

## Study on Epistatic Effects and QTL $\times$ Environment Interaction Effects of QTLs for Panicle Length in Rice (*Oryza sativa* L.)

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**Abstract:** QTLs with epistatic effects and environmental interaction effects for panicle length of rice were studied by mixed-model based QTL mapping with a doubled haploid population from IR64/Azucena in four environments. The results demonstrated the importance of epistasis as a genetic basis of the quantitative traits and also revealed several important features of this phenomenon. In the results, all QTLs except two were involved in epistasis, and 64.7 per cent of the QTLs involved in epistasis were found with significant additive effects. This might mean that the usual estimates of the QTL additive effects could be confounded by epistatic interactions and result in biased estimation. The other 35.3 per cent QTLs did not have any significant additive effects of their own but were also involved in epistatic interactions. Such loci might play the role of modifying agents that tend to activate other loci or modify the action of other loci. The other features of epistasis include that, it was fairly common for the same locus to get involved in interactions with more than one other locus; and epistatic interactions were sensitive to environmental affections. *QE* effects were detected more often than QTL main effects, might indicate that gene expression for quantitative trait could be greatly affected by environments.

**Key words:** quantitative trait locus (QTL); epistatic effects; QTL by environment interaction effects; rice; panicle length

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**摘要:** 利用基于混合模型的QTL定位方法研究了由籼稻品种IR64和粳稻品种Azucena杂交衍生的DH群体在四个环境中穗长的QTL上位性效应和环境互作效应。结果表明上位性可能是数量性状的重要遗传基础,并揭示了上位性的几个重要特点。在本研究中,所有的QTL中只有两个没有参与上位性效应的形成,在参与上位性效应的QTL中,64.7%的QTL还具有本身的加性效应。因此传统方法对QTL加性效应的估算会由于上位性的影响而有偏。其它35.3%的QTL没有本身的加性效应,却参与了上位性互作,这些位点可能通过诱发和修饰其它位点而起作用。上位性的特点还包括,经常发现一个QTL与多个QTL发生互作;大效应的QTL也参与上位性互作;上位性互作易受环境影响。QTL与环境的互作

效应比 QTL 的主效应更多次地被检测到,表明数量性状基因的表达显著地受到环境的调控。

**关键词:** 数量性状位点; 上位性效应; 环境互作效应; 水稻; 穗长

Panicle length in rice is genetically correlated with the production of yield<sup>[1]</sup>. Up to now, a few of QTL mapping studies<sup>[2~5]</sup> have been conducted for panicle length in an attempt to promote the better understanding of its inheritance and in hope of possible gene manipulation for yield improvement in the future. The results of these studies showed that panicle length might be controlled by two to seven QTLs. After comparing QTLs detected in three environments, Zhuang *et al*<sup>[5]</sup> suggested that the QTLs could be affected by environments. But QTL detected separately in each environment could be biased if the real *QE* interaction exists. Zhu<sup>[6]</sup> proposed an indirect method to map QTLs with *QE* effects using predicted total genotype (environment interaction effects). It was shown that some QTLs had both genetic main effects and *QE* interaction effects, although they could be detected in two environments<sup>[7]</sup>. The QTL main effect is the accumulated effect expressed in the same way across different environments, while the *QE* interaction effect is the deviation due to specific environment. At a specific environment, the total effect of a QTL could include the main effects plus *QE* interaction effects at that environment.

In inheritance of quantitative traits, gene expression could be modified by epistatic interaction with other genes as well as by environmental factors<sup>[8]</sup>. Studies in classical quantitative genetics have strongly suggested the importance of epistasis<sup>[9]</sup>, recently QTL mapping experiments have also provided some results regarding the importance of epistasis affecting the phenotypic behavior of quantitative traits in crop population<sup>[10~13]</sup>.

Nevertheless, the epistasis for each trait aforementioned was revealed by two-way analysis of variance using all possible two-marker interactions, not the interactions between QTLs.

