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Quantitative trait loci analysis for the developmental behavior of tiller number in rice (*Oryza sativa L.*)

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Abstract A doubled-haploid rice population of 123 lines from Azucena/IR64 was used for analyzing the developmental behavior of tiller number by conditional and unconditional QTL mapping methods. It was indicated that the number of QTLs significantly affecting tiller number was different at different measuring stages. Many QTLs controlling tiller growth identified at the early stages were undetectable at the final stage. Only one QTL could be detected across the whole growth period. By conditional QTL mapping, more QTLs for tiller number could be detected than that by unconditional mapping. The temporal patterns of gene expression for tiller number could be different at different stages. Even an individual gene or genes at the same genomic region might have opposite genetic effects at various growth stages.

Key words Tiller number · Developmental behavior · Quantitative trait loci (QTL) · Rice (*Oryza sativa* L.)

Introduction

The number of productive tillers per plant plays an important role in the formation of grain yield in rice. The development of tillers is affected by various environmental factors including manuring, planting density, and climatic circumstances such as light, temperature, water supply and so on. Tiller number per plant is a quantitative trait with a relatively low heritability of 29.8–49.6% (Xiong 1992). The genetics of final tiller number at the maturity stage have been well documented by traditional statistical analysis. Li (1977) reported an equal importance of additive and dominant gene effects. Murai and Kinoshita (1986) considered the additive gene effects to be more important than the non-additive effects. Ahmad et al. (1986) showed predominance of additive gene action without the interference of non-additive gene effects, whereas Perera et al. (1986) suggested that both the number of tillers at maturity and the number of panicles per plant were controlled by genes with additive, dominant, and epistatic effects. Using diallel analysis, Xu and Shen (1991) showed that an identical polygenic system appeared to be responsible for the genetic control of tiller number at different growth stages, and that the contributions of additive effects to the variation increased, while those of non-additive effects and environmental factors decreased, with the growth of rice plants.

Genetic studies for quantitative traits have been greatly facilitated by the development of molecular markers (Paterson 1995). Using molecular genetic-linkage maps and QTL mapping technology, it is possible to estimate the number of loci controlling genetic variation and to characterize these loci with regard to their map positions in the genome, as well as their gene action, phenotypic effects, pleiotropic effects, and epistatic interactions with other QTLs. Since the introduction of molecular markers, QTL mapping in numerous species and for various traits has been carried out and is well documented (Tanksley 1993). In rice, many important agronomic traits, such as plant height (Li et al. 1995; Huang et al. 1996), heading date (Li et al. 1995), N2 fixation (Wu et al. 1995 a), japonica/indica hybrid sterility (Wu et al. 1995 b), yield components (Xiao et al. 1995 b), root morphological characters (Yadav et al. 1997), grain shape (Huang et al. 1997), disease resistance (Wang et al. 1994), and heterosis (Xiao et al.

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1995 a; Zhang et al. 1996), have been analyzed by QTL mapping.

In most of these reports, the phenotypic values of traits at a specific developmental stage, usually at the final stage, were used for QTL analysis. These studies, however, have ignored the distinct gene actions at different developmental stages, which is a very important factor influencing the development of quantitative traits. According to the theory of developmental genetics, genes are expressed selectively at different growth stages. The conventional statistical results revealed that the development of morphological traits occurs through the actions and interactions of many genes that might behave differentially during growth periods, and that gene expression is modified by interactions with other genes and by the environment (Atchley and Zhu 1997). It is necessary, therefore, to understand the dynamics of gene expression for a trait at different developmental stages as a basis for quantitative trait manipulation (Xu 1997).

So far, no report has explored the developmental behavior of quantitative traits with molecular markers in rice. In our research program, we plan to exploit the developmental genetics of some important agronomic traits, such as plant height, tiller number, panicle length, panicle weight and biomass of rice, by the QTL molecular-mapping technique. In the present paper, we report the developmental behavior of tiller number. The dynamic QTLs for the developmental behavior of tiller number were investigated with time-dependent measures. Furthermore, the influence of gene expression on quantitative traits at different measuring stages was explored using recently developed statistical procedures (Zhu 1995). The conditional QTLs for tiller number which account for gene expression at a specific period were identified, and the temporal expression of genes for tiller number discussed.

