RESEARCH ARTICLE

Mapping of QTL for tiller number at different stages of growth in wheat using double haploid and immortalized F_2 populations

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Abstract

Effective tiller number is one of the most important traits for wheat (*Triticum aestivum* L.) yield, but the inheritance of tillering is poorly understood. A set of 168 doubled haploid (DH) lines derivatives of a cross between two winter wheat cultivars (Huapei 3 and Yumai 57), and an immortalized F_2 (IF_2) population generated by randomly permutated intermating of these DHs were investigated, and QTLs of tillering related to the maximum tillering of pre-winter (MTW), maximum tillering in spring (MTS), and effective tillering in harvest (ETH) were mapped. Phenotypic data were collected for the two populations from two different environments. Using inclusive composite interval mapping (ICIM), a total of 9 and 18 significant QTL were detected across environments for tillering in the DH and IF_2 populations, respectively. Four QTLs were common between two populations. A major QTL located on the 5D chromosome with the allele originating from Yumai 57 was detected and increased 1.92 and 3.55 tillers in MTW and MTS, respectively. QTLs (*QMts6D, QEth6D*) having a neighbouring marker interval at *Xswes679.1* and *Xcfa2129* on chromosome 6D was detected in MTS and ETH. These results provide a better understanding of the genetic factors for selectively expressing the control of tiller number in different growth stages and facilitate marker-assisted selection strategy in breeding.

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Introduction

Tillering is one of the most important agronomic traits in cereal crops because tiller number per plant determines the number of spikes or panicles per plant, a key component of grain yield and/or biomass. Tillering or the degree of branching determines shoot architecture. The architecture of the shoot system affects a plant's light harvesting potential, the synchrony of flowering and seed set and, ultimately, the reproductive success of a plant (Satorre and Slafer 1999; Yang *et al*. 2006; Kuraparthy *et al*. 2007). Tillers that grow from the main stem are called primary tillers and those grow from primary tillers are called secondary tillers (Kirby and Appleyard 1981). In practice, however, only a few tiller buds grow into a tiller, and only a proportion of these tillers survive to become the ultimate number of tillers, depending on tiller appearance and tiller survival (Hodges 1991; Miralles and Richards 2000; Evers *et al*. 2006). Tillers of different genotypes show various spatial orientations at different developmental stages, giving rise to morphologically distinct plant types. Before the stem elongation, seedling growth habit (SGH) varies from prostrate to semi-prostrate to erect. After anthesis, spikes of the adult plant also differ in their compactness from spreading to compact (Li *et al*. 2002). However, the genetic basis for tillering is not well elucidated.

The application of molecular marker techniques for quantitative trait locus (QTL) analysis has proved to be an effective approach to dissect complex quantitative traits in cereals (Hodges 1991). Although a number of QTL controlled tillering were discovered in rice (Brondani *et al*. 2002; Li *et al*. 2003; Liu *et al*. 2006; Zhao *et al*. 2008; Liu *et al*. 2009), barley (Buck-Sorlin 2002; Babb and Muehlbauer

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2003; Franckowiak *et al*. 2005) and rye (Malyshev *et al*. 2001; Lukaszewski *et al*. 2004; Yamada *et al*. 2004), only few studies have been carried out in wheat. Law (1967) discovered that the factor responsible for tiller number on chromosome 7B in wheat could be either the marker e_1 acting pleiotropically on this character or a factor tightly linked to the marker. Shah *et al*. (1999) mapped a significant QTL (R^2 = 19.4%) for tillering on chromosome arm 3*AL* in wheat. Kato *et al*. (2000) detected three minor QTLs (*Vrn-A1, QTn.ocs-5A.1* and *QTn.ocs-5A.2*) for tillering associated with the vernalization gene on chromosome 5A of wheat. Li *et al*. (2002) reported QTLs with significant effect on tiller number per plant were found to be located on 1D, 2D and 6A in wheat with winter/spring growth characters. Kuraparthy *et al*. (2007) showed a tillering mutant, tiller inhibition (*tin*3) gene which was placed on 3A, and produced one main culm compared to the wild type with many tillers in the F_2 wheat population. However, how to select express tillering QTLs in different growth-stages in wheat is poorly understood. Hua *et al*. (2003) proposed a novel experimental design which was referred to as 'immortalized F_2' (IF_2) population, consisting of hybrid (F_1) individuals created by crossing a set of recombinant inbred lines (RILs). The IF_2 population has a genetic structure resembling the F_2 population, and the genotypes within the population can be duplicated when necessary, with the advantages of permanent conservation such as the RIL and DH populations. Also the IF_2 population allows trials at multiple locations over several years. Moreover, molecular marker data for an IF_2 population can be deduced from that of corresponding DHs. In the present study, QTLs associated with tiller number were identified for three different growth stages in two wheat populations, DH and IF_2. The QTL detected in two populations will be useful for developing further selection strategies in wheat breeding.