Recently, a new methodology was proposed for directly mapping QTLs with additive and epistatic effects as well as their *QE* interaction based on mixed linear model approaches<sup>[14,15]</sup> and the software QTLMapper version 1.0 was developed<sup>[15]</sup> for analyzing the experiment data. To dissect the quantitative inheritance of panicle length of rice, the newly proposed QTL mapping method was employed for detecting QTLs with additive and epistatic effects as well as their *QE* interaction effects in the present research.

## 1 Materials and Methods

A population of 123 double haploid (DH) lines derived from a cross between an irrigated indica variety IR64 and an upland japonica variety Azucena<sup>[16]</sup> was used in the experiments. The genetic map of this population containing 175 markers distributed among 12 chromosomes covering 2 005 cm with an average distance of 11.5 cm between markers<sup>[17]</sup> was used for QTL mapping.

The 123 DH lines and their parents, IR64 and Azucena, were grown in a randomized complete design with two replications at both Hainan in 1995 and Hangzhou in 1996, 1997 and 1998. Hainan Island is located in the Southern China Sea at 18° north latitude while Hangzhou is located in eastern China at ~30 °C north latitude. These two places show great difference in climate, soil conditions,

day length, and even rice growing seasons. At Hangzhou, there were remarkable divergences of temperature, soil conditions among the three years. The experiment was conducted from early December 1995 to late April 1996 at Hainan where rice can grow well all year round. At Hangzhou, experiments were carried out from late May to early November in 1996, 1997 and middle May to middle October in 1998. In all environments, 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 15 cm  $\times$  20 cm. Each plot included three to four lines with eight plants per line. Panicle lengths of 5 central plants of each plot were measured in the field before harvest.

QTLs with additive and additive (additive epistatic effects as well as their environmental interaction effects for panicle length were mapped by the mixed-model based QTL mapping approach<sup>[14,15]</sup> and software of QTLMapper version 1.0<sup>[15]</sup>. The likelihood ratio value of 11.5, which is equal to a LOD score of 2.5<sup>[18]</sup>, was used as a threshold to

declare the detection of QTL or epistasis.

## 2 Results and Analysis

### 2.1 Transgressive segregation of phenotypic behavior

The phenotypic behavior of panicle length for the DH population and its parents under four environments were described in Table 1. The panicle length of parent Azucena was longer than that of IR64 in all environments. Although the mean of DH population under four environments were only slightly different, wide variation occurred among DH lines and transgressive segregants were observed across all four environments with some lines having longer panicle length than that of the parent Azucena, or shorter than that of the parent IR64. The panicle length of the DH population segregated continuously and both skewness and kurtosis values were less than 1.0 (Table 1), as suggested that the data of panicle length were suitable for QTL analysis.

**Table 1 Phenotypic behavior of panicle length under four environments**

| Environment    | Parents |         | DH population |      |      |       |      |       |
|----------------|---------|---------|---------------|------|------|-------|------|-------|
|                | IR64    | Azucena | Mean          | Max  | Min  | Stdev | Skew | Kurt  |
| Hainan in 95   | 21.7    | 25.9    | 23.10         | 30.2 | 16.8 | 3.29  | 0.28 | -0.69 |
| Hangzhou in 96 | 22.9    | 27.2    | 24.67         | 34.0 | 17.9 | 3.60  | 0.42 | -0.32 |
| Hangzhou in 97 | 23.6    | 32.4    | 24.96         | 36.5 | 14.0 | 4.41  | 0.12 | -0.26 |
| Hangzhou in 98 | 25.6    | 29.3    | 25.34         | 33.9 | 18.0 | 3.42  | 0.22 | -0.26 |

Note: Mean, Max, Min, Stdev, Skew and Kurt are the average, maximum, minimum, standard deviation, skewness and kurtosis of all observations for DH lines in a specific environment.

### 2.2 Quantitative Trait Loci for Panicle Length

Altogether 19 QTLs with additive effects and/or additive  $\times$  additive epistasis effects were found to be associated with panicle length on all the 12 chromosomes (Table 2). They were named for panicle length as "Pl" with the chromosomal number. If there were more than one QTL in a chromosome, the

serial number was added after chromosomal number separated by a hyphen. The positions of these QTLs were indicated by the marker interval bracketing the concerned QTL with the estimated distance in morgon (M) from the left marker. The 11 loci (57.9% of all the 19 putative loci) with both detectable additive effects and epistatic interaction effects were presented in regular form while the 6 loci

(31.6% of all the 19 putative loci) involved in epistatic interactions but without detectable additive effects were presented in bold italic letters, the other 2 loci (10.5% of all the 19 putative loci) with only additive effects but no epistatic effects were notified with underling lines. The estimated additive effects and the additive (additive epistatic effects at significance level of 0.01 or 0.005 under different environments were presented in the Table 3 and Table 4, respectively.

