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Mapping quantitative trait loci for plant adaptation and morphology traits in wheat using single nucleotide polymorphisms

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Abstract Wheat (*Triticum aestivum* L.) morphological and adaptation-related traits that are controlled by quantitative trait loci (QTLs) help define potential growing areas of a wheat cultivar. To dissect QTLs for heading date, lodging, shattering (SH), cold tolerance, plant height, spike length, spike compactness, awn length (AL) and chaff color (CC), a high-density genetic map with single nucleotide polymorphism and simple sequence repeat markers were developed using recombinant inbred lines (RILs) derived from 'Ning7840' × 'Clark'. The RILs were evaluated in eight Oklahoma environments from 2001 to 2004. A total of 31 QTLs with additive effects on different traits were mapped on most wheat chromosomes except for 1D, 3A, 3D, 4D, 6D, and 7B. Six chromosome regions showed either tightly linked QTLs or QTLs with pleiotropic effects for two to three traits. Five QTL pairs showed additive × additive effects (AA). Ten additive QTLs were involved in additive × environment (AE) effects, and one epistatic QTL was involved in AAE effects. Among nine traits evaluated only three (SH, AL, and CC) were controlled by single genes in this biparental population. Seven traits were conditioned by multiple QTLs. A total of 127 markers were tightly linked to the QTLs. The findings shed light on the inheritance of wheat morphological and adaptation-related traits and provide DNA markers for manipulating these important traits to improve wheat production.

Keywords *Triticum aestivum* · Adaptation and morphology traits · SNP · Epistasis · QTL × environments interaction

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Introduction

Wheat (*Triticum aestivum* L.) morphological and adaptation-related traits are critical to defining potential growing areas of a wheat cultivar and thus constitute major targets for selection in wheat breeding. These traits are usually controlled by quantitative trait loci (QTLs) and are highly influenced by the production

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environment. QTL analysis has been effectively used to dissect complicated traits into chromosome locations and determine the effects of individual QTL (Båga et al. 2007; Cui et al. 2012; Heidari et al. 2011; Liu et al. 2014; Reif et al. 2011; Sourdille et al. 2002; Verma et al. 2005; Wang et al. 2010, 2009; Zhang et al. 2009). However, most of these QTLs were mapped using low-density maps of simple sequence repeat (SSRs) or other markers. High-density maps may facilitate identification of more closely linked markers to these traits for marker-assisted selection (MAS) in breeding. Single-nucleotide polymorphisms (SNPs) are the most common polymorphism in plant species (Deschamps and Campbell 2010). The availability of high-throughput SNP genotyping platforms makes it possible to develop high-density maps for genetic dissection and MAS of those complex traits (Jannink and Lorenz 2010). To date, a high-density SNP map has not been used to map morphological and adaptation-related traits in wheat.

Many reports on QTL analysis focused only on additive effects of QTLs. However, epistasis between QTLs has been demonstrated to contribute significantly to genetic variance of many important traits (Ma et al. 2005; Rebetzke et al. 2007; Zhang et al. 2008; Reif et al. 2011). In addition, QTL by environment interactions could also affect expression of QTLs (Campbell et al. 2003; Zheng et al. 2010). Therefore, investigating interactions among QTLs, and between QTLs and environments, will provide insight into genetic mechanisms underlying these traits.

In this study, a high-density map was developed using SNP and SSR markers for a RIL population derived from the cross 'Ning7840' × 'Clark', with the overall goal to dissect the QTLs for wheat morphological and adaptation-related traits. Our objectives were to characterize additive and epistatic QTLs, and QTL by environment interactions for plant morphological and adaptation-related traits, and to identify SNP markers tightly linked to the QTLs underlining these traits for eventual MAS in wheat.

Materials and methods

Plant materials and phenotypic data collection

A population of 127 F_{12} recombinant inbred lines (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 high resistance to rust pathogens and *Fusarium graminearum* (Bai et al. 1999). 'Clark' is a soft winter wheat cultivar released from Purdue University, IN, with high yield potential (Ohm et al. 1988).

Phenotypic data were collected from field experiments at three Oklahoma locations, Stillwater (ST), Lahoma (LA), and Altus (AL), in four crop years ending in 2001–2004. The RILs along with the parents were measured for four adaptation traits including heading date (HD), lodging (LD), shattering (SH), and cold tolerance (CT), and five morphological traits including plant height (PH), spike length (SL), spike compactness (SC), awn length (AL), and chaff color (CC). Eight experiments were conducted in various combinations of years and locations, abbreviated here as ST01 to ST04 (Stillwater 2001–2004), LA02 and LA03 (Lahoma 2002 and 2003), 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. The phenotypic data for HD, LD, SH, PH, SL, SC, and CC were collected as previously described (Marza et al. 2006). CT was rated in ST02 using a 1 (tolerant) to 5 (susceptible) scale. AL was estimated at maturity using a 1 (awnless) to 4 (full awn) scale.

DNA extraction and marker analysis

Genomic DNA isolation from both the parents and RILs and PCR for SSR were conducted following previously described protocols (Zhang et al. 2010). PCR fragments were separated by an ABI PRISM 3730 DNA Analyzer (Applied Biosystems, Foster City, CA, USA) and scored using GeneMarker version 1.6 software (Soft Genetics LLC, State College, PA, USA).

