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Major quality trait analysis and QTL detection in hexaploid wheat in humid rain-fed agriculture

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ABSTRACT. Humid rain-fed agriculture is a special environment for wheat (*Triticum aestivum*) culture that tends to negatively affect wheat yield and quality. To identify quality characters of wheat in a humid environment, we conducted quality analysis and quantitative trait loci (QTL) detection in a recombinant inbred line whose parent had a high level of quality for several years. We found that high-quality wheat had less gluten content and lower protein content. Apparently, wheat quality and associated quantity traits were in a dynamic state of equilibrium. We detected 83 QTL for 10 wheat quality traits in this recombinant inbred line population. Nine QTL were detected in both evaluation years; Q.DT.scau-2A, linked to Xwmc522-2A, was detected at the same genetic location in both years. Other QTL for different traits were detected simultaneously in more than one location. Consequently, there appeared to be pleiotropic genes that control wheat quality. Based on previous studies and our research on QTL analysis of grain protein content, we conclude that there must be one or more genes for grain protein content on chromosome 6B, whose expression was little affected by environment. We constructed a consensus map and

projected the QTL on it. It was useful for choosing optimal markers for marker-assisted breeding and map-based cloning.

Key words: Wheat; Quality; Humid; Rain-fed agriculture; QTL; Consensus map

INTRODUCTION

Sichuan Basin, in southwest China, has many overcast, rainy days and high average annual air humidity. The crop grows under a condition of humid rain-fed subsistence agriculture, and the average annual rainfall is about 1000 mm. For example, the rainfall averaged 1117.2 mm (1996) and 1117.6 mm (1988) per year in the Qionglai District (latitude 30°25'N, longitude 103°28'E, and altitude 493.3 m), Chengdu, Sichuan, China (http://number.cnki.net/cyfd/index.aspx). The wheat needs few or no supplementary irrigation during the entire process of growth. This particular climate offers many advantages, such as low cost, dependable crop, easy management, and lower labor requirements, among others. However, it also has disadvantages. Plant diseases and insect pests such as powdery mildew, stripe rust, gibberellic disease, and aphids increase, thereby decreasing yield. Meanwhile, end-use quality is decreased by pre-harvest sprouting (PHS). The development of high-yielding varieties with good end-use quality is a major focus in wheat breeding programs (Ren et al., 2010), especially for wheat grown in humid rain-fed agriculture.

Generally speaking, good cooking quality is related to high or intermediate protein content and high gluten quality (D'Egidio et al., 1990; Blanco et al., 2006). In bread wheat, protein content correlates with bread volume (Finney and Barrimore, 1948). Thus, abundant molecular research has been carried out to understand thoroughly the relationship between wheat quality and its regulating genes. Arbelbide and Bernardo (2006) detected 4 quantitative trait loci (QTL) for dough strength on chromosomes 1A, 1B, 1D, and 5B. Huang et al. (2006) found 3 QTL for mixing development time on chromosomes 1B, 1D, and 3B and 3 QTL for sodium dodecyl sulfate sedimentation volume (SV) on 1B, 2D, and 5D. Numerous studies on milling yield, dough rheology, and baking quality of wheat have been performed (Law et al., 2005; Kunert et al., 2007). Kuchel et al. (2006) mapped QTL for dough rheological traits on chromosomes 1A and 1B, dough strength on chromosome 2A, and loaf volume on chromosome 3A.

Although many studies have been carried on wheat quality, few similar studies in humid rain-fed agriculture have been carried out. In general, PHS due mainly to early breakage of seed dormancy occurred more easily when plants were grown in wet weather for a long time during maturity and harvest (Liu et al., 2008). PHS lowers wheat yield and negatively affects the end-use quality of wheat products (Liu et al., 2008). Effective ways to minimize the quality reduction caused by PHS are to breed and grow cultivars with delayed germination time and reduced germination rate (Liu et al., 2008).

