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Genetic analysis on tiller number and plant height per plant in rice (*Oryza sativa* L.)

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Abstract: Tiller number and plant height are two important agronomic traits of rice. In order to dissect their genetic architecture, QTL mapping for the two traits was conducted by using a DH population derived from an indica-japonica rice cross of IR64 × Azucena. Phenotypic data was evaluated in two crop seasons and analyzed by the mixture-model based on composite interval mapping (MCIM) method. The results showed that tiller number is mainly controlled by both the general genetic factor and the GE interaction factor (with 61.7% of the general heritability and 17.2% of the GE interaction heritability). A total number of 19 QTLs was detected to associate with tiller number. Of these, 9 and 6 QTLs were with single locus effects and digenic effects, respectively. The epistatic effect between QTL I-8 and QTL I-12 was suggested to be a major effect due to the contribution of 21.6% in spring season. Plant height is mainly controlled by the general genetic factor with 92.6% of the general genetic heritability, which is influenced by a total number of 15 QTLs. Of those, 8 QTLs with additive effects, 1 QTL with additive × environment interaction effect and 4 pairs of epistatic QTLs with additive × additive interaction effects were detected. QTL I-15 is suggested as a major QTL and the remaining QTLs were ones with minor effects. Significant negative partial phenotypic correlation was observed between the two traits. However, exploring the genetic basis of trait correlation is still necessary in further study.

Key words: genetic analysis; tiller number; plant height; QTL; rice

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摘要: 水稻分蘖数和株高是两个重要的农艺性状. 为剖解它们的遗传结构, 本研究用一套来源于籼粳组合 IR64 × Azucena 的 DH 群体对这两个性状进行了 QTL 定位分析. 表型数据来源于两个生长季节, 采用基于混合线性模型的方法分析. 结果表明, 分蘖数主要由普通遗传因素和互作遗传因素控制(呈现 61.7% 的普通遗传率和 17.2% 的互作遗传率), 共有 19 个 QTLs 与分蘖数有关, 其中 9 个和 6 对 QTLs 分别具有单位点的遗传效应和 2 位点的互作效应, QTL I-8 和 QTL I-12 的上位性效应由于在春季的

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贡献率达 21.6%,因而认为是一对主效。株高主要由普通遗传因素控制,普通遗传率为 92.6%,共受到 15 个 QTLs 的影响,其中 8 个 QTLs 具有加性效应,1 个 QTL 具有加性与环境的互作效应,4 对上上位性 QTLs 具有加性与加性互作效应。QTL 1-15 被认为是主效 QTL,而其余的是微效 QTLs。两个性状表型之间存在显著的负向部分相关,然而,性状相关的遗传基础仍需做进一步的探讨。

关键词: 遗传分析; 分蘖数; 株高; QTL; 水稻

Tiller number plays an important role in the formation of grain yield in rice, and plant height is also one of the most important traits related to plant status and yield potential. Appropriate tiller number and plant height are the pre-requisite for attaining desired yield in rice breeding programs. Thus, understanding the genetic basis underlying the inheritance of these two traits is of importance for genetic improvement of rice.

There have been many studies attempting to dissect the genetic basis of the two traits by classical genetic analysis. The recent advances in molecular marker technology^[1] have provided a powerful tool for elucidating the genetic basis of quantitative traits. QTLs for tiller number and plant height in rice have been reported before^[2-3].

However, in most of the previous QTL mapping studies, data analysis was only from a single environment^[4-5]. Genetic models used always assumed no epistasis^[6]. And QTL \times environment (*QE*) interaction was usually inferred by applying the methodology of two-way analysis of variance or multiple regressions^[7]. Obviously, all those do not allow reliable and efficient dissection of epistasis and *QE* interactions^[8], which are important genetic components of quantitative traits^[9].

A mixed-model based on composite interval mapping (MCIM) methodology^[9-10] was proposed for mapping QTLs with additive and epistatic effects, as well as their *QE* interaction, and the corresponding software QTL Mapper was also developed for analyzing the experimental data derived from multiple environments. This method to date has been widely applied in QTL mapping

studies^[11-12]. In this study, the genetic bases of tiller number and plant height in rice were analyzed using the MCIM methodology for data derived from a DH population in two environments.

1 Materials and methods

One hundred and thirty five doubled haploid (DH) lines derived from a cross between IR64, an indica variety adapted to irrigated condition, and Azucena, an upland aromatic japonica variety^[13], were used in this experiment. Because the seeds of some DH lines were insufficient, a sub-population of 129 lines was applied in the present trial. The seeds of DH lines were provided by the International Rice Research Institute.