Materials and methods

Plant materials

By microspore culture, 168 DH lines were developed from a cross between Huapei 3 and Yumai 57 (Guo *et al*. 2004; Hai and Kang 2007). The IF_2 population was created following the design of Hua *et al*. (2003). In this design, crossing was done among DHs chosen by random permutations of 168 lines. In each round of permutation, the 168 DHs were randomly divided into two groups, and the lines in two groups were paired up at random without replacement to provide parents for 84 crosses. Each of 168 lines was used only once in each round of pairing and crossing. This procedure was repeated twice, resulting in a population consisting of 168 crosses, which constituted the IF_2 population used.

Field experiments and linkage map

Field experiments were carried out in the year 2008 at Tai'an, Shandong province (116°36'E, 36°57'N) and Jiyuan, Henan province (112°36'E, 35°05'N). Shandong and Henan provinces are the main growing areas for winter wheat in PR China. The field planting followed a randomized complete block design with the DH population and the IF_2 population in each trail. Each plot consisted of three rows: one row for a cross in the IF_2 population and two rows for each of its respective parents (DH lines). There were 20 plants in each row, with a distance of 10 cm between plants within each row and 25 cm between rows. The field management followed the local standard practices. Ten plants in the middle of the inner row were chosen from each plot for trait evaluation, but plants in the plot border were not selected. Tiller number, measured as the number of tillers which arose axillary at least 0.5 cm on every plant in the maximum tillering of prewinter (MTW) and spring (MTS), and the effective tillering at harvest (ETH) was measured as bearing ears. Trait measurements were averaged for 10 plants within each plot for subsequent statistical analyses.

The DH population map built in 2008 had 323 molecular markers, including 284 SSR loci, 37 EST-SSR loci, 1 ISSR loci and 1 HMW loci, that were mapped on 24 linkage groups, covering 2485.7 cM according to the Zhang *et al*. (2009). The genotypes of the IF_2 population were deduced on the basis of DH line genotypes.

Statistical analysis

Analysis of variance (ANOVA) and correlation was performed using statistical software SPSS version 13.0 (SPSS, Chicago, USA). The heritability (h^2) was calculated as: $h^2 = (\sigma_b^2 - \sigma_w^2)/(\sigma_b^2 + (r-1)\,\sigma_w^2)$, where σ_b^2, the between groups variance; σ_w^2, the within groups variance and r, the number of observations. The estimates of σ_b^2, σ_w^2 were obtained from ANOVA.

QTL analyses were performed separately for the DH and IF_2 populations. QTLs were mapped by inclusive composite interval mapping (ICIM) (Li *et al*. 2007, 2008; Zhang *et al*. 2008; Wang 2009). The LOD score for declaring a QTL was 2.0 for two populations and the step of position was 1 cM. The mean QTLs were listed in our study. All QTL names are abbreviations of the trait followed by its respective linkage group number and the chromosome. An alphabetical a or b was added if more than one QTL were found in the same linkage group.

Results

Phenotypic performance

The measurements of tiller number in the three growth stages for both populations as well as two parents are listed in table 1. For the tiller numbers measured, Yumai 57 had higher phenotypic values than Huapei 3. The performance of the IF_2 population was over a larger range of variation than those of the DH population in the three stages, but both had similar averages which were located in the middle of the two parents, and which showed transgressive segregation and distribution in the IF_2 and DH populations. The numbers of tillers

in MTW, MTS and ETH were greater in Tai'an than in Jiyuan in both populations. Both DH and IF_2 populations showed high heritability from 0.77 to 0.95, which also indicates that the environment had relatively small effects on variation in tiller number in the three growth stages.

The correlations among the MTW, MTS and ETH are shown in table 2. The traits were significantly correlated with each other in the DH and IF_2 populations. MTW showed significantly positive correlation with MTS ($P < 0.01$), MTS showed a significantly positive correlation with ETH ($P < 0.01$). MTW showed significantly positive correlation with ETH ($P < 0.05$).

