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ORIGINAL PAPER

Dynamic analysis of QTLs on tiller number in rice (*Oryza sativa* L.) with single segment substitution lines

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Abstract: Twelve single segment substitution lines (SSSLs) in rice, which contain quantitative trait loci (QTLs) for tiller number detected previously, were used to study dynamic expression of the QTLs in this study. These SSSLs and their recipient, Hua-Jing-Xian 74 (HJX74), were used to produce 78 crossing combinations first, and then these combinations and their parents were grown in two planting seasons with three cropping densities. Tiller number was measured at seven developmental stages. QTL effects including main effects (additive, dominance and epistasis), QTL × season and QTL × density interaction effects were analyzed at each measured stage. The additive, dominant and epistatic effects of the 12 QTLs as well as their interaction effects with the seasons and with the densities all display dynamic changes with the development. Eight QTLs are detected with significant additive effects and/or additive × season and/or additive × density interaction effects at least at one developmental stage, and all QTLs have significant dominant and epistatic effects and/or interaction effects involved in. For most of the QTLs dominant effects are much bigger than additive effects, showing overdominance. Each QTL interacts at least with eight other QTLs. Additive and dominant effects of these QTLs are mostly positive while epistatic effects are negative and minor. Most of the QTLs show significant interactions with planting seasons and cropping densities, but the additive effects of QTLs *Tn3-1* and *Tn3-2*, the dominant effects of QTL *Tn7* and *Tn8*, and the epistatic effects of 14 pairs of QTLs are stable across seasons and the dominant effect of QTL *Tn3-3* and the epistatic effects of QTL pairs *Tn2-1*/*Tn6-2, Tn2-1*/*Tn9* and *Tn3-3*/*Tn6-3* are nearly consistent across cropping densities. This paper is the first report of dynamics on dominances and epistasis of QTLs for tiller number in rice and provides abundant information, which is useful to improve rice tiller number via heterosis and/or QTL pyramiding.

G. Liu and H. Zhu contributed equally to this work.

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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 (Yan et al. 1998). On the other hand, tillering is a trait for which the expressing changes over time and can easily be measured. For these reasons, our research group focused on the elucidation of genetic bases influencing tiller number per plant in rice using single segment substitution lines (SSSLs). In 2008, we used 35 SSSLs to evaluate

quantitative trait loci (QTLs) on panicle number per plant, i.e. effective tiller number at final stage in six different environments (Liu et al. 2008). We followed further to analyze the developmental behavior of some of QTLs in single environment and multiple environments (Zhao et al. 2008; Liu et al. 2009, 2010). However, all these researches just applied the homozygous SSSLs as experimental materials to estimate additive effects of QTLs in rice, ignoring the important genetic components of dominant and epistatic effects.

Numerous studies had proved the universality and the importance for dominance and epistasis existed in the genetic system on quantitative traits in plant (Davenport 1908; Bruce 1910; Paterson et al. 1991; Cockerham and Zeng 1996). Dominant and epistatic effects between QTLs have widely been studied by modern molecular quantitative genetics also. Using conventional biparental mapping populations such as backcrossing, selfing F_2, double haploid line and recombination inbred line populations, dominant and epistatic effects between QTLs were estimated for many quantitative traits (Xiao et al. 1995; Yu et al. 1997; Zhuang et al. 1997; Li et al. 1997, 2001, 2003; Wang et al. 1999; Semel et al. 2006; Gao and Zhu 2007; Liu et al. 2007; Li et al. 2008a, b). However, these estimations were always disturbed by the differences in genetic background between individuals or lines within the mapping populations (Eshed and Zamir 1995; McCouch and Doerge 1995; Yamamoto et al. 2000).

Tanksley (1993) suggested analyzing QTL effects via developing novel materials such as near-isogenic lines or single segment substitution lines etc. Eshed and Zamir (1996) estimated the dominant effects and the dominance-by-dominance of epistatic effects of QTLs on yield and its component traits in tomato using a half diallel crossing population derived from SSSLs crossed with their recipient parent. Lin et al. (2000) and Yamamoto et al. (2000) studied the additive effects and the additive-by-additive interaction effects of QTLs on heading date in rice using near-isogenic lines containing two QTLs. In this paper, we used 12 *SSSLs* that have been shown to contain QTLs for tiller number, the recipient *HJX74*, and novel genetic materials of their hybrids F_1 to further study the genetics of tiller number. Especially, these materials allowed the further study of QTL dominant and epistatic effects. Two planting seasons and three cropping densities were used to investigate the interactions of QTL-by-season and QTL-by-density. The results would be helpful for improving tiller number through heterosis and QTL pyramiding in rice.

Materials and methods

Plant materials

Ninety-one genetic entries including 12 *SSSLs* (Table 1 and Fig. 1), the recipient cultivar *HJX74*, twelve crossing combinations of *HJX74* × *SSSLs* and sixty-six $SSSL_i \times SSSL_j$ $(i, j = 1, 2, \ldots, 12,\ i < j)$ were used in this study. The twelve SSSLs were chosen from the large SSSL library developed by Zhang et al. (2004), based on previous mapping results for tiller number (Zhao et al. 2008). *HJX74* is an elite *indica* variety from South China, and 14 *indica* and 10 *japonica* varieties collected worldwide were used as donors to develop SSSLs (Zhang et al. 2004).

