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QTL Analysis of Genetic Main Effects and Genotype (Environment Interaction Effects for Yield Components in Rice *Oryza sativa* L.)

Mebrouk Benmoussa[1], ZHU Jun[1], YAN Ju-qiang[1], HE Ci-xin[1], WU Ping [2](1. *Dept. of Agronomy, Zhejiang University, Hangzhou* 310029, *China*; 2. *Dept. of Bioscience, Zhejiang University, Hangzhou* 310029, *China*)

Abstract: Quantitative trait loci (QTL) for yield components were identified based on an RFLP map from a DH population. The 123 double haploid lines with their parents IR64 and Azucena were evaluated in the field in two different environments (Hangzhou and Hainan). Genetic main effects and GE interaction effects were predicted by an adjusted unbiased prediction (AUP) method and used in QTL mapping. The results indicated that some QTLs detected with QTL main effects might also have QTL environment (QE) interaction effects. In contrast some identified QTLs were mainly controlled by QE interaction effects without significant QTL main effects. The study also indicated that individual QTL showed a range of sensibility to environments as some QTLs were detected only in a single environment while others were detected in two environments. It is also shown that QTL associated with yield components (total grains and full grains) had large additive effects for both QTL main effects and QE interaction effects. These QTLs seem to act as major gene in both environments.

Key words: QTL; yield components; rice (*Oryza sativa*); QTL main effect; QTL × environment interaction effect

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Mebrouk Benmoussa[1], **朱 军**[1], **严菊强**[1], **何慈信**[1], **吴 平**[2](1.**浙江大学 农学系, 浙江 杭州** 310029; 2.**浙江大学 生命科学系, 浙江 杭州** 310029)

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摘 要: **在构建** DH **群体** RFLP **图谱的基础上定位了产量因子的数量性状位点**(QTL). **在杭州和海南两地分别种植包括** 123 **个** DH **原的** DH **群体及其亲本** IR64 **和** Azucena,**并对产量因子性状进行了测定. 运用调整无偏预测**(AUP)**法预测遗传主效应值和** GE **互作效应值,并用于** QTL **定位. 结果表明,一些有主效应的** QTL **同时具有** QTL×**环境**(QE)**互作效应,而一些没有主效应的** QTL **也可以有** QE **互作效应. 研究还表明,**QTL **对环境的敏感性不同,有的** QTL **只能在一个环境中检测到,而另一些** QTL **能在二个环境中都检测到. 产量因子包括总粒数和实粒数的**QTL **无论是主效还是**QE **互作效应均具有较大的加性效应值,这些** QTL **在两个环境中起主基因的作用.**

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关 键 词: QTL; 产量因子; 水稻; QTL 主效; QTL×环境互作效应

Yield and its components are quantitatively inherited and controlled by many genes with small effects and subject to environment effects. The recent advent of molecular markers, RLFP in particular, has greatly facilitated the study of complex quantitative traits and made possible to dissect the polygenes for such traits into individual mendelian factors[1]. Therefore, QTL mapping in numerous species and for various traits has been well-documented[2, 3].

Many studies of QTL mapping have been conducted in individual environment to evaluate the variation of gene expression observed in different environments. Crops grown under natural conditions will be affected by not only genetic effects but also environments, such as weather, soil, cultural practices and management of soil. Therefore it is important to study the genotype by environment (GE) interaction effects of genes which control the performance of the quantitative traits. GE interaction is differential genetic performance across environments. It reduces the association between phenotypic and genotypic values so that plant performs well in one environment may not necessarily perform well in another environment.

Detection of different QTLs in specific environments has been suggested for inferring QTL by environment interactions[4-13]. In most of these studies the QTL analysis was done by comparing QTL detected in separate environments. The QTL identified in all environments are generally considered to be the QTLs for the main effects while those identified in one or the other environment are taken as GE interaction effects. The failure to detect a particular QTL in all environments does not necessarily indicate GE interaction effects. On the other hand, QTL detected in different environments may also not exclude the presence of a true QTL by environment interaction. Therefore, we cannot fully exploit the GE interaction effects by only comparing QTL detected in different environments separately.