QTL mapping

For each growth stage, the analysis was carried out for data in individual environments. Detailed information of QTL detected in individual environments is presented in tables 3 and 4.

Maximum tillering of pre-winter

Seven QTLs were identified for MTW; both parents carried QTL alleles which increased phenotypic values (tables 3 and 4). A major QTL (*QMtw5D*) which was detected in two environments in both the DH and IF_2 populations was mapped to

Table 1. Phenotypic summary of tiller number in maximum tillering of pre-winter, maximum tillering in spring, and effective tillering in harvest for Huapei 3 (P_1), Yumai 57 (P_2), the DH population, and the IF_2 population at Tai'an and Jiyuan in 2008.

	Parents		DH population				IF_2 population			
Tiller period	Huapei 3	Yumai 57	Mean	Min	Max	h^2	Mean	Min	Max	h^2
MTW[a]	19	30	25	14	42	0.95	25	12	38	0.94
MTW[b]	17	19	18	11	32		18	5	30	
MTS[a]	20	27	27	13	44	0.77	26	11	38	0.81
MTS[b]	22	24	23	10	47		22	8	41	
ETH[a]	13	15	16	9	23	0.90	15	8	28	0.91
ETH[b]	19	22	13	7	22		13	5	24	

[a]Environment, 2008 Tai'an; [b]environment, 2008 Jiyuan; min, minimum; max, maximum; h^2, heritability.

Table 2. Coefficients of tiller number in DH population and IF_2 population.

	DH population			IF_2 population		
Trait	MTW	MTS	ETH	MTW	MTS	ETH
MTW						
MTS	0.49**			0.31**		
ETH	0.18*	0.59**		0.20*	0.59**	

*Significant at 0.05 probability level; **significant at 0.01 probability level.

Table 3. Putative QTL for tillering detected in the DH population through ICIM.

Trait	QTL	Position	Interval	A	LOD	$R^2(\%)^c$
MTW[a]	*QMtw6A*	9	*Xgwm459–Xgwm334*	−1.37	3.12	8.06
MTW[b]	*QMtw5D-1*	74	*Xwmc215–Xbarc345*	−2.00	7.67	23.19
MTS[a]	*QMts6D-1*	157	*Xswes679.1–Xcfa2129*	1.74	2.60	8.68
MTS[b]	*QMts4D*	125	*Xcfe188–Xbarc224*	−1.38	2.92	5.53
	QMts5D-1	73	*Xwmc215–Xbarc345*	−3.51	13.03	34.96
ETH[a]	*QEth5B.2*	28	*Xbarc232–Xwmc235*	0.76	2.60	10.91
ETH[b]	*QEth2B*	6	*Xwmc764–Xbarc200*	−0.58	2.15	4.49
	QEth3A	198	*Xbarc1177–Xbarc276.2*	−0.60	2.20	4.62
	QEth6A	43	*Xgwm1055–Xwmc553*	−0.68	2.82	6.03

[a]Environment, 2008 Taian; [b]environment, 2008 Jiyuan; A, additive effect, positive additive effects indicate that the Huapei 3 allele increases the value of the trait; [C]proportion of the phenotypic variation explained by the QTL.

Table 4. Putative QTL for tillering detected in the IF2 population through ICIM.

Trait	QTL	Position	Interval	A	D	LOD	R^2 (%)[c]	D/A[d]
MTWa	*QMtw5A.2*	11	*Xcwem32.2–Xwmc59*	2.06	0.67	3.28	8.21	PD
	QMtw5D-1	79	*Xwmc215–Xbarc345*	−1.92	−2.08	3.79	14.18	OD
MTWb	*QMtw1D*	48	*Xcfd19–Xwmc93*	−1.06	2.15	3.93	9.45	OD
	QMtw4D	1	*Xwmc334–Xwmc331*	0.61	2.62	4.53	7.97	OD
	QMtw5D-2	63	*Xbarc320–Xwmc215*	−2.97	0.37	14.01	26.89	PD
MTSa	*QMts2B*	94	*Xwmc445.2–Xgwm111*	−0.23	2.7	2.57	6.43	OD
	QMts5A.2	3	*Xcfe026.1–Xcwem32.2*	2.76	2.75	8.16	15.91	PD
	QMts5D-2	67	*Xbarc320–Xwmc215*	−2.29	−0.95	6.49	12.71	PD
	QMts6A	67	*Xwmc553–Xgwm732*	0.33	−3.26	2.03	9.51	OD
	QMts6D-2	64	*Xbarc054–Xgwm55*	−0.22	3.58	3.36	11.28	OD
MTSb	*QMtps3A*	107	*Xcfa2134–Xwmc527*	0.85	−2.5	3.58	6.73	OD
	QMts5D-2	68	*Xbarc320–Xwmc215*	−3.55	−0.31	13.08	28.51	PD
ETHa	*QEth4D*	94	*Xgwm194–Xcfa2173*	1.75	−0.64	4.45	21.32	PD
	QEth6D-3	107	*Xgwm133.2–Xswes861.1*	4.67	−2.37	3.9	22.85	PD
	QEth6D-1	132	*Xswes679.1–Xcfa2129*	2.78	−3.68	3.31	16.28	OD
ETHb	*QEth2B*	74	*Xbarc477–Xwmc175*	1.19	−0.14	3.97	9.12	PD
	QEth2D	0	*Xgwm296–Xwmc112*	0.13	1.14	2.11	4.52	OD
	QEth6A	43	*Xgwm1055–Xwmc553*	−1.14	0.22	3.89	8.60	PD

