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ORIGINAL PAPER

Genetic dissection of yield-related traits in a recombinant inbred line population created using a key breeding parent in China's wheat breeding

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Abstract Understanding the genetics underlying yield formation of wheat is important for increasing wheat yield potential in breeding programs. Nanda2419 was a widely used cultivar for wheat production and breeding in China. In this study, we evaluated yield components and a few yield-related traits of a recombinant inbred line (RIL) population created by crossing Nanda2419 with the indigenous cultivar Wangshuibai in three to four trials at different geographical locations. Negative and positive correlations were found among some of these evaluated traits. Five traits had over 50 % trial-wide broad sense heritability. Using a framework marker map of the genome constructed with this population, quantitative trait loci (QTL) were identified for all traits, and epistatic loci were identified for seven of them. Our results confirmed some of the previously reported QTLs in wheat and identified several new ones, including *QSn.nau-6D* for effective tillers, *QGn.nau-4B.2* for kernel number, *QGw.nau-4D* for kernel weight, *QPh.nau-4B.2* and *QPh.nau-4A* for plant height, and *QFlw.nau-5A.1* for flag leaf width. In the investigated population, Nanda2419 contributed all QTLs associated with higher kernel weight, higher leaf chlorophyll content, and a major QTL associated with wider flag leaf. Seven chromosome regions were related to more than one trait. Four QTL clusters contributed positively to breeding goal-based trait improvement through the Nanda2419 alleles and were detected in trials set in different ecological regions. The findings of this study are relevant to the molecular improvement of wheat yield and to the goal of screening cultivars for better breeding parents.

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Introduction

Increasing the yield potential of wheat has been a major focus of most wheat breeding programs around the world. Since the introduction of reduced height (*Rht*) into wheat varieties in the 1960s, wheat production has experienced a tremendous yield increase. However, the breeding gains in wheat yield have substantially slowed in recent years due to the lack of 'breakthrough' germplasms and breeding methodologies. To meet the food security challenges caused by population increase and arable land decrease, new wheat cultivars with higher yield potential must be developed. Achievement of this goal will require full exploitation of various germplasm resources.

The unit grain yield of wheat is determined by three components: number of productive spikes per unit area, number of kernels per spike, and kernel weight. On the individual plant level, yield is a product of spike number, spikelet number per spike, grain number per spikelet, and kernel weight. Although studies have shown that there are negative correlations among the yield components (Fonseca and Patterson 1968; Knott and Talukdar 1971), the degree of correlation could be genotype dependent (Yunus

and Paroda 1982; Shah et al. 1999; Cuthbert et al. 2008; Deng et al. 2011; Wang et al. 2011). Because yield is the final product of plant growth and development, many other traits such as plant height, photosynthetic capability, and biotic and abiotic resistances affect the final yield components. It is feasible to increase the yield potential by coordinative improvement of the yield-related factors through knowledge of their genetic and molecular regulations.

Yield or yield component traits are complex, controlled by polygenes, and affected greatly by environments. In the past decade, with the help of molecular markers and marker-based genetic maps, QTLs for these traits have been identified in a number of germplasms through genome scanning (Kato et al. 1999; Li et al. 2002; Huang et al. 2004; Ma et al. 2007; Cuthbert et al. 2008; Wang et al. 2009; McIntyre et al. 2010). A majority of the reported QTLs are distributed on wheat chromosomes 1A, 1B, 2A, 2D, 3B, 4A, 4B, 4D, and 5A (Zhang et al. 2010a). Major QTLs associated with grain number per spike have been found on chromosome arms 4BS, 4DS, and 7AL (Quarrie et al. 2005, 2006; Kumar et al. 2007; Su et al. 2009; Wang et al. 2009, 2011; Yao et al. 2009; McIntyre et al. 2010; Deng et al. 2011), those associated with grain weight on chromosome arms 4BS, 4DS, and 7DS (Huang et al. 2004, 2006; McCartney et al. 2005; Röder et al. 2008; McIntyre et al. 2010; Wang et al. 2011), and those associated with spike number per plant on chromosome arms 1AL, 3AL, and 4BS (Shah et al. 1999; Kumar et al. 2007; Su et al. 2009; McIntyre et al. 2010; Deng et al. 2011). In addition to the above-mentioned yield and yield component traits, other yield-related traits have also been under comprehensive investigation using molecular genetic tools (Coleman et al. 2001; Yang et al. 2007; Zhang et al. 2009, 2010b). Interestingly, some of the QTLs for different yield components and yield-related traits clustered in common genomic regions.

In China's wheat breeding history, the cultivar Nanda2419, a selection of 'Mentana' (Rieti/Wihelmina//Akagomughi) introduced from Italy in the 1930s, played a significant role in wheat production and breeding. For 40 years, this cultivar was planted all over China but the Northeastern wheat-growing zone, with an annual acreage up to 4,666,000 ha (Zheng 1993). Moreover, use of this cultivar as the breeding parent in different breeding programs has generated more than 130 different cultivars in China. In this study, we investigated the genetic factors contributing to the yield components and to a few other yield-related traits using a recombinant inbred line (RIL) population created from a Nanda2419 x Wangshuibai cross by single seed descent. The goal of the study was to understand the genetic basis of the superior performance of cultivar Nanda2419.

Materials and methods

Plant materials and field trials

Two hundred and thirty RILs produced by single seed descent from the Nanda2419 × Wangshuibai cross and their parental lines were used in this study (Lin et al. 2004).

Field trials were conducted at Jiangpu and Jiangning of Jiangsu (2007JP, 2007JN) and at Taian of Shandong in 2007 (2007SD), and at Jiangpu in 2008 (2008JP). Jiangpu and Jiangning are located in the autumn-sown spring wheat zone of the lower Yangtze Valley (Zone III, latitude from 28°N to 33°N, longitude 105°–123°E); Taian is located in the Huang Huai facultative wheat zone (Zone II, latitude from 33°N to 38°N, longitude 105°–122°E). Zones II and III constitute approximately 60 % of China's wheat-grown area. The trials were performed in randomized complete blocks, each with two replicates. Each plot had two 1.5-m rows spaced 0.5 m apart. At two-leaf stage, only ten evenly distributed plants in each row were retained for further growth. Field management consisted of commonly undertaken practices in wheat production.

Trait evaluation

In each plot, 10 plants were used for trait evaluation. At sampling, plants at the ends of each row were disregarded to minimize within-row edge effects. Grain weight or kernel weight (GW) was measured as the mean weight of two independent samples of 100 grains; grain number per spike (GN) was measured as the mean grain number of 10 main-stem spikes; and effective spike number per plant (SN) was measured as the mean number of spikes of 10 plants. Other measured traits included the following: total tiller number per plant (TN) measured as the mean tiller number of 10 plants investigated at the later jointing stage, plant height (PH), upmost internode length (UIL), flag leaf length (FLL), and flag leaf width (FLW). The last four traits were measured after the flowering stage as the mean values of 10 plants. Flag leaf chlorophyll content (LCC) was measured 15 days after flowering using a portable Minolta chlorophyll meter SPAD-502 (Spectrum Technologies, Inc., Plainfield, IL.). The measurements were taken at the middle point of the fully expanded flag leaf blade next to the main leaf vein. In each plot, leaves from 10 plants were sampled for the measurements. Only GN, PH, and LCC were evaluated at the 2008JP trial.

Statistical analysis and QTL mapping

Analysis of variance (ANOVA) for the phenotypic data was carried out using the general linear model (GLM) function of the SPSS statistical package (SPSS Inc.,

Chicago, IL). The variance of each trait between genotypes was partitioned into $nr\sigma_g^2 + r\sigma_{ge}^2 + \sigma_e^2$, where n is the number of trials, r is the number of replications, σ_g^2 is the genetic variance, σ_{ge}^2 is the variance for genotype-environment interaction, and σ_e^2 is the experimental error. The entry-based broad sense heritability were estimated with the following formula: $H = \sigma_g^2/(\sigma_g^2 + \sigma_{ge}^2 + \sigma_e^2)$. Pearson correlation coefficients were calculated using SPSS.

A simplified framework marker map with 405 loci for QTL mapping was generated using the Kosambi mapping function with the mapping data of Xue et al. (2008). This map covered over 3,360 cM of the wheat genome. QTL detection was performed using Mapmaker/QTL v. 1.9 through simple interval mapping (SIM) and composite interval mapping (CIM) as described in Lin et al. (2004). In CIM analysis, the QTL with the highest LOD score from SIM was fixed at the given peak position using the 'sequence' command for whole map scan. The LOD score for declaring a QTL was 3.0 in SIM and 3.0 higher than that of the fixed QTL in CIM in at least two trails. CIM mapping was used to confirm the positions of the QTLs detected by SIM. For a given trait, QTLs with overlapping confidence intervals were given the same name.

