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Dynamic QTL detection and analysis of tiller number before and after heading in *japonica* rice

Jianmin Bian*, Haohua He, Huan Shi, Changlan Zhu, Xiaosong Peng, Cuijuan Li, Junru Fu, Xiaopeng He, Xiaorong Chen, Lifang Hu, and Linjuan Ouyang

College of Agronomy, Jiangxi Agricultural University/Key Laboratory of Crop Physiology, Ecology and Genetic Breeding, Ministry of Education, The people's Republic of China, Nanchang 330045, China

***Corresponding author: jmbian81@126.com**

Abstract

To understand the static and dynamic information concerning QTLs for tiller production in *japonica* rice, unconditional and conditional QTLs were simultaneously mapped using an introgression line (IL) rice population before and after heading, where all the IL lines had the same *japonica* rice, Sasanishiki, genetic background. The results revealed 14 unconditional and 12 conditional QTLs for tiller number on 9 of the 12 chromosomes. The number and effect of QTLs were different at various stages before and after heading, even an individual gene or genes at the same genomic region might have opposite genetic effects at various growth stages, which indicated that QTLs for tiller number might be differentially spatially and temporally expressed at different development stages. Correlation analysis showed that the number of final effective panicles was highly significantly positively correlated with tiller number around the time of heading. Therefore, the expression of genes (QTLs) around the heading period represented an interesting genetic resource in the context of final effective panicle improvement. Furthermore, most QTLs for heading were not located in the same intervals within the tiller number QTLs of the rice chromosomes. This suggests that distinct genetic systems might be responsible for tiller number and heading date, and pyramiding the heading QTLs with those for tiller number might feasibly together improve final yield.

Keywords: *japonica* rice (*Oryza sativa* L.); introgression line; tiller number; unconditional QTL; conditional QTL.
Abbreviations: IL, Introgression line; QTLs, Quantitative trait loci; DAT, days after transplanting; M-QTLs, main-effect QTLs.

Introduction

Tillering in rice is one of the most important agronomic traits for grain production because tiller number per plant determines panicle number, a key component of grain yield (Liu et al., 2011; Yang et al., 2006; Zhu et al., 2011). Furthermore, tiller number usually serves as a suitable model trait for the study of developmental characteristics, since it changes over time. Hence, the genetic elucidation of tiller number has become a focus in rice genetic and breeding research (Liu et al., 2010). Improving *japonica* tiller number is a major breeding target in rice and many QTLs associated with tiller number at the maturity stage have been well studied by traditional statistical analysis (Fujita et al., 2010). However, it is difficult for breeders to improve tiller number efficiently using phenotypes, since it is controlled by both tiller initiation and tiller survival until spike production (Naruoka et al., 2011), and studies have ignored distinct gene functions at different developmental stages, which are important in the development of the quantitative trait. It is therefore necessary to understand the dynamics of gene expression for tiller number at different developmental stages as a basis for quantitative trait manipulation in breeding application (Xu and Shen, 1991). As an effective method of characterising QTLs in detail, IL rice populations have been constructed (Bian et al., 2010a, b; Kubo et al., 2002; Eshed and Zamir, 1995), and some have already been exploited for the analysis of dynamic QTLs for tiller number across the *indica* rice (*Oryza sativa* L.) genome (Liu et al., 2010; 2012), which showed that temporal expression of QTLs for tiller number and the dynamics of their main effects were probably due to selective gene expression at specific times (Liu et al., 2009). Although these studies provide useful information for tiller number development, the genetic basis remains poorly understood, especially knowledge concerning the stage at which tiller number is correlated with that of the final effective panicles of *japonica*. Therefore, more rice IL populations within the same *japonica* genetic background should be analysed for dynamic QTLs for tiller number before and after heading to further provide valuable information on tiller number for *japonica* rice breeding in the future. In this study, we used a set of ILs within the uniform *japonica* genetic background to explore genetically the developmental trait of tiller number. Unconditional and conditional QTL methods were applied before and after heading. The unconditional QTL mapping was conducted using the genetic effect from tiller initiation to a time point t, while the conditional QTLs were detected with the net genetic effects during the time interval from time t-1 to time t. The objectives of this study were: (1) to explore the dynamics of QTL expression for tiller number throughout ontogeny; (2) to acquire a preliminary understanding of the correlation between tiller number at the measuring stages and in the final effective panicles; (3) to detect the main-effect QTLs (M-QTLs) expressed at most of the measuring stages, which might provide a starting point for improving tiller number through QTL pyramiding in rice.