Table 1 Single segment substitution lines (SSSLs) of HJX74 and substitution segments of chromosomes (Chr.), length (cM), putative QTLs, marker intervals and donors (Zhao et al. 2008; Liu et al. 2008, 2009)

SSSL	Chr.	Length (cM)	Putative QTL	Marker interval	Donor
HJX74					
W11-15-09-03	2	12.5	*Tn2-1*	RM112–RM213	Basmati 370
W27-14-01-09-18	2	23.1	*Tn2-2*	RM526–RM425	IAPAR9
W20-20-05-19-07	3	20.4	*Tn3-1*	RM168–RM571	Chenglongshuijingmi
W20-20-05-05-11	3	6.0	*Tn3-2*	RM135–RM55	Chenglongshuijingmi
W08-16-03-59	3	17.2	*Tn3-3*	PSM304–RM545	IR64
W15-05-07-15	6	8.8	*Tn6-1*	Rm508–Rm225	American jasmine
W17-10-07-05-12	6	8.5	*Tn6-2*	RM133–RM587	Ganxiangnuo
W08-09-05-03	6	28	*Tn6-3*	RM508–RM549	IR64
W19-18-09-06	7	24.5	*Tn7*	RM51–RM214	Kyeema
W17-46-40-10-07-04	8	8.3	*Tn8*	RM515–RM210	Ganxiangnuo
W02-17-06-15	9	17.0	*Tn9*	RM105–RM278	Amol 3
W08-15-06-04-04	12	2.6	*Tn12*	RM235–RM17	IR64

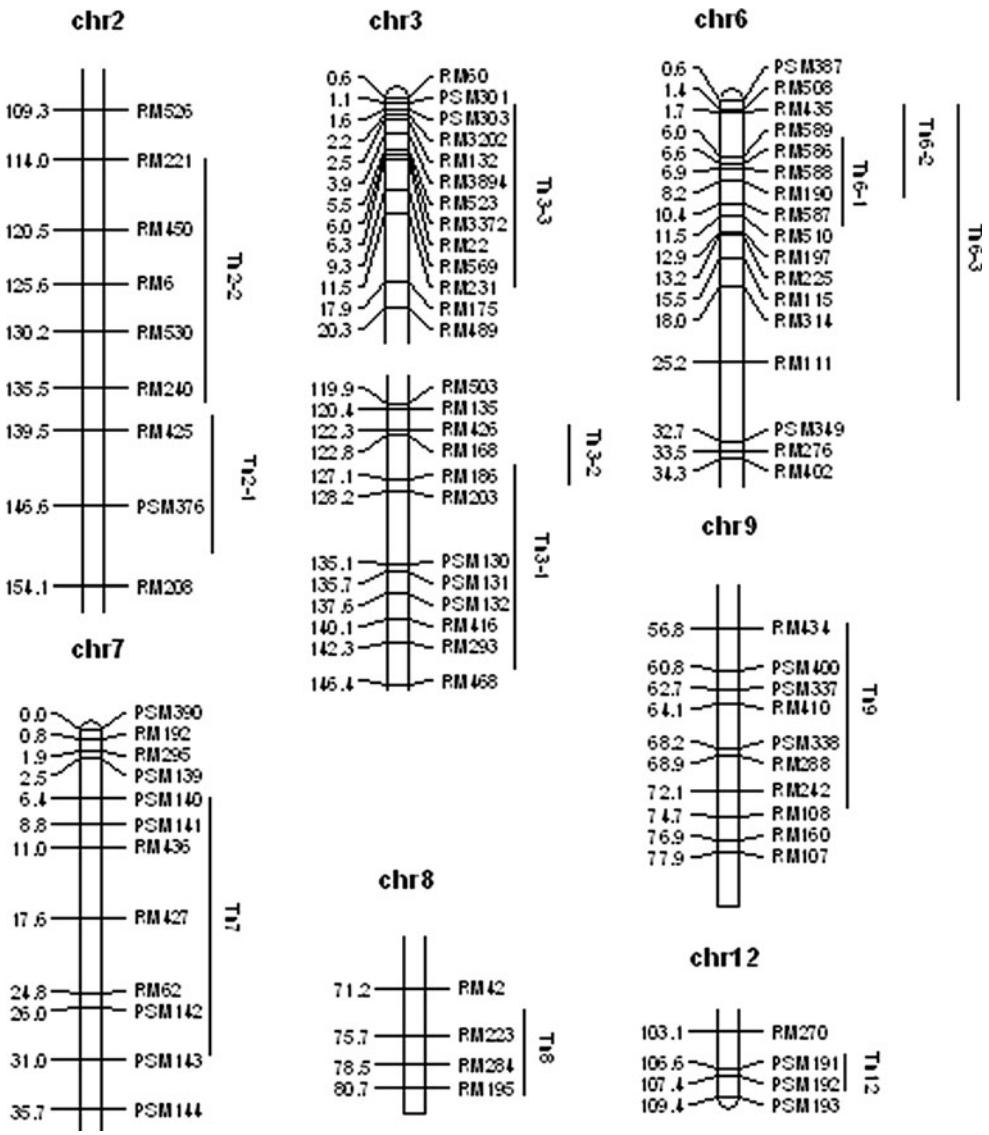

Fig. 1 Chromosomal positions, segment length (cM) of the substituted segments and names of putative QTLs. QTLs are nominated by *Tn* followed by the chromosomal number. Additional number is given as more than one QTL is located in one chromosome. QTL *Tn2-1*, for example, indicates the first QTL of tiller number detected on chromosome 2 (Zhao et al. 2008; Liu et al. 2008, 2009)

Field trials and tiller number evaluations

Phenotypic experiments were conducted at the Experimental Station of South China Agricultural University, Guangzhou, China (at ~113° east longitude and ~23° north latitude). All 91 materials were grown in two seasons, spring (from March to July, *s1*) and fall (from July to November, *s2*) in 2009. Germinated seeds were sown in a seedling bed, and seedlings were transplanted to a paddy field 20 days later with one plant per hill. A completely randomized design with three cropping densities of 10 × 16.7 cm (*c*1), 16.7 × 16.7 cm (*c*2) and 23.3 × 16.7 cm (*c*3), was adopted. Each plot consisted of four 10-plant rows. The management of the field experiments was in accordance with local standard practices. From seven days after transplanting onwards, tiller number per hill was investigated every 7 days on 12 (in spring season) or 10 (in fall season) central plants (fixed through all measuring stages) from each plot until the highest tiller number appeared. Tiller number was continuously recorded for 7 weeks (denoted by *t*1 to *t*7). Tiller number of individual plants in each plot at various measuring stages was used as raw data in the analysis.