Wheat quality traits are expressed as quantitative traits that are forcefully influenced by environments or mutual effects between genotype and environment. In humid rain-fed agriculture, humidity is a major character. So wheat has corresponding quality characters in this special humid environment. In this research, we used a hexaploid wheat population of a R97 x R146 recombinant inbred line (RIL) as our study material and well-understood wheat

quality traits in the environment of humid rain-fed agriculture at the level of physicochemical characteristics and molecular biology.

MATERIAL AND METHODS

Genetic material

A population of a 103 F_{9-10} RIL was constructed through single-seed descent from a cross between R146 as the female and R97 as the male. R146 is a line of resistant PHS wheat grown in southwest China. It has shown a high level of gluten quality and dough rheological characteristics over years.

The RIL and its parents were planted with 2 replications in Qionglai District (altitude 30°25'N, longitude 103°28'E, and altitude 493.3 m), Chengdu, Sichuan, China, in 2008-2009 and 2009-2010. A plot with 2 rows was 3 m long and 25 cm apart, and 90 seeds were sowed in each row. The field management followed standard agricultural practice. Each plot was harvested by hand as soon as more than 70% of the plants reached maturity. The harvested seeds were sun-baked and stored in a ventilated room.

The whole wheat was milled (FOSS 1093 Cyclotec Sample Mill, Sweden) with a 0.5-mm screen. The flour was milled by Laboratory Mill (Brabender Measurement and Control Systems, Germany). The wet gluten content (WGC) and gluten index (GI) were determined with a Glutenmatic 2200 (Perten, Sweden). Gluten protein content (GPC) was determined using a distillation unit B-324 (Buchi, Sweden). Farinograph quality number (FQN) was detected with a Farinograph-E (Brabender, Germany). SV was measured according to a procedure described by Dexter et al. (1980), and falling number (FN) was tested with a Perten 1700 (Sweden).

Statistical analyses

Statistical analyses of wheat quality traits were carried out on the mean of 4 replications using PASW Statistics 18.0 [http://www.umass.edu/statdata/ software/ news/spss/ (accessed August 7, 2012)]. Statistical significance between the parents was evaluated with the Student *t*-test. The correlation coefficient was calculated using Pearson's correlation. Significant differences were determined with a two-tailed test. The coefficient of variation (CV) was calculated on the mean and standard deviation based on 4 replications.

Map construction and QTL detection

Leaves were harvested at the 3-leaf stage, and DNA was isolated from leaf tissue using the CTAB method (Saghai-Maroof et al., 1984). The simple-sequence repeat (SSR) primer pairs of XWMC were catalogued in the GrainGenes database [http://wheat.pw.usda.gov/cgi-bin/graingenes/browse.cgi?Class=marker (accessed August 8, 2012)]. SSR analysis was implemented following procedures published elsewhere (Senior and Heun, 1993; Liu et al., 2008), and a genetic linkage map was composed using MAPMAKER/EXP 3.0b (Lincoln et al., 1993).

WinQTLCart 2.5 [http://statgen.ncsu.edu/qtlcart/WQTLCart.htm (accessed August 8, 2012)] was used to perform composite interval mapping based on model 6. The genome scan was accomplished via composite interval mapping using a backward regression method with

a 10-cM window size. Permutation tests were carried out with 1000 repetitions at a 1-cM walk speed and significance level of 0.05.

Construction of the new consensus map and QTL projection

Wheat mapping data of microsatellite markers Xwmc, Xgwm, and Xbarc from 3 sets of mapping data (Somers et al., 2004; Quarrie et al., 2005; Xue et al., 2008) were used for consensus map construction (Table 1). The 3 high-density genetic maps covered 3522, 4223.1, and 2569 cM and comprised 567, 887, and 1235 markers. The average interval distance ranged from 2.2 to 6.2 cM. Two of the maps were doubled-haploid population and RIL population, respectively. The third map of Somers et al. (2004) was constructed by joining 4 independent genetic maps of bread wheat (3 doubled-haploid and 1 RIL).

Table 1. Summary of 3 individual mapping data for consensus map construction.