Materials and methods

Materials

A population of 123 double-haploid (DH) lines derived from a cross between the irrigated indica variety IR64 and the upland japonica variety Azucena (Guiderdoni et al. 1992) was used in our experiment. Six restriction enzymes (*Dra*I, *Eco*RV, *Hin*dIII, *Sca*I, *Xba*I, *Eco*RI) were employed for a parental polymorphism survey. An RFLP map of the population was established by Huang et al. (1995) from an initial population of 135 DH lines using 135 well-tagged RFLP markers on the 12 chromosomes. This map was recently updated by adding 40 new isozyme and/or RAPD markers and presently contains 175 markers covering 2005 cM, with an average distance of 11.5 cM between pairs of markers (Huang et al. 1997). This new map was used for QTL analysis in our experiment.

Field experiment

The 123 DH lines and their parents, IR64 and Azucena, were evaluated in the field in Hangzhou, China, in a randomized complete design with two replications. The germinated seeds were sown in a seedling bed on May 25,1996, and seedlings were transferred to a paddy field 30 days later, with a single plant per hill spaced at 15 (20 cm. Each plot included 3–4 lines with eight plants per line. After 10 days of transplanting, tiller numbers were measured every 10 days in five central plants from each plot until all lines had headed. The Fertility and cultivation practices were consistent with optimum rice production for this region. The means of the two replications were used for QTL analysis.

Statistical analysis

Genetic behavior measured at time t is the confounded result of genes expressed before time $(t-1)$ and extra effects within the period from $(t-1)$ to t. These two kinds of gene effects are usually not independent. Unconditional QTL mapping was conducted based on phenotypic value at time $t[y_{(t)}]$ by the procedure of composite interval mapping (Zeng 1993; 1994):

$$y_{j(t)} = \beta_{0(t)} + \beta^*_{(t)} X^*_j + \sum_i \beta_{i(t)} X_{ij} + \varepsilon_{i(t)},$$

where $y_{j(t)}$ is the phenotypic value of the jth individual measured at time t; $\beta_{0(t)}$ is the population mean at time t, $\beta^*_{(t)}$ is the accumulated QTL effect at time t; X_j is the coefficient for the QTL effect; $\beta_{i(t)}$ is the accumulated effect for the ith marker at time t; $X_{i(t)}$ is the coefficient for the ith marker effect; and $\varepsilon_{j(t)}$ is the residual error of the jth individual at time t.

Conditional QTL mapping was also conducted, based on the phenotypic mean at time t conditional on the phenotypic mean measured at time $t-1[y_{(t|t-1)}]$, by the procedure of composite interval mapping (Zeng, 1993; 1994):

$$y_{j(t|t-1)} = \beta_{0(t|t-1)} + \beta^*_{(t|t-1)} X^*_j + \sum_i \beta_{i(t|t-1)} X_{ij} + \varepsilon_{i(t|t-1)},$$

where $y_{j(t|t-1)}$ is the conditional phenotypic value of the jth individual; $\beta_{0(t|t-1)}$ is the conditional population mean, $\beta^*_{(t|t-1)}$ is the conditional QTL effect; $\beta_{i(t|t-1)}$ is the conditional effect for the ith marker; and $\varepsilon_{j(t|t-1)}$ is the conditional residual error of the jth individual.

Genetic variation revealed by analyzing developmental behavior at a specific stage could provide information only for cumulative genetic effects at that time (Zhu 1995). The gene effects at time t conditional on the causal effects at time $(t-1)$ imply the new expression of genes which are independent of the causal effects. The conditional phenotypic means $[y_{(t|t-1)}]$ of tiller number in rice were obtained by the mixed-model approach (Zhu 1995). Then both original and conditional values in different measuring stages were used to perform an analysis of the QTLs linked to molecular markers by QTL Cartographer v. 1.1b (Basten et al. 1996). The total percentage of phenotypic variation explained at each stage was estimated within the multiple model, in which all significant QTLs were fitted simultaneously.