The objective of the present study is to evaluate the QTL main effects as well as QTL × Environment (QE) interaction effects for yield and its components.

1 Materials and Method

1.1 Materials

A double haploid population developed by Guiderdoni *et al.*[14] was used in this experiment. This population of 123 lines derived from a cross between the irrigated Indica variety IR64 and the upland Japonica Azucena. Six restriction enzymes (DraI, EcoRV, HindIII, ScaI, XbaI, EcoRI) were used for parental polymorphism survey. An RFLP map was constructed by Huang *et al.*[15] from initial population of 135 DH lines with 135 RLFP markers well tagged on the 12 chromosomes. This map was recently updated by adding 40 new isozymes and/or RAPD markers and presently contains 175 markers covering 2 005 cM with an average distance of 11.5 cM between pairs of markers[16]. This new map has been used for QTL analysis in this experiment.

1.2 Field experiment

The 123 DH lines and their parents IR64 and Azucena were evaluated in the field using a randomised block design with two replications. The agronomic performance of the DH population was evaluated in the field

experiment with two locations, Hangzhou and Hainan Island. Hangzhou is located in eastern China at 30° north latitude. Hainan Island is located in the South China Sea at 18° north latitude. The DH lines were grown in the field in Hangzhou from May to October 1997 and in Hainan from January to June 1996. The germinated seeds were sown in seedling bed and transplanted in the field 30 days later with a single plant hill spaced at 15 cm × 30 cm. Observations were taken on 5 central plants of each plot for each replication for the number of grains per panicle (total grain, TG), the percentage of fertile grains (fertility rate, FR), the number of filled grains (full grain, FG), the number of panicles (productive tillers, PT), and the weight of 1 000 grains (kilogram weight, KG).

1.3 Statistical analysis

For the present genetic experiments of 123 genotypes with 2 replications in 2 locations (as different environments), QTL mapping was conducted based on observations of two locations by a new approach[17,18]. The phenotypic performance of the jth genetic entry in the kth replication within the hth environment can be expressed by the following model:

$$y_{hjk}=\mu+E_h+G_j+GE_{hj}+e_{hjk}$$

Where μ is the population mean, fixed; E_h is the effect of the hth environment, E_h— $(0, \sigma_E^2)$; is the genotype effect, G_j—$(0, \sigma_G^2)$; GE_{hj} is the genotype (environment interaction effect, GE_{hj}—$(0, \sigma_{GE}^2)$; e_{hjk} is the residual effect, e_{hjk}—$(0, \sigma_e^2)$.

The genotype effects (G) and interaction effects (GE) were predicted by the adjusted unbiased prediction method[19,20]. Prediction values were obtained for genetic main effects ($y_{j(G)}=\mu+G_j$) and GE interaction effects in the hth environment ($y_{hj(GE)}=\mu+E_h+G_j+GE_{hj}$). Then the composite interval mapping method[21,22] was applied for analysing the predicted genetic main effects and also the predicted GE interaction effects

The analysis of QTLs linked to molecular markers[15] was conducted by QTL Cartographer v 1.1b[23] for yield components. A likelihood threshold of 9.49 corresponding to a LOD of 2.4 was equivalent to 5% significance level. Therefore any QTL falling within a given interval with a value equal to 9.49 or greater was considered to be significantly associated with that particular trait.

2 Results

2.1 Transgressive segregation of yield components

The phenotypic values for the five traits of the DH population and its parents are presented in table 1. The results indicated that the maximum phenotypic values of the five traits scored were higher than both parents. It was indicated that yield components of the DH population segregated continuously and both the skew and the kurt values were less than 1 except for fertility rate. It was suggested that yield components of the DH population fit normal distribution and is suitable for QTLs analysis. Transgressive segregants with yield components were higher than the parent IR64 or lower than the parent Azucena were observed.