Table 1. Phenotypic values of tiller number of the IL population and its parents at four different measuring stages. DAT: days after transplanting.

Stage	Parents		IL population				
	Sasanishiki	Habatakic	Mean	Min	Max	Skewness	Kurtosis
15 DAT	3.46	3.03	2.96	3.21	2.57	1.57	2.84
29 DAT	10.05	9.80	8.91	11.15	6.90	0.21	-2.15
43 DAT	8.30	9.60	8.72	11.05	7.20	0.41	-1.87
57 DAT	17.15	12.55	15.63	20.05	11.45	0.48	-0.56
15 DAT/initial	3.46	3.03	2.96	3.21	2.57	1.57	2.84
29 DAT/15 DAT	6.59	6.77	5.95	7.95	4.14	0.56	-1.64
43 DAT/29 DAT	-1.75	-0.20	-0.19	2.35	-1.75	0.17	-1.97
57 DAT/43 DAT	8.85	2.95	6.91	11.39	3.00	-0.82	0.02

Results

Phenotypic variation

As shown in Fig. 1, the heading date of the IL population was normally distributed within the range spanned by that of the parents. The parental lines Sasanishiki and Habatakic showed significant differences in heading date (Fig. 1). A mean heading date of 73.8 d ± 0.78 for Sasanishiki and 83.0 d ± 0.85 for Habatakic were obtained in this study, which showed that the heading date of the IL population was continuously distributed as expected for a quantitative trait. Thus, QTLs might be involved in heading date in Sasanishiki. Tiller number for the two parents was significantly different at 43 and 57 days after transplanting (DAT). The mean tiller number of Sasanishiki rapidly increased from 3.46 at 15 DAT to 10.05 at 29 DAT, then decreased to 8.30 at 43 DAT due to the mortality of some young tillers; after heading, the mean tiller number rapidly increased to 17.15 at 57 DAT. For Habatakic, the mean tiller number rapidly increased from 3.03 at 15 DAT to 9.80 at 29 DAT, then decreased to 9.60 at 43 DAT and after heading, increased to 12.55 at 57 DAT (Fig. 2). The phenotypic values of the tiller number within the IL population are presented in Fig. 3. The tiller number of the IL population segregated continuously and both skewness and kurtosis values were less than 1.0 at most measuring stages except at 15 DAT and 15 DAT/initial (Table 1). It appeared that segregation of tiller number within the IL population was normally distributed for most measuring stages and was suitable for QTL analysis. Transgressive segregants, with a tiller number higher or lower than that of the parents, were also observed at all measuring stages (Fig. 3).

Correlation between the number of tillers and final effective panicles

Correlations between tiller number (15 DAT, 29 DAT, 43 DAT, 15 DAT/initial, 29 DAT/15 DAT, 43 DAT/29 DAT and 57 DAT/43 DAT) and final effective panicles (57 DAT) were analysed and evaluated at $P < 0.01$. The results suggested that the number of final effective panicles in the IL population was positively significantly correlated with that of tillers at 43 DAT and 57 DAT/43 DAT ($P < 0.01$), which was the time around the heading period, with correlation coefficients of 0.44 and 0.94, respectively (Table 2). Additionally, the number of final effective panicles was also positively significantly correlated with tiller number at 29 DAT and 29 DAT/15 DAT ($P < 0.01$), with correlation coefficients of 0.36 and 0.33. No significant effects on the number of final effective panicles were detected by tiller number at other measured stages in the ILs (Table 2).

Heading date QTL detection

QTL analysis linked to molecular markers by QTL IciMapping v2.2 Mapping software was performed for heading date in this study. A total of seven significant QTLs were identified on six of the 12 chromosomes and the respective alleles explain 5.83–26.25%, of the total phenotypic variation (Table 3). No QTLs were present on chromosomes 1, 4, 5, 6, 10 or 12. At these loci, the alleles with decreasing heading date were from Sasanishiki for *qHD2, qHD3, qHD7, qHD8.2* and *qHD9*, and those with increasing heading date, from Sasanishiki for *qHD8.1* and *qHD11*.