Mapping population	Total No. of markers	Length of map (cM)	Number of SSR markers						
			Type of markers				Common markers		
			Xbarc	Xgwm	Xwmc	Total	N[b] = 2	N = 3	Total
Chinese Spring x SQ1	567	3522	46	90	86	222	94	83	177
Nanda2419 x Wangshuibai	887	4223.1	95	131	194	420	170	83	253
Consensus map	1235	2569	141	273	357	771	236	83	319

[b]Index common markers in n other populations.

Firstly, 3 linkage maps were constructed with microsatellite markers from 3 sets of mapping data independently by JoinMap® 4 (Van Ooijen, 2006). At the population nodes, we excluded some individuals and loci with many missing observations (missing above 90 genotypes and 38 individuals) and also removed identical loci with a similarity value of 1.0 using the Exclude Identicals function. Trees groupings were obtained by calculating in tabsheets of groupings with the default settings. Groups were created using the grouping tree. Finally, groups of the same chromosome in independent populations were combined into integrated groups, which constructed the new consensus map.

QTL of our mapping experiment were projected on the consensus map with BioMercator 2.1 (Arcade et al., 2004). The major projection procedure was executed as described by Chardon et al. (2004). First, the output QTL from WinQTLCart, consensus map constructed by JoinMap and our map constructed by MapMaker were all converted to text file for BioMercator input. Second, 3 text files of maps were imported into BioMercator, then the QTL file was added to our map. Finally, our map with QTL was projected onto the consensus map.

RESULTS

Analysis of quality traits in the RIL population and parents

All of the traits displayed genetic difference between the 2 parents to some extent. GI, FN, SV, development time (DT), stability time (ST), and FQN in particular showed significant differences based on a *t*-test (Table 2). For all the quality traits, the parent R146 had values higher than those of R97, and most traits reached greatly significant difference ($P < 0.01$). The

mean of all the traits in the RIL was between the values determined for the 2 parents except the mean of GPC, which was higher than the value in both parents. All the traits showed various degrees of transgressive segregation, and GI, FN, and FQN had higher standard deviation and CV (>12). At the same time, the traits demonstrated greatly significant differences between parents. Therefore, the RIL population was suitable for detecting QTL of quality traits.

Table 2. Wheat quality traits of R146, R97, and recombinant inbred lines (RIL) in 2008-2009 and 2009-2010.

Traits	RIL population					Parental lines	
	Mean (%)	Min (%)	Max (%)	SD	CV	R97	R146
GI**	70.1	4.8	98.7	22.9	32.7	57.2	95.4
WGC	28.3	23.8	40.0	3.0	10.5	27.7	28.6
DGC	9.1	7.8	11.9	0.9	9.9	9.0	9.3
WB	19.1	15.8	28.1	2.1	11.0	18.7	19.3
FN**	309.3	153.5	397.5	38.4	12.4	261.3	366.0
SV**	8.3	5.2	12.0	1.5	17.6	6.9	10.8
DT**	4.6	1.3	18.5	2.8	60.9	2.6	7.3
ST**	8.1	1.2	19.1	4.6	57.4	5.4	13.7
FQN**	84.8	26.0	203.0	44.0	51.9	56.0	142.3
GPC	13.2	10.5	17.5	1.1	8.5	12.2	12.8

SD = standard deviation; CV = coefficient of variation; GI = gluten index; WGC = wet gluten content; DGC = dry gluten content; WB = wheat bran; FN = falling number; SV = sedimentation volume; DT = development time; ST = stability time; FQN = farinograph quality number; GPC = gluten protein content. **Indexed significant differences ($P < 0.01$).