Statistical analysis and QTL mapping

For multiple-environment analysis, the phenotypic data for a developmental stage was analyzed using the following linear model,

$$y_{ijkl} = \mu + S_i + G_j + C_k + (GS)_{ij} + (GC)_{jk} + (SC)_{ik} + (GSC)_{ijk} + \varepsilon_{ijkl}$$

where, y_{ijkl} is the *l*th phenotypic observation of the *j*th genetic entry in the *k*th density, *i*th season, μ = population

mean, $S_i = i$th seasonal effect, $G_j = j$th genotypic effect, $C_k = k$th density effect, $(GS)_{ij}$, $(GC)_{jk}$, $(SC)_{ik}$ and $(GSC)_{ijk}$ are their interaction effects, respectively and ε_{ijkl} = residual effect. Effect components were predicted by the Best Linear Unbiased Prediction (BLUP) method, and variance components were estimated by the restricted maximum likelihood (REML) method assuming a complete random model.

Assuming that each SSSL carried no more than one QTL, additive and dominant effect of putative QTL on a *SSSL* could be estimated according to the idiomatic method (Eshed and Zamir 1995, 1996). That is to say additive effect of the QTL on a SSSL can be estimated by $(SSSL - HJX74)/2$ and its dominant effect can be estimated by $(HJX74 \times SSSL - (SSSL + HJX74)/2)$. When two SSSLs were crossed to pyramid into a heterozygousity with double heterozygous substitution segments, $(SSSL_i \times SSSL_j - SSSL_i \times HJX74 - SSSL_j \times HJX74 + HJX742)/4$ was used to estimate the epistatic effect between the two donor segments. Based on the effect components G estimated in the model, QTL main effects [additive (a), dominant (d) and epistatic effect (e)] could be estimated. Based on the effect components GS and GC estimated in the model, QTL interaction effects with seasons (as, ds and es) and with cropping densities (ac, dc and ec) could be acquired, respectively. Contrasts were constructed based on the above definitions of QTL effects that were used in the fixed model version of the above linear model to test the significances of the QTL effects. All calculations were carried out by using R (R Core Development Team 2011).

Results

Phenotypic changes and environmental effects on tiller number

The average tiller number over all plants measured at different stages under three cropping densities in two experimental seasons is shown in Fig. 2. Generally, tiller number continually increases until the highest tillering stage, and then keeps consistency for a moment. After then, it reduces to the effective tiller number. The development curves of tiller number for the two seasons are different. Under the same cropping density, tiller number in spring season is often lower during the prophase of ontogeny (before stage $t5$) but higher during the anaphase than that in fall season. It differs also across cropping densities. In the same season, tiller number reduces with the increase of cropping density, especially during the late-mid-period of ontogenesis. It is obvious that the higher the cropping density, the fewer the tiller number.

The analysis of variances indicates that tiller number in rice is mainly affected by genetic factors (Table 2).

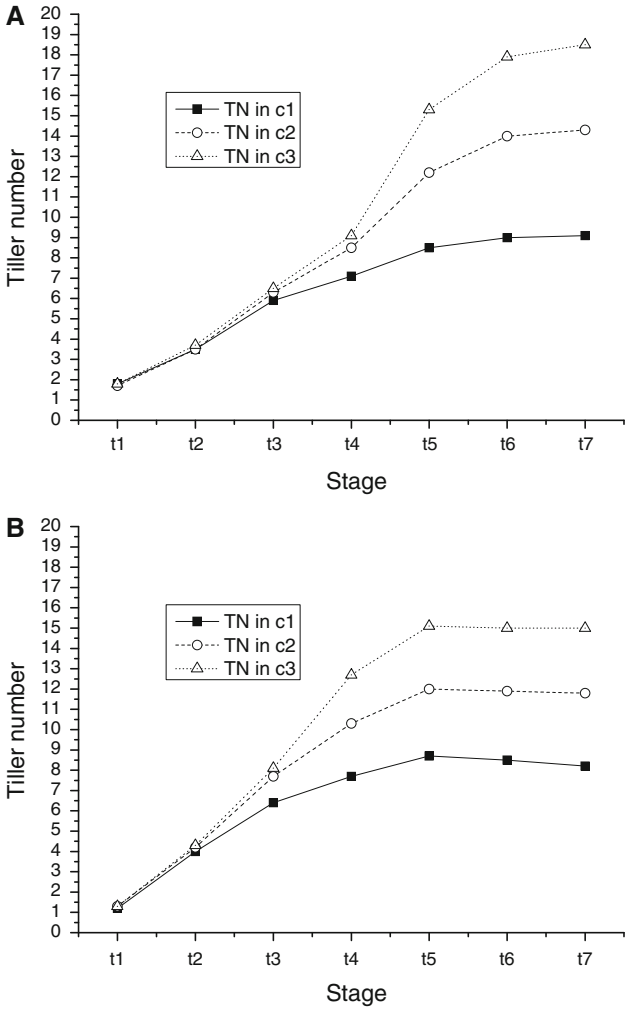

Fig. 2 Dynamics of tiller number under three cropping densities in spring season (**a**) and fall season (**b**). TN is the abbreviation of tiller number. *c1*, *c2* and *c3* represent the three cropping densities of 10 × 16.7, 16.7 × 16.7 and 16.7 × 23.3 cm, respectively. *t*1–*t*7 indicate the developmental stages, setting 7 days between stages, respectively

Phenotypic variances contributed by residuals change from 6.65 to 16.57%, decreasing gradually with developmental stages. The total genetic variances from *G*, *GS*, *GC* and *GSC* account for 83.43–93.35% of phenotypic variations, of which ratios owing to *G* go up from 25.03 at *t*1 to 65.84% at *t*7. The correlation between tiller number and the proportions of genetic variances to phenotypic variances at various stages is very strong with 0.99 of coefficient, of which 0.96 contributes to genetic factor *G*.