The detection of digenic epistatic QTLs in multi-environments was accomplished using the software MQTL version 1.0 (Tinker and Mather 1995a). In this method, the 'B' loci in the genome interacting with a fixed marker locus 'A' were scanned using a walking speed of 1 cM. The basic threshold of the test statistic (TS) for declaring the epistatic QTL was set by performing 1,000 random permutations with a genome-wide type I error rate of 5 %; a higher threshold TS of 20.0 was used to declare significance for every trait, which is equivalent to an LOD value of 4.4 in Mapmaker/QTL (Tinker and Mather 1995b). Linked QTLs were defined as independent when more than 20 cM of genetic distance separated the interval peaks.

Results

Phenotypic analysis

Four different field trials were conducted at three locations over the course of 2 years to evaluate yield components and related traits of the RIL population as well as the cultivars Nanda2419 and Wangshuibai. Nanda2419 consistently had more kernels per spike, shorter height, shorter leaf length, and higher leaf chlorophyll content, whereas Wangshuibai had more total tillers and effective spikes per plant (Table 1). Several traits including kernel weight and upmost internode length did not differ significantly between the two parents. Independent of the differences between the two parents, in all trials there were significant variations in the investigated traits of the RIL populations, with values spanning much larger ranges than those defined by the parental values (Table 1). The phenotypic data of all the traits were normally distributed. The heritability ranged from 25.2 to 79.3 %, with SN and TN occupying the lowest two positions, and GW, UIL, and FLW having values close to 70 % heritability (Table 1).

Correlations among the nine traits in different trials are presented in Table 2. The leaf morphology traits, including FLL and FLW, were significantly related to yield component traits. FLL was positively correlated with SN and TN but had no significant relationships with GN and GW. FLW was positively correlated with GW and with GN in one trial, but was negatively related to SN and TN in almost all of the trials (significant at $P = 0.05$). FLW was also positively related to FLL and LCC in all trials. FLL was positively related to UIL and PH. Interestingly, LCC was significantly positively related to GW and negatively to SN and TN in most of the trials (Table 2). These results suggested that flag leaf-related traits have strong influences on yield component traits. PH was positively correlated with TN, SN, and GW (Table 2). GN was negatively related to GW, and TN negatively affected GW. Unlike TN, SN was not significantly related to GN (Table 2).

QTL mapping

Because genetic variations were present for all of the nine examined traits, chromosome regions associated with these traits were identified by genome scanning through QTL interval mapping.

Yield component traits

TN and SN per plant are two directly related traits that determine the number of spike per unit area. Two chromosome regions showed associations with TN (Table 3). Among them, *QTn.nau-5A* had the highest LOD value and was identified in all three trials with TN data. Three chromosome regions were identified as being associated with SN (Table 3). *QSn.nau-5A* was mapped to the same interval of *QTn.nau-5A* and expressed most stably across the trials with a LOD score >5 in all trials (Table 3; Fig. 1). *QSn.nau-6D* had an LOD value >5 in two trials and mapped to a chromosome region not associated with TN. *QSn.nau-6D* contributed to higher SN through the Nanda2419 alleles. The Wangshuibai alleles of the other two QTLs were associated with more effective spikes.

Among six chromosome regions associated with GN, the two most stably expressed QTLs with the highest LOD values all mapped to chromosome 4B, with the QTL peaks at least 34 cM apart from each other (Table 3; Fig. 1). *QGn.nau-4B.2* explained at least 23.6 % of the phenotypic

Table 1 Parental values, population distribution parameters, and heritability of the investigated yield-related traits

Traits	Environment	Parents		Population		H (%)
		Wangshuibai	Nanda2419	Mean	Min–max	
GN	2007JP	55.0**	69.9	55.5	39.9–75.4	59.6
	2007JN	52.0**	67.5	55.9	37.3–72.1	
	2007SD	43.2**	51.0	45.1	33.3–60.5	
	2008JP	51.7**	60.2	52.6	36.8–71.1	
GW	2007JP	4.3	4.4	4.2	3.3–5.1	69.5
	2007JN	4.4	4.4	4.2	3.0–5.4	
	2007SD	4.3	4.9	4.2	2.8–5.5	
SN	2007JP	23.3**	15.6	16.6	9.0–25.1	25.2
	2007JN	16.2**	10.8	11.7	7.5–17.5	
	2007SD	23.3**	14.8	21.3	14.5–31.7	
TN	2007JP	29.1**	16.5	21.3	12.4–36.4	35.0
	2007JN	18.8**	12.2	13.2	7.7–20.5	
	2007SD	25.6**	17.5	26.0	17.6–41.4	
PH	2007JP	124.3**	102.1	107.3	81.6–128.7	65.4
	2007JN	122.6**	110.2	111.9	94.8–128.7	
	2007SD	139.8**	109.7	120.8	99.0–142.7	
	2008JP	132.8**	113.1	119.6	94.0–141.4	
UIL	2007JP	24.2	25.3	22.1	12.1–29.4	79.3
	2007JN	25.8	25.7	24.2	13.6–31.8	
	2007SD	25.5	26.5	25.2	16.1–32.9	
FLL	2007JP	31.5*	29.5	28.4	20.6–37.2	49.8
	2007JN	29.5	28.7	29.1	20.9–35.7	
	2007SD	23.7**	20.3	21.3	15.3–28.8	
FLW	2007JP	1.8	1.8	1.7	1.3–2.1	72.3
	2007JN	1.6*	1.9	1.7	1.3–2.2	
	2007SD	1.6	1.6	1.5	1.2–1.9	
LCC	2007JP	44.3*	50.7	47.0	41.3–53.9	47.7
	2007JN	38.4*	45.4	42.2	34.4–49.1	
	2007SD	47.2*	50.8	48.7	39.7–54.4	
	2008JP	44.1	45.9	45.3	35.5–51.0	

* And ** indicate significant differences from Nanda2419 at $P = 0.05$ and 0.01, respectively

variation and *QGn.nau-4B.1* explained at least 10.3 % of the phenotypic variation in the four trials (Table 3). *QGn.nau-1B*, *QGn.nau-2A*, *QGn.nau-4D,* and *QGn.nau-6A* were associated with increased grain number per spike through the Nanda2419 alleles.

The evaluation of 100 grain weight in three trials identified four QTLs associated with GW; all QTLs increased GW through the Nanda2419 alleles (Table 3). The confidence intervals of the main and stable QTL *QGw.nau-4B* overlapped with that of *QGn.nau-4B.1* (Fig. 1), which, however, were not additively beneficial to yield increase in terms of the favorite alleles that were from different parents.

Plant height and upmost internode length

Six chromosome regions were found to be associated with plant height (Table 3). *QPh.nau-1A* and *QPh.nau-4B.2* were not detected in the 2007JN trial (Table 3). On average, *QPh.nau-4A* and *QPh.nau-4B.2* had the strongest associations with plant height and explained up to 28 % of the phenotypic variation. Besides *QPh.nau-4A* and *QPh.nau-4B.2*, *QPh.nau-4B.1* had the highest LOD values in at least two trials. Both parents carried QTLs associated with dwarfness, including *QPh.nau-1A*, *QPh.nau-4A* and *QPh.nau-7B* of Nanda2419, and *QPh.nau-4B.1*, *QPh.nau-4B.2* and *QPh.nau-7A* of Wangshuibai.

UIL is a trait highly correlated with PH. Of the six QTL intervals associated with PH, three distributed on chromosomes 4A, 4B, and 7A, were also associated with UIL (Fig. 1). Moreover, three chromosome regions previously having no detectable association with PH were identified in the three trials in which UIL was evaluated; of these three regions, *QUil.nau-6B* explained the highest phenotypic variation, with LOD scores >5 (Table 3). *QUil.nau-6B* was responsible for the reduction of UIL through the Wangshuibai allele.

