

Influence of Epistasis and QTL × Environment Interaction on Heading Date of Rice (*Oryza sativa* L.)

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Abstract: QTLs for heading date of rice (*Oryza sativa* L.) with additive, epistatic, and QTL × environment (QE) interaction effects were studied using a mixed-model-based composite interval mapping (MCIM) method and a double haploid (DH) population derived from IR64/Azucena in two crop seasons. Fourteen QTLs conferring heading date in rice, which were distributed on ten chromosomes except for chromosomes 5 and 9, were detected. Among these QTLs, eight had single-locus effects, five pairs had double-locus interaction effects, and two single-loci and one pair of double-loci showed QTL × environment interaction effects. All predicted values of QTL effects varied from 1.179 days to 2.549 days, with corresponding contribution ratios of 1.04%–4.84%. On the basis of the effects of the QTLs, the total genetic effects on rice heading date for the two parents and the two superior lines were predicted, and the putative reasons for discrepancies between predicted values and observed values, and the genetic potentiality in the DH population for improvement of heading date were discussed. These results are in agreement with previous results for heading date in rice, and the results provide further information, which indicate that both epistasis and QE interaction are important genetic basis for determining heading date in rice.

Keywords: quantitative trait locus (QTL); epistasis; QTL × environment interaction; heading date; rice (*Oryza sativa* L.)

Heading date is an important agronomic trait, which plays a key role in the adaptation and geographic distribution of rice varieties. Appropriate heading date is a prerequisite for attaining the desired yield level. Therefore, identification of the genetic architecture underlying heading date is a major objective in rice breeding programs. Genetic analysis of heading date of rice (*Oryza sativa* L.) revealed that heading date was basically determined by two factors, duration of the basic vegetative growth (BVG) and photoperiod sensitivity (PS)^[1, 2]. Recently, some experiments have been conducted to map QTLs for heading date of rice using molecular markers, resulting in the identification of many QTLs that are in-

involved in the regulation of these factors^[3–6].

Several evidences indicate that important genetic components to quantitative traits include both epistasis^[7–10] and QTL × environment (QE) interaction^[11–14]. In most of the previous QTL mapping studies, researchers used genetic models assuming no epistasis^[15, 16], or analyzed marker interactions based on two-way ANOVA and multiple regression analysis^[3, 9, 17, 18]. In fact, “genetic background effects” on quantitative traits are extraordinarily ubiquitous in rice^[9], and statistical approaches of two-way ANOVA and multiple regressions are only capable of detecting interaction between markers rather than detecting epistasis between QTLs^[19]. Whereas some

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researchers suggested mapping of QTLs in separate environments for inferring the effect of *QE* interaction^[11–13], or considered *QE* interaction without epistasis^[8, 20]; however, these methods do not allow for reliable and efficient dissection of *QE* interactions^[14].

A mixed-model-based composite interval mapping (MCIM) methodology^[19, 21] was proposed for mapping QTLs with additive and epistatic effects, as well as their *QE* interaction, and the corresponding software QTLMapper has been developed for analyzing the experimental data. This method has been applied in many QTL mapping studies^[14, 22–24]. In the present study, the software QTLMapper version 1.6 was used to analyze a set of data on heading date (days-to-heading) in a rice double haploid (DH) population for identifying QTLs with additive effects and additive by additive effects and their interaction effects with environments.

1 Materials and Methods

1.1 Plant materials

The DH population was composed of 135 lines derived from a cross between IR64, an *indica* variety adapted to irrigated conditions, and Azucena, a traditional upland *japonica* variety^[25]. Because the seeds of some lines were insufficient, a subpopulation of 129 lines was applied in the present trial. The molecular marker linkage map containing 175 markers distributed among 12 chromosomes covering 2,005 cM with an average distance of 11.5 cM between markers^[25, 26] was used for QTL mapping. The seeds of DH lines were provided by the International Rice Research Institute.

1.2 Field experiments

Experiments were conducted at the Experimental Farm in South China Agricultural University, Guangzhou, China (at $\sim 23^\circ$ north latitude). The 129 DH lines and two parents, IR64 and Azucena, were grown in two environments, namely, spring season (from

March to August) and fall season (from August to December) in 2002. These crop seasons showed large difference in climate, especially day length. The germinated seeds were sown in a seedling bed, and the 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 4 rows that measured 3 m in length and containing 16 plants in each row, and all the plots were arranged in a completely randomized block design with two replicates. Ten plants from the middle of each row plot were monitored for heading date (HD), which was determined as the number of days from the time of sowing to the first panicle flowering of each plant. The average of the ten observations was used in statistical analysis.