There is, by now, no standard significance threshold (LOD score) being adopted for declaring the detection of a QTL. In most experiments, a LOD score between 2 and 3 is used as the threshold for detecting a QTL. Lander and Botstein (1989) have determined the appropriate threshold of significance for analysis involving a single degree of freedom at each locus. It is applied to QTL mapping in backcross or recombinant inbred populations, or in an intercross when the alleles are constrained to have purely additive, purely recessive, or purely dominant effects. Xu and Zhu (1994) pointed out that the thresholds of LOD scores at $P < 0.05$, 0.01 and 0.001 were about 2.1, 2.9 and 4.0, respectively, for a DH population. Therefore, in the present study, the likelihood ratio (LR) values of 9.5, 13.3 and 18.5, which equal to LOD scores of 2.1, 2.9 and 4.0 (Zeng and Weir 1996), were used as thresholds to declare the detection of QTLs at significance levels of $P < 0.05$, 0.01 and 0.001, respectively.

Results

Phenotypic variation

The phenotypic values of the tiller number of the doubled haploid population and its parents in nine measuring stages are presented in Table 1. The difference in tiller number between the two parents was significant for most stages except at 10 days of transplanting. The average tiller number quickly increased from 1.4 at 10 days to 10.6 at 50 days, then decreased to 8.9 at 90 days due to the mortality of some young tillers. The tiller number of the DH population segregated continuously and both skew and kurtosis values were less than 1.0 in most measuring stages except at 10 days and 90 days. It was suggested that tiller number segregation of the DH population fits a normal distribution for most measuring stages and was suitable for QTL analysis. Transgressive segregants, with a tiller number higher than the high parent IR64 or lower than Azucena, were observed at all measuring stages.

Unconditional QTL mapping

The quantitative trait loci (QTLs) detected for tiller number at nine different measuring stages based on composite interval mapping are shown in Table 2. A total of 15 genomic regions significantly influencing tiller number were identified and located on 8 of the 12 rice chromosomes (Fig. 1). No QTLs were present on chromosomes 5, 9, 10, and 11 ($P < 0.05$). Three QTLs were detected at the final stage between markers RZ730–RZ801 (tn1-4) on chromosome 1, between markers CDO686–Amy1 A/C (tn2-2) on chromosome 2, and between markers CDO87–RG910 (tn3-4) on

Table 1 Phenotypic values of tiller number for the DH population and its parents at nine different measuring stages

Stage (day)	Parents			DH population				
	IR64	Azucena	*t*-value	Max.	Min.	Mean	Skewness	Kurtosis
10	1.50±0.42	1.20±0.28	1.88	2.5	1.0	1.40±0.33	1.14	1.41
20	4.00±0.57	2.00±0.07	11.01**	5.1	1.2	2.56±0.78	0.57	0.13
30	12.50±0.73	5.50±0.71	21.74**	13.2	3.5	7.79±2.12	0.21	−0.54
40	14.10±0.71	6.70±0.16	32.15**	15.8	5.6	10.31±2.52	0.23	−0.63
50	14.60±1.13	6.50±0.14	22.50**	18.7	6.0	10.63±2.91	0.52	−0.29
60	14.90±0.70	6.10±0.42	33.20**	20.5	5.9	10.04±3.01	0.89	0.78
70	11.40±0.99	6.20±0.28	15.98**	17.9	5.5	9.31±2.64	0.91	0.85
80	11.10±0.42	5.90±0.17	36.29**	16.6	5.5	8.91±2.38	0.93	0.71
90	11.10±0.42	5.90±0.17	36.29**	17.3	5.1	8.88±2.44	1.06	1.31

** Indicates significant difference at 0.01 levels

Table 2 Estimated unconditional genetic effects of QTLs detected for the tiller number of the DH population at different stages based on unconditional composite interval mapping