Table 2 Correlation coefficients between the nine traits in the RIL population in different trials

	FLW	LCC	UIL	PH	TN	SN	GN	GW
FLL	0.18**	0.12	0.43**	0.31**	0.21**	0.18**	−0.12	−0.02
	0.19**	0.16*	0.43**	0.41**	0.30**	0.33**	0.06	−0.02
	0.24**	−0.10	0.45**	0.38**	0.24**	0.17*	−0.11	0.04
FLW		0.48**	0.23**	0.21**	−0.30**	−0.17*	0.01	0.35**
		0.39**	0.17*	0.23**	−0.17*	−0.13	0.19**	0.38**
		0.45**	0.17*	0.01	−0.38**	−0.40**	0.07	0.39**
LCC			0.02	−0.20**	−0.28**	−0.18**	0.05	0.15*
			0.03	−0.02	−0.04	−0.00	0.12	0.20**
			−0.01	−0.12	−0.32**	−0.32**	0.22**	0.31**
				−0.03			0.28**	
UIL				0.56**	−0.03	−0.11	−0.17*	0.12
				0.67**	0.20**	0.13	−0.17*	0.16*
				0.61**	−0.05	−0.09	−0.21**	0.13
PH					0.30**	0.22**	−0.18**	0.24**
					0.36**	0.32**	−0.08	0.33 **
					0.14*	0.14*	−0.18*	0.30**
							−0.24**	
TN						0.84**	−0.25**	−0.18**
						0.90**	−0.13*	−0.21**
						0.84**	−0.06	−0.32**
SN							−0.12	−0.13
							−0.00	−0.25**
							−0.03	−0.25**
GN								−0.35**
								−0.23**
								−0.31**

For each trait, the correlation coefficients from 2007JP, 2007JN, 2007SD, and 2008JP are represented in the first, second, third, and forth rows, respectively

* And ** indicate significance at $P = 0.05$ and 0.01, respectively

Flag leaf-related trait

Three chromosome regions were found to be associated with FLL in at least two trials and conditioned shorter leaves through the Nanda2419 alleles (Table 3). Three chromosome regions were found to be associated with FLW (Table 3). *QFlw.nau-2D* and *QFlw.nau-5A.1* were detected in every trial. *QFlw.nau-5A.2* was identified in the 2007JP and 2007SD trials. *QFlw.nau-5A.1*, with a LOD score larger than 14.4, had the strongest effects on FLW and explained more than 28 % of phenotypic variation. The Nanda2419 allele of *QFlw.nau-5A.1* was associated with wider leaves, whereas those of the other QTLs were associated with narrower leaves (Table 3).

Two major QTLs were identified for LCC (Table 3). *QLcc.nau-5A* explained more than 10 % of the phenotypic variation in three trials, and its LOD values ranged from 3.9 to 6.9. *QLcc.nau-2D* was identified in two trials. Their Nanda2419 alleles were associated with higher chlorophyll content (Table 3).

Chromosome regions involved in digenic epistasis

Using the given threshold, epistatic loci were identified across environments for TN, GN, GW, PH, UIL, FLL, and FLW (Table 4). These epistatic loci were distributed in 38 different chromosome regions. The epistatic chromosome region flanked by *Xmag4365-Xmag557* (associated with GW) overlapped with the confidence interval of *QGw.nau-3A* (Fig. 1).

Discussion

In this study, the wheat yield component traits GN, GW, and SN and the yield-related traits TN, FLL, FLW, LCC, PH, and UIL were evaluated in an RIL population derived

Table 3 QTLs identified for yield component and yield-related traits

Trial	QTL	QTL peak[a]		AE[b]	LOD	R^2 (%)	Multiple model	
		Interval	Position				LOD	R^2 (%)
TN								
2007JP	*QTn.nau-4A*	*Xcfd2-Xmag1353*	5.0	−2.1	3.8	9.4	9.4	20.2
	QTn.nau-5A[c]	*Xbarc56-Xgwm156.1*	1.0	−2.3	5.6	11.4		
2007JN	*QTn.nau-4A*	*Xcfd2-Xmag1353*	11.0	−1.1	3.3	9.9	8.8	18.8
	QTn.nau-5A[c]	*Xbarc56-Xgwm156.1*	0.0	−1.1	4.5	9.0		
2007SD	*QTn.nau-5A*[c]	*Xbarc56-Xgwm156.1*	0.0	−2.9	11.3	21.3	11.3	21.3
SN								
2007JP	*QSn.nau-4B*	*Xwmc349-Xwmc47*	0.0	−1.7	3.8	8.8	15.0	29.5
	QSn.nau-5A[c]	*Xbarc56-Xgwm156.1*	0.0	−2.1	7.1	13.7		
	QSn.nau-6D	*Xwmc773-Xgdm98*	8.0	2.1	6.3	12.9		
2007JN	*QSn.nau-5A*[c]	*Xbarc56-Xgwm156.1*	0.0	−1.1	5.4	10.5	5.4	10.5
2007SD	*QSn.nau-4B*	*Xwmc349-Xwmc47*	0.0	−1.4	3.0	6.0	13.8	26.1
	QSn.nau-5A[c]	*Xmag1281-Xbarc56*	7.0	−1.9	6.4	12.9		
	QSn.nau-6D	*Xwmc773-Xgdm98*	7.0	1.8	5.3	11.8		
GN								
2007JP	*QGn.nau-4B.1*[c]	*Xwmc238-Xgwm495*	2.0	−4.2	5.5	11.2	11.9	40.4
	QGn.nau-4B.2	*Xwmc413-Xmag4087*	14.0	−6.3	5.4	24.3		
	QGn.nau-4D	*Xmag1652-Xwmc8*	18.0	4.9	3.9	14.2		
2007JN	*QGn.nau-1B*	*Xmag2064-Xwmc419*	1.0	3.1	3.7	13.9	24.2	65.0
	QGn.nau-2A	*Xgwm47.3-Xwmc181.2*	11.0	3.4	4.0	3.0		
	QGn.nau-4B.1	*Xwmc238-Xgwm495*	2.0	−4.8	8.3	16.8		
	QGn.nau-4B.2[c]	*Xwmc413-Xmag4087*	16.0	−8.6	11.2	53.4		
	QGn.nau-4D	*Xbarc1118-Xgpw94042*	0.0	2.9	3.4	2.4		
	QGn.nau-6A	*Xmag1470-Xbarc118*	0.0	2.7	3.0	3.1		
2007SD	*QGn.nau-2A*	*Xgwm47.3-Xwmc181.2*	16.0	2.4	3.8	7.6	17.0	45.2
	QGn.nau-4B.1	*Xmag983-Xwmc238*	6.0	−2.8	4.8	10.3		
	QGn.nau-4B.2[c]	*Xwmc413-Xmag4087*	19.0	−4.2	5.5	23.6		
	QGn.nau-4D	*Xmag1652-Xwmc8*	14.0	3.4	3.2	13.9		
	QGn.nau-6A	*Xmag1470-Xbarc118*	2.0	2.7	4.5	10.1		
2008JP	*QGn.nau-1B*	*Xwmc611-Xmag2064*	5.0	3.4	3.4	8.5	16.2	43.0
	QGn.nau-4B.1[c]	*Xgwm495-Xgwm149*	0.0	−4.9	8.3	17.2		
	QGn.nau-4B.2	*Xwmc413-Xmag4087*	18.0	−7.5	8.1	40.7		
	QGn.nau-6A	*Xmag1470-Xbarc118*	0.0	3.3	3.5	7.7		
GW								
2007JP	*QGw.nau-3A*	*Xmag557-Xwmc322*	15.0	0.3	6.2	13.4	26.5	56.7
	QGw.nau-4B[c]	*Xgwm495-Xgwm149*	1.0	0.3	11.7	23.0		
	QGw.nau-4D	*Xmag1163-Xgdm93.1*	6.0	0.2	3.5	10.7		
	QGw.nau-5A	*Xmag1281-Xbarc56*	4.0	0.2	5.4	9.7		
2007JN	*QGw.nau-3A*	*Xmag557-Xwmc322*	11.0	0.2	3.3	9.3	22.6	45.0
	QGw.nau-4B	*Xgwm495-Xgwm149*	0.0	0.2	5.3	7.6		
	QGw.nau-4D	*Xmag1163-Xgdm93.1*	5.0	0.2	3.4	9.4		
	QGw.nau-5A[c]	*Xmag1281-Xbarc56*	2.0	0.3	10.4	21.9		
2007SD	*QGw.nau-3A*	*Xmag4365-Xwmc153*	16.0	0.2	3.0	4.2	22.2	42.3
	QGw.nau-4B	*Xwmc238-Xgwm495*	1.0	0.2	3.0	4.2		
	QGw.nau-4D	*Xmag1163-Xgdm93.1*	7.0	0.3	3.3	9.8		
	QGw.nau-5A[c]	*Xmag1281-Xbarc56*	3.0	0.5	14.0	30.5		