Additive effects of QTLs and their interactions with planting seasons and cropping densities

QTL mapping in single environment can provide comprehensive information about QTL effects (see Supplementary

Table 2 Proportions of phenotypic variances contributed by various effects and residuals on tiller number in the population investigated

Factor[a]	*t*1[b]	*t*2	*t*3	*t*4	*t*5	*t*6	*t*7
G	0.2503[c]	0.3833	0.3912	0.4394	0.6292	0.6491	0.6584
GS	0.2503	0.1916	0.2186	0.1872	0.0542	0.0329	0.0451
GC	0.0834	0.0767	0.0230	0.0542	0.0759	0.0878	0.0932
GSC	0.2503	0.2172	0.2569	0.2170	0.1591	0.1599	0.1368
ε	0.1657	0.1313	0.1103	0.1022	0.0815	0.0702	0.0665

[a] G, *GS*, *GC*, *GSC* and ε indicate genotype, genotype × seasons, genotype × densities, genotype × season × densities and residual, respectively

[b] *t*1–*t*7 indicate measuring stages of tiller number, setting 7 days between stages

[c] Proportions are calculated by the formula of V_i/V_P, where V_i is corresponding variance component, and V_P is phenotypic variance, $V_P = \sigma^2_\varepsilon/(\text{nsc}) + \sigma^2_{g\times s\times c}/(\text{sc}) + \sigma^2_{g\times s}/s + \sigma^2_{g\times c}/c + \sigma^2_g$ (σ^2 represents variance component estimated, *n*, *s*, and *c* indicate the numbers of replications, seasons and densities, respectively)

Table 1–3). However, using jointly analysis of multiple environmental data can divide the comprehensive effect of QTLs in single environment into QTL effect components, main effects (*a, d* and *e*) and interaction effects with planting seasons (*as*, *ds* and *es*) and with cropping densities (*ac*, *dc* and *ec*).

A total of eight QTLs are detected with significant additive effects and/or interaction effects with seasons and/or densities (Table 3), distributed on chromosomes 2, 3, 6 and 7. All QTLs express additive effects with dynamic patterns during the whole stage of rice growth. First, the additive effects of most QTLs are statistically significant only at certain stages. QTL *Tn6-3* does not have significant additive effect at all stages. QTLs *Tn2-2* and *Tn6-1* are detectable at all stages. QTLs *Tn7* can be detected only at stage *t*3 when its additive effects reaches the maxinum value. Many QTLs cannot be detected at a given stage since their accumulated effects are too small at that stage. The number of QTLs with significant additive effects is different at various stages, with the variations from three at stage *t*1 to 7 at stage *t*3. Secondly, the additive effects of each QTL differ greatly across developmental stages. One common feature is that additive effect of each QTL increases to a maximum value and then decreases. The additive effect of QTL *Tn2-1*, for instance, increases from 0.16 at stage *t*1 to a peak point of 0.59 at stage *t*4, and then decreases to 0.15 at stage *t*7.

Additive effects of QTLs are affected by planting seasons and cropping densities. For most of the QTLs, the additive × season interactions are significant at one or more measurement stages. For QTL *Tn2-1*, for instance, the additive × season interactions are significant at all stages but *t*7. QTLs *Tn3-1* and *Tn3-2* do not show any significant interaction effects, indicating that the two QTLs are stable across the two planting seasons. QTLs *Tn6-3* and *Tn7* do not have significant additive effects at most stages, but their interaction effects with seasons are often significant. For QTL *Tn2-1*, the additive × season interaction effects are always larger than the additive effects. Like the additive effects of QTLs, the additive × season interaction effects vary across developmental stages also. With development the interaction effects increase first and then decrease. For QTLs *Tn2-1, Tn2-2, Tn6-3* and *Tn7*, their interaction effects with s1 are positive at all stages, while the inverse cases are true for QTLs *Tn3-1, Tn3-2* and *Tn6-1*. An exception is that QTL *Tn6-2* has negative interaction effects with *s*1 from stages *t*1 to *t*4 but positive after then.

Additive-by-density interactions are also significant for most of the QTLs at most stages. QTL × density interaction effects vary with development. QTL *Tn2-1* has significant interaction effect only at stage *t*1. The other seven QTLs are often detected with significant additive × density interaction effects. Specially, QTLs *Tn3-2, Tn6-1* and *Tn6-3* frequently show large interaction effects, indicating great changes on their additive effects with the changes of cropping densities. QTLs such as *Tn2-2, Tn3-1, Tn6-2* and *Tn6-3* have significant interactions with cropping densities mainly at the late-mid-period of development, but QTLs *Tn2-1* and *Tn7* interact with densities only at stages *t*1 and *t*3, respectively. QTLs *Tn3-2* and *Tn6-1* have significant interactions with cropping densities at all developmental stages. During stages of *t*5 and *t*6, interaction effect values on QTLs of *Tn2-1, Tn2-2, Tn3-1, Tn3-2* and *Tn6-1* increase with densities and the other QTLs have the utmost values mainly at the density of *c*2.

Dominant effects of QTLs and their interactions with planting seasons and cropping densities

All the 12 QTLs have significant dominant effects on tiller number at one or more stages (Table 4). The number of QTLs with significant dominant effects is between 5 at stage *t*7 and 11 at stage *t*3. QTL *Tn2-1*, for example, has significant dominant effects at stages *t*1, *t*2 and *t*3, and its effect values rise from 0.34 to 1.07 and then decrease. Each

Table 3 QTL additive effects and their interaction effects with planting seasons and cropping densities estimated at various stages