[a]Environment, 2008 Tai'an; [b]environment, 2008 Jiyuan; A, additive effect; D, dominance effect. Positive additive effects indicate that the Huapei 3 allele increases the value of the trait; [c]proportion of the phenotypic variation explained by the QTL; [d]ratio of estimated dominant effect to the absolute value of additive effect. When a ratio is larger than unity it is regarded as overdominance; ratio falling between 0 and 1 is regarded as partial dominance.

the *Xwmc215–Xbarc345* interval on chromosome 5D (figure 1), explaining phenotypic variation form 14.18% to 26.89%. In the DH population, the QTL *QMtw6A* on 6A was detected in Tai'an (in 2008), but it was not significant in the IF_2 population. At the same time, QTLs distributed on chromosomes 1D, 4D and 5A.2 were detected in two trials in the IF_2 population but it did not show a significant effect in the DH population. Its D/A ratio were near *QMtw5D* and showed an overdominance effect in Tai'an (in 2008) but showed a partial dominance in Jiyuan (in 2008), with the dominant allele originating from Yumai 57 and conferring lower tillers.

Maximum tillering in spring

A total of 10 regions were found to have effects on MTS. Of these QTLs, Yumai 57 alleles increased tiller number and had additive effects of 0.22 and 3.55, which accounted for 5.53% and 34.96% of the phenotypic variance, respectively. *QMts5D* and *QMts6D* were identified in both DH and IF_2 populations, but *QMts5D-1* (DH) mapped to the *Xwmc215–Xbarc345* interval while *QMts5D-2* (IF_2) were in the *Xbarc320-Xwmc215* interval. Similarly, *QMts6D-1* (DH) in the *Xswes679.1–Xcfa2129* interval while *QMts6D-2* (IF_2) in the *Xbarc054–Xgwm55* interval (Figure.1). However, the remaining QTLs (*QMts2B, QMts3A, QMts4D* etc.) were only detected once in DH or IF_2, likely because of this trait's higher sensitivity to environments (tables 3 and 4).

