw.hwwgr-4BS, QTkw.hwwgr-5AL,* and *QTkw.hwwgr-7DS*, also increased TKW, but each one was significant in only one environment and explained from 3.6 to 15.1 % of the phenotypic variance.

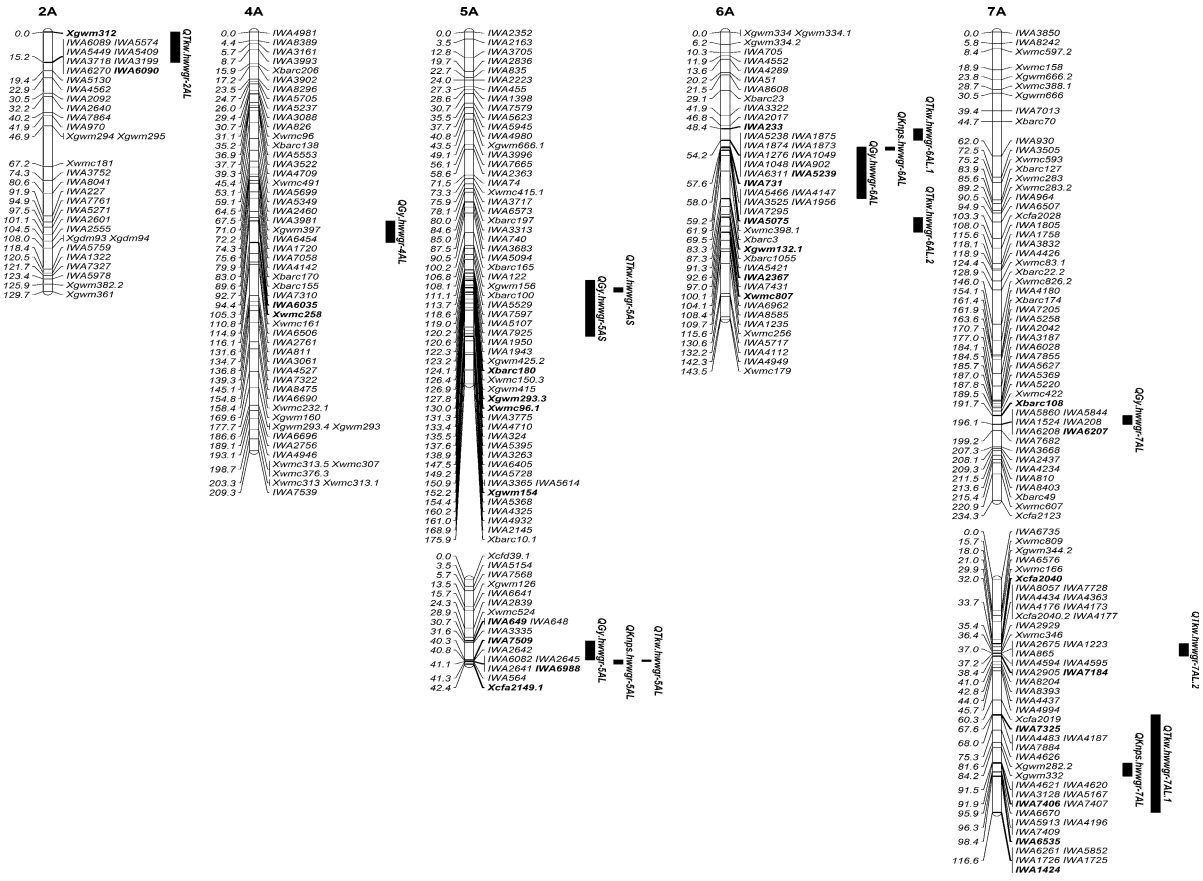

Fig. 1 Additive QTL for wheat yield traits in the 'Ning7840' × 'Clark' RIL population. QTL confidence interval is shown by *bold* marker names as flanking markers and a *vertical bar*

