



## QTL analysis of genetic main effects and genotype × environment interaction effects for yield components in rice (*Oryza sativa* L.)

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### 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). The genetic effect of a QTL has been partitioned into genetic main effect and GE interaction effect. These two genetic effects were predicted by an adjusted unbiased prediction (AUP) method and used in QTL mapping. The results indicate that some QTL detected for the genetic main effects might also have GE interaction effects. In contrast some identified QTL were mainly controlled by GE interaction effects without significant genetic main effects. The study also revealed that individual QTL showed a range of sensibility to environments as some QTL were detected only in a single environment while others were detected in two environments. It is also shown that QTL associated with total grains and full grains tightly linked to markers RZ675-RG163 on chromosome 4 had high additive effects and high likelihood ratio for both main effects and GE interaction effects seem to act as major gene controlled by genetic main effects and GE interaction effects.

**Key words:** QTL, yield components, rice, main effect, GE interaction effects.

### Introduction

Genetic studies for quantitative traits have been greatly facilitated by the development of molecular markers <sup>1</sup>. Using molecular genetic-linkage maps and QTL mapping technology, it is possible to estimate the number of loci controlling genetic variation and to characterize these loci with regard to their map positions in the genome, as well as their gene action, phenotic effects, pleiotropic effects and epistatic interactions with other QTL. Since the introduction of molecular markers, QTL mapping in numerous species and for various traits has been well documented <sup>8, 9</sup>. Genotype by environment interaction is differential genotypic performance across environments. It reduces the association between phenotypic and genotypic values and thus plant that performs well in one environment may not necessarily perform well in another environment. The objective of plant breeder is an attempt to select genotypes that perform well or are stable across environments <sup>10</sup>. In most of these studies the QTL analysis was done 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 one or the other environment are taken as GE interaction effects.

The objectives of the present study were 1) to assess the value for a new methodology for QTL mapping with genetic main effects and GE interaction effects; 2) to describe the genetic analysis for yield components resistance genes and localise QTL involved in controlling these traits on the molecular map of rice.

### Materials and Methods

**Materials:** A double haploid 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. This map contains 175 markers covering 2005cM with an average distance of 11.5cM between pairs of markers <sup>3</sup>. This new map has been used for QTL analysis in this experiment.

**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 located at 32 N and Hainan located at 18 N. The DH lines were grown in the field in Hangzhou from May to October 2003 and in Hainan from January to June 2003. 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 1000 grains (kilogram weight, KG).

**Statistical analysis:** For the present genetic experiments of 123 genotypes with 2 replications in 2 locations (as different environments), QTL mapping was firstly conducted based on phenotypic values at each location by the procedure of composite interval mapping <sup>10</sup>. For CIM analysis between markers *i* and *i+1* using DH population, the statistical model is:

$$\hat{y}_j = \beta_0 + \beta^* X_j^* + \sum_i \beta_i X_{ij} + \varepsilon_j \quad (1)$$

where  $\hat{y}_j$  is the phenotypic value of the  $j$ th individual measured;  $\beta_0$  is the population mean,  $\beta^*$  is the QTL effect;  $X_j^*$  is the coefficient for QTL effect;  $\beta_i$  is the effect for the  $i$ th marker;  $X_{ij}$  is the coefficient for the  $i$ th marker effect of the  $j$ th individual; and  $\varepsilon_j$  is the residual error of the  $j$ th individual.

The QTL mapping was then also conducted based on observations of two locations by a new approach<sup>13</sup>. The phenotypic performance of the  $j$ th genetic entry in the  $k$ th replication within the  $h$ th environment can be expressed by the following model:  $y_{hjk} = \mu + E_h + G_j + GE_{hj} + e_{hjk}$  where  $\mu$  is population mean, fixed;  $E_h$  is effect of the  $h$ th environment,  $E_h \sim (0, \sigma_E^2)$ ;  $G_j$  is genotype effect,  $G_j \sim (0, \sigma_G^2)$ ;  $GE_{hj}$  is genotype  $\times$  environment interaction effect,  $GE_{hj} \sim (0, \sigma_{GE}^2)$ ;  $e_{hjk}$  is residual effect,  $e_{hjk} \sim (0, \sigma_e^2)$ . The genotype effects (G) and interaction effects (GE) were predicted by the adjusted unbiased prediction method<sup>12</sup>. Prediction values were obtained for genetic main effects ( $y_{j(G)} = \mu + G_j$ ) and genotype  $\times$  environment interaction effects in the  $h$ th environment ( $y_{hj(GE)} = \mu + E_h + G_j + GE_{hj}$ ). Then the composite interval mapping method<sup>12</sup> was applied for analysing the predicted genetic main effects of