2.2 Detection of QTL for yield components

2.2.1 Total grains　A total of 4 QTLs (tg3, tg4, tg10, tg11) were detected in Hangzhou location for the DH population (Table 2) and were located on chromosome 3, 4, 10, and 11, respectively. All these QTLs had a positive additive effect except for QTL tg11 which was associated with a decrease in

additive effect. The QTL tg4 located on chromosome 4 within the markers RZ675-RG163 accounted for 22.63 number of grains increases in total grains.

There were 5 QTLs detected in total from the DH population evaluated in Hainan (Table 2) and had the same genetic direction as those found in Hangzhou but with a smaller effect. The QTL tg10 mapped to chromosome 10

Table 1 Phenotypic values of yield components for the DH population and its parents

Location	Trauts	Parents		DH population					
		Azucena	IR64	Max	Min	Mean	Stdev	Kurt	Skew
Hangzhou	Prod. Till	10.1	13.4	15.3	4.5	8.9	2.4	−0.1	0.6
	kg weight	24.9	25.6	33.8	17.8	25.4	2.9	0.2	0.2
	Total Gr	82.7	51.0	215.3	47.1	117.4	35.5	−0.1	0.3
	Full gr	78.8	35.7	182.1	20.3	94.1	32.0	−0.4	0.1
	Fer. Rate	1.0	0.7	1.0	0.3	0.8	0.1	2.5	−1.4
Hainan	Prod. Till	3.5	6.1	11.6	3.8	6.7	1.5	0.1	0.5
	kg weight	29.0	27.1	40.3	19.3	27.0	4.2	−0.1	0.4
	Total Gr	81.8	61.9	130.8	34.7	67.6	17.4	0.9	0.6
	Full grain	66.5	46.8	106.7	0.7	37.0	18.1	1.1	0.5
	Fertily	0.8	0.8	0.9	0.0	0.6	0.2	−0.3	−0.6

Table 2 Estimated genetic effects of QTL for yield components across environments

Trait	Chr	Locus	Marker interval	Hangzhou	Hainan	Main effect	GE in Hangzhou	GE in Hainan
TG	2	tg2-1	Amy1A/C-RG95				6.69*	−3.00*
		tg2-2	RG437-RG544					−4.29*
	3	tg3-1	RG191-RG678		−4.55*	−4.56*		
		tg3-2	RZ337A-RZ448	8.24**	6.9*	4.68*		−3.31*
	4	tg4	RZ675-RG163	22.63**	7.20*	11.47**	10.48**	
	10	tg10	RZ257-RG241	−7.65*	−9.23**	−4.25*		6.35*
	11	tg11	Adh1-RG1094	−7.07*	−5.70*	−5.77*		
	12	tg12	RZ816-RG341	8.40**				
FR	1	fr1	RG146-RG345	4.16*	3.72*	5.90*		
	2	fr2	Amy1A/C-RG95	7.11**			8.00**	
	4	fr4	RZ449-RZ788	3.50*	7.20**	3.30*		
	6	fr6	RZ144-RG667		6.30*	8.23**		
FG	3	fg3	RG179-CDO337	10.39**	7.90**	3.57*	8.94**	
	4	fg4-1	RG675-RG163	16.65**	9.84**	6.55*	12.12**	−4.29*
		fg4-2	RG214-RG143				10.98**	−4.29*
PT	1	pt1	RG690-RZ730	−0.51**	0.71**	0.53*	0.93**	
	2	pt2	Amy1A/C-RG95		0.45*			0.71**
	3	pt3	Pgi-CD087		0.32*	0.64**		0.73**
	4	pt4	RG675-RG163	0.85**			1.08**	
	8	pt8	TGMS1.2A10K20	0.51**	0.61**	0.93**		
KG	1	kg1-1	W1-RG173		−1.26**			
		kg1-2	RG690-RZ730	1.28**		1.10**		1.21**
	2	kg2	Pall-RZ58	0.93**				
		kg3-2	CDO87-RG910			0.99**		0.86**
	4	kg4	RG190-RG908	−1.16**				
	10	kg10	CDO98-G2155	−1.37**	−0.75*	−0.78*		
	11	kg11	Adh1-RG1094				−0.55*	