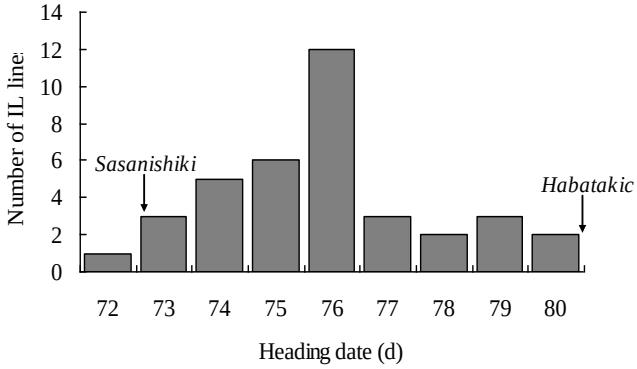

Fig. 1 Frequency distribution for heading date of 37 IL lines.

QTL detection for tiller number by unconditional mapping

A total of 14 unconditional QTLs that significantly influenced tiller number were identified on chromosomes 1, 2, 4, 5, 6, 7, 8 and 10 (Table 4; Fig. 4). Six QTLs were detected at the formation stage of effective panicle number around marker RM7600 (*qUTn1.3*) on chromosome 1, around marker RM3534 (*qUTn4*) on chromosome 4, around marker RM5642 (*qUTn5.2*) on chromosome 5, around marker RM3286 (*qUTn5.3*) on chromosome 5, around marker RM1370 (*qUTn6*) on chromosome 5, and around marker RM6838 (*qUTn8*) on chromosome 8. All these QTLs could be detected after heading. t these loci, the alleles associated with decreasing tiller number were from Sasanishiki for *qUTn4 qUTn5.2* and *qUTn5.3*, and those with increasing number, from Sasanishiki for *qUTn1.3, qUTn6* and *qUTn8*. Apart from these six significant QTLs detected at the final stage, another eight regions also showed significant QTLs at one or several measuring stages. Most of these QTLs were found prior to 57 DAT, implying that many genes for tiller number were expressed before heading. Of these QTLs, *qUTn1.3*, was detected during separate stages, indicating that the accumulated effects of this QTL were too small to be detected at the intermediate stage, even though it was subsequently stably expressed. Furthermore, *qUTn4* and

Table 2. Correlations between tiller number (15 DAT, 29 DAT, 43 DAT, 15 DAT/initial, 29 DAT/15 DAT, 43 DAT/29 DAT and 57 DAT/43 DAT) and final effective panicles (57 DAT) based on 37 IL lines.

Stage	*Unconditional tiller number*			*Conditional tiller number*			
	15 DAT	29 DAT	43 DAT	15 DAT/initial	29 DAT/15 DAT	43 DAT/29 DAT	57 DAT/43 DAT
57 DAT	0.31	0.36*	0.44**	0.31	0.33*	0.06	0.94**

* 5% levels of significance; ** 1% levels of significance; DAT: days after transplanting.

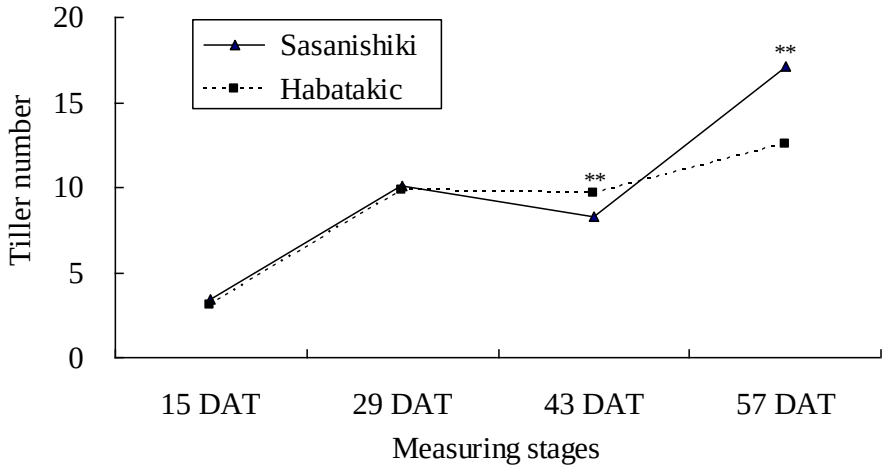

Fig 2. Tiller numbers averaged Sasanishiki and Habatakic at four stages before and after heading. DAT: days after transplanting; ** signify a significant difference at the 1% level between Sasanishiki and Habatakic according to the *t*-test.

Table 3. Quantitative trait loci (QTLs) for heading date based on 37 IL lines.