1.3 Statistical analysis

QTLs with additive and additive \times additive epistatic effects (*a* and *aa*), as well as their environmental interaction effects (*ae* and *aae*) in the DH population, were analyzed by QTLMapper version 1.6^[27]. The likelihood ratio threshold was chosen at $\alpha \leq 0.005$ (e.g., LR = 7.8497) for claiming putative QTLs, and the genetic effects were further tested by a *t*-test with jackknife resampling procedure. QTLs for heading date were designated as “*Hd*” followed by the relevant chromosomal number. If there was more than one QTL on a chromosome, serial letters were added after the chromosomal number.

2 Results

2.1 Phenotypic variation

The phenotypic values of heading date for the DH population and its parental lines, IR64 and Azucena, in the two environments are presented in Table 1. The variation between the two parental lines was small, whereas the phenotypic variation among the DH lines was large. Transgressive segregants with heading date later than that of IR64 and earlier than that of Azucena were observed in both the environm-

Table 1 Summary of statistics of phenotypic values for heading date (days) of rice

Growing season	Mean for parents		DH population		
	IR64	Azucena	Mean	SD	Min.–Max.
Spring season	123.35	116.44	123.32	7.54	94.00–146.00
Fall season	106.53	105.25	104.44	5.44	91.00–117.00

SD: Standard deviation; Min: Minimum; Max:Maximum.

ents. In addition, the days-to-heading of both parents and DH population in the spring season was larger than that in the fall season, indicating that environmental conditions might influence heading in rice.

2.2 QTLs with additive effects and additive × environment interaction effects

QTLs detected with additive effects and additive × environment interaction effects on heading date in rice are shown in Table 2. Eight QTLs with additive effects and/or additive × environment interaction effects were mapped to chromosomes 1, 2, 3, 4, 7, and 10. All the eight QTLs were identified with significant additive effects. The IR64 alleles at two loci (*Hd1* and *Hd10a*) reduced days-to-heading by 2.516 and 1.608 days due to additive effects, but increased days-to-heading from 1.446 days to 2.549 days for the remaining six loci (Table 2). This suggests that alleles for increased heading date were dispersed within the two parents, resulting in small differences of phenotypic values between parents and transgressive segregants among the DH population. Two QTLs (*Hd3a*

and *Hd3b*) showed significant *ae* interaction effects, which increased days-to-heading in spring season. The two QTLs with *ae* effects could be classified into photoperiod-sensitive QTLs based on functions that are differently expressed in the two crop seasons^[18]. The IR64 alleles on the two loci prolonged flowering time in spring season by 1.376 days and 1.411 days due to *ae* effects, respectively. For all the QTLs detected, the predicted effect values varied from 1.375 days to 2.549 days, with corresponding contributions from 1.32% to 4.84%. This suggests that the effect of each QTL on heading date was minor and that the expressions of some QTLs were modified by environmental conditions^[28].

2.3 Epistasis and epistasis × environment interaction

Five pairs of QTLs, which had interactions with each other, were mapped on chromosomes 1, 3, 6, 8, 10, 11, and 12 (Table 3). Among these epistatic interactions, four pairs were identified with *aa* effects, and

Table 2 Estimated additive effects and additive × environment interaction effects of QTLs for heading date (days) in two environments

QTL	Marker interval	Site (M)	<i>a</i>	h_a^2	<i>ae</i>	h_{ae}^2
<i>Hd1</i>	RG810–RG331	0.00	–2.516	0.047		
<i>Hd2</i>	RG437–RG544	0.00	1.446	0.016		
<i>Hd3a</i>	RZ574–RZ284	0.08	1.779	0.024	1.376	0.013
<i>Hd3b</i>	Pgi-1–CDO87	0.06	1.878	0.026	1.411	0.015
<i>Hd4</i>	RG908–RG91	0.06	1.603	0.019		
<i>Hd7</i>	RG477–PGMS0.7	0.02	2.549	0.048		
<i>Hd10a</i>	RG241–RZ625	0.00	–1.608	0.019		
<i>Hd10c</i>	CDO98–G2155	0.14	1.659	0.021		

QTLs were designated as “*Hd chromosomal number (serial letter)*”. Site (M) denotes the genetic distance in Morgan between left marker and QTL. *a* and *ae* denote additive effect and additive × environment interaction effect of QTL, respectively. h^2 represents the contribution ratio of QTL effect. All the estimated values were significant at 0.005 probability level.