QTL[a]	Effect[b]	*t*1[c]	*t*2	*t*3	*t*4	*t*5	*t*6	*t*7
Tn2-1	*a*	0.16*, [d]	0.21*	0.44**	0.59**	0.35**	0.33**	0.15
	as1	0.25**	0.35**	0.65**	0.69**	0.38*	0.50**	0.32
	ac1	0.18*	0.15	0.24	0.07	−0.01	−0.09	−0.24
Tn2-2	*a*	0.26**	0.50**	0.99**	1.13**	1.17**	1.20**	1.09**
	as1	0.13*	0.08	−0.11	0.06	0.31	0.47*	0.56**
	ac1	0.04	0.09	−0.04	−0.23	−0.52	−0.63*	−0.83**
	ac3	−0.02	0.01	0.07	0.53*	0.78**	0.88**	0.96**
Tn3-1	*a*	0.02	0.19*	0.61**	0.96**	1.27**	1.24**	1.22**
	ac1	0.07	0.16	−0.19	−0.35	−0.61*	−0.80**	−0.79**
	ac3	−0.08	−0.17	−0.14	0.01	0.32	0.29	0.54*
Tn3-2	*a*	0.10	0.17	0.51**	0.85**	1.13**	1.17**	1.05**
	ac1	−0.21*	−0.20	−0.53*	−0.99**	−1.06**	−1.15**	−1.23**
	ac3	0.23**	0.24	0.70**	0.94**	1.43**	1.36**	1.39**
Tn6-1	*a*	0.14*	0.54**	0.94**	1.18**	1.43**	1.72**	1.70**
	as1	−0.14*	−0.23*	−0.51**	−0.69**	−0.72**	−0.77**	−0.77**
	ac1	−0.19*	−0.29*	−0.77**	−0.79**	−1.23**	−1.43**	−1.41**
	ac2	0.18*	0.31*	0.50*	0.12	0.42	0.07	0.13
	ac3	0.02	−0.02	0.26	0.67**	0.81**	1.36**	1.28**
Tn6-2	*a*	−0.05	0.06	0.34*	0.40*	0.58**	0.83**	0.76**
	as1	−0.02	−0.06	−0.31*	−0.17	0.24	0.48*	0.41*
	ac2	0.05	0.13	0.36	0.21	0.58*	0.68*	0.44
Tn6-3	*as1*	−0.02	0.10	0.20	0.29	0.38*	0.62**	0.56*
	ac1	0.02	−0.12	−0.37	−0.31	−0.56*	−0.64*	−0.61*
	ac2	0.01	0.1	0.32	0.34	0.58*	0.55*	0.59*
Tn7	*a*	0.07	0.12	0.36*	0.30	0.16	−0.03	−0.19
	as1	0.11*	0.21*	0.31*	0.38**	0.24	0.13	−0.03
	ac1	−0.14	−0.20	−0.47*	−0.33	0.06	0.06	0.15
	ac3	0.16*	0.27*	0.49*	0.33	0.16	0.07	−0.02

[a] QTLs are nominated by *Tn* followed by the chromosomal number. Additional number is given as more than one QTL is located in one chromosome. QTL *Tn2-1*, for example, indicates the first QTL of tiller number detected on chromosome 2

[b] Effects of *a*, *as* and *ac* indicate the additive effects, additive × seasons and additive × densities of interaction effects respectively, which are estimated based on genetic effect components of the mapping population. *s1* represents the planting season of spring. *c1, c2* and *c3* represent the three cropping densities of 10 × 16.7, 16.7 × 16.7 and 16.7 × 23.3 cm, respectively

[c] *t*1–*t*7 indicate measuring stages of tiller number, setting 7 days between stages

[d] The numbers and the signs showed in the Table indicate the estimated values and the directions of the effects of the donor alleles, respectively. "* and **" show the significances at 0.005 and 0.001 of probability levels, respectively

QTL exhibits the developmental schedule of itself, having at least one peak values on dominant effects during the whole developmental period.

Great differences on dominant effects are found between the two seasons. All QTLs except *Tn7* and *Tn8* show significant interactions with seasons. This result indicates that these QTLs are seasonal sensitive, especially QTLs *Tn-2-2, Tn3-2, Tn6-1, Tn6-2, Tn6-3, Tn9* and *Tn12* showing large interaction effects. The dominant effects of QTLs *Tn7* and *Tn8* are relatively stable across seasons since they are less often detected with significant interaction effects with seasons. Factors in the season of *s1* tend to reduce dominant effects of QTLs *Tn2-2, Tn3-3* and *Tn6-2*, but enhance dominant effects of others.

Dominance-by-density interactions are also frequently observed. All the 12 QTLs are detected with significant interactions at certain stages in certain densities. For example, QTL *Tn2-1* has significant interaction effects only at stages *t*2 ∼ *t*7 in *c*2 and *t*2, *t*4 in *c*3. Dynamics also occurs on dominance-by-density interaction effects of these QTLs, which vary across stages. Similar to the additive × density interaction effects, large estimations for dominance × density interaction effects are often obtained, indicating that cropping densities play an important role on dominance of QTLs.

Table 4 QTL dominant effects and their interaction effects with planting seasons and cropping densities estimated at various stages