Chrom.	QTL	Marker interval	10D	20D	30D	40D	50D	60D	70D	80D	90D
1	tn 1-3	RG381–RZ19			0.77**	1.05**	1.07*				
1	tn 1-4	RZ730–RZ801	0.09*	0.25*	0.79***	1.03***	1.64***	1.69***	1.23***	1.13**	1.22***
2	tn 2-1	RG171–RG157				0.66*		0.89			
2	tn 2-2	CDO686–Amy1A/C								−0.73*	−0.72*
2	tn 2-3	RG95–RG654				−0.53*					
2	tn 2-4	RZ123–RG520					−0.68*				
3	tn 3-2	RZ284–RZ394	−0.13***	−0.19*							
3	tn 3-3	RZ403–RG179				−0.68**					
3	tn 3-4	CDO87–RG910					0.91*	1.56***	1.41***	0.86*	1.05**
3	tn 3-5	RG910–RG418A							−1.37*		
4	tn 4-3	RG143–RG620				0.77**	0.96**				
6	tn 6	DCO544–RG653	0.10*	0.24*	0.68**	0.56*	0.73*				
7	tn 7	CD497–CDO418					0.72*				
8	tn 8	Amp 2–CDO99	0.08*								
12	tn 12	CDO344–RG958	0.10**	0.23*	0.64*	0.96**	1.02**				
% Variability for multiple-QTL model			37.5	38.6	34.7	54.7	58.5	39.5	34.3	33.8	34.6