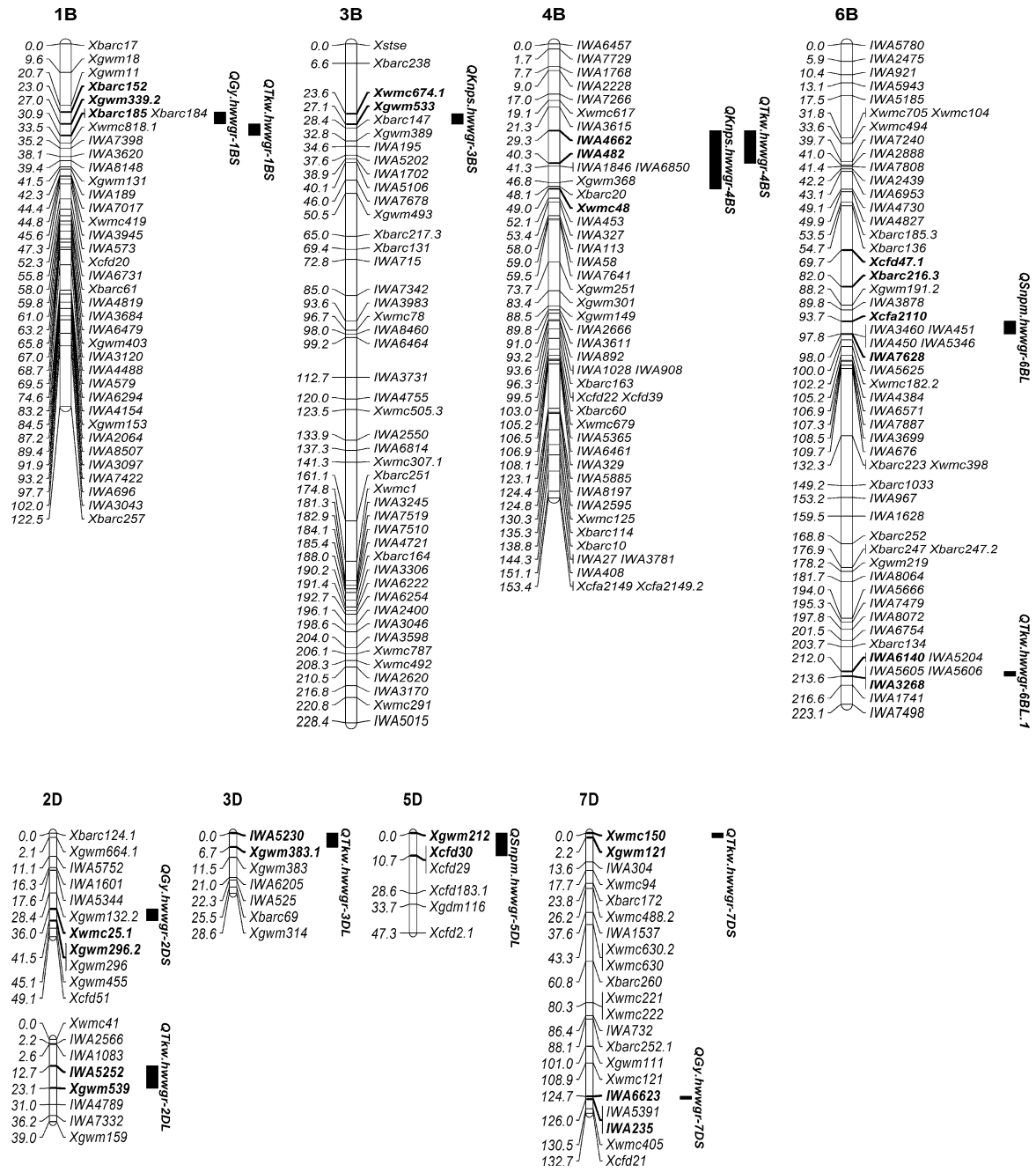

Fig. 1 continued

Epistatic QTL for yield traits

Digenic epistatic QTL were identified using inclusive composite interval mapping. Eight pairs of epistatic QTL were identified for GY, KNPS, and TKW (Table 2). Among these pairs, GY epistatic QTL were identified on 2AL/6DS, 5DL/6DL, 7AS/4AL, and 1BL/5DL. Among them, only *QGy.hwwgr-7AS/4AL* reduced the GY and explained 8.5 % of the phenotypic variance. The other QTL increased GY, accounting for