Genetic correlations between wheat quality traits

To comprehend the interrelationship among the traits we detected, all data from the wheat RIL population were analyzed with Pearson's linear correlation. The genetic correlation coefficients between traits are shown in Table 3. All traits showed different degrees of correlation. GI was significantly negatively correlated with WGC (r = -0.490, P = 0.000), dry gluten content (DGC; r = -0.437, P = 0.000), and wheat bran (WB; r = -0.503, P = 0.000). WGC, DGC, and WB were strongly positively correlated with one another. SV was significantly positively correlated with GI (r = 0.384, P = 0.000), WGC (r = 0.390, P = 0.000), DGC (r = 0.407, P = 0.000), and WB (r = 0.374, P = 0.000). GPC was strong positive correlated with WGC (r = 0.709, P = 0.000), DGC (r = 0.667, P = 0.000), WB (r = 0.712, P = 0.000), and SV (r = 0.276, P = 0.006), and strong negative correlated with GI (r = -0.285, P = 0.004). GI was correlated or strongly correlated with dough rheological characteristics of DT (r = 0.201, P = 0.047), ST (r = 0.678, P = 0.000), and FQN (r = 0.480, P = 0.000). FN was correlated with DT (r = 0.243, P = 0.016) and FQN (r = 0.201, P = 0.047). FQN was negative correlated with WB (r = -0.202, P = 0.046). ST was strong negative correlated with WGC (r = -0.394, P = 0.000), DGC (r = -0.342, P = 0.001), and WB (r = -0.408, P = 0.000). We found that FQN, ST, FN, and GI were all negative correlated with GPC, WGC, and DGC. The increased quality may have been usually accompanied by decreased content of quantity traits (e.g., gluten content and GPC).

QTL analysis for grain quality traits

Wheat quality traits were quantity traits. Genotype-environment interactions on QTL were embodied in the wheat development. To understand the quality trait variation in multiple

environments, the nature of genetic variation in major wheat quality traits was investigated in an RIL population by mapping QTL for 2 years.

Table 3. Genetic correlation between wheat quality traits in wheat recombinant inbred lines (RIL) and their parents.

	WGC	DGC	WB	FN	SV	DT	ST	FQN	GPC
GI	-0.491**	-0.437**	-0.503**	-0.051	0.384**	0.201*	0.678**	0.480**	-0.285**
WGC		0.965**	0.994**	-0.070	0.390**	0.001	-0.395**	-0.191	0.709**
DGC			0.930**	-0.127	0.408**	0.007	-0.343**	-0.155	0.668**
WB				-0.044	0.374**	-0.02	-0.409**	-0.202*	0.712**
FN					0.107	0.243*	0.070	0.201*	-0.053
SV						0.065	0.158	0.179	0.276**
DT							0.636**	0.816**	0.045
ST								0.882**	-0.273**
FQN									-0.119

*,**Indicate significance at $P < 0.05$ and $P < 0.01$, respectively. For abbreviations, see legend to Table 2.

Dough rheological characteristics

Ten QTL for DT and FQN were detected in 2008 and 2009 (Table 4). Five and 1 stable QTL were detected in both years for DT and FQN, respectively. Two QTL (Q.DT.scau-1A.1 and Q.DT.scau-1A.2) of DT were both linked to the molecular marker xwmc611-1A. Q.DT.scau-4D linked to xwmc473-4D had a higher LOD score and phenotypic variation (LOD > 5.4, $R^2 > 5.7$) and displayed stability in both years. We found that Q.DT.scau-7D and Q.FQN-scau-7D were both linked to the same marker, xwmc634-7D, and had similar genetic locations. In the QTL analysis for dough rheological characteristics, we detected only 2 QTL of ST at a time.

Table 4. QTL analysis of dough rheological characteristics in R146 x R97 RIL population for 2 years.