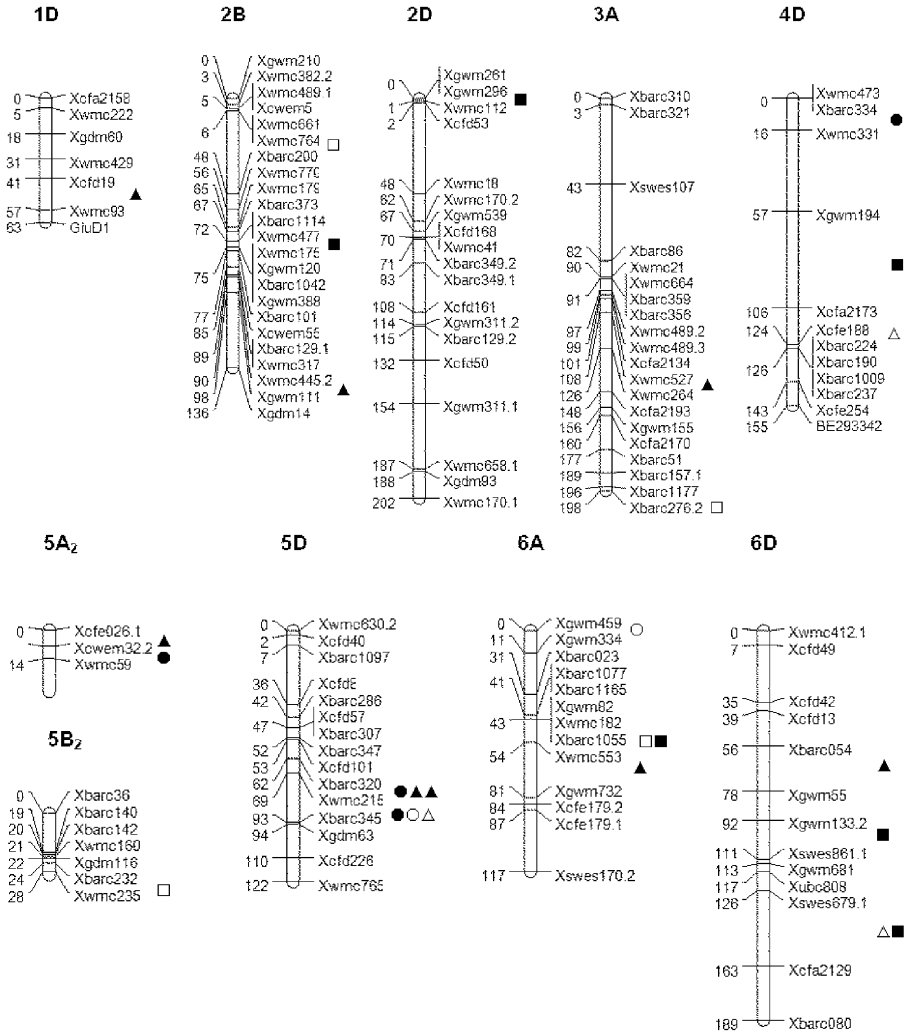
Both *QMts5A.2* and *QMts5D* showed partial dominance but the dominant alleles originated from Huapei 3 and Yumai 57, respectively. *QMts3A* and *QMts6A* showed overdominance with Huapei 3 contributing the dominant allele, respectively, both increasing tillers.

Effective tillering in harvest

Ten QTLs were detected for ETH. The QTL on chromosomes 2B and 6A were both identified in two populations; additionally, *QEth6A* was identified in the interval *Xgwm1055–Xwmc553* in DH and IF_2, where again the allele had an additive effect of 0.68 and 1.14 on tiller numbers, which accounted for 6.03% and 8.60% of the phenotypic variance, respectively. Two QTLs (*QEth5B.2* and *QEth3A*) were detected in the DH population (table 3), but neither of them were significant in the IF_2 population. On the contrary, four QTLs on 2D, 4D and 6D (*QEth2D, QEth4D* and *QEth6D*) were detected in the IF_2 population, but they were not detected in the DH population. The Huapei 3 allele of *QEth2D* and *QEth4D* increased tillers; the former showed overdominance and the latter showed partial dominance.

Discussion

In the present study, the IF_2 as well as the DH population derived from Huapei 3 × Yumai 57 were used to identify the tillering QTLs determining the MTW, MTS, and ETH. Some QTLs revealed in IF_2 were detected at the exact marker interval or neighbouring marker interval in at least one, other investigation in the DH (tables 3 and 4), indicated that both kinds of populations were equally effective in mapping QTLs. At the same time, more QTLs were detected in the IF_2. This also indicated that the IF_2 population had a relatively higher



○ QTL for MTW in DH; ● QTL for MTW in IF2; △ QTL for MTS in DH; ▲ QTL for MTS in IF2; □ QTL for ETH in DH; ■ QTL for ETH in IF2

Figure 1. Positions of QTLs associated with tillering at different period in the DH and IF2 populations derived from Huapei 3 × Yumai 57 by ICIM.

efficiency of QTL detection than the DH population, because the IF_2 population could be generated by an artificial random intermating of DH lines and it had several distinct advantages for QTL analysis as the genotypes and their proportions are similar to those in F_2 population. Hua (2001) and Tian *et al*. (2008) had shown similar results. In this study, we used the same significance level in declaring putative QTLs in the IF_2 and in the DH population, in order to reduce the number of false positives that might be caused by the unknown homology and dominant/recessive relationship between alleles from the DHs. Indeed, many more putative QTLs, but unrelated between trials, would have been declared if a lower LOD (e.g., 1.5) value was used as the threshold. In ICIM, we also used a strict threshold (e.g., 2.5, 3, data not shown), to reduce the false positives. As expected, the traits with higher heritability generally had more phenotypic variation explained by the QTLs detected. For each tillering growth stage, alleles increasing the trait values were found in both parents, providing supportive evidence for transgressive segregation in phenotypes (table 1). These also could increase the scope for identifying QTL and facilitate the comparisons of QTL among different types of populations. In summary, 9 and 18 QTLs were detected across environments for tillering in the DH and IF_2 populations, respectively.