Table 3 continued

Trial	QTL	QTL peak[a]		AE[b]	LOD	R^2 (%)	Multiple model	
		Interval	Position				LOD	R^2 (%)
PH								
2007JP	*QPh.nau-1A*	*Xwmc329.1-Xwmc24*	9.0	−3.8	3.9	6.1	23.4	53.5
	QPh.nau-4A[c]	*Xcfd2-Xmag1353*	13.0	−7.0	9.7	28.5		
	QPh.nau-4B.1	*Xwmc238-Xgwm495*	0.0	4.0	5.7	8.6		
	QPh.nau-4B.2	*Xwmc413-Xmag4087*	22.0	5.8	4.5	18.9		
	QPh.nau-7A	*Xbarc195-Xmag274.2*	3.0	4.0	3.7	9.1		
	QPh.nau-7B	*Xgwm537-Xmag2110*	10.0	−4.5	3.4	11.6		
2007JN	*QPh.nau-4A*	*Xmag1353-Xwmc420*	3.0	−3.8	4.0	8.6	16.2	34.3
	QPh.nau-4B.1[c]	*Xwmc238-Xgwm495*	0.0	4.5	5.7	11.7		
	QPh.nau-7A	*Xwmc17-Xmag3302*	5.0	4.0	3.5	8.8		
	QPh.nau-7B	*Xgwm537-Xmag2110*	1.0	−3.2	3.0	6.3		
2007SD	*QPh.nau-1A*	*Xwmc329.1-Xwmc24*	7.0	−5.2	3.3	10.2	20.4	42.5
	QPh.nau-4A	*Xmag1353-Xwmc420*	0.0	−4.2	3.7	6.6		
	QPh.nau-4B.1[c]	*Xwmc238-Xgwm495*	0.0	6.1	7.0	14.2		
	QPh.nau-4B.2	*Xwmc413-Xmag4087*	19.0	8.3	3.9	26.1		
	QPh.nau-7A	*Xmag3302-Xbarc195*	5.0	5.1	3.9	9.7		
	QPh.nau-7B	*Xgwm537-Xmag2110*	9.0	−5.1	3.1	9.9		
2008JP	*QPh.nau-1A*	*Xwmc24-Xmag1022.2*	1.0	−4.3	3.6	7.2	21.4	50.0
	QPh.nau-4A[c]	*Xcfd2-Xmag1353*	13.0	−7.0	6.7	21.1		
	QPh.nau-4B.1	*Xwmc238-Xgwm495*	0.0	4.0	3.8	5.8		
	QPh.nau-4B.2	*Xwmc413-Xmag4087*	18.0	8.1	4.1	27.8		
	QPh.nau-7A	*Xmag3302-Xbarc195*	4.0	4.4	3.1	8.3		
	QPh.nau-7B	*Xgwm537-Xmag2110*	10.0	−5.7	3.8	14.1		
UIL								
2007JP	*QUil.nau-4A*	*Xcfd2-Xmag1353*	13.0	−1.7	4.2	20.8	24.9	58.5
	QUil.nau-4B	*Xgwm495-Xgwm149*	0.0	1.7	5.9	19.1		
	QUil.nau-5A	*Xcfa2185.2-Xsts-psr1201*	16.0	−2.2	4.8	24.1		
	QUil.nau-6B[c]	*Xmag3298.2-Xbarc79*	2.0	2.9	7.0	25.0		
	QUil.nau-6D	*Xgdm98-Xmag1459*	3.0	−1.8	4.9	20.8		
	QUil.nau-7A	*Xmag3302-Xbarc195*	7.0	1.5	4.2	18.0		
2007JN	*QUil.nau-4A*	*Xcfd2-Xmag1353*	13.0	−1.8	3.4	7.8	24.0	55.3
	QUil.nau-4B	*Xgwm495-Xgwm149*	0.0	1.7	4.2	5.7		
	QUil.nau-6B[c]	*Xmag3298.2-Xbarc79*	2.0	3.7	9.2	32.2		
	QUil.nau-6D	*Xgdm98-Xmag1459*	7.0	−2.1	5.1	9.9		
	QUil.nau-7A	*Xmag3302-Xbarc195*	8.0	1.6	3.5	5.1		
2007SD	*QUil.nau-4A*	*Xmag1353-Xwmc420*	6.0	−1.5	3.0	5.4	20.0	46.7
	QUil.nau-4B[c]	*Xmag983-Xwmc238*	6.0	2.7	9.2	19.4		
	QUil.nau-5A	*Xcfa2185.2-Xsts-psr1201*	20.0	−2.3	4.0	13.3		
	QUil.nau-6B	*Xgwm644-Xmag3298.2*	5.0	2.4	5.0	15.1		
	QUil.nau-6D	*Xgdm98-Xmag1459*	4.0	−1.8	3.1	8.9		
	QUil.nau-7A	*Xbarc195-Xmag274.2*	2.0	1.6	3.2	7.3		
FLL								
2007JP	*QFll.nau-1B*	*Xcfa2292-Xbarc80*	3.0	−1.4	3.7	6.9	10.2	27.6
	QFll.nau-3A	*Xwmc428-Xcfa2262*	2.0	−1.7	3.3	10.9		
	QFll.nau-4A	*Xcfd2-Xmag1353*	10.0	−1.6	3.3	10.0		
2007JN	*QFll.nau-1B*	*Xcfa2292-Xbarc80*	2.0	-1.5	3.3	8.8	3.3	8.8

Table 3 continued

Trial	QTL	QTL peak[a]		AE[b]	LOD	R^2 (%)	Multiple model	
		Interval	Position				LOD	R^2 (%)
2007SD	*QFll.nau-3A*	*Xwmc664-Xwmc627*	1.0	−1.5	3.2	8.6	7.1	20.4
	QFll.nau-4A[c]	*Xcfd2-Xmag1353*	13.0	−1.5	3.9	11.6		
FLW								
2007JP	*QFlw.nau-2D*	*Xgwm296-Xwmc112*	4.0	-0.1	3.9	5.5	27.5	50.0
	QFlw.nau-5A.1[c]	*Xbarc56-Xgwm156.1*	0.0	0.2	20.7	35.6		
	QFlw.nau-5A.2	*Xcfa2185.2-Xsts-psr1201*	16.0	−0.1	3.2	9.8		
2007JN	*QFlw.nau-2D*	*Xwmc112-Xgwm261*	1.0	−0.1	3.1	4.9	17.5	33.5
	QFlw.nau-5A.1[c]	*Xbarc56-Xgwm156.1*	1.0	0.2	14.4	28.7		
2007SD	*QFlw.nau-2D*	*Xgwm296-Xwmc112*	4.0	−0.1	4.6	6.2	31.4	58.7
	QFlw.nau-5A.1[c]	*Xbarc56-Xgwm156.1*	1.0	0.2	19.1	35.3		
	QFlw.nau-5A.2	*Xcfa2185.2-Xsts-psr1201*	16.0	−0.1	5.8	16.8		
LCC								
2007JP	*QLcc.nau-5A*[c]	*Xbarc56-Xgwm156.1*	0.0	1.5	6.9	13.8	6.9	13.8
2007JN	*QLcc.nau-5A*[c]	*Xbarc56-Xgwm156.1*	1.0	1.7	3.9	10.3	3.9	10.3
2007SD	*QLcc.nau-2D*	*Xsts-bsd183-Xgwm265.1*	0.0	1.4	4.5	9.2	9.7	21.0
	QLcc.nau-5A[c]	*Xbarc56-Xgwm156.1*	3.0	1.5	5.2	11.8		
2008JP	*QLcc.nau-2D*[c]	*Xsts-bsd183-Xgwm265.1*	0.0	1.9	5.9	13.3	10.0	21.4
	QLcc.nau-5A	*Xmag1281-Xbarc56*	6.0	1.5	4.1	8.2		

[a] The position was the distance from the left-side marker of the peak interval

[b] Additive effect. Positive and negative, Nanda2419 and Wangshuibai allele produced larger value, respectively

[c] Fixed QTL in CIM

from the cross of an elite cultivar Nanda2419 with Wangshuibai; four different field trials were conducted in two wheat-growing ecological zones for the evaluation of these traits. Through whole-genome scanning, 35 QTLs were identified for the nine investigated traits, which explained 8.8–65.0 % of the phenotypic variation in multiple QTL models (Table 3). QTL detection was less effective for traits with low heritability, such as TN, SN, FLL, and LCC, as shown by the small portion of phenotypic variation in a multiple QTL model. However, a major QTL for each of these traits was consistently detected in every trial. For GN, GW, PH, UIL, and FLW, on average, over 40 % of the total phenotypic variation was explained by the identified QTLs. The highest amounts of phenotypic variation explained in a single trial for each of these five traits were 65.0, 56.7, 53.5, 58.5, and 58.7 %, respectively (Table 1).