*, **, *** Indicate significance at 0.05, 0.01 and 0.001 levels, respectively

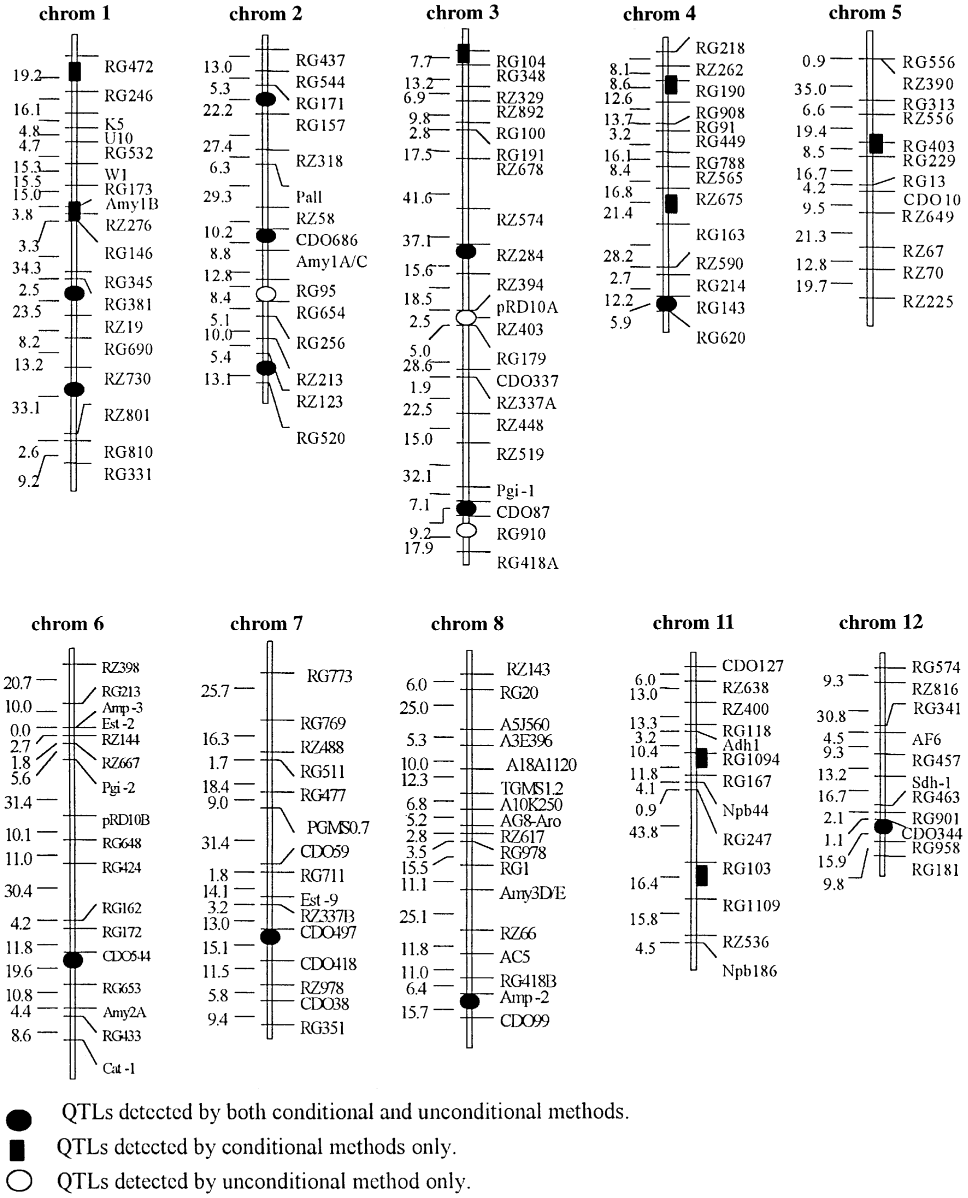

Fig. 1 Molecular linkage map showing locations of QTLs for tiller number in the DH population of IR64/Azucena. Designations to the right of the chromosome represent marker names and to the left represent map distances in cM based on the Kosambi function

chromosome 3. Of these, tn1-4 was also detected for all other stages, whereas tn3-4 could be detected from day 50 to day 90 and tn2-2 only from day 80 to day 90. At these loci, the alleles increasing tiller number were from IR64 for tn1-4 and tn3-4, and from Azucena for tn2-2.

Besides significant QTLs on these three chromosomal regions detected at the final stage, another 12 regions also showed significant QTLs at one or several measuring stages. Most of these QTLs were detected prior to 50 days, indicating that many genes for tiller number were expressed at early stages. This explains the genetic reasons for the rapid increase of tillers at these periods. The failure of detecting these QTLs at advanced stages indicated that the cumulative effects of the QTLs expressed at the early stages were not significant for the final tiller number.

The number of QTLs significantly affecting tiller number varied at different measuring stages. At early stages, from 10 to 30 days, there were 4–5 QTLs which accounted for about 35% of the total phenotypic variability. The number of QTLs increased to eight at 40–50 days, which accounted for 54.7–58.5% of the total phenotypic variation. After this, the number of QTLs rapidly decreased to three at later stages, which explained from 33.8% to 39.5% of the total phenotypic variability. The total genetic effect of QTLs increased from 0.5 at 10 days to 7.7 at 50 days and then decreased to about 3.0 at 80–90 days. It paralleled the rapid increase of tiller number at early stages to reach the peak period at about 50 days, then decreased afterwards because of the mortality of later-developed young tillers.

From the above analysis, it was concluded that more QTLs could be detected from measures during plant growth stages than at the final stage. It was implied, by the detection of different QTLs at different stages, that genes controlling tiller number might be expressed differently during the growth period. The analysis of unconditional effects only provided inference for the cumulative gene effects from the initial time to time *t*. Therefore, the temporal patterns of gene expression cannot be appropriately explained by the unconditional QTL mapping results (Yan et al. 1998).

Conditional QTL mapping

The conditional QTL mapping results are presented in Table 3. For conditional analysis, (20D|10D) denotes measures at 20 days given the phenotype values measured at 10 days, (30D|20D) for those at 30 days relative to the measures at 20 days, and so on. But (10D|initial) denotes the measures at 10 days after transplanting conditional on those at the initial time of planting, which should be equal to the unconditional measure at 10 days. QTLs found at time *t* have cumulative genetic effects due to genes expressed from the initial time to time *t*, while QTLs detected for time $(t\,|\,t(1)$ will have net genetic effects of genes expressed only through time $(t-1)$ to time *t*.

A total of 20 genomic regions showing conditional QTLs significantly affecting tiller number at different measuring stages was detected (Table 3). These 20 regions were mapped to 10 out of the 12 rice chromosomes (Fig. 1). Five chromosomes (5, 6, 7, 8 and 12) carried only one and the others 2–4 significant regions. In 13 out of the 20 genomic locations, QTLs were significantly detected at only one specific stage. For the other seven locations (tn1-3, tn1-4, tn2-1, tn3-2, tn3-4, tn6 and tn8), time-specific QTLs were identified at 2–4 different measuring stages.