The relationship among MTW, MTS and ETH

Generally speaking, wheat is sown in October in Shandong and Henan provinces. From 10 to 15 days after seeding, tillers begin to grow and increase with the adding of leaves to the stem. The peak period of tillering quickly reaches before winter. The tiller growth stops when the mean temperature is below 0°C (first 10 days of December), this stage

of the tillering is MTW. In the following year, a great number of new tillers are formed again when the mean temperature reaches 10°C (late February). At the jointing stage, the number of tillers becomes the largest and is called MTS. The MTW, MTS and ETH are important traits which determined the population structure during the lifetime. MTW, reflecting the wheat population growth status before winter; is the most important factor for high-yield cultivars because MTW has earlier growth, larger leaf area, stronger roots, and higher spike rate, etc. MTW accounted for 70% to 80% of the total number of tillers while MTS accounted for 20% to 30%. MTS reflected the growth of wheat in spring, which determined the ears per hectare and grains per ear. The pistil and stamen differentiation also occurred simultaneously in this stage. MTS is not only affected by the number of MTW but also highly affected by spring temperature and fertilization. Very small MTS seriously affects the wheat production by reducing the wheat population and lowering the light utility efficiency (LUE). If the MTS is too large, it might lead to over-shading and light deficiency at the tillering and jointing stages, and significantly reduce ETH. Therefore, the number and growth status of tillers are very important factors for determining the structure, physiological function and yields of wheat. Overall, according to the characteristics of the tillers at different periods, wheat with high yield and high quality can be created by reducing the number of ineffective tillers and increasing the rate of effective tillers under rational field management.

QTLs of MTW, MTS and ETH

QTLs for tillering were detected in different chromosomes in MTW, MTS and ETH. Many QTLs affecting tiller number in this study, such as those in map regions 1D, 2D, 3A, 5A.2 and 6A, had also been reported previously by Shah *et al*. (1999), Kato *et al*. (2000), Li *et al*. (2002) and Kuraparthy *et al*. (2007), in different populations or mutant plants. Li *et al*. (2002) had reported a region near *Gli-A2* (*Xpsr10*) on the short arm of chromosome 6A strongly affecting tiller number. Similarly, two regions on 1D chromosome arm 1DS and on 2D chromosome arm 2DS also affected tiller number. In our study , QTL on 2D and 6A were detected at similar regions on chromosome arms 2DS and 6AS (figure 1), and we also identified a QTL on chromosome 1D, but that had a different region on 1D compared with *Xmwg837- Xmwg337* in Li *et al*. (2002). In view of the above results (figure 1), there were two QTL on 3A and 5A.2 controlling tiller number that could be detected under different environments and in different populations. The former QTL was detected on the same chromosome by Shah *et al*. (1999) and Kuraparthy *et al*. (2007), and the latter QTL was detected on chromosome 5A.2 (Kato *et al*. 2000). Kato *et al*. (2000) also detected a QTL with significant effects on tiller number on 5A.1. Shah *et al*. (1999) mapped a significant QTL for tillering on chromosome arm 7B. Both Huang *et al*. (2003) and Narasimhamoorthy *et al*. (2006) detected a QTL on 3B, but unfortunately we failed to detect any QTL on chromosome 3B, 5A.1 and 7B in the DH and IF_2 populations by ICIM. Fortunately, we did find some new QTLs which affected tiller number in different periods in the DH or/and IF_2 populations. For example, a major QTL on 5D chromosome, which was detected at MTW and MTS in two populations and explained 12.71%–34.96% of the phenotypic variation, played an important role in an early-developing tillers. A QTL on chromosome 6D was detected in MTS and ETH which had a great influence on later-developing tillers. At the same time, some QTLs on 2B, 4D and 5B.2 may effect the entire period of wheat tiller growth phases.