SNP genotyping was performed using the Infinium™ iSelect SNP genotyping assay containing 9000 wheat SNPs developed by Illumina Inc. (San Diego, CA, USA). The assay was designed under the protocols of the International Wheat SNP Consortium (Cavanagh et al. 2013). SNP calls were performed using GenomeStudio v2011.1 software (Illumina, San Diego, CA, USA). The genotyping assay was conducted at the USDA Northern Small Grains Genotyping Laboratory in Fargo, ND.

Linkage map construction and QTL identification

A linkage map was constructed using the MAP function in QTL IciMapping 3.2 software (Wang et al. 2012), along with the Kosambi mapping function and a minimum LOD value of 5.0. The linkage map was initially constructed using all polymorphic markers segregating across the population, and then reconstructed following removal of markers less than 1 cM apart. Ordering of markers and assignment of linkage groups to chromosomes were considered in the context of previously published wheat maps (Somers et al. 2004; Cavanagh et al. 2013).

QTL mapping was performed using Inclusive Composite Interval Mapping of Additive (ICIM-ADD) and Epistatic QTL (ICIM-EPI) functions in QTL IciMapping version 3.2 software (Wang et al. 2012). Additive QTL was detected using 1.0 cM steps. Significance tests were conducted at the 0.001 level for stepwise regression. Significant LOD thresholds were determined for each dataset by 1000 permutations using a Type I error set at $P < 0.05$. Epistatic QTL were detected using a scanning step of 5 cM, 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) function. Additive × environment (AE) effects and additive × additive × environment (AAE) effects were identified using ICIM-ADD and ICIM-EPI functions in QTL IciMapping. AE and AAE interactions were detected using 1.0 cM scanning steps, a probability of 0.001 in stepwise regression, and a LOD threshold of 2.5 for claiming QTLs 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

QTLs for plant morphological and adaptation traits

Of the 9000 SNPs screened, 2404 were polymorphic in the 'Ning7840' × 'Clark' population, indicating a high level of polymorphism in this population (26.7 %). These polymorphic SNPs were used to construct an initial map. To select SNPs for final map construction, all markers within 1 cM distances were removed from the initial map. The remaining 594 SNPs and 413 polymorphic SSR markers were used to construct a final map with 998 markers (594 SNPs and 404 SSRs) in 47 linkage groups covering 4225.7 cM across all 21 wheat chromosomes. The final map was used to identify QTLs for plant adaptation and morphological traits.

Thirty-one putative QTLs with additive effects on different traits were distributed across all wheat chromosomes except 1D, 3A, 3D, 4D, 6D, and 7B (Table 1; Fig. 1). Six QTLs on chromosome arms 1BS, 2DS, 4BS, 5DL, 7AL and 7DS showed simultaneous additive effects on two traits, involving LD–CC, SL–SC, SL–PH, PH–CT and HD–CT. One QTL on chromosome arm 5AL showed a simultaneous additive effect on three traits (HD–PH–AL). Among the 31 QTLs, 14 (45.2 %) were located on the A genome, 9 (29.0 %) on the B genome, and 8 (25.8 %) on the D genome. The numbers of additive QTL on homoeologous groups one to seven were 3, 6, 1, 6, 6, 3 and 6, respectively. A total of 127 markers (97 SNPs and 30 SSRs) showed tight linkage to these QTLs (Table 1), and most of them may be useful for MAS of the linked QTLs.

Plant adaptation traits HD, LD, SH and CT were measured in 4, 3, 6 and 1 environments, respectively. Nine QTLs for plant adaptation were identified, but most of them were significant only in one environment (Table 1). Three HD QTLs were detected on chromosomes 5AL, 6BS and 7DS, with the early heading alleles provided by 'Clark'. *QHd.hwwgr-5AL* was located in the marker interval *IWA7509-IWA6988*, and explained 19.2 % of the phenotypic variance for HD. *QHd.hwwgr-6BS* was flanked by markers *IWA4827* and *Xbarc185.3* and accounted for 13.3 % of the phenotypic variance for HD. *QHd.hwwgr-7DS* was positioned between markers *IWA8075* and *Xcfd41* and explained 12.1 % of the phenotypic variance for HD. Three additive QTLs for lodging differences were found on chromosomes 1BS, 2AS, and 4AL with the lodging resistance alleles at *QLd.hwwgr-1BS* and *QLd.hwwgr-4AL* from 'Ning7840', and at *QLd.hwwgr-2AS* from 'Clark'. These three QTLs explained 19.9, 13.0, and 13.3 % of the phenotypic variance, respectively. Only one major QTL was found for SH on chromosome 2DS in two of six environments tested (Table 1). This QTL, namely *QSh.hwwgr-2DS*, explained 19.1 (LA03) and 15.9 % (ST04) of the phenotypic variance and was positioned

in marker interval *Xwmc25.1-Xgwm296.2* on chromosome arm 2DS, with the 'Ning7840' allele conferring shattering tendency. For CT, two QTLs were mapped to marker intervals *Xgwm212-Xcfd30* on chromosome 5DL and *Xbarc184.1-IWA8075* on 7DS, accounting for 34.6 and 12.5 % of the phenotypic variance, respectively (Table 1). The favorable CT allele at *QCt.hwwgr-5DL* was contributed by 'Clark', and that at *QCt.hwwgr-7DS* was from 'Ning7840'.