QTL[a]	Effect[b]	*t*1[c]	*t*2	*t*3	*t*4	*t*5	*t*6	*t*7
Tn2-1	*d*	0.34**, [d]	0.65**	1.07**	0.30	0.04	−0.10	−0.04
	ds1	−0.02	−0.59**	−0.38	−0.06	0.24	0.20	0.32
	dc2	0.04	0.48*	1.25**	1.08*	1.02*	1.08*	1.08*
	dc3	−0.04	−0.64**	−0.7	−1.00*	−0.65	−0.75	−0.91
Tn2-2	*d*	0.02	0.43**	0.90**	0.76*	0.62**	0.66*	0.74*
	ds1	−0.23*	−0.62**	−1.20**	−0.84**	−1.13**	−0.90**	−0.77**
	dc1	−0.42**	−0.42	−1.40**	−1.59**	−1.39**	−1.07*	−1.41**
	dc2	0.51**	0.80**	1.65**	1.72**	1.12*	1.12*	1.04*
Tn3-1	*d*	0.36**	0.53**	0.94**	0.81**	0.82**	0.75*	0.50
	ds1	0.25*	0.14	0.15	0.04	0.39	0.85*	0.55
	dc1	0.27	0.04	0.51	1.36**	1.17**	0.87	0.81
	dc3	−0.22	−0.30	−0.40	−1.01*	−1.33**	−1.25**	−1.25**
Tn3-2	*d*	0.13	0.50**	0.80**	0.26	−0.05	0.31	0.20
	ds1	0.07	−0.05	−0.23	0.34	0.41	1.09**	1.29**
	dc1	0.29*	0.72**	1.20**	1.49**	1.58**	1.13*	0.80
	dc3	−0.48**	−0.71**	-1.43**	−1.30**	−2.08**	−1.27**	−1.03*
Tn3-3	*d*	0.24*	0.30	0.91**	0.15	−1.04**	−1.41**	−1.37**
	ds1	0.24*	0.07	0	0.11	−0.31	−0.56	−0.51
	dc3	0.28*	0.01	0.20	0	0.44	0.17	−0.19
Tn6-1	*d*	0.33**	0.51**	1.11**	1.34**	1.57**	1.19**	0.92**
	ds1	0.39**	0.14	0.54*	0.99**	1.90**	1.99**	2.12**
	dc2	−0.35*	−0.80**	−0.31	−0.74	−1.92**	−1.81**	−2.15**
	dc3	0.06	0.39	0.28	0.14	1.43**	1.10*	2.15**
Tn6-2	*d*	0.37**	0.52**	0.74**	0.80**	0.89**	0.82*	0.72*
	ds1	0.20*	0.13	0.16	−0.29	−1.01**	−1.23**	−1.33**
	dc1	−0.25	−0.50*	−0.97*	−0.88*	−1.19*	−1.61**	−1.62**
	dc2	−0.30*	−0.14	−0.55	−0.49	−0.65	−1.10*	−0.84
	dc3	0.55**	0.63**	1.53**	1.37**	1.84**	2.71**	2.46**
Tn6-3	*d*	0.54**	0.51**	1.07**	1.33**	0.76*	0.33	−0.08
	ds1	0.51**	0.10	0.66*	0.45	−0.37	−0.56	−0.94**
	dc1	0.14	0.03	0.70	0.81	1.07*	0.98*	0.60
Tn7	*d*	0.49**	0.67**	1.39**	0.89**	0.81**	0.64	0.35
	dc2	0.01	0.18	0.41	0.72	1.29**	1.60**	1.35**
Tn8	*d*	0.21*	0.19	0.38	0.59	0.89**	0.92**	0.83*
	dc1	−0.21	−0.34	−0.05	−0.07	0.74	1.04*	0.56
	dc2	0.37**	0.58*	1.24**	1.31**	0.43	0.3	0.32
	dc3	−0.15	−0.23	−1.19**	−1.24**	−1.17*	−1.34**	−0.88
Tn9	*d*	0.13	0.52**	1.03**	1.40**	0.99**	0.86*	0.45
	ds1	0.07	−0.03	0.14	0.22	0.72*	0.77*	0.65
	dc1	0.14	0.05	−1.00**	0.08	1.23*	1.62**	1.61**
	dc2	−0.08	0.05	0.90*	0.56	0.34	−0.14	0.02
	dc3	−0.06	−0.10	0.10	−0.64	−1.56**	−1.48**	−1.64**
Tn12	*d*	0.26**	0.57**	0.62*	0.28	0.22	−0.11	−0.33
	ds1	0.22*	0.14	0.24	0.59	1.51**	1.44**	1.59**
	dc2	−0.20	−0.50*	−0.53	−0.68	−1.07*	−0.70	−0.6
	dc3	0.22	0.28	0.39	0.73	1.33**	0.70	0.96*

[a] QTLs are nominated by *Tn* followed by the chromosomal number. Additional number is given as more than one QTL is located in one chromosome. QTL *Tn2-1*, for example, indicates the first QTL of tiller number detected on chromosome 2

[b] Effects of *d*, *ds* and *dc* indicate the dominant effects, dominance × seasons and dominance × densities of interaction effects respectively, which are estimated based on the genetic effect components of the mapping population. *s1* represents the planting season of spring. *c1, c2* and *c3* represent the three cropping densities, 10 × 16.7, 16.7 × 16.7 and 16.7 × 23.3 cm

[c] *t*1–*t*7 indicate measuring stages, setting 7 days between stages

[d] The numbers and the signs showed in the Table indicate the estimated values and the directions of the effects of the donor alleles, respectively. "* and **" show the significances at 0.005 and 0.001 of probability levels, respectively

Degrees of dominance (d/a) and their interaction values with seasons ($(ds)/(as)$) and with densities ($(dc)/(ac)$) are calculated (data no list). The results indicate that the degrees of dominance for QTL *Tn2-2* are always less than 1 at all developmental stages. For QTLs *Tn6-3* and *Tn7* the degrees of dominance are always larger than 1 and are overdominant. For the other five QTLs the degrees of dominance are larger than one at the prophase of development and smaller than one at the late-mid-period. Degrees of dominance for each QTL are also affected by seasons and cropping densities. Interaction values estimated between degrees of dominance and seasons and between degrees of dominance and cropping densities vary greatly.

Epistatic effects of QTLs and their interactions with planting seasons and cropping densities

A total of 61 pairs of QTLs are detected with significant epistatic effects (abbreviating as *e*) on tiller number (see Supplementary Table 4). They distribute in corresponding marker intervals on all chromosomes involved. Five pairs of QTLs, *Tn2-1/Tn3-1, Tn2-2/Tn3-2, Tn3-1/Tn7, Tn3-1/Tn8,* and *Tn7/Tn12,* are not detected with significant epistasis. All epistatic effects change dynamically with development. Only at certain stages QTL epistatic effects are significant, and their estimations change across stages. QTL pair of *Tn2-1/Tn2-2*, for example, has significant epistatic effects only at stages $t1$, $t2$, $t3$ and $t4$, and its effect values wave between -0.5 and 0.01.

Planting seasons and cropping densities greatly influence the epistatic effects. The epistatic effects of 52 QTL pairs have significant interactions with seasons (abbreviating as es) at least at one stage. The epistasis-by-season interactions are insignificant for some of the QTL pairs at certain stages, indicating they are stable across the two seasons. Epistasis × season interaction effects show also dynamic changes across stages. In addition, the effect directions (contributing to trait performance positively or negatively) are also special. Under certain seasons, the directions of epistasis × season interactions keep mostly consistent across stages.