QTL[a]	Chr.	Marker[b]	LOD[c]	Additive effect[d]	% of variance explained
qHD2	2	RM1211	7.64	1.76	16.41
qHD3	3	RM5748	8.74	2.31	14.52
qHD7	7	RM1364	5.00	1.54	6.42
qHD8.1	8	RM5891	3.14	-1.05	5.83
qHD8.2	8	RM6070	13.06	3.11	26.25
qHD9	9	P414D03	11.78	1.61	19.93
qHD11	11	RM1341	4.76	-1.49	6.01

[a] Individual QTLs are shown with the italic abbreviation of the trait and the chromosome number. [b] The marker nearest the putative QTL. [c] The LOD score. [d] A negative value indicates that the allele from Sasanishiki increased the phenotypic value.

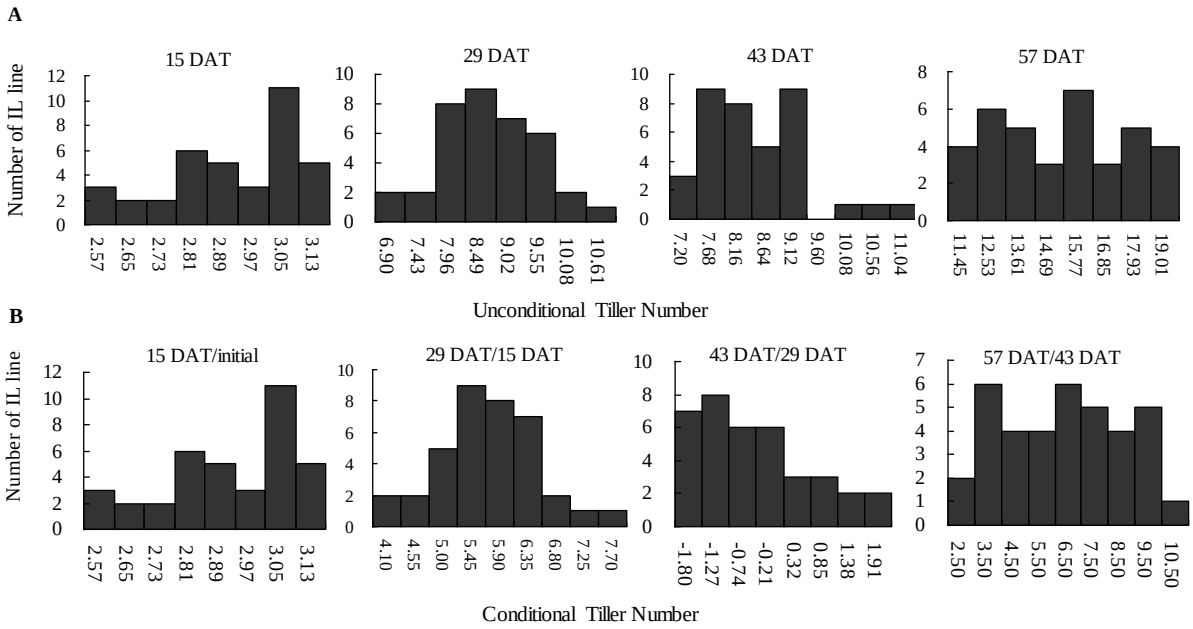

Fig 3. Frequency distribution of tiller number at four stages in ILs by unconditional method (A) and conditional method (B). DAT: days after transplanting.

qUTn6 were detected at all measuring stages except at 15 DAT, when the Sasanishiki alleles decreased and increased tiller number, respectively, which indicated that some M-QTLs responsible for tiller initiation might begin to be stably expressed two weeks after transplantation.

QTL detection for tiller number by conditional mapping

In total, 12 conditional QTLs were identified for tiller number on eight of the 12 rice chromosomes (Table 5; Fig. 4). No QTLs were present on chromosomes 8, 9, 11 and 12. At seven of the 12 genomic locations, QTLs were significantly detected at only one specific stage. For the other five locations (*qCTn1.1*, *qCTn1.4*, *qCTn2.1*, *qCTn3 and qCTn7*), temporal-specific QTLs were identified at two different measuring stages. Although these QTLs were identified at two different measuring stages, all of them demonstrated opposite effects between those times. A total of four conditional QTLs (*qCTn1.2*, *qCTn1.3*, *qCTn1.4* and *qCTn7*) that affected tiller number were detected at 15 DAT/initial, demonstrating that about half of them were expressed at the start of tiller initiation. The number of conditional QTLs was six for 29 DAT/15 DAT, five for 43 DAT/29 DAT, and two for 57 DAT/43 DAT. Of these QTLs, four QTLs were detected consecutively. These results indicated that novel genes regulating tiller number were expressed as the plant developed.