Five conditional QTLs in total affecting tiller number were detected for (10D|initial), which indicated that there were five QTLs expressed from the initial time to 10 days after transplanting. The number of conditional QTLs were three for (20D|10D) and (30D|20D), and increased to six for (40D|30D), then decreased to only one for (90D|80D). The percentage of phenotypic variation accounted for by the conditional QTLs was 37.5% for (10D|initial). It was near 30% for (20D|10D) and (30D|20D), and increased to about 40% for (40D|30D), then decreased to 6.2% for (90D|80D). The summed genetic effects of conditional QTLs were 0.50 for (10D|initial), and increased to 3.06 for (40D|30D), then decreased to 0.1 for (90D|80D). These results indicated that, with the growth of rice

Table 3 Estimated conditional genetic effects of QTLs detected for the tiller number of the DH population at different stages based on conditional composite interval mapping

Chrom.	QTL	Marker interval	10D|initial	20D|10D	30D|20D	40D|30D	50D|40D	60D|50D	70D|60D	80D|70D	90D|80D
1	tn 1-1	RG472–RG246				0.50*					
1	tn 1-2	Amy 1B–RZ276									−0.1
1	tn 1-3	RG381–RZ19			0.40**	0.45*					
1	tn 1-4	RZ730–RZ801	0.09*			0.44*	0.44*		−0.28*		
2	tn 2-1	RG171–RG157						0.50*	−0.28**		
2	tn 2-2	CDO686–Amy1A/C								−0.31**	
2	tn 2-4	RZ123–RG520				−0.49*					
3	tn 3-1	RG104–RG348		0.15**							
3	tn 3-2	RZ284–RZ394	−0.13***							−0.34*	
3	tn 3-4	CDO87–RG910				0.64**	0.64**				
4	tn 4-1	RG190–RG908			0.36*						
4	tn 4-2	RZ675–RG163					0.72**				
4	tn 4-3	RG143–RG620				0.55**					
5	tn 5	RG403–RG229		0.22***							
6	tn 6	CDO544–RG653	0.10*	0.14*				−0.22*			
7	tn 7	CDO497–CDO418					0.48*				
8	tn 8	Amp2–CDO99	0.08*				−0.55*				
11	tn 11-1	RG1094–RG167						0.59*			
11	tn 11-2	RG103–RG1109			−0.35*						
12	tn 12	CDO344–RG958	0.10**								
% Variability for multiple-QTL model			37.5	28.2	27.3	40.7	29.5	11.4	13.5	11.3	6.2

*, **, *** Indicate significance at 0.05, 0.01 and 0.001 levels, respectively

plants, the expression of new genes for tiller number increased and reached the peak point at 40 days, which was earlier than the peak point of the cumulative effects. The results also showed that conditional QTLs detected prior to 50 days were different from those detected after 50 days (Table 3). For most conditional QTLs detected before 50 days, the alleles which increased tiller number were except for tn2-4, tn8 and tn11-2, from IR64. But for all QTLs detected after 60 days, the alleles from IR64 decreased tiller number.

Discussion

There are two kinds of data that can be used to analyze the developmental genetics of quantitative traits. One is of the measurement of trait development according to its real growth stage, such as maximum tillering stage and heading stage in rice, and the other is of time-specific measures. In most cases, the materials used in the genetic analysis of the developmental behavior of quantitative traits segregated not only for the trait to be studied, but also for other traits, such as heading date. It is very difficult, even impossible in some cases, to measure trait development in a segregating population according to its real growth stage. Therefore, time-specific measures have been commonly used to exploit the genetic basis of quantitative trait development in both plants and animals (Xu and Shen 1991; Zhu 1995; Atchley and Zhu 1997).

In the present study, we found three QTLs for tiller number at the final stage, which agreed with previous reports that only 1–2 QTLs were detected for tiller number at the final stage (Xiao et al. 1995 a, b; Lin et al. 1996; Wu et al. 1996). But with time-specific measures of tiller number, we could identify 15 QTLs at different stages. At the peak tillering stages, from 40 to 50 days, eight QTLs were identified. With conditional mapping, 20 chromosomal regions significantly affecting tiller number in different growth periods were found. About 70% of these time-specific QTLs were detected before 50 days. It was evident that more QTLs had been expressed for the growth of tillers at the early stages than for the QTLs detected at the maturity stage. Therefore, it is impossible to determine the genetic basis for tiller number by QTL mapping at maturity only.