Table 3 Estimated epistasis and epistasis \times environment interaction effects of QTLs for heading date (days) in two environments

QTLi	Marker interval	Site (M)	QTLj	Marker interval	Site (M)	<i>aa</i>	h_{aa}^2	<i>aae</i>	h_{aae}^2
<i>Hd1</i>	RG810–RG331	0.00	<i>Hd6</i>	RG162–RG172	0.04	–1.179	0.010		
<i>Hd3b</i>	Pgi-1–CDO87	0.06	<i>Hd8</i>	Amy3DE–RZ66	0.18	–2.306	0.030		
<i>Hd10a</i>	RG241–RZ625	0.00	<i>Hd10c</i>	CDO98–G2155	0.14			–1.273	0.012
<i>Hd10b</i>	CDO93–CDO98	0.00	<i>Hd11b</i>	RZ536–Npb186	0.04	–1.418	0.015		
<i>Hd11a</i>	RG1094–RG167	0.00	<i>Hd12</i>	RG341–AF6	0.00	1.441	0.016		

QTLs were designated as “*Hd chromosomal number (serial letter)*”. Site (M) denotes the genetic distance in Morgan between left marker and QTL. *aa* and *aae* denote epistatic effect and epistasis \times environment interaction effect of QTL, respectively. h^2 represents the contribution ratio of QTL effect. All estimated values were significant at 0.005 probability level.

Table 4 Predicted genetic effects for parents, positive superior line (PSL), and negative superior line (NSL) on heading date in rice

Entry	$\mu + G_G$	$\mu_1 + G_1$	$\mu_2 + G_2$
IR64	117.21	128.16	106.25
Azucena	103.63	109.01	98.25
PSL	135.26	148.76	121.76
NSL	92.50	100.42	79.00

The estimated population means (μ) was 113.88 days, and the predicted population means in spring season (μ_1) and fall season (μ_2) were 123.32 days and 104.44 days, respectively. G_G denotes the general genetic effect. G_1 and G_2 are the total genetic effects in the spring season and the fall season, respectively.

only one pair exhibited *aae* effect. For one pair of QTL, *Hd11a* and *Hd12*, the additive \times additive epistatic effect in parental type increased days-to-heading by 1.441 days. The other four epistatic effects in parental type reduced heading date from 1.179 days to 2.306 days. The epistatic effect between *Hd10a* and *Hd10c* was modified by environments. In the spring season, the epistatic effect in parental type reduced heading date to 1.273 days. In addition, all the epistatic effects had corresponding contributions from 1.04% to 3.96%.

2.4 Prediction of superior lines based on QTL effects

Using the estimated effects of all the QTLs, this study predicted the total genetic effects of the two parents (IR64 and Azucena), positive superior lines (PSL), and negative superior lines (NSL) derived from the mapping population (Table 4). The predicted genetic effects of days-to-heading for IR64 and Azucena did not show good match with their ob-

served phenotypic values (Table 1), indicating considerable residuals remained. In the DH population, the genetic potentiality for improvement of heading date ranged from 92.498 to 135.262 days in general, ranging from 100.424 to 148.762 days in the spring season, and 78.998 to 121.762 days in the fall season, respectively. These results revealed potential genetic gains if selection of heading date was conducted in offspring derived from the mapping population. In addition, the prediction of this study revealed that *a* effect, *aa*, *ae*, and *aae* effects were important components of the predicted genetic effects, providing a strong evidence to the importance of epistatic and *QE* interaction effects as genetic factors on heading date of rice.

3 Discussion

3.1 The importance of epistasis and *QE* interaction

Epistasis as an important genetic basis of com

plex traits has been well demonstrated in recent QTL mapping studies [22, 30]. Lin *et al.* [4] provided strong evidence for the presence of epistatic interactions on heading date using near-isogenic lines. Li *et al.* [14] showed that the number of detectable epistatic QTL pairs affecting heading date in each of the nine environments ranged from 5 to 11. In the present study, five pairs of QTLs with interaction effects were detected, four of which showed *aa* effects and one showed *aae* effect. This result further revealed that epistasis on heading date of rice was ubiquitous. Genotype \times environment (*GE*) interaction is another important genetic component for the variation of quantitative traits in plant breeding and evolution. Thus, it has been the subject of extensive investigations for quantitative traits. With DNA markers and appropriate experimental designs, *GE* interaction can be further dissected into components of *QE* interactions, which are of importance for marker-assisted selection in crop improvement [19]. Selection based on QTLs with *QE* interaction effects could result in unstable offspring across environments. In most previous studies, it is impossible to predict the real *QE* interaction effects due to the limitation of genetic models and statistical methods [19]. Recently, Li *et al.* [14] reported significant *QE* interaction effects associated with plant height and heading date. In this study, two additive QTLs and one pair of epistatic QTLs were identified with *QE* interaction effects, suggesting that many QTLs for heading date of rice were environmentally sensitive.