**Table 2** Positions of QTLs with additive effect and/or additive  $\times$  additive epistasis effect for panicle length

| Chrom.   | QTL                 | Marker interval            | Distance/m  |
|----------|---------------------|----------------------------|-------------|
| 1        | <b><i>PI1-1</i></b> | <b><i>RG246-K5</i></b>     | 0.06        |
| 1        | PI1-2               | RZ730-RZ801                | 0.18        |
| 2        | <b><i>PI2-1</i></b> | <b><i>RG437-RG544</i></b>  | 0           |
| 2        | PI2-2               | RG95-RG654                 | 0.04        |
| 3        | <b><i>PI3-1</i></b> | <b><i>RG104-RG348</i></b>  | 0           |
| 3        | PI3-2               | RZ403-RG179                | 0.04        |
| <u>3</u> | <u>PI3-3</u>        | <u>CDO87-RG910</u>         | <u>0.08</u> |
| 4        | PI4-1               | RZ262-RG190                | 0.08        |
| 4        | PI4-2               | RG163-RZ590                | 0.18        |
| 5        | PI5                 | RZ67-RZ70                  | 0.12        |
| 6        | PI6                 | Amy2A -RG433               | 0.04        |
| 7        | PI7-1               | RG511-RG477                | 0.18        |
| 7        | <b><i>PI7-2</i></b> | <b><i>RG711-Est-9</i></b>  | 0.08        |
| 8        | <b><i>PI8</i></b>   | <b><i>RZ143-RG20</i></b>   | 0.06        |
| <u>9</u> | <u>PI9</u>          | <u>RZ422-Amy3ABC</u>       | <u>0.26</u> |
| 10       | PI10-1              | RG257-RG241                | 0.26        |
| 10       | PI10-2              | G2155- RG134               | 0.02        |
| 11       | <b><i>PI11</i></b>  | <b><i>RG103-RG1109</i></b> | 0.16        |
| 12       | PI12                | RG901-CDO344               | 0           |

Note: QTLs with both detectable additive effect and epistatic effect were presented in regular form while the QTLs involved in epistasis but without detectable additive effect were presented in bold italic form, and the QTLs with only additive effects but not epistatic effects were notified with underlines.

### 2.3 Analysis for QTL additive effects

The thirteen QTLs with additive main effect ( $a$ ) and/or additive by environment interaction effect ( $ae$ ) were shown in Table 3. Of the 13 QTLs, 2 and 3 were found with only significant  $a$  and  $ae$  effects, respectively, while the other 8 with both  $a$  and  $ae$  effects. The additive main effects had both negative and positive directions at different loci might suggest that alleles for panicle length be

dispersed within the two parents. So parading of all alleles increasing panicle length from the two parents could produce the segregants superior to the parents. The absolute magnitude of additive main effects ranged from 0.54 cm to 1.52 cm. The QTL PI1-2 with the highest magnitude of additive main effects was located into the same marker interval where the major gene Sd-1 for plant height might locate, as might suggest pleiotropism or close linkage of these two loci. As to QTLs with  $ae$  effects, two QTLs (PI5 and PI9) were detected in only one environment, while the other eleven QTLs had opposite directions of  $ae$  effects in two or more environments. Notably, most of the 13 QTLs had both additive main effects and additive by environment interaction effects. So, at a specific environment, the total effect of a QTL could include the main effects plus  $QE$  interaction effects at that environment. The results of additive (environment interaction effects were often detected along with additive main effects might suggest that  $QE$  interaction which caused by gene expression in spatial pattern, be an important component of genetic basis of quantitative traits.