QTL epistatic effects also differ among cropping densities. 63 pairs of QTLs are detected with significant epistasis × density interaction effects (abbreviating as ec) at least at one stage. *Tn2-1/Tn6-2, Tn3-2/Tn6-2* and *Tn3-3/Tn6-3* do not have significant epistasis × density interaction effects, indicating that the epistatic effects of these QTL pairs are stable across cropping densities. Epistasis × density effects show also dynamic changes across stages. In addition, the effect directions of QTL epistasis × density differ across densities.

Several types of QTL pairs are found, (1) stable QTLs like *Tn2-1/Tn6-2* only with *e*; (2) season-sensitive QTLs like *Tn2-2/Tn6-3* having *e* and *es*; (3) density-sensitive QTLs as *Tn2-1/Tn3-1* and *Tn2-1/Tn3-3* with significant *ec*; and (4) special QTLs as *Tn2-1/Tn2-2* and *Tn7/Tn12* with both *es* and *ec* (Table 5).

Discussions

Based on previous studies, we further investigated in this study the dynamics of QTLs on rice tiller number with 12 SSSLs, recurrent parent (HJX74) and their crossing combinations. The F_1 hybrids between SSSLs and HJX74, and between two SSSLs allow the estimation of dominant and epistatic effects for QTLs on tiller number in rice, and interactions of QTLs × planting seasons and QTLs × cropping densities. Results show that the additive, dominant and epistatic effects of these QTLs as well as their interaction effects with seasons and with densities display dynamic changes with development. Eight QTLs are detected with significant additive effects and/or additive × season and/or additive × density interaction effects at least at one developmental stage, and all QTLs have significant dominant and epistatic effects. For most QTLs, the dominant effects are much greater than the additive effects, showing overdominance. Each QTL interacts at least with eight other QTLs. Additive and dominant effects of these QTLs are mostly positive while epistatic effects are negative and minor. Most QTLs show significant interactions with planting seasons and cropping densities. These information are useful in improving rice tiller number via heterosis or QTL pyramiding.

Some results in this study are different from those previously reported (Zhao et al. 2008; Liu et al. 2009). Six SSSLs with putative QTLs *Tn2-2, Tn3-1, Tn3-2, Tn6-1, Tn6-2* and *Tn8* were used simultaneously in the three trials. QTL *Tn8* was detected with significant additive effects only at stages $t1$ and $t2$ in Zhao et al. (2008). QTLs *Tn3-2* and *Tn6-1* were not detected in Liu et al. (2009). QTL *Tn3-1* was found with opposite additive effects from previous reports. These may be understandable when taking genotype by environmental interactions into consideration.

Tiller number in rice was controlled by a polygenic system and were affected by environmental factors such as manuring, planting density, and climatic circumstances of light, temperature, water supply and so on (Xiong 1992). In this study, phenotypiing on tiller number was carried out under three cropping densities, and it was indicated that the higher the cropping density, the less the tiller number. We also recorded the temperatures at noon every day during experiments (no list data) and tried to explore the relation between tiller number and temperature. We found that the

Table 5 Part of QTLs with different types of epistatic effects

QTL[a]	Effect[b]	*t*1[c]	*t*2	*t*3	*t*4	*t*5	*t*6	*t*7
Tn2-1/Tn2-2	*e*	−0.15**[,d]	−0.25**	−0.50**	−0.39**	−0.2	0.01	−0.11
	es1	−0.11**	−0.01	−0.03	−0.17	−0.05	0.10	−0.03
	ec1	0.02	−0.01	0.34*	0.36*	0.75**	0.61**	0.60**
	ec2	−0.05	−0.14	−0.55**	−0.44*	−0.43*	−0.54**	−0.49*
Tn2-1/Tn3-1	*ec2*	−0.02	−0.20	−0.43**	−0.40*	−0.49*	−0.41*	−0.42*
	ec3	0.07	0.20	0.33*	0.73**	0.84**	0.62**	0.67**
Tn2-1/Tn3-3	*e*	−0.05	−0.07	−0.2	0.17	0.48**	0.54**	0.55**
	ec2	0.12*	0.02	−0.19	−0.34	−0.38*	−0.46*	−0.47*
	ec3	−0.02	0.14	0.18	0.49**	0.38	0.50**	0.55**
Tn2-1/Tn6-2	*e*	−0.10*	−0.14*	−0.24*	−0.13	0.10	−0.01	−0.04
Tn2-2/Tn6-3	*e*	−0.13**	−0.16*	−0.41**	−0.39**	−0.32*	−0.25	−0.17
	es1	−0.06	0.11	0.19	0.14	0.33*	0.36**	0.38**
Tn7/Tn12	*es1*	−0.04	−0.07	−0.20	−0.29*	−0.51**	−0.50**	−0.39**
	ec3	−0.07	−0.19*	−0.23	−0.32	−0.15	0.02	−0.05

[a] QTLs are nominated by *Tn* followed by the chromosomal number. Additional number is given as more than one QTL is located in one chromosome. QTL *Tn2-1*, for example, indicates the first QTL of tiller number detected on chromosome 2

[b] Effects of *e*, *es* and *ec* indicate the epistatic effects, epistasis × seasons and epistasis × densities of interaction effects respectively, which are estimated based on the genetic effect components of the mapping population. *s1* represents the planting season of spring. *c1, c2* and *c3* represent the three cropping densities of 10 × 16.7, 16.7 × 16.7 and 16.7 × 23.3 cm, respectively

[c] *t*1–*t*7 indicate measuring stages of tiller number, setting 7 days between stages

[d] The numbers and the signs showed in the Table indicate the estimated values and the directions of the effects of the donor alleles, respectively. "* and **" show the significances at 0.005 and 0.001 of probability levels, respectively

correlation coefficients between tiller number and the average temperature over 7 days for each stage measured are 0.85** in *e1* and −0.77* in *e2*, respectively. This suggests that the development of tiller number is inconsistent with the change of temperatures. As discussed in previous study, tiller number may depend on photothermal quotient (PTQ, i.e. radiation/temperature) (Liu et al. 2009). A low PTQ means little growth during the window for tiller appearance and hence little excess assimilates to produce tillers. While relatively high PTQ would increase tiller number (Leon et al. 2001). In summary, since tiller number in rice has a low heritability (Xu and Shen 1991), the QTLs identified on tiller number are often inconsistent across studies. On magnitude, significant QE and QD interactions existed in this study provide well practice evidences. Large interaction effects of QTLs are often as the requirment to evaluate the stability of QTLs.