The field experiments in a randomized complete block design with two replications, were conducted in spring season (from March to August) and fall season (from August to December) in 2002, respectively, at the experimental farm in South China Agricultural University, Guangzhou, China. The germinated seeds were sown in a seedling bed and seedlings were transplanted to a paddy field 30 days later, with a single plant per hill spaced at 0.3 m \times 0.2 m. Each plot consisted of four 3 m long rows with 16 plants. The management of the field experiments was in accordance with local standard practices.

Ten plants in the middle of the inner two rows of each plot were investigated to score tiller number (TN, the tiller numbers per plant on 45

th day after transplanting) and plant height (PH, the height per plant in cm from the soil surface to the tip of the tallest panicle at maturity excluding awn), and the average for ten plants was used in the analysis.

The linkage map used in this study was established in a previous study^[14]. The preliminary data set of RFLP markers on rice chromosome map generated from the initial population of 135 DH lines. A total of 175 markers covered all 12 rice chromosomes with a total genome size of 2005 cM and an average distance of 11.5 cM between adjacent markers^[14].

The software package QGA Station was used for the analysis of inheritance of the quantitative traits, based on the genetic model developed by Zhu^[15] and the MINQUE method^[16]. QTLs with additive and additive × additive epistatic effects, as well as their interaction effects with environments were analyzed by QTLMapper^[10].

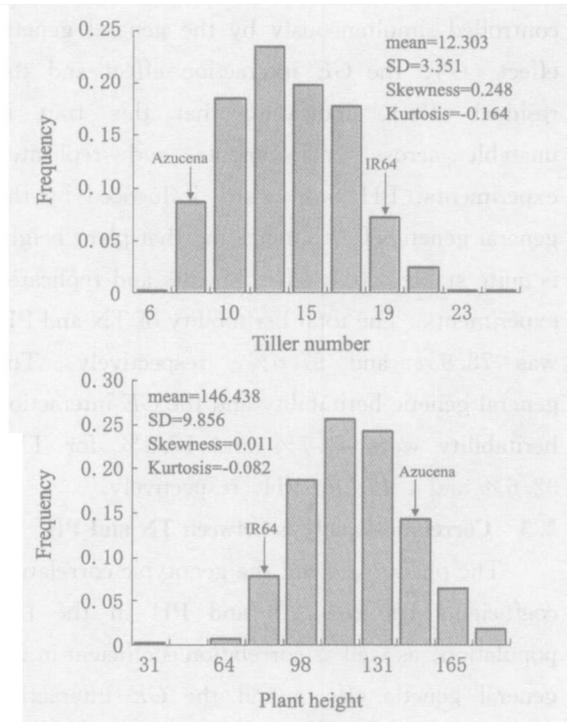
2 Results

2.1 Trait performance and frequency distribution

Trait performance of two parents, IR64 and Azucena, and frequency distribution in the DH population for TN and PH of rice were shown in Fig. 1.

Comparing the phenotypic values of two parents, IR64 was larger on TN but smaller on PH than Azucena. The variation of each trait was large and continuous (Fig. 1). The standard deviation (SD) was 3.351 for TN and 9.856 for PH. Both skewness and kurtosis were less than 1.0 in absolute value for each trait, indicating both traits had approximately normal distribution.

Significant transgressive segregations were observed for two traits in the current study (Fig. 1), which could be directly attributed to the gathering of alleles with the same effect direction



Arrow marks directed the phenotypic performances of parents.

Fig 1 Summary statistics of phenotypic values for TN and PH in rice

(positive or negative) at the multiple QTLs in a line. It is necessary to further analyze the allele distributions of QTLs in parents.

2.2 Components of variances and heritabilities of TN and PH

Genetic variances and heritabilities estimated for TN and PH were presented in Table 1.

Table 1 Estimates of some parameters for two traits in the DH population

Trait	V_G	V_{GE}	V	h_G^2	h_{GE}^2
TN	6.335 *	1.763 *	2.176 *	0.617 **	0.172 **
PH	466.726 *	22.263	15.193	0.926 **	0.044 **

Notes: * and ** indicated significant difference from zero at the 0.05 and 0.01 levels of probability, respectively. V_G , V_{GE} and V were the general genetic variance, the GE interaction genetic variances and the residual variance, respectively. h_G^2 and h_{GE}^2 are the general heritability and the interaction heritability, respectively.