Yield component QTLs

QTLs were identified for all yield component traits in all trials. We found that in Wangshuibai, *QSn.nau-5A* and *QTn.nau-5A*, which both mapped to the same interval on chromosome 5A, were associated with increased total tillers and spikes per plant. The associations of these intervals with TN and SN had average LOD values of 7.1 and 6.3 and explained, on average, 13.9 and 12.4 % of the phenotypic variation in three trials. These observations imply that this interval on chromosome 5A contains a major QTL that determines the number of tillers and the number of effective spikes per plant. Su et al. (2009) have related this interval to a minor QTL for ear number per plant in a doubled haploid population derived from the Hanxuan10 x Lumai14 cross. *QSn.nau-4B* detected in the present study shared the same interval as *QSn.sdau-4B* (Deng et al. 2011). *QSn.nau-4B* and *QSn.nau-6D* intervals in Nanda2419 did not affect total tiller number but increased effective spikes per plant and could thus be useful for raising spike formation efficiency. *QTn.nau-4A* did not affect effective spikes per plant and are thus likely less important for breeding purposes.

Of the six QTLs associated with GN, four were identified in at least three trials (Table 3). Two GN QTLs were mapped to chromosome 4B and were associated with increased grain number through the Wangshuibai alleles, but only the *QGn.nau-4B.1* interval has been previously reported to be associated with kernel number and linked to the *Rht-B* locus (Somers et al. 2004; Quarrie et al. 2005; Deng et al. 2011). The *QGn.nau-4D* interval shown in this study was in the chromosome region near the *Rht-D* locus (Somers et al. 2004). Because the presence of *Rht-B1b* and *Rht-D1b* can lead to increased grain numbers per spike

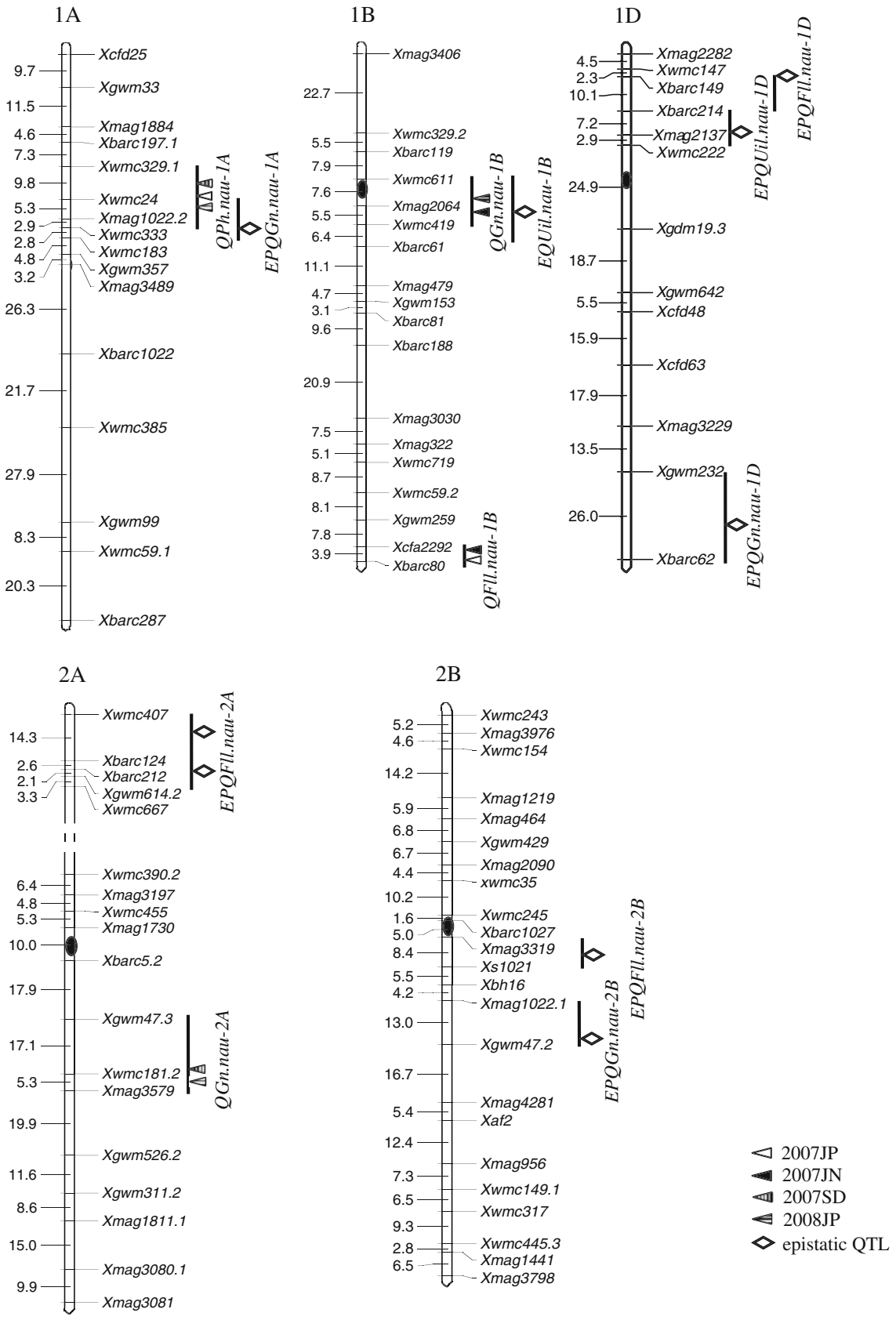

Fig. 1 Distribution of the detected QTLs and epistatic loci. The framework map was generated using data of Xue et al. (2008). The *vertical solid line* represents the QTL peak interval