Note：QTLs are named by traits abbreviations and chromosome number，TG：total grains，FR：fertility rate，FG：full grains，PT：Productive tillers，KG：kilograin weight；

* and * * were significant at 0.05 and 0.01 levels.

between markers RZ257-RG241 had a negative additive effect of −9.23 grains with a high likelihood ratio of 34.22. At this locus，the alleles increasing total grains were from IR64.

A total of four QTLs were detected being common to both environments (Table 2) and were located on chromosome 3，4，10，and 11 between markers RZ337A-RZ448，RZ675-RG163，RZ257-RG241 and Adh1-RG1094 respectively.

Four QTLs have been identified (Table 2) for the genetic main effects and were located on chromosome 3，4，10，and 11，respectively. The QTL tg4 bordered by the markers RG675-RG163 gave the highest additive effect of 11.47 grains and with a very high likelihood value equal to 56.94. This QTL was detected when using phenotypic data in Hangzhou but was not identified in Hainan. The locus tg3-1 located on chromosome 3 within markers RG191-RG678 was also detected for the genetic main effects but only in Hangzhou location. The results indicated that these loci were controlled by genetic main effects without significant interaction with the environment.

A total of 2 QTLs were found (Table 2) for the QE interaction effects in Hangzhou. Among these，the QTL tg2-1 mapped to chromosome 2 had a significant interaction effects for both environments. It was suggested that this locus was mainly controlled by QE interaction effects without significant main effects. The other QTL tg4 located on chromosome 4 was mapped to the same position as the QTL main effect，showing that the genetic effects of this locus was cumulative results of genetic main effects and QE interaction effects.

A total of 4 QTLs were mapped (Table 2) for QE interaction effects in Hainan. These loci have a negative additive effect with alleles increasing total grains deriving from IR64. Results indicated that the QTLs tg2-1 and tg2-2 located on chromosome 2 were mainly controlled by QE interaction effects. In contrast the QTLs tg3-2 and tg10 were controlled by QTL main effects as well as QE interaction effects.

2.2.2 Fertility rate　Three QTLs fr1，fr2 and fr4 were identified as being significant in Hangzhou location (Table2) and were located respectively on chromosome 1，2，and 4. These QTLs had a significant additive effect of about 4% and 7% for seed set. All these QTLs had a positive additive effect and the contributing alleles were from Azucena.

A total of 3 QTLs (fr1，fr4，fr6) have been detected in Hainan environment (Table 2). The QTL fr1 occupied the same position as the one identified in Hangzhou location. All these QTLs had a positive additive effect and the alleles increasing fertility rate were from Azucena.

Two QTLs were detected on chromosome 1 and 4 being common for both environments and were bordered by markers RG146-RG345and RZ449-RZ788 respectively (Table 2).

Three QTLs in total fr1，fr4 and fr6 (chromosome 1，4 and 6) were detected (Table 2) from the DH population and evaluated in Hangzhou for the genetic main effects. Among these，the locus fr6 was identified in Hainan but not detected in Hangzhou with phenotypic data，the alleles at that locus increased fertility rate and were

from Azucena.

Only one QTL fr2 located on chromosome 2 between markers Amy1A/C-RG95 has been identified in Hangzhou for QE interaction effects (Table 2), showing that locus was mainly controlled by QE interaction effects without any QTL main effects.

No QTL with the QE interaction effects has been detected in Hainan.