The dominance and overdominance of QTLs

Utilization of heterosis has become a major strategy for increasing productivity of plants and animals. For rice, hybrid varieties have contributed greatly worldwide to the production of food crops. However, the genetic basis of heterosis is still not well understood. Genetic analyses of heterosis using linkage mapping have been reported in rice (Xiao et al. 1995; Yu et al. 1997; Li et al. 2008b). They suggested that dominance and/or overdominance play a significant role in heterosis. In this study, all the 12 QTLs have significant dominant effects at most of the developmental stages. This includes the four QTLs without significant additive effects, indicating overdominance. The results indicate that a total of 33 degrees of dominance are with absolute values more than one, occupying 58.9% of all cases (Table 3). Especially, QTLs *Tn6-3* and *Tn7* have degrees of dominance larger than one at all stages. Therefore, overdominance plays an important role in observed heterosis. The remaining QTLs (41.1%) have degrees of dominance between −1 and 1, showing partial dominance in these heterozygotes. QTL *Tn2-2* dose not have more than one degrees of dominance at all stages. Similarly, QTLs *Tn2-1, Tn3-1* and *Tn3-2* have degrees of dominance <1 during stages *t*4–*t*7, and QTLs *Tn6-1* and *Tn6-2* during *t*6–*t*7. Therefore, it is difficult for crossing combinations with these QTLs to get transgressive segregations at these developmental stages.

The epistasis between QTLs

Epistatic interactions play an important role in the genetic basis of quantitative traits. Xing et al. (2002) detected eight digenic interactions for the numbers of tillers per plant. Liu et al. (2006) reported that four pairs of epistatic QTLs with additive × additive interaction effects were associated

with tiller number in rice. However, these studies used conventional biparental mapping populations, where results were often biased since these populations segregated the whole genome simultaneously. This study used HJX74 and its single segment substitution lines and their F_1 hybrids as genetic materials. Apparently, this population segregated at most two loci of the whole genome to avoid the disturbing of genetic background differences. Results show that all the 12 QTLs have significant epistatic effects with more than one other QTLs across the developmental stages, and only five pairs of QTLs (7.58%) have no significant epistatic effects. All epistatic effects change with developmental stages, seasons and cropping densities. Two remarkable findings are detected that all epistatic estimates are on magnitude <1 and most are negative. Since the effects of the single-locus mostly depend on the genotypes of other loci, as can be seen from this analysis, thus an attempt for utilization of the QTLs in the breeding programs has to take into account of the epistatic effects.

However, how to estimate epistasis is an unsettled issue for long time. Tanksley (1993) proposed to apply near-isogenic lines that aggregate two QTLs as materials to analysis epistasis. Then some researchers followed this suggestion in different crops (Eshed and Zamir 1996; Lin et al. 2000; Yamamoto et al. 2000). In this paper, we estimate the dominant × dominant epistasis among tiller number QTLs in rice. In fact, such a way is based on the supposing that each SSSL carried only with single locus effects as additive or dominance and without dual-locus effect as epistasis. It is unable to distinguish the types of epistasis like additive × additive, additive × dominant, dominant × additive and dominant × dominant interaction since without enough information of genotypes is provided by this study. An improved approach is to construct a F_2 population derived from $SSSL_i \times SSSL_j$, in which nine genotypes could be differentiated by marker assistant selection (MAS), and then all the four types of epistasis could be estimated well.

The dynamics of QTL effects on tiller number in rice

Similar to our previous study (Liu et al. 2009), this paper reveals also the dynamics of QTL expressing on tiller number in rice. Under three cropping densities in two planting seasons, dynamics of phenotype on tiller number is in evidence during the whole developmental period of individual (Fig. 1). Generally, tiller number was investigated until the period of heading date, and then the process of increase and decrease on tiller number was explored genetically. Biology however tells us that the decrease of tiller number after heading date is perhaps irrelevant with genetic factors but depends on environmental factors. Thus in this study tiller number was observed only to the period of highest tiller and the period of tiller reduction was ignored. Genetic components, including additive, dominance and epistasis of QTLs and their interactions with planting seasons and cropping densities, were constantly tracked at seven stages. The results indicate that all genetic components play important roles for phenotypic dynamics on tillers. Not surprisingly, the genetic determinations of tiller number also displays dynamic characteristics. Although the dynamic expressions of QTLs controlling tiller number has been reported previously, no studies have considered in dominant and epistatic effects. As the first report, dynamics of dominant and epistatic effects for 12 QTLs measured on tiller number are revealed in this study. Mostly, they ascend (reduce) first and then turn to reduce (ascend) in developmental curves of themselves. On magnitude, the additives change between −0.04 and 1.72, dominances between −1.41 and 1.57, and epistasis between −0.86 and 0.55. The additive and the dominant effects of the 12 QTLs are mostly positive, indicating that the additive of alleles from the donors basically increase tiller number. It is interesting to note that the epistatic effects of most QTL pairs tend to decrease tiller number. These phenomena may have implications in heterosis utilization and QTL pyramiding on tiller number in rice. We can select these SSSLs to cross with the receptor HJX74, and it is expected to get better combinations with heterosis. Although epistasis between QTLs on tiller number are pervasive, the contributions of epistasis to trait performance are generally small for all the QTL pairs. Thus the effect of pyramiding two QTLs is predictable using the additive and the dominant effects of the QTLs.

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