Table 2 Epistatic QTL for wheat grain yield and yield components

Bi-locus	Env.[a]	Marker interval (QTL1)	Marker interval (QTL2)	LOD[b]	PVE %[c]	AA[d]
GY						
QGy.hwwgr-2AL/6DS	AL03	*Xgwm295–Xwmc181*	*Xwmc416–Xcfd33*	5.1	10.9	288.4
QGy.hwwgr-5DL/6DL	AL03	*Xcfd7–IWA1681*	*Xbarc175–IWA4042*	5.9	10.1	294
QGy.hwwgr-7AS/4AL	ST01	*Xwmc597.2–Xwmc158*	*IWA7322–IWA8475*	6.2	8.5	−231.4
QGy.hwwgr-1BL/5DL	ST01	*IWA6294–IWA4154*	*Xcfd7–IWA1681*	5.2	7.5	216.7
KNPS						
QKnps.hwwgr-1BS/3DL	LA03	*Xgwm18–Xgwm11*	*Xgwm132–Xgwm52*	5.4	10.9	−1.5
QKnps.hwwgr-6BS/7DS	ST01	*IWA5780–IWA2475*	*Xcfd41–Xcfd31*	5.6	10.4	−2.4
TKW						
QTkw.hwwgr-4BS/7BL	ST03	*IWA6457–IWA7729*	*IWA1722–IWA5129*	6.5	4.7	−1.1
QTkw.hwwgr-6BL/1AS	AL02	*IWA4384–IWA6571*	*IWA944–IWA7796*	5.3	1.0	0.7

[a] Environments: ST01, ST02, ST03, LA02, LA03, AL02, and AL03, refer to Stillwater 2001, Stillwater 2002, Stillwater 2003, Lahoma 2002, Lahoma 2003, Altus 2002, and Altus 2003, respectively

[b] LOD score for epistatic QTL

[c] Phenotypic variation explained by epistatic QTL effects

[d] Additive by additive effect of QTL at the two scanning positions. A positive value indicates that the epistatic QTL increased the phenotypic value whereas a negative value indicates the epistatic QTL decreased the phenotypic value

10.9 (*QGy.hwwgr-2AL/6DS*), 10.1 (*QGy.hwwgr-5DL/6DL*), and 7.5 % (*QGy.hwwgr-1BL/5DL*) of the phenotypic variances.

Two pairs of epistatic QTL for KNPS were detected on chromosomes 1BS/3DL and 6BS/7DS. These QTL pairs showed a negative effect on KNPS, accounting for 10.9 (*QKnps.hwwgr-1BS/3DL*) and 10.4 % (*QKnps.hwwgr-6BS/7DS*) of the phenotypic variance.

Two pairs of epistatic QTL on chromosomes 4BS/7BL and 6BL/1AS showed significant effects on TKW. *QTkw.hwwgr-4BS/7BL* had a negative effect on TKW and explained 4.7 % of the phenotypic variance. *QTkw.hwwgr-6BL/1AS* had a positive effect on TKW but accounted for only 1.0 % of the phenotypic variance.

Environmental effects on QTL for yield traits

Evaluation of additive QTL × environment (AE) interactions from multi-environment trials identified four QTL with AE interactions, two for GY and two for KNPS (Table 3). Two GY QTL with AE interactions were detected on chromosomes 5AL and 5AS, explaining 2.4 and 1.0 % of the phenotypic variance, respectively. Two AE QTL exhibited opposite effects on GY, with *QGy.hwwgr-5AL* increasing GY and *QGy.hwwgr-5AS* decreasing GY. Two AE QTL for KNPS were on chromosomes 7AL and 4BS, with increased KNPS for *QKnps.hwwgr-7AL* and decreased KNPS for *QKnps.hwwgr-4BS*. AAE interactions were not found.

Discussion

QTL for wheat yield

We identified 29 additive QTL for GY and its components. These QTL were distributed across 13 chromosomes: 2A, 4A, 5A, 6A, 7A, 1B, 3B, 4B, and 6B 2D, 3D, 5D, and 7D. Most were reported in previous studies (Hyne et al. 1994; Kato et al. 2000; Groos et al. 2003; Marza et al. 2006; Li et al. 2007; Kuchel et al. 2007; Kumar et al. 2007; Kirigwi et al. 2007; Cuthbert et al. 2008; McIntyre et al. 2010; Heidari et al. 2011; Bennett et al. 2012; Mason et al. 2013; Edae et al. 2014). Positive alleles for each trait were dispersed between the two parents, resulting in transgressive segregation in the RIL population, but with relatively small differences between the parents.