Discussion

Introgression lines (ILs) enable the genetic analysis of japonica *tiller number*

Tiller number is an important trait in rice breeding, however, it is usually evaluated at a single developmental stage, especially at maturity (Thomson et al., 2003). Recently, several studies have begun to identify dynamic QTLs for this quantitative trait, using different *indica* rice populations (Liu et al., 2012; Wu et al., 1999), however, the genetic basis remains poorly understood, especially for *japonica* rice. In this study, an elite *japonica* variety, Sasanishiki, was used to detect and analyse dynamic QTLs for tiller number before and after heading. To improve the detection efficiency of QTLs for tiller number in Sasanishiki, an introgression line (IL) rice population (an *indica* rice variety Habataki with genomic fragments substituted into the Sasanishiki genetic background) was selected, and a total number of 14 and 12 significant QTLs were uncovered by unconditional and conditional QTL mapping methods, respectively. Of these, only six unconditional QTLs for tiller number at the final stage were found, which demonstrated that more genes participated in *japonica* rice tiller number development at times other than at panicle maturity. Moreover, the number of these QTLs was greater than has been previously reported (Yan et al., 1998), which showed that ILs were ideally suited for the identification

Table 4. Quantitative trait loci (QTLs) for tiller number in rice identified by unconditional method.

QTL[a]	Chr.	Marker[b]	15 DAT[e]			29 DAT			43 DAT			57 DAT		
			LOD[c]	Additive effect[d]	% of variance explained	LOD	Additive effect	% of variance explained	LOD	Additive effect	% of variance explained	LOD	Additive effect	% of variance explained
qUTn1.1	1	RM6887				3.22	-0.66	5.68						
qUTn1.2	1	RM7124	3.30	-0.18	9.35									
qUTn1.3	1	RM7600	4.86	-0.23	15.23							3.68	-2.21	8.17
qUTn1.4	1	RM1387	4.86	-0.23	15.23									
qUTn2.1	2	RM2770				4.69	-0.84	9.10						
qUTn2.2	2	RM1211							14.99	1.10	32.14			
qUTn4	4	RM3534				6.87	1.09	15.45	14.58	1.21	19.86	3.34	2.09	7.25
qUTn5.1	5	RM2744							7.54	-0.67	6.11			
qUTn5.2	5	RM5642										3.26	2.06	7.04
qUTn5.3	5	RM3286										2.76	1.86	5.77
qUTn6	6	RM1370				6.42	-1.04	13.98	8.27	-0.72	7.06	2.83	-1.89	5.94
qUTn7	7	RM1364	3.76	-0.20	10.96									
qUTn8	8	RM6838							7.17	-0.64	5.66	3.28	-2.06	7.10
qUTn10	10	RM7217				3.38	0.66	11.06						

[a] Individual QTLs were showed with the italic abbreviation of the trait and the chromosome number. [b] The marker nearest the putative QTL. [c] The LOD score. [d] A negative value indicates that the allele from Sasanishiki increased the phenotypic value. [e] DAT: days after transplanting.