Plant morphological traits PH, SL, SC, AL and CC were measured in 5, 5, 4, 4 and 2 environments, respectively. Nine PH QTLs were identified on chromosome arms 2BL, 4AL, 4BS, 5AL, 5DL, 6AL and 7DS, and many of them were significant in multiple environments. For example, two major QTLs, *QPh.hwwgr-4BS.1* flanked by markers *IWA4662* and *IWA482* on 4BS and *QPh.hwwgr-5AL* in the interval *IWA649-Xcfa2149.1* on 5AL were detected in four of the five environments tested, with reduced PH alleles contributed by 'Clark'. The two QTLs explained 18.9–30.6 % and 9.9–13.1 % of the phenotypic variance, respectively. Three QTLs on 5DL (*QPh.hwwgr-5DL*), 6AL (*QPh.hwwgr-6AL.1*) and 7DS (*QPh.hwwgr-7DS*) were detected in two environments (ST02 and LA02). For *QPh.hwwgr-5DL* and *QPh.hwwgr-6AL.1*, 'Ning7840' contributed reduced PH alleles, with 6.9 % (ST02) and 17.5 % (LA02) of the phenotypic variance explained by *QPh.hwwgr-5DL* and 8.7 % (ST02) and 5.1 % (LA02) of the phenotypic variance explained by *QPh.hwwgr-6AL.1*. *QPh.hwwgr-7DS* explained 6.8 and 7.6 % of the phenotypic variance at the ST02 and LA02 environments, respectively, with 'Clark' contributing the reduced PH allele. Another four QTLs, *QPh.hwwgr-4BS.2*, *QPh.hwwgr-2BL*, *QPh.hwwgr-6AL.2*, and *QPh.hwwgr-4AL*, were detected only in single environments and explained 7.3–11.7 % of the phenotypic variance.

Nine SL QTLs were detected on chromosome arms 1AL, 2AS, 2DS, 3BS, 4AL, 4BS, 5BS, and 7AL. Among them, *QSl.hwwgr-2DS* was detected consistently across three of five environments and had the most effect on wheat spike morphology. This QTL was positioned between markers *IWA5344* and *Xgwm132.2* on chromosome arm 2DS, with the long-spike allele from 'Clark' explaining 7.5–19.1 % of the phenotypic variance among three environments. *QSl.hwwgr-7AL.1* and *QSl.hwwgr-5BS* were detected in two environments. *QSl.hwwgr-7AL.1* was located in the marker interval *Xgwm282.2-IWA7406*, and explained 9.1 and 16.9 % of the phenotypic variance, respectively, with the long-spike allele contributed by 'Clark'. *QSl.hwwgr-5BS* was located between *Xbarc15* and *Xbarc4*, and accounted for 12.3 and 9.9 % of the phenotypic variance, with 'Ning7840' contributing the long-spike allele. Another six SL QTLs, *QSl.hwwgr-1AL*, *QSl.hwwgr-2AS*, *QSl.hwwgr-3BS*, *QSl.hwwgr-4AL*, *QSl.hwwgr-4BS*, and *QSl.hwwgr-7AL.2*, were significant in single environments and explained 7.1–17.0 % of the phenotypic variation. Two SC QTLs on chromosomes 2DS and 7AL were significant and explained 16.9 and 17.6 % of phenotypic variance with all compact-spike alleles contributed by 'Ning7840'. One major QTL for AL, *QAl.hwwgr-5AL*, identified on chromosome 5AL in all environments evaluated (ST01-ST04), was flanked by markers *IWA7509* and *Xcfa2149.1*, separated by about 2.1 cM, and explained 49.6–99.3 % of the phenotypic variance in different environments. The allele from 'Ning7840' conferred awn presence. Similarly, a single major QTL for CC was detected on chromosome 1BS across both environments CC was recorded. This QTL, namely *QCc.hwwgr-1BS*, was located between loci *Xwmc818.1* and *IWA7398,* and explained 90.0 % of the phenotypic variance in both environments, with the bronze glume allele coming from 'Clark'.

Epistatic effects for plant morphological and adaptation traits

Five digenic epistatic QTLs for plant adaptation and morphological traits were detected on wheat chromosomes 1AL/1DL for HD, 5BS/7BL, 5DS/7DL and 7BL/1DL for PH, and 7AL/6DL for SC (Table 2). *QHd.hwwgr-1AL/1DL* explained 9.9 % of the phenotypic variance in HD. Among the three pairs of epistatic loci associated with PH, *QPh.hwwgr-5BS/7BL* and *QPh.hwwgr-5DS/7DL* accounted for 2.3 and 2.5 % of the phenotypic variance, whereas *QPh.hwwgr-7BL/1DL* explained 1.8 % of the phenotypic variance. *QSc.hwwgr-7AL/6DL* explained 14.9 % of the phenotypic variance in SC.

Table 1 Chromosome location, marker interval, interval distance, associated markers, LOD value and phenotypic variance explained by and additive effect of QTL, and additive × environment effect detected for plant adaptation and morphologic traits in Oklahoma from 2001 to 2004