It was suggested that the modes of inheritance for two traits were different. TN was

controlled simultaneously by the general genetic effect (G), the GE interaction effect and the residual effect, indicating that this trait is unstable across environments and replicated experiments. PH was mostly influenced by the general genetic effect, indicating that plant height is quite stable across environments and replicated experiments. The total heritability of TN and PH was 78.9% and 97.0%, respectively. The general genetic heritability and the GE interaction heritability were 61.7% and 17.2% for TN, 92.6% and 4.4% for PH, respectively.

2.3 Correlation analysis between TN and PH

The phenotypic and the genotypic correlation coefficients between TN and PH in the DH population, as well as correlation coefficient in the general genetic effects and the GE interaction effects, were estimated. Significant phenotypic relationship ($r_p = -0.323^*$) existed between these two traits. However, the phenotypic relationship is disturbed by the residual error. The genetic relationship excludes the interference of residual error, which is heritable. The correlation coefficient between TN and PH was -0.383^{**} for r_{G+GE} and -0.454^{**} for r_G . Accordingly, breeders might appropriately establish their selective strategies in order to implement various environmental breeding targets utilizing correlation between traits.

2.4 QTLs with single-locus effects for TN and PH

The genetic main effects of QTLs (a and aa) are stable across different environments, while the QE interaction effects (ae and aae) are the deviation due to a specific environment. In any environment, the total genetic effect of a QTL is the sum of the QTL main effects and QE interaction effects. The positions and genetic effects of QTLs for TN and PH were listed in Table 2.

A total number of 17 QTLs with additive effects and/or additive \times environment interaction effects for TN and PH was detected, distributing

Table 2 Effects and contributions of QTLs with single locus effects for TN and PH

QTL	Marker interval	a	ae	$h^2(a)$	$h^2(ae)$
TN					
1-2	K5—U10	1.332		0.074	
1-12	RG381—RZ19	0.739	0.525	0.043	0.023
1-17	RZ801—RG331	0.609		0.016	
3-20	Pgi1—RG910	0.901		0.034	
5-2	RG556—RG313	-0.464		0.009	
7-11	RZ337B—CDO497	0.537		0.012	
8-14	AC5—RG418B	1.125	0.730	0.053	0.045
10-1	G1084—RG257		-0.650		0.035
12-9	CDO344—RG958	1.295		0.070	
PH					
1-15	RZ730—RZ801	-21.704		0.140	
2-11	RG95—RG654	7.042		0.026	
3-20	Pgi1—RG910	-5.298		0.015	
4-3	RG190—RG908	9.579	4.064	0.048	0.017
4-6	RG91—RG449	-4.317		0.010	
4-10	RG163—RG214	-6.787		0.024	
7-5	RG477—PGMS0.7	4.974		0.013	
9-5	RZ206—RZ422	-5.205		0.014	

Note: QTLs were named with the relevant chromosomal number-interval number of markers. All estimated values of effects were significant at level of $P < 0.005$. The sign indicated the direction of the effect of the IR64 allele. ae indicated the interaction effect value between QTL and spring season.

on ten out of the 12 chromosomes (except for chromosomes 6 and 11). 9 QTLs affecting TN were mapped on 7 chromosomes. 8 PH QTLs were detected with single-locus effects on 6 chromosomes.

A total number of 16 additive effects (a) and 4 additive \times environment interaction effects (ae) of QTLs was identified for these two traits. There were 10 QTLs having positive additive effects, indicating that the alleles from IR64 at these loci will increase corresponding trait values. There were 3 QTLs having positive ae effects, indicating that the alleles of IR64 at these loci can increase corresponding trait in spring season, but decrease them in fall season.

A major QTL for plant height in rice linked

to marker RZ730 on chromosome 1 was inferred to be the location of the *sd1* gene^[2]. A major QTL for tiller number was also detected before^[3]. In the present study, QTL *I-15* for PH was detected with a distance of 22 cM from the marker RZ730 on chromosome 1. For this QTL, the alleles from IR64 might reduce PH by 21.704 cm with 14.0% of contribution. Thus the QTL could be suggested as a major QTL, being concordance with the previous results.

2.5 Digenic epistatic QTLs for TN and PH

Epistasis, describing the interaction of genes in two diverse locus, is an important factor affecting expression of genes and genetic variation in populations. Table 3 showed digenic epistatic QTLs underlying TN and PH.