Table 3 QTL with additive × environment interactions for grain yield and yield components

b	Position	Marker interval	LOD (A)[a]	LOD (AE)[b]	*P* value	PVE %[c]	AE[d]
QGy.hwwgr-5AL	31	*IWA649–IWA7509*	5.1	6.8	0.009	2.4	94.7
QGy.hwwgr-5AS	126	*Xbarc180–Xwmc150.3*	4.7	4.4	0.03	1.0	−86.8
QKnps.hwwgr-7AL	95	*IWA7406–IWA6670*	11.4	4.2	0.04	2.1	1.1
QKnps.hwwgr-4BS	49	*Xbarc20–Xwmc48*	2.9	4.7	0.03	1.2	−0.6

[a] LOD score for additive effects

[b] LOD score for additive by environment effects

[c] Phenotypic variation explained by additive by environment effects at the current scanning position

[d] Additive × environment effect of QTL × environment interactions at the current scanning positions. A positive value implies that QTL × environment interaction increased the phenotypic value, whereas a negative value implies the QTL × environment interaction decreased the phenotypic value

Both additive (8 QTL) and additive types of epistatic effects (4 QTL pairs) contributed to GY variation among the RILs. GY QTL on chromosome 5A (*QGy.hwwgr-5AL* and *QGy.hwwgr-5AS*) appeared to be environmentally sensitive. Four of the chromosomes, 1BS, 4AL, 5AS, and 7AL, were the same as reported by Marza et al. (2006). *QGy.hwwgr-1BS* may be the same as reported in several previous studies (Huang et al. 2003; Kuchel et al. 2007; Zhang et al. 2010b), and *QGy.hwwgr-4AL* appears to be the QTL that controlled GY under drought conditions mapped by Kirigwi et al. (2007). Among other QTL on chromosomes 5AL, 6AL, 7DS, and 2DS identified in the new map, *QGy.hwwgr-7DS* between *Xwmc121* and *Xwmc405* may be the same as that reported by Groos et al. (2003). *QGy.hwwgr-5AL*, *QGy.hwwgr-6AL*, and *QGy.hwwgr-2DS* were not reported previously.

SNPM was measured only in the ST01 and ST02 experiments. In the previous study Marza et al. (2006) found one QTL on 3BS in a single environment, and the 'Ning7840' allele increased SNPM by 12 %. However, we detected two major QTL on chromosomes 5DL and 6BL in ST02 and ST01, respectively. The favorable *QSnpm.hwwgr-5DL* allele was from 'Clark', whereas the desirable *QSnpm.hwwgr-6BL* allele was from 'Ning7840'. The discrepancy in QTL position between the two maps may be due to changes in marker position between the maps. The earlier map used fewer SSR and AFLP (Marza et al. 2006) whereas the new map contains more SNP and SSR and should be more reliable. That only two QTL for SNPM were detected in single environments indicates that SNPM is not a stable yield component and is vulnerable to environmental variation. Epistatic effects were not detected.

Five additive QTL and two pairs of epistatic QTL for KNPS explained 10 % or more of the phenotypic variance, suggesting that both additive and epistatic effects contributed to KNPS. Among the additive QTL, *QKnps.hwwgr-7AL* and *QKnps.hwwgr-4BS* showed AE interactions that explained a small portion of the phenotypic variance (1.2–2.1 %). Three of the five QTL on chromosomes 3BS, 4BS, and 6AL were the same as reported by Marza et al. (2006). *QKnps.hwwgr-3BS* was near marker *Xgwm389* where spike weight (*QAsw.crc-3B*) and kernel number (*QSns.crc-3B*) QTL were reported previously (Cuthbert et al. 2008). The same QTL regions on 3BS for yield and other agronomic traits were reported in previous studies (Huang et al. 2003; Maccaferri et al. 2008; Bennett et al. 2012). Wang et al. (2009) indicated that this genomic region showed pleiotropic effects on wheat yield-related traits. In addition, a QTL in interval *Xwmc48–IWA4662* on 4BS had a pleiotropic effect on KNPS and TKW. In previous reports, this genetic region was associated with other agronomic traits such as yield, plant height, heading date, kernel weight, average kernel weight per spike, harvest index, SNPM, KNPS, and maturity (Groos et al. 2003; Huang et al. 2003; Cuthbert et al. 2008; Maccaferri et al. 2008; Wang et al. 2009). Therefore, this 4BS chromosome region should be a focus for further intensive study of wheat agronomic traits. In addition, we identified two major and stable QTL on chromosomes 7AL and 5AL in the newly developed

map. *QKnps.hwwgr-7AL* had a highly significant effect on KNPS that explained 12.9–21.9 % of the phenotypic variance in different environments; *QKnps.hwwgr-5AL* was identified in ST03 and ST01, where it accounted for 10.3 and 9.8 % of the phenotypic variance, respectively.