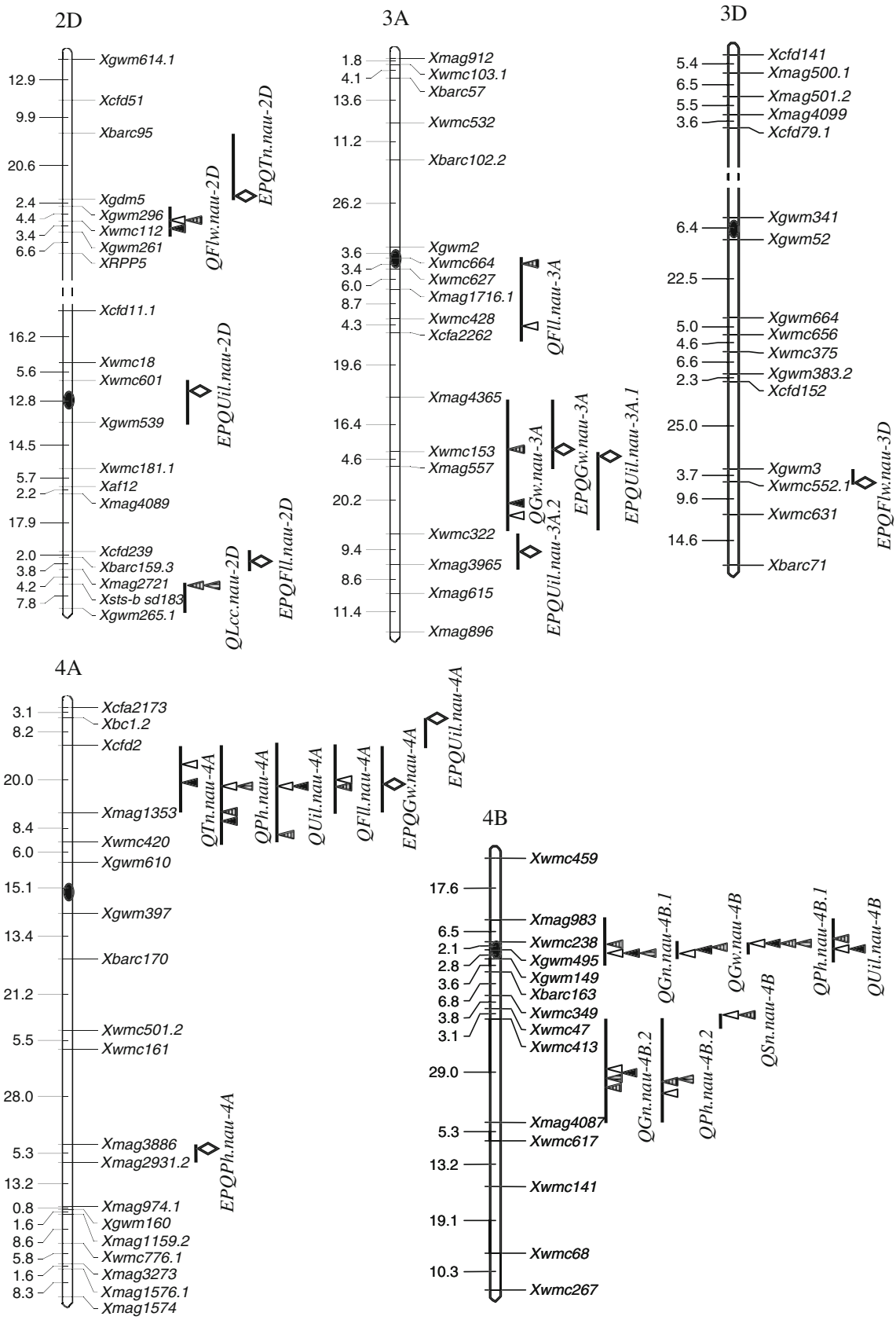

Fig. 1 continued

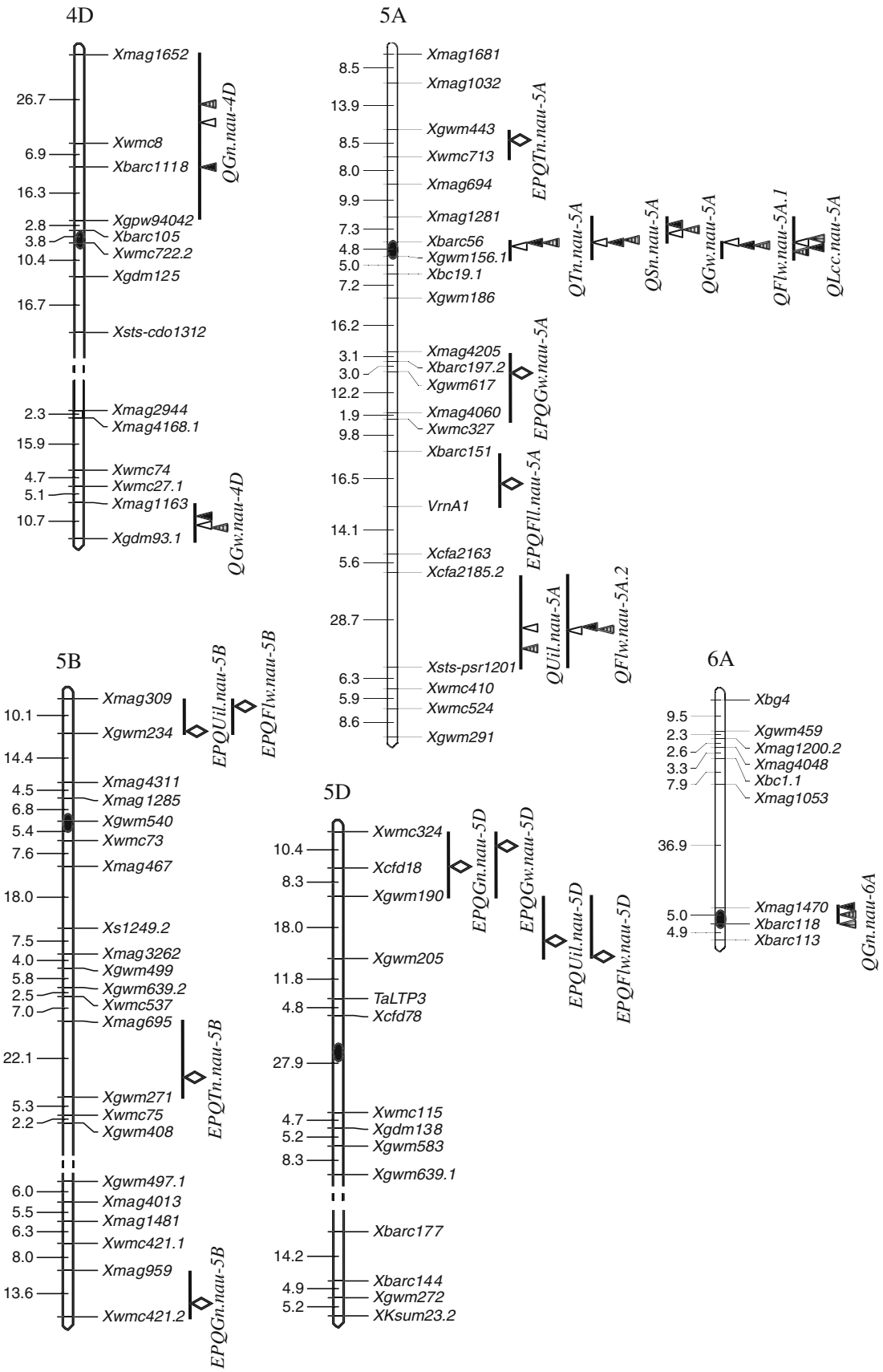

Fig. 1 continued

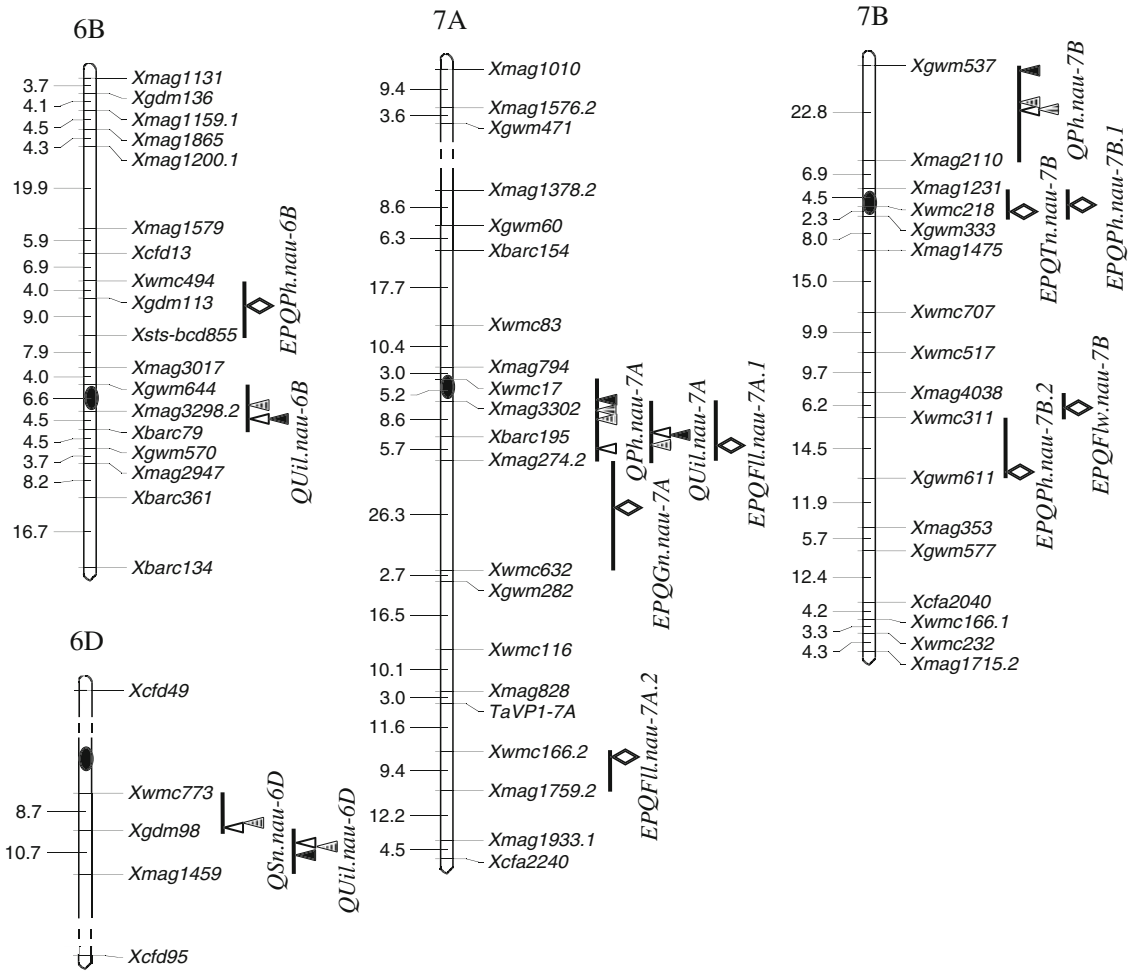

Fig. 1 continued

(Allan 1989; Borrell et al. 1991; Börner et al. 1993; Li et al. 1998; Rebetzke et al. 2011), it is likely that these two QTLs are related to the effects of dwarfing genes. However, the examination of the parent cultivars (Nanda2419 and Wangshuibai) with markers for *Rht-B1b* and *Rht-D1b* (Ellis et al. 2002) indicated that the parent cultivars do not carry both of these genes (data not shown); the plant heights of the parent cultivars (over 110 cm, Table 1) further support this conclusion. In fact, the *QGn.nau-4D* and *Rht-D* intervals are located in different deletion bins (Xue et al. 2008; Erayman et al. 2004). McIntyre et al. (2010) detected a QTL for grain number per spike in the *Xwmc48.2-Xcfd23* interval on chromosome 4DS, but its relationship with *QGn.nau-4D* could not be determined. Other QTLs associated with GN detected in all trials included *QGn.nau-2A* and *QGn.nau-6A*. The *QGn.nau-2A* interval has been related to GN in association analyses with 137 wheat germplasm accessions (Yao et al. 2009). Peng et al. (2003) identified a major QTL associated with kernel number in this interval in a wild emmer wheat population, accounting for 38.3 % of the phenotypic variation. The association of *QGn.nau-6A* with GN has not been well documented before.

Of the four chromosome regions associated with kernel weight, the *QGw.nau-4D* intervals have not previously been reported, although certain QTLs associated with grain weight have been mapped to 4D (McCartney et al. 2005; Huang et al. 2006). *QGw.nau-4B* and *QGw.nau-5A* were two major QTLs identified as being associated with higher kernel weight in Nanda2419. Cuthbert et al. (2008) identified one major QTL associated with kernel weight in the same region of chromosome 4B in the wheat line BW278 and one major QTL associated with kernel weight in the same region of chromosome 5A in the Superb cultivar. The associations of the 4B and 5A intervals with kernel weight have also been reported in other studies (Zhang et al. 2008; Sun et al. 2010; Wang et al. 2011). However, contrary to conclusions of Cuthbert et al. (2008), the effect of the *QGw.nau-4B* interval was not likely associated with the *Rht-B1b* interval of chromosome 4B, because neither mapping parent carries this gene. *QGw.nau-3A* was found in the same chromosomal region as *Tgw.ipk-3A* in the

XX86 variety (Huang et al. 2004). Moreover, the interaction between Nanda2419 allele of *QGw.nau-3A* and genetic factor in the *Xcfd2-Xmag1353* interval of chromosome 4A of Wangshuibai also contributed to increased kernel weight (Table 4). It was unexpected that all the detected GW QTLs increased kernel weight through Nanda2419 alleles, since Wangshuibai and Nanda2419 had a similar kernel weight. Similar phenomenon was noted in one durum mapping population using elite breeding line UC1113 as one of the parents (Zhang et al. 2008). This could be due to the fact that GN is determined developmentally earlier than GW and there is a negative association between GW and GN.

PH and UIL QTL