2.2.3 Full grains A total of two QTLs were found for full grains in Hangzhou (Table 2) and were mapped to chromosome 3 between markers RG179-CDO337, chromosome 4 between markers RZ675-RZ163 and markers RG214-RG143. The increase in full grain for these QTL was associated with azucena alleles. The loci tg4-1 mapped to chromosome 4 between markersRZ675-RZ163 had a high additive effect of 16.65 grains and high likelihood ratio and seems to act as major gene.

There were two QTLs detected in Hainan (Table 2) and were located on chromosome 3 between markers RG179-CDO337 and chromosome 4 between the markers RG675-RG163. These QTLs occupy also the same locus as that identified in Hangzhou but with a minor effect.

Two QTLs were found to be common for both environments and were located on chromosome 3 and 4 between markers RG179-CDO337 and RG675-RG163 respectively (Table 2). Two QTLs fg3 and fg4-1 were detected (Table 2) for the genetic main effect. These QTLs were identified when mapping phenotypic data in both environments separately. At these loci, the alleles increasing full grains were associated with azucena. The QTL located on chromosome 4 between markers RG675-RG163 had the highest additive effect with 6.65 grains and a very high likelihood ratio of 34.18 and might be a major gene because of its effect.

There were in total three QTLs detected (Table 2) in Hangzhou for the QE interaction effects. Among these, the QTL fg3 and fg4-1 were mapped to the same loci as the QTL main effects on chromosome 3 and 4 respectively. Therefore the genetic effects of these two QTL are cumulative of QTL main effects and QE interaction effects. However the QTL fg4-2 was controlled only by QE interaction effect without significant QTL main effects.

Two QTLs were detected for QE interaction effects in Hainan (Table 2) with alleles increasing full grains derived from IR64. The QTL fg4-1 occupied the same locus as the QTL main effects when using the phenotypic data in both environments. In contrast the locus fg4-2 was mainly controlled by QE interaction effects.

2.2.4 Productive tillers Three QTLs were mapped for productive tillers and were significant for Hangzhou environment (Table 2). These QTLs were located on chromosome 1, 2, and 8 respectively. All the alleles increasing productive tillers were from Azucena except for locus pt1 bordered by markers RG690-RZ730 that had a negative additive effect and the alleles contributing for the increase were from IR64. No QTL controlling this trait was identified on chromosome 5, 6, 7, 9, 10, 11, and 12. The QTL located on chromosome 4 gave the highest additive effect of -0.85 with a very high likelihood ratio.

There were 4 QTLs (pt1, pt2, pt3, pt8) identified in Hainan (Table 2). Among these QTLs, only one was detected in Hangzhou and having an opposite direction effect.

Two QTLs were found to be common for both environments and were located on chromosome 1 and 8 between markers RG690-

RZ730 and TGMS1. 2-A10K250 respectively (Table 2).

Three significant QTLs pt1, pt3, and pt8 (Table2) showed association with productive tillers and were detected for the genetic main effects. These QTLs were also identified with phenotypic data in both environments except for locus 3 which fails to be identified in Hangzhou location.

Two QTLs pt1, and pt4 (chromosome 1, and pt4) were significantly mapped for QE effects in Hangzhou location (Table 2). At these loci the alleles Azucena were associated with an increase in productive tillers number. Of these, the QTL pt1 was detected at the same position as the QTL with main effects showing that the genetic effects of these loci was cumulative results of QTL main effects and QE interaction effects.

Two QTLs pt2, and pt3 were identified (Table 2), in hainan for QE interaction effects and were located respectively on chromosome 2, and 3 with alleles increasing productive tillers derived from Azucena. Among these QTL, the locus pt2 was controlled mainly with QE interaction effects. In contrast the QTL pt3 was detected at the same position as the main effects and its genetic effect is cumulative of QTL main effects and QE interaction effects.

2. 2. 5 kilogram weight　A total of 4 QTLs affecting grain weight were detected (Table 2) in Hangzhou and were located respectively on chromosome 1, 2, 4, 10. The alleles from Azucena at loci kg1-2 and kg2 increased grain weight. In contrast the alleles from IR64 were associated with an increase in grain weight at loci kg4 and kg10 (chromosome 4 and 10). The highest additive effect was obtained by the QTL kg10 and was 1. 37 g with a likelihood equal to 16. 79.