QTL	Environment	QTL position (cM)	Marker interval	Interval (cM)	LOD[a]	PVE %[b]	ADD[c]	Linked markers	AE[d]	Common QTL reported previously[e]
Plant adaptation traits										
Heading date (HD)										
QHd.hwwgr-5AL	LA02	41	*IWA7509-IWA6988*	0.8	5.9	19.2	1.5	*IWA7509, IWA2642, IWA6082, IWA2645, IWA2641, IWA6988*	–	Reif et al. (2011)
QHd.hwwgr-6BS	ST03	50	*IWA4827-Xbarc185.3*	3.5	3.5	13.3	0.9	*IWA4827, IWA7979, IWA7896, IWA7625, IWA7452, IWA7198, IWA5043, IWA5042, IWA4826, IWA4825, IWA4824, IWA4823, IWA3677, IWA2420, IWA2419, IWA2417, IWA1662, IWA1655, IWA7974, Xbarc185.3*	–	Marza et al. (2006)
QHd.hwwgr-7DS	ST02	20	*IWA8075-Xcfd41*	15.6	3.8	12.1	1.0	*IWA8075, Xcfd41*	–	–
Lodging (LD)										
QLd.hwwgr-1BS	ST02	33	*Xbarc184-Xwmc818.1*	2.6	7.3	19.9	−0.4	*Xbarc184, Xwmc818.1*	4.15	Keller et al. (1999) Marza et al. (2006)
QLd.hwwgr-2AS	ST02	16	*IWA2797-IWA3520*	1.3	5.0	13.3	0.3	*IWA2797, IWA2798, IWA6384, IWA3520*	–	Keller et al. (1999)
QLd.hwwgr-4AL	LA03	72	*Xgwm397-IWA6454*	1.2	4.0	13.0	−0.3	*Xgwm397, IWA6454*	–	Marza et al. (2006)
Shattering (SH)										
QSh.hwwgr-2DS	LA03	36	*Xwmc25.1-Xgwm296.2*	5.5	5.1	19.1	0.3	*Xwmc25.1, Xgwm296.2*	1.09	–
	ST04	36	*Xwmc25.1-Xgwm296.2*	5.5	4.9	15.9	0.4	*Xwmc25.1, Xgwm296.2*		
Cold tolerance (CT)										
QCt.hwwgr-5DL	ST02	0	*Xgwm212-Xcfd30*	10.7	14.4	34.6	0.6	*Xgwm212, Xcfd29, Xcfd30*	–	–
QCt.hwwgr-7DS	ST02	19	*Xbarc184.1-IWA8075*	2.6	6.1	12.5	−0.4	*Xbarc184.1, IWA8075*	–	–

Table 1 continued

QTL	Environment	QTL position (cM)	Marker interval	Interval (cM)	LOD[a]	PVE %[b]	ADD[c]	Linked markers	AE[d]	Common QTL reported previously[e]
Plant morphology traits										
Plant height (PH)										
QPh.hwwgr-4BS.1	ST01	40	*IWA4662-IWA482*	11.0	9.0	19.5	3.0	*IWA4662, IWA482*	2.54	Marza et al. (2006)
										Zhang et al. (2008)
	ST02	40	*IWA4662-IWA482*	11.0	10.4	18.9	3.0	*IWA4662, IWA482*		Mao et al. (2010)
	LA02	40	*IWA4662-IWA482*	11.0	20.6	36.0	5.4	*IWA4662, IWA482*		–
	ST03	37	*IWA4662-IWA482*	11.0	5.9	21.7	3.3	*IWA4662, IWA482*		
QPh.hwwgr-5DL	ST02	0	*Xgwm212-Xcfd30*	10.7	4.4	6.9	−1.8	*Xgwm212, Xcfd29, Xcfd30*	2.98	Cui et al. (2011)
	LA02	0	*Xgwm212-Xcfd30*	10.7	12.0	17.5	−3.8	*Xgwm212, Xcfd29, Xcfd30*		
QPh.hwwgr-5AL	ST01	40	*IWA649-IWA7509*	9.6	6.4	13.1	2.5	*IWA649, IWA648, IWA3335, IWA7509*	0.97	Cui et al. (2011)
	ST02	40	*IWA649-IWA7509*	9.6	6.7	11.3	2.3	*IWA649, IWA648, IWA3335, IWA7509*		
	LA02	42	*IWA6988-Xcfa2149.1*	1.3	7.3	9.9	2.8	*IWA6988, IWA6082, IWA2645, IWA2641, Xsp564, Xcfa2149.1*		
	ST03	41	*IWA7509-IWA6988*	0.8	4.0	11.7	2.4	*IWA7509, IWA2642, IWA6082, IWA2645, IWA2641, IWA6988*		
QPh.hwwgr-6AL.1	ST02	88	*Xbarc1055-IWA5421*	4.0	5.2	8.7	−2.0	*Xbarc1055, IWA4370, IWA3782, IWA1285, IWA5421*	–	Marza et al. (2006)
										Mao et al. (2010)
	LA02	89	*Xbarc1055-IWA5421*	4.0	3.8	5.1	−2.0	*Xbarc1055, IWA4370, IWA3782, IWA1285, IWA5421*		
QPh.hwwgr-7DS	ST02	13	*IWA5971-IWA4131*	0.8	4.3	6.8	1.8	*IWA5971, Xwmc646, IWA8096, IWA5972, IWA906, IWA827, IWA3750, IWA3746, IWA4131, IWA4133, IWA3749, IWA3745, IWA3744, IWA7039, IWA4131*	1.63	–
	LA02	13	*IWA5971-IWA4131*	0.8	5.8	7.6	2.5	*IWA5971, Xwmc646, IWA8096, IWA5972, IWA906, IWA827, IWA3750, IWA3746, IWA4131, IWA4133, IWA3749, IWA3745, IWA3744, IWA7039, IWA4131*		