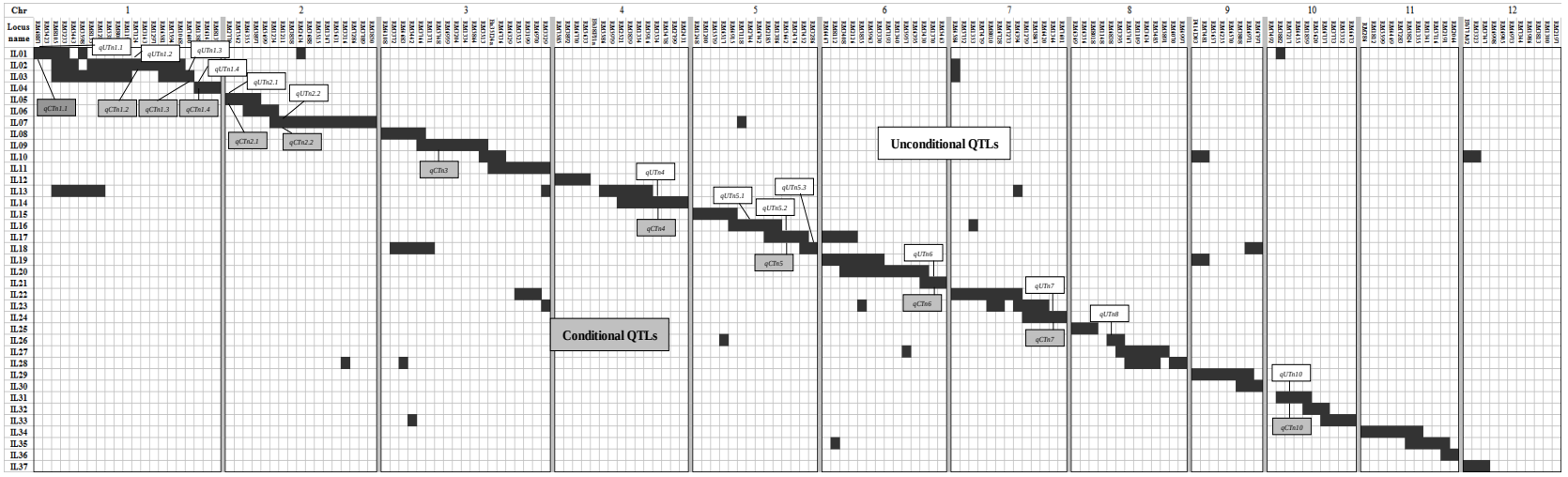

Fig 4. Chromosomal locations of quantitative trait loci (QTL) for tiller number. Quantitative trait loci detected by unconditional mapping method and conditional mapping method are labeled in the upper right and lower left corners, respectively. White indicates homozygosity for Sasanishiki alleles, black indicates homozygosity for Habatakia alleles.

Table 5. Quantitative trait loci (QTLs) for tiller number in rice identified by conditional method.

QTL[a]	Chr.	Marker[b]	15 DAT/initial			29 DAT/15 DAT[e]			43 DAT/29 DAT			57 DAT/43 DAT		
			LOD[c]	Additive effect[d]	% of variance explained	LOD	Additive effect	% of variance explained	LOD	Additive effect	% of variance explained	LOD	Additive effect	% of variance explained
qCTn1.1	1	RM6887							6.46	1.18	11.72	2.70	-1.93	7.58
qCTn1.2	1	RM7124	3.30	-0.18	9.35									
qCTn1.3	1	RM7600	4.86	-0.23	15.23									
qCTn1.4	1	RM1387	4.86	-0.23	15.23				4.38	0.91	6.91			
qCTn2.1	2	RM2770				5.94	-0.83	11.07	4.75	0.96	7.69			
qCTn2.2	2	RM1211							10.07	1.47	35.30			
qCTn3	3	RM5748				4.17	-0.66	6.90	6.46	1.18	11.72			
qCTn4	4	RM3534				7.45	0.98	15.40						
qCTn5	5	RM5642										3.25	2.16	9.43
qCTn6	6	RM1370				6.91	-0.93	13.75						
qCTn7	7	RM1364	3.76	-0.20	10.96	3.96	0.63	6.46						
qCTn10	10	RM7217				3.94	0.62	11.81						

[a] Individual QTLs are shown with the italic abbreviation of the trait and the chromosome number. [b] The marker nearest the putative QTL. [c] The LOD score. [d] A negative value indicates that the allele from Sasanishiki increased the phenotypic value. [e] DAT: days after transplanting.