Selective expression of genes

Tiller number can be changed over the entire duration of wheat growth phases, and the tiller number at a certain stage was determined by the sum of QTL effects estimated by the unconditional method, while the change in tiller numbers at certain periods was controlled by the total QTL effects estimated by the conditional method (Zhu 1995; Yan *et al*. 1998; Zhao *et al*. 2008). In fact, QTLs have different effects at various stages, and exhibited the feature of time expression (Zhao *et al*. 2008). In our study, a QTL on the 6A chromosome influenced tiller numbers during the three growth periods, which were expressed with specific effects and at specific periods. For example, the QTL alleles originated from Huapei 3 which increased tillers in MTP and ETH, decreased tillers in MTS. Some QTLs were detected to relate to tiller numbers, which had specific functional periods and effects themselves. For instance, a major QTL, located on the 5D chromosome, was detected in MTW and MTS, but was not found in ETS. Similarly, a QTL on chromosome 6D was detected in MTS and ETH, but not in MTW. The final aim of QTL mapping was to effectively utilize QTLs detected. The molecular marker of these QTL detected in MTW can be used to select those wheats which have more tillers in prewinter (wheat sown in October), while the QTL markers of MTS can be used in selecting these wheats with more tillers in the spring (sown in November). The results showed that the numbers and effects of QTLs affecting tiller number were different at various periods, which could provide information for selection strategy in breeding.

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References

Babb S. and Muehlbauer G. J. 2003 Genetic and morphological characterization of the barley uniculm2 (*cul2*) mutant. *Theor. Appl. Genet*. **106**, 846–857.

Brondani C., Rangel P., Brondani R. and Ferreira M. 2002 QTL mapping and introgression of yield related traits from *Oryza glumaepatula* to cultivated rice (*Oryza sativa*) using microsatellite markers. *Theor. Appl. Genet*. **104**, 1192–1203.

Buck-Sorlin G. H. 2002 The search for QTL in barley (*Hordeum vulgare* L.) using a new mapping population. *Cell Mol. Biol. Lett*. **7**, 523–535.

Evers J. B., Vos J., Andrieu B. and Struik P. C. 2006 Cessation of tillering in spring wheat in relation to light interception and red: far-red ratio. *Ann. Bot*. **97**, 649–658.

Franckowiak J. D., Kleinhofs A. and Lundqvist U. 2005 Descriptions of barley genetic stocks for 2005. *Barley Genet. Newslett*. **35**, 155–210 (in Chinese).

Guo C. Q., Bai Z. A., Liao P. A. and Jin W. K. 2004 New high quality and yield wheat variety Yumai 57. *China Seed* **4**, 54 (in Chinese).

Hai Y. and Kang M.-H. 2007 Breeding of a new wheat variety Huapei 3 with high yield and early maturing. *Henan Agric. Sci*. **5**, 36–37 (in Chinese).

Hodges T. 1991 *Predicting crop phenology*. CRC Press, Boca Raton, USA.

Hua J. P. 2001 *Genetic disseetion on the basis of heterosis using an 'Immortalized F_2' population*. Ph. D. thesis, Huazhong Agricultural University, Wuhan, P R China.

Hua J. P., Xing Y. Z., Wu W. R., Xu C. G., Sun X. L., Yu S. B. and Zhang Q. F. 2003 Single-locus heterotic effects and dominance by dominance interaction can adequately explain the genetic basis of heterosis in an elite hybrid. *Proc. Natl. Acad. Sci. USA* **100**, 2574–2579.

Huang X. Q., Coster H., Ganal M. W. and Röder M. S. 2003 Advanced backcross QTL analysis for the identification of quantitative trait loci alleles from wild relatives of wheat (*Triticum aestivum* L.). *Theor. Appl. Genet*. **106**, 1379–1389.

Kato K., Miura H. and Sawada S. 2000 Mapping QTLs controlling grain yield and its components on chromosome 5A of wheat. *Theor. Appl. Genet*. **101**, 1114–1121.

Kirby E. J. M. and Appleyard M. 1981 *Cereal development guide*. Cereal Unit, National Agricultural Centre, Stoneleigh, UK.

Kuraparthy V., Sood S., Dhaliwal H. S., Chhuneja P. and Gill B. S. 2007 Identification and mapping of a tiller inhibition gene (*tin3*) in wheat. *Theor. Appl. Genet*. **114**, 285–294.

Law C. N. 1967 The location of genetic factors controlling a number of quantitative characters in wheat. *Genetics* **56**, 445–461.

Li H., Ye G. and Wang J. 2007 A modified algorithm for the improvement of composite interval mapping. *Genetics* **175**, 361–374.

Li H., Ribaut J. M., Li Z. and Wang J. 2008 Inclusive composite interval mapping (ICIM) for digenic epistasis of quantitative traits in biparental populations. *Theor. Appl. Genet*. **116**, 243–260.