Table 3 Epistasis (aa) and epistasis × environment interaction (aae) effects and their contributions (h²) of QTLs for TN and PH

QTL _i	QTL _j	aa	aae	h ² (aa)	h ² (aae)
TN					
<i>I-8</i>	<i>I-12</i>		1.609		0.216
<i>2-5</i>	<i>9-6</i>	0.646		0.017	
<i>4-10</i>	<i>8-11</i>	0.575		0.014	
<i>5-8</i>	<i>9-6</i>		-0.571		0.027
<i>6-5</i>	<i>8-2</i>	-0.888		0.033	
<i>7-6</i>	<i>9-8</i>		0.614		0.031
PH					
<i>I-7</i>	<i>I-16</i>	-5.256		0.015	
<i>2-6</i>	<i>3-5</i>	3.423		0.006	
<i>3-3</i>	<i>3-12</i>	-2.912		0.005	
<i>8-1</i>	<i>10-4</i>	4.601		0.011	

Note: All effects were significant at level of $P < 0.005$. The signs indicated the directions of the epistatic effects of the parental (IR64 or Azucena) alleles. *aae* indicated the interaction effect values between QTL epistasis and season.

A total number of 10 epistasis and/or epistasis × environment interaction effects was identified for TN and PH, involving in 19 epistatic QTLs with one interacted by other two loci. For TN, 6 epistasis and/or epistasis × environment interaction effects, or 11 epistatic QTLs were detected, which involved in 8

chromosomes. For PH, a total number of 4 epistasis and/or epistasis × environment interaction effects, or 8 epistatic QTLs were detected on 5 chromosomes.

A total number of 7 additive epistatic effects (*aa*) and 3 additive epistasis × environment interaction effects (*aae*) was identified for the two traits. The effects ranged from 0.571 (for TN) to 5.256 (cm, for PH), with contributions from 0.5% (for PH) to 21.6% (for TN). All *aae* effect values except for that between QTL *I-8* and *I-12* for TN appeared minor and with contributions less than 10%.

Of 7 additive epistatic effects, 4 were positive, indicating that the digenic interactions of parental no-alleles at pairs of these loci increased corresponding traits due to *aa* effects. On the contrary, the remaining 3 had negative effects on traits, but recombination no-alleles increased them at pairs of these loci due to *aa* effects. Of 3 epistasis × environment interaction effects, 2 were positive, indicating that the combination of parental no-alleles at these loci could increase corresponding traits in spring season but decrease them in fall season due to *aae* effects. The remainder was negative, indicating that the combination of parental no-alleles at pairs of the locus could decrease corresponding traits in spring season but increase them in fall season due to *aae* effects.

Of 6 pairs of epistatic QTLs for TN, separate 3 were with only *aa* effects and with only *aae* effects, respectively. No pairs of epistatic QTLs with both *aa* and *aae* effects were detected. The *aae* effect between QTL *I-8* and *I-12* for TN was 1.609 with 21.6% of the contribution in spring season, which might be considered as a major effect for TN. For PH, only *aa* effects were detected. Of those, two *aa* effects appeared to increase PH, and the remaining two decreased it. Therefore, the influence of epistatic effects on PH might be minor due to the counteraction of

effects.

2.6 Relationships between QTLs

Comparing the single-locus effect QTLs (Table 2) with the digenic epistatic effect QTLs (Table 3) for the two traits, some QTLs on common regions of chromosomes were found. A total number of 32 QTLs with single-locus effects and/or digenic interaction effects was detected for the two traits. Of these QTLs, 13 were only with single-locus effects, 16 only with digenic interaction effects and the remaining 3 with both single-locus and digenic epistatic effects. QTL (3-20) controlled simultaneously both TN and PH. Of 9 QTLs with single-locus effects affecting TN, one (1-12) was involved in digenic interactions for TN, and one (1-17) was associated with digenic interactions for PH. Of 11 epistatic loci for TN, one (4-10) was with single-locus effects for PH.

3 Discussion

3.1 Features of parents

The two parents of the population used in this study have a quite different morphology on most traits investigated. 'IR64' appeared more tiller numbers, while 'Azucena' was taller in plant height. The parents, IR64 and Azucena, are representatives of two highly differentiated gene pools^[13-14], although both adapt well to similar environments. Generally, it is suggested that phenotypic similarity between parents may provide little information on the loci contributing to genetic variation of quantitative traits. However, when large numbers of complementary loci are involved, considerable variation of quantitative traits could be maintained in populations derived from two similar phenotypic parents. The same phenotype of a quantitative trait may be generated by very different allelic combinations of QTLs. For TN and PH evaluated, 9 and 8 single-locus QTLs were

detected with opposite genetic effects, respectively (Table 2). The results indicated that alleles with positive and negative effect (increasing or decreasing trait values) were dispersed between the two parents. This may provide an explanation on the occurrence of the transgression in a population^[17].