$$\hat{y}_{j(G)} = \beta_{0(G)} + \beta_{(G)}^* X_j^* + \sum_i \beta_{i(G)} X_{ij} + \varepsilon_{j(G)} \quad (2)$$

and also the predicted GE interaction effects

$$\hat{y}_{hj(GE)} = \beta_{0(GE_h)} + \beta_{(GE_h)}^* X_{hj}^* + \sum_i \beta_{i(GE_h)} X_{hij} + \varepsilon_{hj(GE)} \quad (3)$$

The analysis of QTLs linked to molecular markers<sup>3</sup> was conducted by QTL Cartographer v 1.1b<sup>2</sup> 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. QTL detected by model (2) will have additive main effects for both environments, while those detected by model (3) will have additive by environment interaction effects.

## Results and Discussion

**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.

### Detection of QTL for yield components

**Total grains:** A total of 4 QTL were detected in Hangzhou location for the DH population (Table 2, Fig. 1) and were located on chromosome 3, 4, 10 and 11, respectively. All these QTL 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 QTL detected in total from the DH population evaluated in Hainan (Table 2, Fig. 1) and had the same genetic

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

Location	Trait	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
	Kgweight	24.9	25.6	33.8	17.8	25.4	2.9	0.2	0.2
	TotalGr	82.7	51.0	215.3	47.1	117.4	35.5	-0.1	0.3
	Fullgr	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
	Kgweight	29.0	27.1	40.3	19.3	27.0	4.2	-0.1	0.4
	TotalGr	81.8	61.9	130.8	34.7	67.6	17.4	0.9	0.6
	Fullgrain	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

direction as those found in Hangzhou but with a smaller effect. The QTL tg10 mapped to chromosome 10 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 QTL 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 QTL have been identified (Table 2, Fig. 1) for the genetic main effects and was 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 QTL were found (Table 2, Fig. 1) for the GE 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 GE interaction effects without significant main effects. The other QTL tg4 located on chromosome 4 was mapped to the same position as the genetic main effect, showing that the genetic effects of this locus was cumulative results of genetic main effects and GE interaction effects.

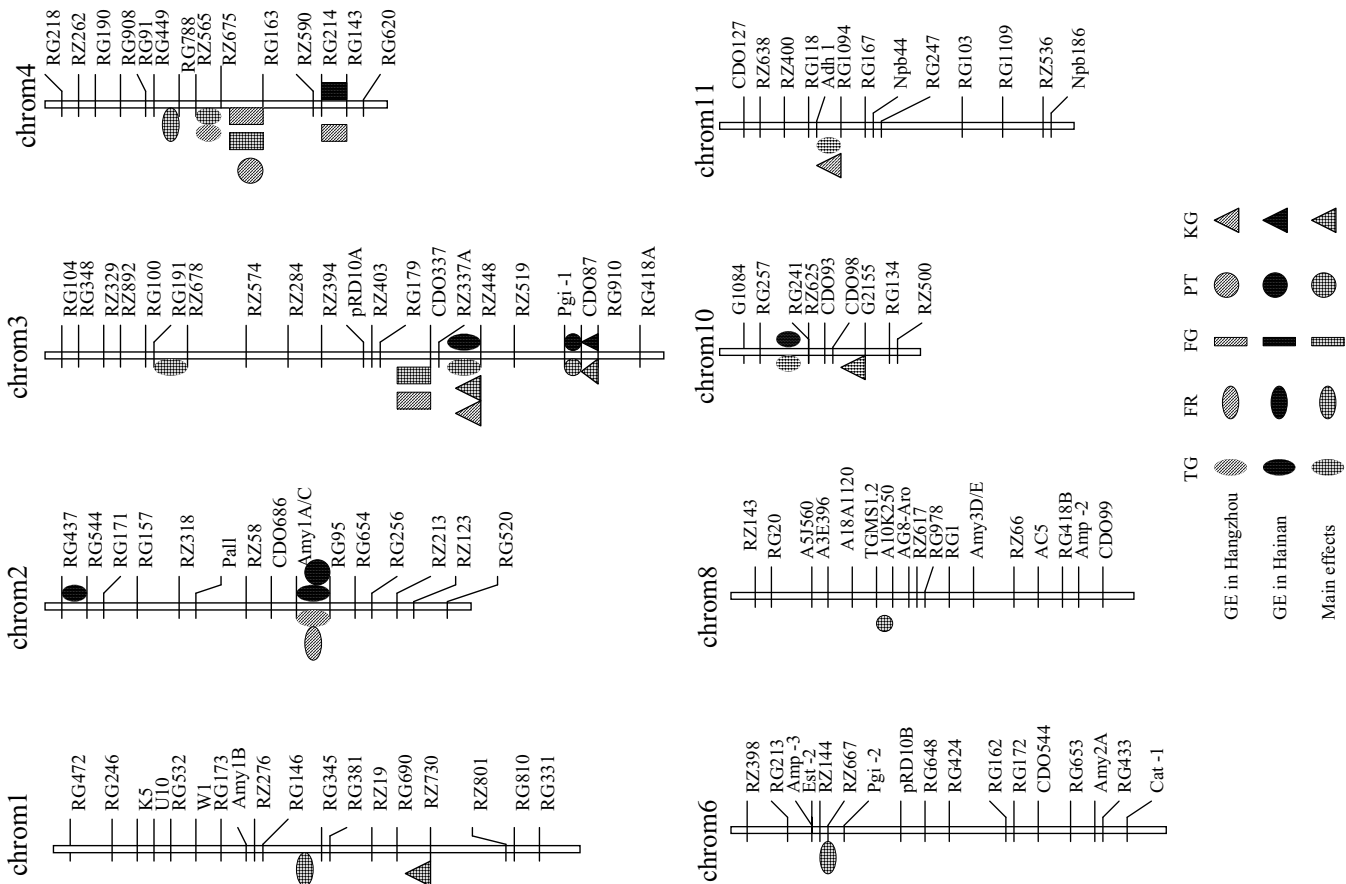
A total of 4 QTL were mapped (Table 2, Fig. 1) for GE interaction effects in Hainan. These loci have a negative additive effect with alleles increasing total grains deriving from IR64. Results indicated that the QTL tg2-1 and tg2-2 located on chromosome 2 were mainly controlled by GE interaction effects.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