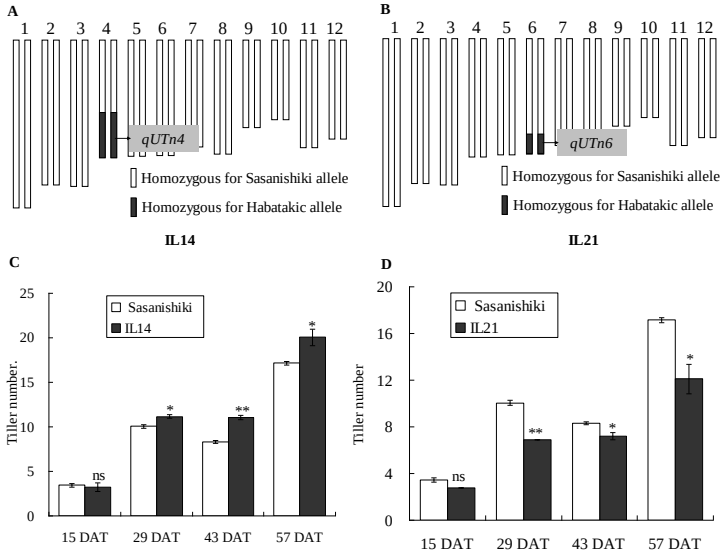

Fig 5. Graphical genotypes and phenotypic characterization of IL14 and IL21. A Graphical genotypes of IL14. B Graphical genotypes of IL21. C Tiller number of Sasanishiki and IL14 of the four measuring stages. D Tiller number of Sasanishiki and IL21 of the four measuring stages. DAT: days after transplanting, Each value represents the mean ± SE, *, ** signify a significant difference at the 5% and 1% level respectively according to the *t*-test, ns signify no significant difference.

of dynamic QTLs for tiller number and that this analysis is more productive when evaluating *japonica* rice tiller number development.

The expression of QTLs for* japonica *tiller number

Some studies have shown that distinct genetic systems might be responsible for the early and late growth of tiller number for *indica* or upland *japonica* (Yan et al., 1998). In this study, three out of the four QTLs (*qUTn1.2*, *qUTn1.3*, *qUTn1.4* and *qUTn7*) that affect tiller number at 15 DAT were not responsible for tiller number at the formation stage of effective panicle number (57 DAT) in Sasanishiki (Table 4), implying that distinct genetic systems might also be responsible for tiller number in *japonica* rice before and after heading, and a thorough and dynamic QTL analysis for *japonica* formation was necessary. In addition, multiple patterns of gene expression were also identified, with some QTLs only expressed at only one stage, and others in two consecutive stages or in non-sequential intervals, such as *qUTn1.3*, possibly because some genes reiterate their expression at different developmental timepoints (Sun et al., 2006). Furthermore, *qCTn1.1* detected in different stages showed opposing genetic effects (Table 5), which suggested that the expression of these genes might play different roles (control the growth or the mortality of tillers) at different developmental stages. Moreover, *qCTn3* detected by the conditional mapping method was not detected by the unconditional method, and the QTL data showed that *qCTn3* was expressed at 29 DAT/15 DAT and 43 DAT/29 DAT. This shows that the variation in cumulative gene functions might be reduced due to opposing genetic effects at the same or at nearby locations (Zheng et al., 2011). This might have also been the case with QTL *qCTn2.1* and *qCTn7* in this study.

The potential use of QTLs for tiller number

In this study, 26 QTLs for tiller number located on 9 of the different 12 rice chromosomes were uncovered at the Nanchang site and most of these QTLs coincided with loci described in the literature (www.gramene.org) e.g., the *qCTn3* locus on chromosome 3 (around RM5748) maps to a similar location of *tn3c* detected by Wu et al. (1999); *qUTn6* and *qCTn6* (around RM1370) are probably the same locus as that described by Yan et al. (1998), whereas *qUTn7* and *qCTn7* (around RM1364) appear to be the same locus on chromosome 7 locus as that detected by Liu et al. (2010). Furthermore, *qUTn2.2* and *qCTn2.1* (around RM1211) share the same locus with a QTL for tiller number detected by Liu et al. (2012) and *qUTn1.3* (between RM6581 and RM7600) is probably the same locus *qPN1* described by Zhu et al. (2011) for tiller number. In view of these results, some stable QTLs controlled tiller number, which could be detected under different environments and in different populations. However, *qUTn4*, which was stably detected two weeks after transplantation, has not been previously identified. The IL14 carrying this M-QTL Sasanishiki allele showed a lower tiller number at later consecutive stages (Fig. 5), thus, the Habataki genomic fragments harboring this QTL represented a good candidate for marker-assisted selection for tiller number, and hence for grain yield itself. A further M-QTL, *qUTn6*, was also stably detected on chromosome 6, two weeks after transplantation. IL21, which carried this Sasanishiki QTL allele, showed an increased tiller number at later consecutive stages (Fig. 5). However, the other 24 QTLs were environment-specific, as their significant effects were only detected at 1, 2 or 3 different developmental stages (Table 4 and Table 5); for example, *qCTn4* showed a great contribution at 29 DAT/15DAT, but was not detected in other stages. These QTLs also represent an interesting genetic resource in the context of rice yield improvement at different developmental stages, for a design-breeding approach in the future, as described by Wang et al. (2007). Correlation analysis revealed that the number of final effective panicles was highly significantly positively correlated with tiller number at the time around the heading period. To some extent, this result showed that tiller number around the heading period had a strong promoting effect on the formation of final effective panicles, therefore, the expression of genes (QTLs) around the heading period represented an interesting genetic resource in the context of the final effective panicle improvement.