**Table 3** Additive and/or additive  $\times$  environment interaction effects of QTLs across four environments

| Ch-Ini       | $a$           | $ae1$          | $ae2$          | $ae3$         | $ae4$          |
|--------------|---------------|----------------|----------------|---------------|----------------|
| PI1-2        | -1.52**       | 0.30**         | -0.75**        | 0.20**        |                |
| PI2-2        | 0.55*         | -0.54**        |                | 0.79**        |                |
| PI3-2        | 0.72**        | 1.21**         | -2.53**        | -0.17**       | 1.49**         |
| <u>PI3-3</u> | <u>-0.81*</u> | <u>-0.46**</u> | <u>-1.52**</u> | <u>2.62**</u> | <u>-0.64**</u> |
| PI4-1        | 0.54*         |                |                | 0.77**        | -0.73**        |
| PI4-2        | -0.93**       | 0.89**         | -0.82**        |               |                |
| PI5          | -0.54**       |                |                | -0.23**       |                |
| PI6          | 0.87**        |                |                |               |                |
| PI7-1        |               |                | 0.29**         |               | -0.28**        |
| <u>PI9</u>   |               |                |                |               | 0.72*          |
| PI10-1       | 0.59*         |                |                |               |                |
| PI10-2       | 0.70**        |                | -2.64**        | 1.29**        | 1.44**         |
| PI12         |               |                | -0.27**        |               | 0.22**         |

Note:  $a$ ,  $ae1$ ,  $ae2$ ,  $ae3$ ,  $ae4$  represent additive main effect and additive  $\times$  environment interaction effect at Hainan in 1995, at Hangzhou in 1996, 1997 and 1998, respectively. \* and \*\* represent the significance level of  $P = 0.01$  and 0.005, respectively.

## 2.4 Analysis for QTL epistatic effects

Altogether 19 digenic epistatic interactions with epistatic main effect (*aa*) and/or epistasis by environment interaction effect (*aae*) were detected to be associated with panicle length (Table 4). Among them, 6 pairs had *aa* effects and 17 pairs had *aae* effects in one to four environments while 4 pairs had both *aa* and *aae* effects. The absolute magnitude of the effects for the detected epistatic interactions varied from 0.55 cm to 0.98 cm for epistatic main effects and from 0.14 cm to 2.09 cm for epistasis by environment interaction effects. The wider range of epistasis (environment interaction effects than that of epistasis main effects along with that epistasis (environment interaction effects were more often detected than epistasis main effects, might indicate that although digenic interactions could have both main effects and environmental interaction effects, they were more easily subjected to environmental influence.

As to composition, epistatic interactions for panicle length involved not only all the QTLs with additive effects except PI3-3 and PI9, but also six loci without detectable QTL additive effects. So it might be important when doing QTL analysis to keep the concept in mind that the loci without detectable QTL additive effect can also be putative QTLs. Another important case was that it was fairly common for one locus to interact with more than one non-allelic locus. For panicle length, the 19 interactions were composed of 17 interacting loci with 10 loci (58.8 per cent) being involved in more than one distinct interaction. This might indicate the possibility of multilocus associations for the trait development. Furthermore, the QTL PI1-2 with relatively high magnitude at the similar position of major QTL Ph1-2 for plant height interacted with six non-allelic loci, as apparently indicated that QTLs with relatively high magnitude of effects might also be involved in epistasis.