Among 14 QTL identified for TKW, favorable alleles were about equally distributed between the two parents. In addition, two epistatic loci for TKW were identified with relatively minor effects. A major, consistent QTL, *QTkw.hwwgr-7AL.1*, was mapped to the interval *IWA7325–IWA1424*. This is a new QTL showing pleiotropic effects on KNPS and TKW. Ramya et al. (2010) reported one TKW QTL on chromosome 2DL near *Xgwm539*, and another on 4BS near *Xwmc617*, and these QTL were in the same genomic regions as *QTkw.hwwgr-2DL* and *QTkw.hwwgr-4BS*. *QTkw.hwwgr-2DL* in interval *IWA5252–Xgwm539* accounted for the largest proportion of variance to TKW (19.2 %); *QTkw.hwwgr-4BS* was located near *Xwmc617* and explained 14.4 % of the phenotypic variance in TKW.

Co-localization of QTL

It is well known that correlated traits are likely to map to similar locations (Kato et al. 2000). Identifying co-locations of QTL controlling different traits will lead to markers for more effective MAS of correlated traits. Co-localizations of QTL for yield-related traits were reported in other research (Groos et al. 2003; Kirigwi et al. 2007; Kumar et al. 2007; Li et al. 2007; Wang et al. 2009). In the present study, seven QTL on chromosomes 1BS (GY–TKW), 4BS (KNPS–TKW), 5AS (GY–TKW), 5AL (GY–KNPS–TKW), 6AL (GY–KNPS–TKW), 6BL (SNPM–TKW), and 7AL (KNPS–TKW) exhibited pleiotropic effects. Chromosome 5A was previously reported to harbor several genes for different agronomic traits (Miura and Kuroshima 1996; Kato et al. 2000; Börner et al. 2002; Sourdille et al. 2002; Toth et al. 2003; Huang et al. 2004; Marza et al. 2006; Kumar et al. 2007; Cuthbert et al. 2008; Wang et al. 2009; Reif et al. 2011). We identified two QTL on both arms of chromosome 5A. QTL for GY and TKW were both located in interval *Xgwm293.3–Xgwm154* on 5AS with the favorable allele from 'Clark'. QTL for GY, KNPS, and TKW were co-located on 5AL in interval *IWA649–Xcfa2149.1,* with 'Ning7840' contributing the positive allele for GY and TKW, but negative allele for KNPS. These two QTL regions on 5A were coincident with MQTL40, MQTL39, and MQTL42 reported by Zhang et al. (2010b). These results indicated that this QTL for TKW contributed significantly to GY. Another co-located QTL associated with GY, KNPS, and TKW in interval *IWA731–Xwmc807* on 6AL was coincident with previously reported QTL for several wheat traits including GY, test weight, plant height, spikelets per spike, kernel diameter, and spikelet compactness (Huang et al. 2003; Heidari et al. 2011; Kuchel et al. 2007; Kumar et al. 2007). At this QTL, the 'Ning7840' allele conferred increased GY and KNPS but decreased TKW, suggesting that this QTL affected GY in a different way than the QTL on 5AS. Another important yield QTL in interval *IWA7325–IWA1424* on chromosome 7AL affected TKW and KNPS across multiple environments, but with opposite effects on each trait. Two other co-located QTL for GY–TKW and KNPS–TKW were present in marker intervals *Xbarc152–Xbarc185* on chromosome 1BS and *IWA4662–Xwmc48* on 4BS, respectively. The 'Ning7840' allele of QTL on 1BS had positive effects on GY and TKW, but with negative effects on KNPS and TKW on 4BS. We also identified a co-located QTL for SNPM and TKW in *Xcfd47.1–IWA7628* on chromosome 6BL, again with the 'Ning7840' allele conferring opposite effects on the two traits. These results indicated that although some QTL show the widely recognized compensatory relationship of yield components, more specifically, that increasing TKW may lead to decreases in KNPS or SNPM, many other QTL affecting TKW may positively affect, or do not affect, other yield components, thus selecting favorable alleles of these QTL may simultaneously improve TKW and other yield components (Zhang et al. 2012).

Conclusion

A total of 29 additive QTL and eight pairs of epistatic QTL were mapped on 13 chromosomes. Four additive QTL also showed additive × environment (AE) interactions. The most QTL were identified for TKW (8), with the least for SNPM. QTL that were repeatable in multiple environments were identified for all traits except SNPM. Positive alleles for all traits were dispersed between both parents. Seven loci showed

co-localized QTL for at least two traits; however, all co-localized loci affected TKW, and four of them affected GY. Thus, selecting QTL for TKW may spontaneously select for or against other yield components in breeding populations. Because many QTL reported in this study were reported previously in different populations, markers tightly linked to different QTL developed in this study can be used in MAS for these traits.

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