Traits	QTL[a]	Marker[b]	Position	2008~2009		R^2	Position	2009~2010		R^2
				LOD score	Additive effect			LOD score	Additive effect	
DT	Q.DT.scau-1A.1	Xwmc611-1A	2.9	7.7	-0.2	>0.0	2.7	8.0	-0.2	0.3
	Q.DT.scau-1A.2	Xwmc611-1A	16.4	7.6	-0.1	>0.0	17.2	7.9	-0.2	>0.0
	Q.DT.scau-1A.3	Xwmc329-1A					1.6	6.9	-0.1	>0.0
	Q.DT.scau-1B	Xwmc419-1B	56.2	6.3	-0.6	4.6	54.7	6.8	-0.3	0.8
	Q.DT.scau-1D	Xwmc222-1D					1.0	7.1	>0.0	0.1
	Q.DT.scau-2A	Xwmc522-2A	16.1	6.5	0.4	3.6	16.1	7.7	0.4	3.2
	Q.DT.scau-4D	Xwmc473-4D	33.9	5.4	-0.4	5.7	34.2	5.6	-0.3	5.8
	Q.DT.scau-7D	Xwmc634-7D	66.7	7.3	0.6	3.5				
FQN	Q.FQN.scau-4A	Xwmc161-4A	4.5	4.4	-5.2	0.7				
	Q.FQN.scau-7D	Xwmc634-7D	64.7	6.5	2.1	4.8	65.0	6.6	5.8	1.3

[a]Refers to QTL that are detected in both years or links to markers and the marker linked to QTL of other traits; [b]is for the marker that is nearest to corresponding QTL. For abbreviations, see legend to Table 2.

Wheat protein and its correlated traits

As shown in Table 5, 3 stable QTL for 2 traits (WB and GPC) were found through QTL analysis. Q.GPC.scau-6B linked to marker xwmc419-6B was the only stable QTL for GPC. Three QTL (Q.GPC.scau-1B, Q.WB.scau-1B, and Q.WGC.scau-1B) were found all linked to the same marker, xwmc728-1B, at similar genetic locations. Q.WB.scau-1B was

detected during both years. A stable QTL of Q.WB.scau-7D.1 linked to xwmc634-7D was detected at the genetic location of 66.1 and 66.3 cM for 2 years. At a similar genetic location, we also detected 2 QTL for DT and FQN (see Table 4).

Table 5. QTL analysis of protein and its correlated traits in R146 x R97 RIL population for 2 years.

Traits	QTL[a]	Marker[b]	Position	2008~2009		R^2	Position	2009~2010		R^2
				LOD score	Additive effect			LOD score	Additive effect	
GPC	Q.GPC.scau-1A.1	Xwmc329-1A	1.6	4.6	0.1	>0.0				
	Q.GPC.scau-1A.2	Xwmc611-1A					2.7	3.3	>0.0	0.2
	Q.GPC.scau-1B	Xwmc728-1B	77.7	3.5	>0.0	0.4				
	Q.GPC.scau-1D	Xwmc222-1D	1.0	4.8	0.1	0.5				
	Q.GPC.scau-2A	Xwmc522-2A					16.1	3.7	-0.1	0.1
	Q.GPC.scau-4A	Xwmc161-4A	5.5	4.0	>0.0	0.5				
	Q.GPC.scau-6B	Xwmc419-6B	65.7	3.6	>0.0	0.1	66.4	3.4	>0.0	0.6
WB	Q.WB.scau-1B	Xwmc728-1B	77.0	4.3	0.2	1.4	77.2	3.4	0.2	1.0
	Q.WB.scau-1D	Xwmc222-1D					1.0	4.2	-0.2	0.7
	Q.WB.scau-6B	Xwmc388a	47.1	3.0	>0.0	0.7				
	Q.WB.scau-7D.1	Xwmc634-7D	66.1	5.3	0.3	>0.0	66.3	3.0	0.1	0.1
	Q.WB.scau-7D.2	Xwmc473c					1.0	4.6	0.4	1.8
WGC	Q.WGC.scau-1B	Xwmc728-1B	78.5	5.4	0.2	1.1				
	Q.WGC.scau-1D	Xwmc222-1D					1.0	3.1	0.5	2.0
	Q.WGC.scau-6B	Xwmc388a	46.5	4.2	>0.0	1.3				
	Q.WGC.scau-7D	Xwmc473c					1.0	4.1	0.6	2.0

[a]Refers to QTL that are detected in both years or links to markers and the marker linked to QTL of other traits; [b]is for the marker that is nearest to corresponding QTL. For abbreviations, see legend to Table 2.