**Table 4 Epistasis and epistasis by environment interaction effects of QTLs across four environments cm**

| QTLi         | QTLj        | <i>aa</i> | <i>aae1</i> | <i>aae2</i> | <i>aae3</i> | <i>aae4</i> |
|--------------|-------------|-----------|-------------|-------------|-------------|-------------|
| <b>PI1-1</b> | PI10-2      | 0.98**    |             |             |             |             |
| PI1-2        | PI3-2       | -0.84**   |             | -0.82**     |             | 0.56*       |
| PI1-2        | PI4-1       |           |             | -0.31**     |             |             |
| PI1-2        | PI4-2       |           |             | 0.39**      |             |             |
| PI1-2        | PI5         |           | -0.39*      |             |             |             |
| PI1-2        | PI6         |           | 0.79**      | -0.50*      |             |             |
| PI1-2        | PI7-1       |           |             | -1.02**     | 0.58*       |             |
| <b>PI2-1</b> | PI4-2       |           | -0.22*      |             |             |             |
| PI2-2        | PI4-2       |           |             |             |             | 0.33**      |
| PI2-2        | PI5         |           | -0.54**     | -0.26**     | 0.32**      | 0.48**      |
| <b>PI3-1</b> | PI10-1      |           | -0.14**     |             |             |             |
| PI3-2        | <b>PI8</b>  |           |             | 0.27**      | -0.16**     |             |
| PI3-2        | <b>PI11</b> | 0.64*     |             |             |             |             |
| PI4-1        | PI4-2       |           | 0.25**      | -0.29**     | 0.21**      |             |
| PI4-1        | PI7-1       | -0.55**   | -0.24**     |             | 0.25**      |             |
| PI5          | PI10-1      |           | -0.53*      |             |             |             |
| PI5          | PI10-2      | 0.86**    | 1.07**      | -2.09**     | 1.05**      |             |
| PI7-1        | PI12        |           |             | -0.49**     |             |             |
| <b>PI7-2</b> | PI12        | -0.68**   | 0.54*       |             |             |             |

Note: *aa*, *aae1*, *aae2*, *aae3*, *aae4* represent epistatic main effect and epistasis  $\times$  environment interaction effect at Hainan in 1995, at Hangzhou in 1996, 1997 and 1998, respectively. \* and \*\* represent the significance level of  $P = 0.01$  and  $0.005$ .

respectively.

### 3 Discussion

Both epistatic interaction effects and QTL (environment interaction effects are important components of genetic basis. But many of researches have been based on models assuming neither epistatic effects nor *QE* interaction effects due to lacking of valid statistical method. To indicate the possibility of *QE* interaction, QTL mapping results in different environments were simply compared<sup>[5]</sup>. For inferring epistasis between QTLs, interaction effects between molecular markers were widely assayed by two-way analysis of variance<sup>[10,13]</sup> But this method usually cannot give unbiased estimation for QTL parameters. Here we adopt mixed-model based QTL mapping to detect QTLs with epistasis and *QE* interaction and estimate their effects. The study demonstrated the importance of epistasis as a genetic basis of the quantitative traits and also revealed several important features of this phenomenon. Partitioning of epistasis from other genetic components of variation would, no doubted, help to obtain more reliable estimates of the QTL effects. Moreover, consideration of epistasis in the QTL analysis would enhance our understanding about the inheritance of quantitative traits.

In the present study, only two loci with significant additive effects were not involved in epistasis. This means that the usual estimated effects of most QTLs could be confounded by epistatic interactions and resulted biased estimation unless epistatic effect is separated. In fact, the actual genetic effects of many QTLs are reasonably dependent on other loci. There were six loci

involved in epistasis did not have any significant additive effects of their own. Successful detection of significant epistatic effects resulting from QTLs without additive effects indicated that many loci even without significantly affecting the traits on their own could still affect the trait in combination with other loci. These loci might play the role of modifying agents that tend to activate other loci or modify the action of other loci.

For that it was fairly common for the same locus to get involved in interactions with more than one other locus, referred as multiepistasitivity by Li *et al.*<sup>[12]</sup>, the real genetic effect of any locus would be necessarily different from genotype to genotype due to involvement of different interacting loci. This was alike that the interaction between QTL and background or modifying loci might be prevalent epistasis affecting the behavior of quantitative traits<sup>[10,13]</sup>. Furthermore, as interactions were observed to be greatly affected by environments, the contribution of any locus to the trait, should also vary according to the growing environment.

In quantitative genetics, the trait behavior is resulted from the combined effects of many genes under different environments<sup>[8]</sup>. Usually, *QE* effects are treated as random effects especially in different years. They imply the extents that QTLs would be affected by unknown environments. At a specific environment, the total effects of a QTL should include all the genetic main effects and *QE* interaction effects at that environment. It was implied, by the fact of some QTLs and epistatic interactions having only *QE* effects, that gene expression of these QTLs and epistatic interactions could be

mainly induced by environments.

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