The six QTLs associated with PH identified in this study were all detectable in at least three of the four trials (Table 3). All of the QTLs, except the *QPh.nau-4B.2* and *QPh.nau-4A* intervals, have been related to plant height in other studies (Huang et al. 2004; Liu et al. 2006; Chu et al. 2008; Tsilo et al. 2010; Cui et al. 2011). *QPh.nau-4B.1* was mapped to the same chromosome region as the QTLs associated with PH on chromosome 4B reported by Huang et al. (2004), Liu et al. (2006) and Tsilo et al. (2010), and these QTLs were identified with similar LOD values in different studies. Cui et al. (2011) mapped a QTL associated with plant height in the same interval as that of *QPh.nau-1A* in a RIL population derived from a Weimai 8 × Jimai 20 cross. The QTL intervals for *QPh.nau-7A* and *QPh.nau-7B* on chromosome arms 7AL and 7BS were coincident or overlapped with the intervals of reported QTLs on 7AL (Huang et al. 2004; Zhang et al. 2011) and 7BS (Huang et al. 2006; Liu et al. 2011), respectively. Because the Akagomughi cultivar carries *Rht9* on chromosome 7BS (Worland et al. 1984) and is the parent of Nanda2419 (Mentana), it would be interesting to determine the relationship between *QPh.nau-7B* and *Rht9*. The *QPh.nau-7B* interval was also related to flowering time (Lin et al. 2008) and kernel weight (Hai et al. 2008).

UIL is a component of plant height. As expected, three of the six QTLs associated with UIL, including those mapping to chromosomes 4A, 4B and 7A, were located at the same intervals as QTLs associated with plant height (Table 3). However, the *QPh.nau-1A* and *QPh.nau-7B* intervals were not related to UIL, and *QUil.nau-6B* and *QUil.nau-6D* were not found to have any effect on plant height. It should be noted that *QUil.nau-6B* was most

Table 4 Digenic epistatic loci for the investigated traits across environments

Traits	Locus A		Locus B		LOD	Phenotype means[a]			
	Interval/chr.	Peak position[b]	Interval/chr.	Peak position		aabb	AAbb	aaBB	AABB
TN	*Xbarc95-Xgdm5*/2D	20.0	*Xmag695-Xgwm271*/5B	17.0	4.7	16.2	18.3	18.2	16.8
	Xgwm443-Xwmc713/5A	3.0	*Xmag1231-Xgwm333*/7B	6.0	4.8	16.0	18.4	18.1	16.8
GN	*Xwmc24-Xwmc183*/1A	8.0	*Xgwm232-Xbarc62*/1D	15.0	4.6	50.5	52.7	55.3	50.1
	Xmag1022.1-Xgwm47.2/2B	11.0	*Xmag959-Xwmc421.2*/5B	9.0	5.3	55.2	51.8	47.4	53.1
	Xwmc324-Xgwm190/5D	10.0	*Xmag274.2-Xwmc632*/7A	12.0	5.5	49.7	55.4	53.9	50.9
GW	*Xmag4365-Xmag557*/3A	16.0	*Xcfd2-Xmag1353*/4A	12.0	4.9	4.2	4.2	4.5	4.0
	Xmag4205-Xwmc327/5A	6.0	*Xwmc324-Xgwm190*/5D	4.0	6.1	4.4	4.0	4.1	4.3
PH	*Xmag3886-Xmag2931.2*/4A	1.0	*Xmag1231-Xgwm333*/7B	4.0	4.6	115.5	111.9	113.4	118.4
	Xwmc494-Xsts-bcd855/6B	6.0	*Xwmc311-Xgwm611*/7B	14.0	5.9	112.0	115.9	120.5	112.0
UIL	*Xwmc611-Xbarc61*/1B	8.0	*Xmag3093-Xgwm234*/5B	10.0	6.0	24.9	21.5	24.0	25.1
	Xbarc214-Xwmc222/1D	7.0	*Xgwm190-Xgwm205*/5D	13.0	5.6	22.8	25.1	24.9	22.4
	Xwmc601-Xgwm539/2D	3.0	*Xwmc322-Xmag3965*/3A	5.0	5.0	24.6	22.9	22.8	25.1
	Xwmc153-Xwmc322/3A	1.0	*Xbc1.2-Xcfd2*/4A	0.0	4.9	22.4	24.3	25.7	23.7
FLL	*Xbarc149-Xbarc214*/1D	0.0	*Xbarc124-Xgwm614.2*/2A	3.0	4.9	25.6	27.0	27.2	25.1
	Xmag3319-Xs1021/2B	5.0	*Xwmc166.2-Xmag1759.2*/7A	1.0	4.5	27.2	24.8	25.5	26.6
	Xcfd239-Xmag2721/2D	3.0	*Xwmc407-Xbarc124*/2A	6.0	4.5	27.3	25.5	25.1	26.6
	Xbarc151-VrnA1/5A	9.0	*Xmag3302-Xmag274.2*/7A	11.0	6.6	27.8	25.5	24.6	26.4
FLW	*Xgwm3-Xwmc552.1*/3D	3.0	*Xgwm190-Xgwm205*/5D	18.0	5.2	1.6	1.7	1.7	1.6
	Xmag3093-Xgwm234/5B	2.0	*Xmag4038-Xwmc311*/7B	4.0	4.9	1.5	1.7	1.7	1.6

[a] Shaded row represents synergistic epistatic loci beneficial for yield increase. The capital letter under 'Phenotype means' represents Wangshuibai allele

[b] Epistatic QTL peak distance from the left-side marker of the interval

strongly associated with UIL and had the highest LOD scores of all of the QTLs associated with UIL.