Salih and Adelson (2009) stated that genes with similar functions may be grouped in specific locales and can contribute to QTL traits. In our study, QTL of some traits were detected in the same or similar genetic locations (Table 6). Q.DT.scau-1D, Q.GPC.scau-1D, Q.WB.scau-1D, and Q.WGC.scau-1D were all linked to molecule marker xwmc222-1D at the 1 cM genetic position. In 2009, QTL for trait pairs WGC and WB and DT and GPC were located at the genetic position 1 (linked to xwmc473c, 7D) and 2.7 cM (linked to xwmc611-1A, 1A), respectively. We found that 4 locations on chromosome 1A (xwmc329-1A 1.6 cM and xwmc611-1A 2.7 cM), 2A (xwmc522-2A 16.1 cM), and 1D (xwmc222-1D 1 cM) harbored QTL of DT and GPC. These coincidences may be due to pleiotropy or genetic linkage (Heidari et al., 2011).

Consensus map and QTL projection

Two hundred and fifty and 83 markers were shared by 2 and 3 individual maps that were used for construction of the new consensus map (Table 1). We checked the 3 map data with JoinMap and excluded 40 markers and 35 individuals, which had many missing observations. Finally, this consensus map comprised 617 markers, including 119 Xbarc, 187 Xgwm and 311 Xwmc. All these markers were distributed on 21 linkage groups covering 1881.1 cM with an average interval distance of 3.0 cM (Figure S1). On the consensus map, only 4 linkage groups (1D, 4D, 5D, and 6D) had the lower marker density and the lowest was 8.3 cM per marker in 1D, and there were no effective fixed orders in fixed-order file. Moreover, there were 32 common markers between our map data and the consensus map. It was feasible to project our map and QTL on to the consensus map (Figure 1).

Table 6. QTL with the same or close location of genetic position in combined analysis.

Traits	QTL[a]	Marker[b]	Position	LOD score	Additive effect	R^2
FQN	Q.FQN.scau-4A	Xwmc161-4A	4.5	4.4	-5.2	0.7
GPC	Q.GPC.scau-4A	Xwmc161-4A	5.5	4.0	>0.0	0.5
DT	Q.DT.scau-1D	Xwmc222-1D	1.0	7.1	>0.0	0.1
GPC	Q.GPC.scau-1D	Xwmc222-1D	1.0	4.8	0.1	0.5
WB	Q.WB.scau-1D	Xwmc222-1D	1.0	4.2	-0.2	0.7
WGC	Q.WGC.scau-1D	Xwmc222-1D	1.0	3.1	0.5	2.0
DT	Q.DT.scau-1A.3	Xwmc329-1A	1.6	6.9	-0.1	>0.0
GPC	Q.GPC.scau-1A.1	Xwmc329-1A	1.6	4.6	0.1	>0.0
WB	Q.WB.scau-6B	Xwmc388a	47.1	3.0	>0.0	0.7
WGC	Q.WGC.scau-6B	Xwmc388a	46.5	4.2	>0.0	1.3
WB	Q.WB.scau-7D.2	Xwmc473c	1.0	4.6	0.4	1.8
WGC	Q.WGC.scau-7D	Xwmc473c	1.0	4.1	0.6	2.0
DT	Q.DT.scau-2A	Xwmc522-2A	16.1	7.7	0.4	3.2
GPC	Q.GPC.scau-2A	Xwmc522-2A	16.1	3.7	-0.1	0.1
DT	Q.DT.scau-1A.1	Xwmc611-1A	2.7	8.0	-0.2	0.3
GPC	Q.GPC.scau-1A.2	Xwmc611-1A	2.7	3.3	>0.0	0.2
FQN	Q.FQN.scau-7D	Xwmc634-7D	65.0	6.6	5.8	1.3
WB	Q.WB.scau-7D.1	Xwmc634-7D	66.3	3.0	0.1	0.1
DT	Q.DT.scau-7D	Xwmc634-7D	66.7	7.3	0.6	3.5
GPC	Q.GPC.scau-1B	Xwmc728-1B	77.7	3.5	>0.0	0.4
WB	Q.WB.scau-1B	Xwmc728-1B	77.2	3.4	0.2	1.0
WGC	Q.WGC.scau-1B	Xwmc728-1B	78.5	5.4	0.2	1.1