Two QTLs were identified as being significant in Hainan environment (Table 2). These QTLs had all a negative additive effect. The alleles IR64 increased this parameter at locus kg1-1 and kg10 (chromosome 1 and 10). Among these QTLs identified only one was the same as that detected in Hangzhou. Only one QTL has been detected being common for both environments and was located on chromosome 10 between markers CD098-G2155 (Table 2).

Four QTLs affecting grain weight were detected (Table 2) for the QTL main effects. They were mapped on chromosome 1 between RG690-RZ730, chromosome 3 between RZ337A-RZ448 and between markers CDO87-RG910, chromosome 10 between CDO98-G2155 with alleles increasing kilogram weight derived from Azucena at loci kg1-2, kg3-1, kg3-2 and from IR64 at locus kg10.

Two QTLs were detected for the QE interaction effect in Hangzhou location (Table 2). Of these, kg3-1 was mapped to chromosome 3 between markers RZ337A-RZ448 to the same position as that of the QTL main effects but was not detected in both environments when using phenotypic data. The other QTL was located on chromosome 11 between markers Adh1-RG1094 with alleles increasing grain weight derived from IR64. No QTL has been identified at the same locus for the QTL main effects. Therefore the genetic effect for this QTL detected in Hangzhou was mainly controlled by QE interaction effects.

Three QTLs have been detected for the QE interaction effects in Hainan (Table 2). The alleles Azucena increased this parameter at kg1-2 and kg3-2 (chromosome 1 and 3). In contrast the alleles IR64 was associated with an increase in grain weight at locus kg3-1 and also mapped to the same position as the QTL main effects, indicating that this QTL is

controlled with QTL main effects and QE interaction effects.

3 Discussion

Breeding population typically exhibits environment interaction when tested in different environments. In the case of such interaction one would expect that at least some of the genes underlying QTL would also show GE interaction[24]. Quantitative geneticists have long recognised the importance of genotype by environment interaction and have documented numerous crops and for various traits. However, in most of these studies the QTL analysis was performed by comparing QTL detected separately in each environment. The QTL identified in all environments are generally considered to be the QTL for the main effects while those identified in only one or the other environment are taken as GE interaction effects. Although environment specific QTL may be detected this way, the approach is intrinsically weak because the interaction is not part of the genetic model that is fitted in the model[6]. Therefore the failure to identify a particular QTL in all environments does not necessarily indicate the GE interaction effects.

In this study the total genetic effects were partitioned into genetic main effects and GE interaction effects. The genetic main effects (G) and interaction effects (GE) were predicted by the Adjusted Unbiased Prediction (AUP) method[19,20]. In this situation if pattern of environment specific QTL really results from QTL by environment interaction this is readily, and more powerfully detected by QTL main effects and QE interaction effects. Results indicate that some QTLs detected in all environments may still have QE interaction effects. In this case the genetic effect is cumulative, consisting of QTL main effects and QE interaction effects.

This study also reveals that QTLs show a range of sensitivity to environments as some QTLs were detected only in single environment while others were detected in all environments. The relative rankings of genotypes may well differ in different environments and the relationship may be quite complex[25]. These QTLs might be described with their sensitivity to environment and this agrees with the results reported by Paterson[4], Zhang[12], and Lee[11]. QTL associated with total grain (tg3-1, tg3-2, tg4, tg10, tg11) and QTL affecting full grain (fg3, fg4-1, fg4-2) showing the largest effect in one environment were also more likely to be detected in another environment. Therefore, these results tend to support the conclusion made by Tanksley[2] that a substantial proportion of QTLs affecting quantitative trait in one environment will be active in other environments and that this especially true for QTL with major effect. Therefore identifying QTL that are consistent across environments would be desirable in a marked selection program[4].

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