Flag leaf-related trait QTLs

None of the QTLs for FLL and FLW overlapped (Fig. 1). *QFlw.nau-5A.1* on chromosome 5A was a major QTL associated with FLW and explained 28.7–35.6 % of phenotypic variation. *QFlw.nau-2D* was located at the interval associated with FLW in the Cranbrook × Halberd doubled haploid population (Coleman et al. 2001). This 2DS interval was also related to QTLs associated with flag leaf weight, greenness (Su et al. 2006), and spike length (Ma et al. 2007). The other QTLs associated with FLW and the three QTL intervals associated with FLL have not been reported elsewhere. *QFll.nau-1B* interval was related to flowering time in the same population (Lin et al. 2008).

Of the two QTL intervals associated with LCC, *QLcc.nau-5A* and *QLcc.nau-2D* were consistent with the minor QTL associated with LCC on chromosome 5A reported by Yang et al. (2007) and with the minor QTL associated with chlorophyll b content on chromosome arm 2DS reported by Zhang et al. (2009), respectively. *QLcc.nau-5A,* with LOD values ranging from 3.9 to 6.9, had the largest effect on LCC in this study; this interval furthermore overlapped with the interval of *QFlw.nau-5A.1,* the major QTL associated with FLW, which partially explains the positive correlation of LCC with FLW (Table 2).

Trait correlations and QTL clustering

We found that some of the yield components investigated in this study were correlated to certain degree (Table 2). This finding could partially explain the phenomenon of QTL clustering in some chromosome regions (Fig. 1).

PH was positively related to FLL, TN, SN, and GW. With regard to PH and FLL, *QPh.nau-4A* and *QFll.nau-4A* mapped to an identical interval with the Nanda2419 alleles always conditioned dwarfing and shorter flag leaves. *EPQFll.nau-7A.1* was located at the same interval as *QPh.nau-7A*; the Nanda2419 allele for the latter QTL was associated with increased PH, whereas the Nanda2419 allele of the former QTL contributed to longer flag leaves by interacting with the Nanda2419 allele at *EPQFll.nau-5A*. It has been documented that genes for reduced plant height, such as *Rht-B1b*, *Rht-B1c,* and *Rht-D1b*, have pleiotropic effects on the leaf, stem, and ear through the inhibition of cell elongation and the reduction of cell size (Keyes et al. 1989; Youssefian et al. 1992; Tonkinson et al. 1995; Miralles et al. 1998). Thus, both linkage and pleiotropic effects could lead to the clustering of these related traits.

One of the major QTLs associated with PH, *QPh.nau-4B.1,* was related to all yield component traits but not to leaf traits (Fig. 1). The Wangshuibai allele of this QTL produced shorter plants and more tillers and kernels, but lighter kernel weight. This finding is consistent with the negative correlation between PH and GN and the positive correlation between PH and GW (Table 2). The same is true for *QPh.nau-4B.2* and *QGn.nau-4B.2,* which mapped to identical intervals. McCartney et al. (2005) also reported a positive correlation between PH and GW at the *QPh.nau-4B.1* interval. Similarly, Rattey et al. (2009) and McIntyre et al. (2010) identified an interval on chromosome 1D related to PH and GW. The associations between PH and yield components were also shown in epistatic analysis. The Nanda2419 allele of *QPh.nau-1A* was associated with short PH and increased GN when interacting with the Wangshuibai allele of *EPQGn.nau-1D* (Table 4). The 4A QTL interval associated with TN, PH, UIL, and FLL had epistatic effects on GW when interacting with the interval *Xmag4365-Xmag557*. The allele for higher PH and less TN was beneficial to GW.

The chromosome region surrounding *Xmag1281-Xbarc56* carried one of the major QTLs associated with GW, FLW, LCC, TN, and SN. The Nanda2419 allele of this interval produced higher FLW, LCC, and GW and was negatively related to TN/SN. Similar to this result, Quarrie et al. (2006) identified a QTL interval on 7AL in the breeding line SQ1 that increased FLW, LCC, GW, and grain yield per ear.

The end goal of wheat breeding is higher yield. The significantly negative correlation between GW and SN and no correlation between GN and SN (Table 2) indicate that increasing tillers or spikes per plant has a more significant impact on kernel weight than on kernel number, whereas the significantly negative correlation between GW and GN suggests that floret differentiation and grain filling are in direct competition with each other for assimilates (Bremner and Rawson 1978; Borrás et al. 2004). This relationship has been well documented in the opposing effects of QTLs on these traits. For example, the QTLs on chromosomes 3B (Cuthbert et al. 2008), 7A (McIntyre et al. 2010), 4BL, and 5AL (Wang et al. 2011) produce opposing effects on GW and GN, whereas the 4BS (Cuthbert et al. 2008) and 5AL intervals (Kato et al. 2000) produce opposing effects on SN and GW. Thus, in breeding practice, adjusting the weight of individual yield components in yield formation according to the ecological conditions of the growing area is very important to increasing the yield potential. Moreover, more attention should be paid to QTLs that do not negatively affect yield components, such as *QGw.nau-3A*, *QGw.nau-4D*, *QGn.nau-2A*, *QGn.nau-4D,* and so on. FLW and LCC had significant positive effects on GW and environment-dependent effects on GN, indicating that increasing FLW

and LCC could be helpful for increasing kernel weight and yield potential.

Genetic complexity of yield formation

Yield formation is determined by complicated genetic interactions. This is reflected not only in QTL mapping and correlation analysis of the yield components and yield-related traits but also in epistatic analysis. Of 38 epistatic loci, 12 were associated with QTL intervals or epistatic loci for at least one other trait examined in this study (Fig. 1). In particular, the 36.7-cM chromosome region flanked by *Xwmc324-Xgwm205* on chromosome 5D was implicated in four pairs of epistatic interactions associated with GN, GW, UIL, and FLW (Table 4).

Based on the associations of individual traits with yield, 13 pairs of the epistatic loci showed antagonistic epistasis, and six pairs of the epistatic loci showed synergistic epistasis beneficial to yield increase (Table 4). In antagonistic epistasis, pyramiding the beneficial alleles of two epistatic loci produced fewer effects than expected based on the allelic effects of the individual locus under no genetic interaction; in synergistic epistasis, pyramiding the beneficial alleles of two epistatic loci produced larger effects than expected based on the allelic effects of the individual locus under no genetic interaction.

QTLs in Nanda2419 for greater yield potential

One of the two mapping parents used in this study was Wangshuibai, an indigenous cultivar with poor agronomical traits; the other parent was Nanda2419, an elite cultivar and strong breeding parent. We were able to compare the genetic compositions of these two cultivars as they related to yield potential. We found that Nanda2419 contributed all QTLs associated with higher kernel weight, higher LCC and the major QTL associated with wider flag leaf, and three of six QTLs associated with reduced height. Nanda2419 also carried QTLs associated with higher numbers of effective tillers and higher grain number; however, for these two traits, Wangshuibai seemed to play a greater role. Four QTL clusters in Nanda2419 and three in Wangshuibai contributed to the improvement of multiple traits. The QTL clusters surrounding *Xwmc238-Xgwm495* and *Xmag1281-Xbarc56* had opposing effects on yield components. In both intervals, the Nanda2419 alleles improved kernel weight. Because of negative correlations between yield-related traits, the intervals affecting fewer traits could be more useful in breeding. In this study, 11 Nanda2419 intervals and two Wangshuibai intervals improved a single trait associated with breeding goals. A majority of these QTLs or QTL clusters were detected in all the trials set in Zone II and III wheat-producing regions, with Nanda2419 contributing to greater breeding potential. These results suggested that Nanda2419 is superior to Wangshuibai in terms of numbers, organization, and expression stability of useful QTLs.

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