3.2 Prediction of total genetic effects based on QTL effects

It is difficult to determine the relationship between the observed phenotypic values and the estimated genotypic effects for the parents [3]. When the heritability of the studied trait is sufficiently large, it can be inferred that the estimation of QTL effects is reliable if the estimated genetic effects match the observation values. However, in the present research,

the estimated genetic effect values for heading date for the parents were different from the observed phenotypic values. These discrepancies might be explained partly by an imprecise estimation of *QTL* effect values. Another explanation might be attributed to the failure of detecting additional QTLs responsible for heading date, because it is difficult to determine an optimal probability threshold for claiming putative QTLs. The predicted genetic effects of superior lines can be used to measure the potentialities of an improved population, thereby enabling breeders to obtain prior information on the optimal genetic gains for selection. In the DH population, the genetic potentiality for improvement of heading date was 92.498 days in general, 100.424 days in the spring season, and 78.998 days in the fall season. This suggests that the IR64/Azucena cross still had large breeding potential to be exploited for heading date.

3.3 Comparison of the present study with previous researches

It is obvious that the QTLs detected depend on the mapping populations employed and the environments involved. Thus, it is an important aspect of rice breeding to detect the common loci controlling heading date among different populations in various environments [3]. There have been many QTL mapping studies on rice heading date. One of the most comprehensive studies was probably conducted by Yano *et al.* [18], who identified fourteen QTLs controlling flowering time in rice, using several types of progeny derived from a single cross between rice cv. Nipponbare (*japonica*) and rice cv. Kasalath (*indica*). More recently, Li *et al.* [14] have identified twenty additive QTLs affecting heading date using a DH population of IR64/Azucena in nine different environments. In the present study, at least fourteen QTLs were responsible for heading date. Most QTLs detected in Yano's research could be found on corresponding chromosomes in the present study. However, some QTLs identified in the two studies were different.

These differences might be attributed to differences in mapping populations, experimental environments, and especially QTL mapping approaches used in both studies. Seven out of eight additive QTLs identified in this study fell in the vicinity of the additive QTLs affecting heading date identified in the research of Li *et al.*^[14]. Certainly, some differences were also observed between the results of the two studies, which might be caused by different environmental conditions or even by different options when using the QTLMapper software in the two studies.

3.4 Relationship between additive QTLs and epistatic QTLs

It would be interesting to study relationships between the additive QTLs and the epistatic QTLs identified. Li *et al.*^[9] drew two major conclusions on the relationship. First, the majority (87.1%) of loci involved in the digenic interactions did not appear to have significant single-locus effects on three grain yield components in rice. Second, a significant proportion (45.0%) of the identified QTLs were involved in digenic interactions with background loci. In the present study, six out of ten epistatic QTLs had no significant single-locus effects, and four out of eight additive QTLs were involved in digenic epistatic interactions. These results were in agreement with the Li's results^[9], suggesting that many epistatic QTLs were not detected and some of the additive QTLs might be detected with effects confounded by epistatic effects, if the effects of epistasis were ignored in QTL mapping. Thus, breeders have to take into account such complexity and test the effects of individual loci in the targeted genetic background to obtain the expected phenotypes for the genes of interest^[10].

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上位性和 QTL \times 环境互作对水稻(*Oryza sativa* L.)抽穗期的影响

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摘要: 水稻抽穗期是重要的农艺性状之一, 对水稻品种的地理分布和适应性起到关键性作用。适宜的抽穗期是获得高产的前提。因此确定水稻抽穗期的遗传基础在育种计划中具有重要的意义。本研究用一套来源于亲本 IR64/Azucena 的双单倍体 (DH) 群体在两个种植季节的试验资料, 用基于混合线性模型的复合区间作图方法, 对水稻抽穗期 QTL 的加性、上位性及其与环境互作效应进行了研究。结果表明共有 14 个 QTL 影响水稻抽穗期, 它们分布在除第 5 和第 9 条染色体外的 10 条染色体上, 有 8 个位点携带单位点效应, 5 对位点携带双位点互作效应, 2 个单位点和 1 对双位点存在与环境的互作, 所有效应值介于 1.179~2.549 天之间, 相应的贡献率为 1.04%~4.84%。基于所估算的 QTL 效应值, 本研究预测了两个亲本和两个极端型品系的遗传效应值, 并讨论了影响遗传效应值与实际观测值偏差的可能原因, 以及研究群体所具有的遗传潜力。对水稻抽穗期 QTL 的定位结果与前人研究基本一致, 并进一步证实了上位性和 *QE* 互作效应是水稻抽穗期的重要遗传基础。

关键词: 数量性状位点(QTL); 上位性; QTL 与环境互作; 抽穗期; 水稻 (*Oryza sativa* L.)

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