Table 1 continued

QTL	Environment	QTL position (cM)	Marker interval	Interval (cM)	LOD[a]	PVE %[b]	ADD[c]	Linked markers	AE[d]	Common QTL reported previously[e]
QPh.hwwgr-4BS.2	LA02	52	*Xwmc48-IWA453*	3.1	8.6	11.7	−3.0	*Xwmc48, IWA453*	2.64	Marza et al. (2006), Zhang et al. (2008), Mao et al. (2010), –
QPh.hwwgr-2BL	ST01	129	*Xwmc441-IWA6453*	5.1	4.5	9.3	−2.1	*Xwmc441, IWA6453*	–	–
QPh.hwwgr-6AL.2	ST01	17	*Xgwm427-Xwmc580*	1.7	3.7	7.3	1.8	*Xgwm427, Xwmc580*	–	Mao et al. (2010)
QPh.hwwgr-4AL	LA02	118	*IWA2761-IWA811*	14.5	4.6	6.8	−2.3	*IWA2761, IWA811*	1.14	–
Spike length (SL)										
QSl.hwwgr-2DS	ST01	23	*IWA5344-Xgwm132.2*	10.8	7.5	19.1	−0.4	*IWA5344, IWA4354, IWA1107, IWA965, Xgwm132.2*	–	Heidari et al. (2011)
	ST03	26	*IWA5344-Xgwm132.2*	10.8	3.7	7.5	−0.2	*IWA5344, IWA4354, IWA1107, IWA965, Xgwm132.2*		
	LA03	25	*IWA5344-Xgwm132.2*	10.8	3.7	16.9	−0.3	*IWA5344, IWA4354, IWA1107, IWA965, Xgwm132.2*		
QSl.hwwgr-7AL.1	ST01	89	*Xgwm332-IWA7406*	7.7	3.9	9.1	−0.3	*Xgwm332, IWA4621, IWA4620, IWA3128, IWA5167, IWA7407, IWA7406*	–	Patil et al. (2013)
	ST03	83	*Xgwm282.2-Xgwm332*	2.6	8.6	16.9	−0.4	*Xgwm282.2, Xgwm332*		
QSl.hwwgr-5BS	ST01	19	*Xcfd45-Xbarc4*	5.3	5.8	12.3	0.3	*Xcfd45, Xbarc4*	–	Marza et al. (2006)
	ST02	16	*Xbarc15-Xcfd45*	5.1	3.7	9.9	0.3	*Xbarc15, Xcfd45*		
QSl.hwwgr-4BS	ST02	49	*Xbarc20-Xwmc48*	0.9	6.4	17.0	−0.4	*Xbarc20, Xwmc48*	–	Marza et al. (2006)
QSl.hwwgr-2AS	AL02	17	*IWA2907-Xgwm71*	7.7	4.8	14.8	0.3	*IWA2907, Xgwm71*	–	–
QSl.hwwgr-4AL	ST03	37	*IWA5553-IWA3522*	0.8	6.8	12.6	0.3	*IWA5553, IWA3826, IWA1327, IWA4876, IWA6103, IWA5335, IWA3877, IWA3324, IWA3118, IWA2699, IWA6443, IWA3522*	–	–
QSl.hwwgr-3BS	ST01	55	*Xgwm493-Xbarc217.3*	14.5	4.0	10.7	−0.3	*Xgwm493, Xbrc217.3*	–	–
QSl.hwwgr-1AL	ST03	30	*Xcfa2129-IWA4511*	7.9	4.9	9.3	−0.3	*Xcfa2129, IWA2540, IWA931, IWA605, IWA4511*	–	–

Table 1 continued

QTL	Environment	QTL position (cM)	Marker interval	Interval (cM)	LOD[a]	PVE %[b]	ADD[c]	Linked markers	AE[d]	Common QTL reported previously[e]
QSl.hwwgr-7AL.2	ST03	185	*IWA7855-IWA5627*	1.2	4.1	7.1	−0.2	*IWA7855, IWA5887, IWA3616, IWA6124, IWA4482, IWA2497, IWA7590, IWA5627*	–	Marza et al. (2006)
Spike compactness (SC)										
QSc.hwwgr-2DS	ST01	27	*IWA5344-Xgwm132.2*	10.8	7.1	16.9	−0.3	*IWA5344, IWA4354, IWA1107, IWA965, Xgwm132.2*	–	–
QSc.hwwgr-7AL	ST04	82	*Xgwm282.2-Xgwm332*	2.6	4.8	17.6	−0.3	*Xgwm282.2, Xgwm332*	–	–
Awn length (AL)										
QAl.hwwgr-5AL	ST01	42	*IWA6988-Xcfa2149.1*	1.3	131.3	99.3	1.5	*IWA6988, IWA6082, IWA2645, IWA2641, IWA564, Xcfa2149.1*	4.68	Torada et al. (2006)
	ST02	42	*IWA6988-Xcfa2149.1*	1.3	112.4	98.6	1.5	*IWA6988, IWA6082, IWA2645, IWA2641, IWA564, Xcfa2149.1*		
	ST03	41	*IWA7509-IWA6988*	0.8	75.3	49.6	0.7	*IWA7509, IWA2642, IWA6082, IWA2645, IWA2641, IWA6988*		
	ST04	42	*IWA6988-Xcfa2149.1*	1.3	51.8	92.3	1.2	*IWA6988, IWA6082, IWA2645, IWA2641, IWA564, Xcfa2149.1*		
Chaff color (CC)										
QCc.hwwgr-1BS	ST01	35	*Xwmc818.1-IWA7398*	1.7	62.2	90.0	0.9	*Xwmc818.1, IWA3123, IWA7398*	0.71	–
	ST04	35	*Xwmc818.1-IWA7398*	1.7	48.7	89.4	0.9	*Xwmc818.1, IWA3123, IWA7398*		