About 2/3rds of the chromosomal regions showed QTLs affecting tiller number at early stages but not at later stages (Table 2). This implies that distinct genetic systems might be responsible for the early and later growth of tiller number in rice. Similar results have been observed in mapping QTLs for the body weight growth of mice. Here, most of the QTLs affecting early growth were undetected at later stages (Cheverud et al., 1996). It was shown by the conditional QTL mapping results that most QTLs detected before 50 days had positive genetic effects, but were negative afterwards (Table 3). Therefore, the expression of genes at early stages prior to 50 days might control the growth of tillers, but genes expressed at later stages might control the mortality of tillers.

By comparing the conditional and unconditional mapping results (Fig. 1), we found that 12 out of the 15 map locations of the QTLs detected by unconditional mapping were also detectable by conditional mapping, except for tn2-3, tn3-2, tn3-3, and tn3-5. But there were eight conditional QTLs that were undetectable by the unconditional method. This is because conditional mapping can detect QTLs acting at a specific growth period but not affected by the genes expressed in the previous stages. Since the unconditional QTLs explain the cumulative gene actions from initial time to time *t*, the variation of cumulative gene effects might be diminished if genes with opposite genetic effects were expressed at the same or nearby locations, such as at the map locations of tn2-1 and tn6. It might also explain why some conditional QTLs were not detected by unconditional mapping.

In this study on unconditional mapping, a major QTL (tn1-4) was detected on chromosome 1 between markers RZ730 and RZ810 at all measuring stages with a similar gene action throughout (Table 2). But it was suggested by the conditional QTL mapping results that the real temporal pattern of gene expression at this locus was quite different. With conditional mapping, differential gene expression at the region was detected for (10D|initial), (40D|30D), (50D|40D) and (70D|60D), respectively. This indicated that the gene or genes for tiller number at this region were expressed prior to 10 days, between 30 to 50 days, and between 60 to 70 days. Alleles from IR64 increased tiller number at the early stages, but decreased it for (70D|60D). Similar results were also observed in other genomic regions, such as tn2-1 and tn6. At the map location of tn6, an unconditional QTL was detected before 50 days, but not afterwards. This observation can be well explained by the conditional QTL mapping result. A conditional QTL with a negative genetic effect was detected for (60D|50D), which might counteract the early gene effects at this locus. It is possible that an individual gene might have opposite genetic effects at various growth stages, or that multiple genes at the same genomic location might be expressed differently at various stages.

At the genomic region of tn3-4, unconditional QTLs were detected from 50 days until the end, but conditional QTLs were only detected for (40D|30D) and (50D|40D). This observation suggested that those unconditional QTLs detected at 50 days and after were due to the cumulative gene effects expressed from 30 to 50 days. Therefore, conditional QTL mapping results can well explain the dynamic gene expression of quantitative traits.

It has long been noted by rice breeders and geneticists that semi-dwarf varieties generally have a higher tillering ability than tall varieties. A highly negative correlation between plant height and tiller number at corresponding measuring stages has been observed in our study (data not shown). By comparing the map locations for tiller number with those for plant height, we found that most QTLs for tiller number, especially those with large genetic effects, mapped to approximately the same chromosomal regions as plant height, but with opposite genetic effects (Yan et al. 1997). For example, the major QTL (tn1-4) mapped to the same genomic region as the semi-dwarf gene *sd*-1 but with an opposite genetic effect. Conditional QTLs for both tiller number and plant height were detected for (10D|initial), which indicates that the gene (or genes) at this genomic region for these two traits has (or have) expressed prior to 10 days after transplanting. Conditional QTL mapping results also showed that the gene (or genes) for plant height were expressed again between 40 to 80 days, which is parallel to the rapid increase of plant height at these stages (Yan et al. 1997). For tiller number, conditional QTLs were detected with positive genetic effects for (40D|30) and (50D|40), but with negative genetic effects for (70D|60D) (Table 3). This conforms with the fact that tiller number begins to decline at the onset of stem elongation and panicle initiation. It was evident that, even though the gene (or genes) at this region controlled both tiller number and plant height, its (their) expression stages and gene effects was (were) different. Therefore, further evaluation is needed to resolve whether these two traits are controlled by the same *sd*-1 gene with pleiotropic effects or by different closely linked genes.

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