Li W. L., Nelson J. C., Chu C. Y., Shi L. H., Huang S. H. and Liu D. J. 2002 Chromosomal locations and genetic relationships of tiller and spike characters in wheat. *Euphytica* **125**, 357–366.

Li X. Y., Qian Q., Fu Z. M., Wang Y. H., Xiong G. S., Zeng D. L. *et al*. 2003 Control of tillering in rice. *Nature* **422**, 618–621.

Liu G. F., Xu H. M., Yang J. and Zhu J. 2006 Genetic analysis on tiller number and plant height per plant in rice (*Oryza sativa* L.). *J. Zhejiang University* **32**, 527–534 (in Chinese).

Liu G. F., Zeng R. Z., Zhu H. T., Zhang Z. M., Ding X. H., Zhao F. M. *et al*. 2009 Dynamic expression of nine QTLs for tiller number detected with single segment substitution lines in rice. *Theor. Appl. Genet*.**118**, 443–453.

Lukaszewski A. J., Rybka K., Korzun V., Malyshev S. V., Lapinski B. and Whitkus R. 2004 Genetic and physical mapping of homoeologous recombination points involving wheat chromosome 2B and rye chromosome 2R. *Genome* **47**, 36–45.

Malyshev S., Korzun V., Voylokov A., Smirnov V. and Börner A. 2001 Linkage mapping of mutant loci in rye (*Secale cereale* L.). *Theor. Appl. Genet*. **103**, 70–74.

Miralles D. J. and Richards R. A. 2000 Responses of leaf and tiller emergence and primordium initiation in wheat and barley to interchanged photoperiod. *Ann. Bot*. **85**, 655–663.

Narasimhamoorthy B., Gill B. S., Fritz A. K., Nelson J. C. and Brown-Guedira G. L. 2006 Advanced backcross QTL analysis of a hard winter wheat × synthetic wheat population. *Theor. Appl. Genet*. **112**, 787–796.

Satorre E. H. and Slafer G. A. 1999 *Wheat: ecology and physiology of yield determination*. Haworth Press, Binghamton, USA.

Shah M. M., Gill K. S., Baenziger P. S., Yen Y., Kaeppler S. M. and Ariyarathne H. M. 1999 Molecular mapping of loci for agronomic traits on chromosome 3A of bread wheat. *Crop Sci*. **39**, 1728–1732.

Tian D. G., Lin F., Zhang C. Q., Zhang Z. Z., Xue S. L., Cao Y. *et al*. 2008 Mapping QTLs associated with resistance to *Fusarium* head blight using an "Immortalized F_2" population. *Acta Agron. Sin*. **34**, 539–544.

Wang J. K. 2009 Inclusive composite interval mapping of quantitative trait genes. *Acta Agron. Sin*. **35**, 1–7.

Yamada T., Jones E. S., Cogan N. O. I., Vecchies A. C., Nomura T., Hisano H. *et al*. 2004 QTL analysis of morphological, developmental, and winter hardiness-associated traits in perennial rye grass. *Crop Sci*. **44**, 925–935.

Yan J. Q., Zhu J., He C. X., Benmoussa M. and Wu P. 1998 Quantitative trait loci analysis for the developmental behavior of tiller number in rice (*Oryza sativa* L.). *Theor. Appl. Genet*. **97**, 267–274.

Yang G. H., Xing Y. Z., Li S., Ding J. Z., Yue B., Deng K. *et al*. 2006 Molecular dissection of developmental behavior of tiller number and plant height and their relationship in rice (*Oryza sativa* L.). *Hereditas* **143**, 236–245.

Zhang L., Li H., Li Z. and Wang J. 2008 Interactions between markers can be caused by the dominance effect of QTL. *Genetics* **180**, 1177–1190.

Zhang K. P., Tian J. C., Zhao L., Liu B. and Chen G. F. 2009 Detection of quantitative trait loci for heading date based on the doubled haploid progeny of two elite Chinese wheat cultivars. *Genetica* **135**, 257–265.

Zhao F. M., Liu G. F., Zhu H. T., Ding X. H., Zeng R. H., Zhang Z. M. *et al*. 2008 Unconditional and conditional QTL mapping for tiller numbers at various stages with single segment substitution lines in rice (*Oryza sativa* L.). *Agric. Sci. Chin*. **713**, 257–265 (in Chinese).

Zhu J. 1995 Analysis of conditional genetic effects and variance components in developmental genetics. *Genetics* **141**, 1633–1639.

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