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

**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		
		tg3-1	RG191-RG678		-4.55	4.56				
		tg3-2	RZ337A-RZ448	8.24	6.9	4.68				
		tg4	RZ675-RG163	22.63	7.20	11.47	10.48			
		tg10	RZ257-RG241	-7.65	-9.23	-4.25		6.35		
		tg11	Adh1-RG1094	-7.07	-5.70	-5.77				
		tg12	RZ816-RG341	8.40						
		FR	1	fr1	RG146-RG345	4.16	3.72	5.90		
				fr2	Amy1A/C-RG95	7.11		8.00		
				fr4	RZ449-RZ788	3.50	7.20	3.30		
				fr6	RZ144-RG667		6.30	8.23		
fr3	RG179-CDO337			10.39	7.90	3.57	8.94			
fr4-1	RG675-RG163			16.65	9.84	6.55	12.12	-4.29		
FG	4	fg4-2	RG214-RG143				10.98	-4.29		
		pt1	RG690-RZ730	-0.51	0.71	0.53	0.93			
PT	2	pt2	Amy1A/C-RG95		0.45	0.64		0.71		
		pt3	Pgi-CD087		0.32	0.64		0.73		
		pt4	RG675-RG163	0.85	0.61	0.93	1.08			
KG	1	kg1-1	W1-RG173		-1.26	1.10		1.21		
		kg1-2	RG690-RZ730	1.28						
	2	kg2	Pall-RZ58	0.93						
		kg3-1	RZ337A-RZ448			0.68	0.50	-1.14		
	3	kg3-2	CDO87-RG910			0.99		0.86		
		kg4	RG190-RG908	-1.16						
	10	kg10	CDO98-G2155	-1.37	-0.75	-0.78				
		kg11	Adh1-RG1094					-0.55		

\*QTLs are named by traits abbreviations and chromosome number, TG: total grains, FR: fertility rate, FG: full grains, PT: Productive tillers, KG: kilogram weight.



**Figure 1.** RFLP linkage map showing location of QTL for rice yield components in the DH population of IR64/Azucena. Numbers at the top indicate chromosomes. Markers are indicated on the right of the chromosomes

A total of 3 QTL (fr1, fr4, fr6) have been detected in Hainan environment (Table 2, Fig. 1). The QTL fr1 occupied the same position as the one identified in Hangzhou location. All these QTL had a positive additive effect and the alleles increasing fertility rate were from Azucena.

Two QTL were detected on chromosome 1 and 4 being common for both environments and were bordered by markers RG146-RG345 and RZ449-RZ788 respectively (Table 2).