[a] LOD value at the center of the additive QTL

[b] Phenotypic variance explained by the additive QTL

[c] Additive effect; a positive value implies alleles for late HD, susceptible to lodging, shattering, and cold, increasing PH or SL, non-compact spike, long awn, light chaff color contributed by 'Ning7840', whereas a negative value indicates the alleles from 'Clark'

[d] Phenotypic variance explained by the additive QTL × environment interaction. '−' indicates no additive × environment effect

[e] Previously reported in the same chromosome region; '−' indicates that the QTL was not reported previously

Interactions between QTLs and environments

Ten QTLs with AE interactions and one pair of QTLs with an AAE interaction were identified for PH, LD, SH, AL, CC and HD (Table 1, Table 2). AE interactions for six PH QTLs (*QPh.hwwgr-4AL*, *QPh.hwwgr-4BS.1*, *QPh.hwwgr-4BS.2*, *QPh.hwwgr-5AL*, *QPh.hwwgr-5DL*, and *QPh.hwwgr-7DS*) explained 0.97–2.98 % of the phenotypic variance. Another four QTLs, *QLd.hwwgr-1BS*, *QSh.hwwgr-2DS*, *QAl.hwwgr-5AL*, and *QCc.hwwgr-1BS* showed AE interactions that accounted for 4.15, 1.09, 4.68, and 0.71 % of the phenotypic variance, respectively (Table 1). The QTL pair, *QHd.hwwgr-1AL/1DL*, was involved in an AAE interaction, and explained 1.27 % of the phenotypic variance in HD (Table 2).

Discussion

Using the high-density map constructed by combining SNP and SSR markers, we identified 31 QTLs for adaptation and morphological traits at 23 locations across 15 chromosomes (Fig. 1). Previously, Marza et al. (2006) mapped 35 additive QTLs for these adaptation and morphological traits using the same population. Because the previous map for QTL analysis was constructed using 363 AFLP and 47 SSR markers with much lower genome coverage, the resulting QTLs for the same trait differed in number and chromosome location between the two studies. In this study, we scored 2404 SNPs and 413 SSRs in the RIL population and selected 594 evenly distributed SNPs and all the SSRs for mapping. The resulting map has significantly improved map density and genome coverage. The new map provided new QTLs with closer markers. In addition, we identified five pairs of epistatic QTLs for HD, PH, and SC, and one epistatic QTL pair involved in genotype-environment interaction.

HD showed additive main effects, but also bi-locus interactions of additive effects, indicating that HD is a complex trait influenced by epistasis and GE interactions. Only the epistatic QTL pair, *QHd.hwwgr-1AL/1DL*, which explained 9.9 % of the variation in HD, was involved in GE interactions in this study. Nonetheless, additive gene action was still the major genetic component controlling HD. Three additive QTLs (*QHd.hwwgr-5AL, QHd.hwwgr-6BS* and *QHd.hwwgr-7DS*) showed major effects on HD with earlier heading alleles contributed by 'Clark'. Reif et al. (2011) used association mapping to identify two QTLs for HD on chromosomes 5AL and 7DS. Based on the locations of markers closely linked to the QTLs in both studies, the two QTLs identified in Reif et al. (2011) are most likely the same as *QHd.hwwgr-5AL* and *QHd.hwwgr-7DS* identified in this study. However, *QHd.hwwgr-5AL* is close to vernalization locus *Vrn-A1*, suggesting that a *Vrn-A1* allele was responsible for early HD in 'Clark'. *QHd.hwwgr-7DS* was found in the same chromosome region as *QCt.hwwgr-7DS* for CT. These two QTLs are most likely closely linked or identical, and might have pleiotropic effects on CT and HD. The 'Clark' allele conferred earlier heading with lower CT than 'Ning7840'. *QHd.hwwgr-6BS* was reported in Marza et al. (2006) but not in other studies.

LD can strongly affect both wheat grain yield and quality especially where high yield is expected. Previous research has shown that LD is controlled by several genes with some of them showing major effects (Keller et al. 1999). Berry and Berry (2015) suggested that LD was affected by wide genetic variation in lodging-associated traits, including PH, components of stem strength, components of anchorage strength, ear area and shoot number per plant. In this study, three major additive QTLs, *QLd.hwwgr-1BS*, *QLd.hwwgr-2AS*, and *QLd.hwwgr-4AL*, were found. Two of them, *QLd.hwwgr-4AL* and *QLd.hwwgr-1BS* with the lodging-sensitive alleles from 'Clark', were also reported by Marza et al. (2006). *QLd.hwwgr-1BS* coincided with QTLs for grain yield and thousand-kernel weight found in the same population and alleles from 'Clark' increased grain yield and thousand-kernel weight (Li et al. 2015). Furthermore, in the present study, *QLd.hwwgr-1BS* also coincided with a QTL (*QCc.hwwgr-1BS*) for CC. *QLd.hwwgr-1BS* also showed a minor AE effect and is most likely the same QTL reported by Keller et al. (1999), because both reside near marker *Xgwm18*. Keller et al. (1999) also reported that the QTL on 1BS coincided with QTLs for PH, culm stiffness and leaf width. These results indicated that LD gene expression was not only correlated with the genetic control of lodging-associated traits but also influenced by the environment.