[a]Refers to QTL that are detected in both years or links to markers and the marker linked to QTL of other traits; [b]is for the marker that is nearest to corresponding QTL. For abbreviations, see legend to Table 2.

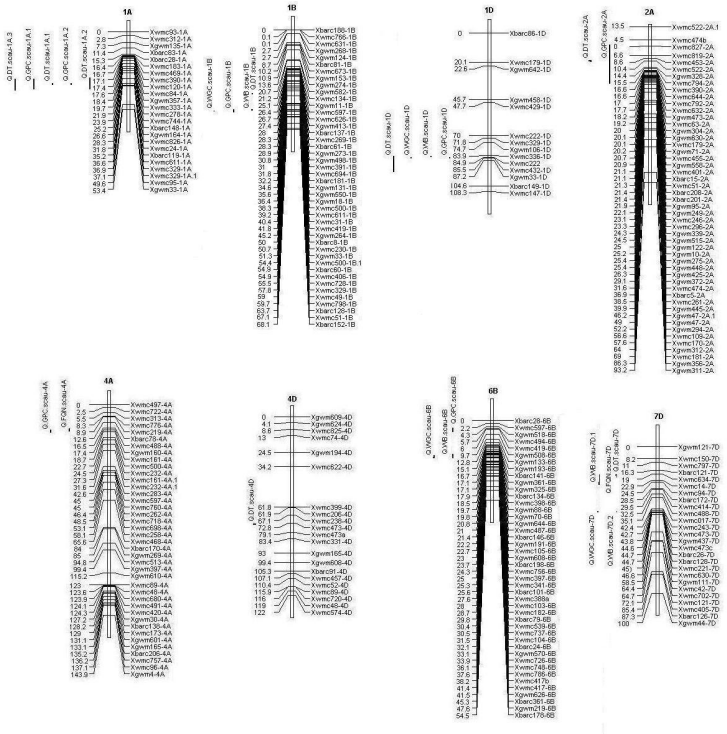

Figure 1. Positions of QTL associated with major quality traits of wheat in the R146 x R97 RIL population.

DISCUSSION

Gluten strength is a function of both protein concentration and protein composition (Guttieri et al., 2001). Gluten composed of glutenin and gliadin proteins is one of the major determinants of the elasticity of dough; it forms a network in dough and confers viscoelasticity, which are necessary to produce high-quality bread (Yahata et al., 2006). GI is expressed as the ratio of wet gluten remaining on a sieve after centrifuging to the total wet gluten weight. This index has become the standard procedure for evaluating gluten strength and correlates well with sodium dodecyl sulfate (Cubadda et al., 1992). Generally speaking, the higher the GI, the higher the gluten quality (Hu et al., 2004) and dough rheological characteristics. In our present study (see Table 3), GI was significantly positive correlated with SV ($r = 0.384$, $P = 0.000$) and positive correlated or strong positive correlated with the dough rheological characteristics DT ($r = 0.201$, $P = 0.047$), ST ($r = 0.678$, $P = 0.000$), and FQN ($r = 0.480$, $P = 0.000$). We also found that GI was strongly negatively correlated with WGC ($r = -0.490$, $P = 0.000$), DGC ($r = -0.437$, $P = 0.000$), WB ($r = -0.503$, $P = 0.000$), and GPC ($r = -0.285$, $P = 0.004$). ST, a dough rheological characteristic, was strong correlated with GI and significantly negative correlated with gluten characters (WGC, DGC, WB, and GPC). FQN was loosely negative correlated with WGC, DGC, and GPC. These correlations meant that high-quality wheat contained less gluten and had a lower GPC. In the QTL analysis, the QTL of quality (FQN and DT) and quantity (GPC) traits linked to these markers (red type) had the opposite additive effect (see Table 6). Hu and Shang (2007) also indicated that high-quality wheat varieties contain less wet gluten but have a higher GI. We believed that wheat quality and associated quantity trait content was in a dynamic state of equilibrium, and the increased quality was usually accompanied by decreased quantity traits (e.g., gluten content and GPC) based on the data.