Three QTL in total fr1, fr4 and fr6 (chromosome 1, 4 and 6) were detected (Table 2, Fig. 1) 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 GE interaction effects (Table 2, Fig. 1), showing that locus was mainly controlled by GE interaction effects without any genetic main effects.

No QTL for the GE interaction effects has been detected in Hainan.

**Full grains:** A total of two QTL were found for full grains in Hangzhou (Table 2, Fig. 1) 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 markers RZ675-RZ163 had a high additive effect of 16.65 grains and high likelihood ratio and seems to act as major gene.

There were two QTL detected in Hainan (Table 2, Fig. 1) and were located on chromosome 3 between markers RG179-CDO337 and chromosome 4 between the markers RG675-RG163. These QTL occupy also the same locus as that identified in Hangzhou but with a minor effect.

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

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

**Productive tillers:** Three QTL were mapped for productive tillers and were significant for Hangzhou environment (Table 2, Fig. 1). These QTL 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 QTL (pt1, pt2, pt3, pt8) identified in Hainan (Table 2, Fig. 1). Among these QTL, only one was detected in Hangzhou and having an opposite direction effect.

Two QTL 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 QTL pt1, pt3, and pt8 (Table 2, Fig. 1) showed association with productive tillers and were detected for the genetic main effect. These QTL were also identified with phenotypic data in both environments except for locus 3 which fails to be identified in Hangzhou location.

Two QTL pt1, and pt4 (chromosome 1, and pt4) were significantly mapped for GE effects in Hangzhou location (Table 2, Fig. 1). 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 for genetic main effects showing that the genetic effects of these loci was cumulative results of genetic main effects and GE interaction effects.

Two QTL pt2, and pt3 were identified (Table 2, Fig. 1), in Hainan for GE 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 GE interaction effects. In contrast the QTL pt3 was detected at the same position as the main effects and its genetic effect is cumulative of genetic main effects and GE interaction effects.

**Kilogram weight:** A total of 4 QTL affecting grain weight were detected (Table 2, Fig. 1) in Hangzhou and were located respectively on chromosome 1, 2, 4, 10. The alleles from Azucena at loci kgwt1-2 and kgwt2 increased grain weight. In contrast the alleles from IR64 were associated with an increase in grain weight at loci kgwt4 and kgwt10 (chromosome 4 and 10). The highest additive effect was obtained by the QTL kgwt10 and was 1.37 g with a likelihood equal to 16.79.

Two QTL were identified as being significant in Hainan environment (Table 2, Fig. 1). These QTL had all a negative additive effect. The alleles IR64 increased this parameter at locus kgwt1-1 and kgwt10 (chromosome 1 and 10). Among these QTL 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 QTL affecting grain weight were detected (Table 2, Fig. 1) for the genetic 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 kgwt1-2, kgwt3-1, kgwt3-2 and from IR64 at locus kgwt10.

Two QTL were detected for the GE interaction effect in Hangzhou location (Table 2, Fig. 1). Of these, kgwt3-1 was mapped to chromosome 3 between markers RZ337A-RZ448 to the same position as that of the genetic 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 genetic main effect. Therefore, the genetic effect for this QTL detected in Hangzhou was mainly controlled by GE interaction effects.

Three QTL have been detected for the GE interaction effects in Hainan (Table 2, Fig. 1). The alleles Azucena increased this parameter at kgwt1-2 and kgwt3-2 (chromosome 1 and 3). In contrast the alleles IR64 were associated with an increase in grain weight at locus kgwt3-1 and also mapped to the same position as the genetic main effects, indicating that this QTL is controlled with genetic main effects and environment interaction effects.

### Conclusions

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<sup>13</sup>. 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 effect 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<sup>4</sup>. 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 effect and GE interaction effects. The genetic main effects (G) and interaction effects (GE) were predicted by the Adjusted Unbiased Prediction (AUP) method<sup>12</sup>. In this situation if pattern of environment specific QTL really results from QTL by environment interaction this is readily and more powerfully detected by genetic main effect and GE interaction effects. Results indicate that some QTL detected in all environments may still have GE interaction effects. In this case the genetic effect is cumulative, consisting of genetic main effects and GE interaction effects. Therefore, just by detecting QTL, in different environments separately, we cannot be conclusive on the absence of GE interaction effects. In contrast some QTL identified were mainly controlled by GE interaction effects without significant genetic main effects. Therefore, with this methodology more QTL could be mapped for yield components and one might explore better the magnitude and nature of QTL × environment.

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