The relationship between heading date and tiller number

In most cases, the materials used in the genetic analysis of the developmental behavior of tiller number segregated not only for the trait to be studied, but also for heading date. However, little is known about the relationship between heading date and dynamic tiller number development. In this study, we found that many heading date QTLs, e.g., *qHD8.1*, *qHD8.2*, *qHD9* and *qHD11*, were not located within the same intervals within the tiller number QTLs of the rice chromosomes, which further confirmed that distinct genetic systems might be responsible for tiller number and heading date. It is, therefore, possible to improve tiller number and heading date separately, and pyramid these heading QTLs with those for tiller number to improve the final yield simultaneously.

Materials and Methods

Plant materials

Sasanishiki, an elite *japonica* variety, was selected as the recipient, and Habataki, an *indica* elite variety, was used as donor. The flow chart of the development ILs, through backcrossing and SSR marker selection, was described previously by Ando et al. (2008). Of all the 39 introgressive lines, 37 IL lines (SL401-SL437) were selected and renumbered as IL01-IL37 in this research. Each contains a major segment inherited from Habataki, along with a variable number of minor segments in Sasanishiki genetic background, and the selected IL population covered most of the genome, only one small region at the middle of chromosome 4 (defined by Bb38P21a), one small region at the middle of chromosome 8 (defined by RM1148), one small region at the distal end of the long arm of chromosome 10 (defined by SSR locus RM7492), and one larger segment of chromosome 12 (SSR loci RM6998 and RM2197) are not represented. A linkage map was constructed according the distance described by Ando et al. (2008).

Field trials and traits measured

The 37 IL lines and their parents, Sasanishiki and Habatakic, were sown on 19 May 2012 in Jiangxi Agricultural University, Nanchang site, China. Their seedlings were transplanted on 20 June and were grown under natural conditions in a completely randomized block design with two replications. Each plot was consisted of four rows separated by 30 cm, with each row consisting of ten plants, each separated from its neighbour by 20 cm. Crop management followed normal procedures for rice.
After 2 weeks of transplanting, tiller numbers were measured every 14 days in 10-15 central plants from each plot until the formation of effective panicle number (about one week after heading of all the lines). The means of the two replications were used for QTL analysis. We divided the course of tiller

number into four stages according the recipient phonotype: (1) The beginning stage of tiller number, 0 to 15 DAT; (2) vertices stage of tiller number, 15 to 29 DAT; (3) decline stage of tiller number, 29 to 43 DAT; and (4) formation stage of effective panicle number, 43 to 57 DAT. The heading date was scored in ten plants per line and mean values of the two replications were calculated for each line.

Statistical analysis

According to the report by Zhu et al. (1995), conditional QTLs reflected the genes expression at a specific growth period but not the previous stages. Since the unconditional QTLs reflected the accumulated gene effects from initial time to time t. To explore dynamics of QTL expression during whole ontogeny, both original and conditional values in different measuring stages were used to perform the dynamic QTLs analysis linked to molecular markers by QTL IciMapping v2.2 Mapping software (Li et al., 2008), applying a threshold LOD of 2.5, which was used for non-ideal ILs population QTL detection (http://www.isbreeding.net/). QTL nomenclature followed the recommendations of McCouch & CGSNL (Rice Genetics Cooperative 2008). The heading date QTL detection was also conducted by using IciMapping v2.2 Mapping software (Li et al., 2008), applying a threshold LOD of 2.5. Correlation analysis was performed to detect association between tiller number and the final effective panicles of IL population using SPSS software.

Conclusion

The analysis of dynamic QTLs for tiller number before and after heading using *japonica* rice ILs, shows that distinct genetic systems might be responsible for the early and late initiation of tillers in *japonica* rice. Correlation analysis showed that the number of final effective panicles was highly significantly positively correlated with tiller number at the time of heading, and the expression of genes (QTLs) around the heading period represents a relevant genetic resource in the context of final effective panicle improvement. The IL lines harboring these M-QTLs also represent a useful genetic resource for rice yield improvement at different developmental stages via a design-breeding approach in the future. Furthermore, QTL analysis suggests that many heading-date QTLs are not located within the same intervals on the rice chromosomes as those containing QTLs for tiller number, which suggests a way to pyramid these heading QTLs with those for tiller number to improve the final yield simultaneously.

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