Among 83 QTL for 10 traits in this study, 9 QTL were detected across 2 environments (years): 5 for DT, 1 for FQN, 2 for WB, and 1 for GPC. GPC, DT, and FQN were important factors in wheat end-using quality. It had generally been believed that stable QTL that expressed across different environments had more potential to be used in marker-assisted breeding (MAB) and further research (Wei et al., 2009). Hence, we were able to find more appropriate markers for these important traits based on the new consensus map.

Three stable QTL for the dough rheological character DT were located on chromosome 1A (Q.DT.scau-1A.1 and Q.DT.scau-1A.2, both linked to xwmc611-1A) and 1B (Q.DT.scau-1B, linked to xwmc419-1B). Previous research (Campbell et al., 2001; Kuchel et al., 2006; Nelson et al., 2006) has also reported additional QTL for dough rheological traits on chromosomes 1A and 1B. These dough rheological traits may be influenced by their placement in specific regions of chromosomes 1A and 1B (Nelson et al., 2006). A number of reports have identified GPC QTL on various chromosomes, and they have all detected at least one GPC QTL on chromosome 6B (Joppa and Cantrell, 1990; Blanco et al., 1996; Steiger et al., 1996; Olmos et al., 2003; Prasad et al., 2003; Distelfeld et al., 2004; Turner et al., 2004). Prasad et al. (2003) identified 2 GPC QTL on 6Bs, one of which linked to marker xgwm133-6B. On chromosomes 6B and 7B, we also detected 2 GPC QTL linked to xwmc419-6B (see Table 5) and xwmc232-7B (data not shown), respectively. Two markers of xgwm133-6B and xwmc419-6B had close genetic distance in our consensus map (see Figure 1). Olmos et al. (2003) also found 1 GPC QTL with similar genetic distance on chromosome arm 6Bs. So, 1 or more genes for GPC that can stably express with smaller environmental impact must be pres-

ent on chromosome 6B. We believe that some (or specific) chromosomes may harbor specific regions or multi-genes (but only one or few genes can express) for 1 trait.

Genes with similar functions may be grouped in specific locales and could contribute to QTL traits (Salih and Adelson, 2009). In the study of gene clusters (see Table 6), we found that QTL for more traits were detected in more than 1 genetic location simultaneously. Therefore, these locations must contain genes with pleiotropy, and these genes interweave a web of wheat quality. The pleiotropy may strongly constrain possible mutational avenues because of the interwoven web of genetic and physiological interactions that were involved in development and function (Hodgkin, 1998). In wheat breeding, wheat quality traits were almost quantity traits. Genetically speaking, all quality traits had a definite relationship with one another. Wheat quality traits controlled by more pleiotropic genes may conceivably be involved in wheat quality breeding. The pleiotropic genes have constrained possible mutation over the long term of wheat breeding, and hence have slowed wheat quality breeding.

Our dense genetic map was very useful for MAB. It was furthermore important for map-based cloning and genome sequencing projects (Varshney et al., 2006, 2007). To date, a large number of markers have been developed and mapped in populations. However, these markers diffused in different populations, so they cannot offer additional information like markers mapped in a single mapping population. Varshney et al. (2007) described an alternative way to prepare a dense genetic map that combines various genetic maps by exploiting common markers. The density of the genetic map in our research was enhanced greatly through consensus map construction and QTL projecting. Meanwhile, the reflection of QTL on a consensus map provided a convenient way to choose optimal markers for MAB and map-based cloning.

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Supplementary material

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