PH determines plant architecture and influences grain yield. Many genes or QTLs controlling PH have

been mapped. In this study, nine QTLs for PH were identified on chromosomes 2BL, 4AL, 4BS, 5AL, 5DL, 6AL and 7DS. Both parents contributed alleles for reduced PH about equally. Using QTL meta-analysis Mao et al. (2010) identified chromosome arms 4BS and 6AL as harboring two meta-QTLs for PH, also identified in this study. The two QTLs on 4BS, *QPh.hwwgr-4BS.1* and *QPh.hwwgr-4BS.*2, with PH-reducing alleles from different parents, were located between loci *IWA4662* and *IWA453* spanning about 23 cM apart (Table 1), where PH-associated QTLs were positioned in previous reports (Marza et al. 2006; Zhang et al. 2008; Griffiths et al.). *QPh.hwwgr-4BS.1* was the QTL with the largest effect on PH ($R^2 = 36$) in all three locations and was coincident with the widely used wheat semi-dwarf gene *Rht1*. *QPh.hwwgr-4BS.2* co-located with *QSl.hwwgr-4BS*, with the taller plant and longer-spike alleles coming from 'Clark'. Cui et al. (2011) detected PH QTLs on chromosomes 5AL and 5DL near markers *Xwmc524* and *Xbarc320,* respectively. These are most likely in the same chromosome regions as *QPh.hwwgr-5AL* and *QPh.hwwgr-5DL* identified in this study. These QTLs were not reported in Marza et al. (2006). *QPh.hwwgr-5DL* was closely linked to *QCt.hwwgr-5DL*, with 'Clark' contributing the taller allele and greater CT. *QPh.hwwgr-7DS* was detected in two environments, and 'Ning7840' contributed the taller allele. This QTL was not reported previously. Additionally, three pairs of epistatic QTLs for PH were identified, and six additive QTLs, namely *QPh.hwwgr-4AL*, *QPh.hwwgr-4BS.1*, *QPh.hwwgr-4BS.2*, *QPh.hwwgr-5AL*, *QPh.hwwgr-5DL*, and *QPh.hwwgr-7DS*, were involved in AE interactions. PH proved to be a complex trait in this biparental population, with additive, epistatic, and environmental effects and pleiotropism with other traits.

SH of the mature wheat spike can cause severe yield losses. Porter (1959) reported that shattering resistance was controlled by two major genes, together with a number of minor genes or polygenes depending on different genotypes. Marza et al. (2006) identified six SH QTLs on chromosomes 4B, 5A, 6A, 6B and 7D in the 'Ning7840' × 'Clark' population, indicating complex inheritance of SH. Using the same population but a different linkage map, only the SH QTL, *QSh.hwwgr-2DS*, was detected in two (LA03 and ST04) of six environments tested. This QTL was not detected by Marza et al. (2006). The inconsistency between the two studies might be explained by the use of different linkage maps and different LOD scores for declaration of QTLs. Zhang et al. (2009) identified four genomic regions on chromosomes 2B, 3B, and 7A that were associated with SH. These studies further indicated that SH was a complex quantitative trait and controlled by major and minor QTLs and affected by the environment.

Fig. 1 Additive QTLs for plant adaptation and morphology traits in the 'Ning7840' × 'Clark' RIL population. QTL confidence intervals are indicated by vertical bars and bold script ▶

CT is an important economic trait in winter wheat (*Triticum aestivum* L.) that determines the plant's ability to survive harsh winter conditions. Båga et al. (2007) suggested that essential elements of the CT mechanism are associated with winter growth habit controlled by vernalization loci on group 5 chromosomes. They identified a 5A QTL at 46 cM proximal to vernalization locus *Vrn-A1,* explaining 40 % of the CT variance. In our study, *QCt.hwwgr-5DL* flanked by markers *Xgwm212* and *Xcfd30* was detected on chromosome 5DL. The 'Clark' allele explained 34.6 % of the variation in CT. This QTL was about 50 cM proximal to the *Vrn-D4* locus, which is present in the centromeric region (Yoshida et al. 2010). Thus group 5 chromosomes are important in vernalization response and CT. Another CT QTL, *QCt.hwwgr-7DS*, was mapped to a 2.6 cM interval between markers *Xbarc184.1* and *IWA8075* on chromosome 7DS. The CT allele at this locus was from 'Ning7840'. This QTL co-located with QTL-*QHd.hwwgr-7DS* for HD, with the late-heading allele contributed by 'Ning7840'. These results suggest that both parents contributed CT QTLs in the RIL population, but the 'Clark' QTL showed a larger effect. The QTL for CT in 'Ning7840' is likely due to the pleiotropic effect of *QHd.hwwgr-7DS*, which delayed the transition from the vegetative to reproductive growth stages and a possible escape mechanism from cold damage.

SL was conditioned by additive QTLs only, with no significant interactions between QTLs or between QTLs and environments. Among nine additive QTLs, *QSl.hwwgr-2DS* consistently showed the largest effect in three environments at two locations, with 'Clark' contributing the allele for longer spikes. This QTL might be the same as the one reported by Heidari et al.