3.2 Inheritance of TN and PH

TN plays an important role in the formation of grain yield in rice. Its genetic mechanism has been well documented by traditional analysis^[18]. Recently, QTL action of tiller number at different growth stages has been well discussed by QTL mapping analysis^[3]. In the present study, tiller number on 45 th day after transplanting in rice was evaluated and analyzed. The result suggested that tiller number was with a relatively high heritability of 78.9% and was controlled by both the general genetic factor and the *GE* interaction factor (with 61.7% of h_G^2 and 17.2% of h_{GE}^2). The variation of TN in the DH population, therefore, was mostly ascribed to the different genotypes among lines. TN appeared different genetic variations across environments. A total number of 19 QTLs was detected to associate with TN. Of these, 8 were with single locus effects, 10 involved in digenic epistatic effects, and 1 was with both effects. 8 QTLs were identified with *a* effects ranged from -0.464 to 1.332 and corresponding contributions from 0.9% to 7.4% and an associated contribution of 31.0%. IR64 alleles increased TN at 7 loci but decreased it at 1 locus. 3 QTLs were detected with *ae* effects, which values were sequentially 0.525, 0.730 and -0.650 with the corresponding contributions of 2.3%, 4.5% and 3.5%. 6 pairs of epistatic QTLs were detected with 3 of *aa* effects and 3 of *aae* effects, varying from 0.571 to 1.609 with the corresponding contributions ranged from 2.7% to 21.6%. One pair of epistatic QTLs was suggested to be with large effect. Since the existence of *ae* and *aae* the

tiller numbers appeared different across environments.

PH is one of the most important traits related to yield potential in rice. There have been several reports based on molecular marker genetic analysis of PH in rice, which detected a number of QTLs on nine of the 12 chromosomes^[19]. Recently, QTLs of plant height at different growth stages have also been mapped on molecular linkage groups^[2, 20]. In the present study, plant height was suggested with a relatively high heritability of 97.0%, indicating that PH is mainly controlled by genetic factors. Further analysis showed that PH was largely controlled by the general genetic factor (h_G^2 was 92.6%) and little influenced by the GE interaction factor (h_{GE}^2 was 4.4% only). Therefore, PH is stable in different generations and environments. A total number of 15 QTLs was detected to associate with this trait, which distributed on 8 chromosomes except chromosomes 5, 6, 11 and 12. Of those, 7 were with single locus effects, 7 involved in digenic epistatic effects, and 1 was with both effects. 8 QTLs were identified with *a* effects, which were with 3 positive and 5 negative in sign and ranged from 4.317 to 21.704 cm in magnitude with corresponding contributions from 1.0% to 14.0%. One QTL was detected with *ae* effect of 4.064 cm (the corresponding contribution of 1.7%). 4 pairs of epistatic QTLs were with *aa* effects, with two positive and two negative in sign and from 2.912 to 5.256 cm in magnitude with the corresponding contributions from 0.5% to 1.5%. QTL *I-15*, being identified with large effect, was suggested as a major QTL.

3.3 Correlations between TN and PH

Significant phenotypic correlation was observed between TN and PH with -0.323^* of r_p , which derived mainly from the significant genetic correlation. The genetic correlation between TN and PH was -0.383^{**} . However,

the genetic correlation is unstable due to the influence of the GE interaction effect. The component of the general genetic correlation is thus used as the criterion of describing the true genetic correlation between two traits. The general genetic correlation between TN and PH was estimated with -0.454^{**} of r_G , which was stable across generations and environments. Traditionally, the pleiotropy or very close linkage of QTLs was suggested as the basis of trait correlation^[21-22]. QTL *3-20* was detected with opposite additive effects on TN and PH. Single-locus effect QTL *I-17* on TN and QTL *4-10* on PH involved in digenic interaction effects on another trait, respectively. All these associations of QTLs between TN and PH might partially be responsible for their genetic correlation. However, no evidence showed that the pleiotropy or very close linkage of QTLs would result in genetic correlation between traits. It is impossible to reveal the complex genetic basis of trait correlation so far^[23-24].

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