1A
2AS
4A
5A
6A
7A
1B
2B
3B
4B
5B
6B
2D
5D
7D
QSl.hwwgr-1AL
QLd.hwwgr-2AS
QSl.hwwgr-2AS
QSl.hwwgr-4AL
QLd.hwwgr-4AL
QPh.hwwgr-4AL
QAl.hwwgr-5AL
QHd.hwwgr-5AL
QPh.hwwgr-6AL.1
QPh.hwwgr-6AL.2
QSl.hwwgr-7AL.2
QSc.hwwgr-7AL
QSl.hwwgr-7AL.1
QLd.hwwgr-1BS
QCc.hwwgr-1BS
QPh.hwwgr-2BL
QSl.hwwgr-3BS
QPh.hwwgr-4BS.1
QSl.hwwgr-4BS
QSl.hwwgr-5BS
QHd.hwwgr-6BS
QSl.hwwgr-2DS
QSc.hwwgr-2DS
QSh.hwwgr-2DS
QCt.hwwgr-5DL
QPh.hwwgr-5DL
QHd.hwwgr-7DS
QCt.hwwgr-7DS
QPh.hwwgr-7DS

Table 2 Marker intervals, LOD values, phenotypic variance attributable to additive × addtive effects of epistatic QTL, and additive × additive × environment effect detected for plant adaptation and morphology traits in three Oklahoma locations from 2001–2004

Epistasis	Environment	Marker interval (Ch1)	Marker interval (Ch2)	LOD[a]	PVE(%)[b]	AA[c]	AAE[d]
HD							
QHd.hwwgr-1AL/1DL	LA02	*IWA3434-IWA135*	*Xgdm126-Xbarc66*	5.2	9.9	−1.2	1.27
PH							
QPh.hwwgr-5DS/7DL	LA02	*Xcfa2104-Xgwm190*	*Xwmc634-Xgwm428*	5.3	2.5	−2.4	–
QPh.hwwgr-5BS/7BL	LA02	*Xgwm443-IWA4790*	*Xwmc232-Xbarc63*	5.1	2.3	−2.3	–
QPh.hwwgr-7BL/1DL	LA02	*IWA5001-Xgwm611*	*IWA342-IWA7154*	5.2	1.8	2.0	–
SC							
QSc.hwwgr-7AL/6DL	ST04	*IWA6535-IWA1424*	*IWA619-IWA7816*	5.2	14.9	−0.3	–

[a] LOD score for epistatic effects

[b] Phenotypic variance explained by epistatic QTLs

[c] Epistatic effect between two loci; a negative number indicates decreased trait value; a positive number indicates increased trait value

[d] Phenotypic variance explained by the epistatic QTL × environment interaction. '–' indicates no additive × additive × environment effect

(2011), and was not reported by Marza et al. (2006). The second major QTL is *QSl.hwwgr-7AL.1*, again with the long-spike allele contributed by 'Clark'. This QTL was detected at ST in two of the three years tested, but was not detected in Marza et al. (2006). It is most likely the same QTL (*QSl.macs-7A*) as reported by Patil et al. (2013) in durum, because both were tightly linked to the marker *Xgwm282*. The third QTL, *QSl.hwwgr-5BS*, was detected in ST01 and ST02 and 'Ning7840' contributed increased SL at this locus. Marza et al. (2006) also detected this QTL.

SC usually correlates with SL. Generally more compact spikes are shorter. In our study, two additive QTLs for SC were detected on chromosomes 2DS (*QSc.hwwgr-2DS*) and 7AL (*QSc.hwwgr-7AL*). As expected, they co-located with *QSl.hwwgr-2DS* and *QSl.hwwgr-7AL.1,* with 'Ning7840' contributing the more compact and shorter-spike alleles. In addition, one pair of epistatic additive QTLs involved chromosomes 7AL and 6DL. The epistatic QTL showed the largest effect ($R^2 = 14.9$ %) among the identified AA epistatic QTLs for all traits in this study. The results also confirm that QTLs for SC usually have a pleiotropic effects on SL, but some QTLs for SL may be independent of SC. Therefore it should be still possible to breed wheat varieties with long but more compact spikes as one way of increasing yield via a greater number of kernels per spike.

In wheat, awns may contribute up to 40 % of the photosynthetic assimilates accumulated in the grain (Peleg et al. 2010). The genetic control of this trait was generally found to be simple, and three genes (*hd*, *b1* and *b2*) are involved in the differences between awned and awnless varieties. Accordingly, three dominant inhibitors *Hd*, *B1* and *B2* are respectively located on chromosomes 4AS, 5AL and 6BL. Wheat genotypes carrying the three recessive alleles are fully awned whereas those with either *HdB2* or *B1B2* are awnless (Sourdille et al. 2002). In this study, 'Ning7840' produced long awns (score: 4) and 'Clark' was apically awnletted (score: 1). In the RIL population, the segregation ratio between long and short awns was about 1 to 1, and fitted a single gene segregation ratio. A single QTL, *QAl.hwwgr-5AL,* mapped to chromosome arm 5AS in all four environments (ST01-ST04) tested for this trait, was positioned distally to *Xwmc524* on 5AS, and was flanked by markers *IWA7509* and *Xcfa2149.1* spanning about 2.1 cM. *Xwmc524* is very close to *Xgwm291* (Somers et al. 2004), which is closely linked to the B1 awn inhibitor locus on 5AL (Torada et al. 2006; Kosuge et al. 2008; Yu et al. 2014). 'Clark' contributed the apically awnletted allele. Six other SNP markers were also mapped into the same QTL region. *QAl.hwwgr-5AL* was also closely linked to HD and PH, with 'Clark' contributing alleles for decreased PH and early HD.

Based on the preponderance of evidence from this and similar studies, and the presence of consistent and strong additive gene effects, certain QTLs constitute reasonable targets for breeding for improved adaptation in the southern plains of the USA. High priority might be placed on the repeatedly detected QTLs for PH, shattering, and certain spike morphologies reported in this study.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

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