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MAPPING OF QTLS FOR YIELD AND ITS COMPONENTS IN A RICE RECOMBINANT INBRED LINE POPULATION

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Abstract

Quantitative trait loci (QTLs) for rice (*Oryza sativa* L.) yield and related components have been reported in recent years. However, due to differences between the genetic backgrounds, type of molecular markers and the tested environment the results describing the number of QTLs, chromosomal regions and nature of the additive effects could be different. The purpose of this study was to map QTLs conferring the yield and yield related components in a rice recombinant inbred line (RIL) population. A linkage map consisting of 119 simple sequence repeat (SSR) markers was constructed based on an RIL population with 307 lines derived from a cross between Guanghui 116 (male) and LaGrue (female). Mapping of the QTLs for grain yield per plant, number of grains per panicle, 1000-grain weight, seed-setting rate and number of tillers per hill, was carried out based on the composite interval–mapping method. The additive effects and the percentage of phenotypic variation for all the traits involved were also estimated. Fifteen QTLs were detected on chromosomes 1-6, 8, 9 and 12. Among these, nine QTLs were reported earlier, indicating their stability across genetic backgrounds. The markers, *qTL*-3, *qTL-6*, *qTL-12*, *qSS-5*, *qSS-9* and *qGY-8*, which control the tiller number, seed-setting rate and grain yield per plant, have not been detected in previous studies.

Introduction

Yield-related traits in rice (O*ryza sativa* L.) are typical quantitative traits showing continuous variation in segregating populations. Each quantitative trait is governed by many non-allelic genes or polygenes and may additionally be influenced significantly by environmental factors and genetic basis, which makes it more complicated. With the development of molecular markers, construction of high-density genetic-linkage maps and improvement of statistical analysis methods, one can probe multiple quantitative trait loci (QTLs) for a single Mendelian genetic dissection study and can further clarify the genetic effects of their size and mode of action(Meng *et al.*, 2012). This is important not only for an understanding of the genetic mechanism of agronomic traits in rice, but also for molecular marker–assisted selection.

A few studies about the mapping of QTLs that are used to control rice yield and its components have been reported (Fan *et al*., 2005; Gutiérrez *et al*., 2010; Liu, Shao *et al*., 2010; Liu, Zhang *et al*., 2010; Rahman *et al*., 2007; Tan *et al*., 2008; Tian *et al*., 2006; Yoon *et al*., 2006; Zou *et al*., 2005; Saleem *et al*., 2011). Fu *et al*., (2010) detected 26 QTLs for yield-related traits and the alleles of 10 (38.5%) QTLs originating from *O. rufipogon* showed a beneficial effect for yield-related traits in the indica 93-11 genetic background. In another study (Rahman *et al*., 2007), 530 markers including SSR and sequence-tagged-site (STS) were used for the QTL analysis of 16 agronomic traits in an introgression line, a cross between IR71033 and a Korean japonica cultivar consisting of 146 lines, and 36 single-locus QTLs and 45 digenic epistasis loci were identified.

As important components of yield-related traits, more researches on QTLs for rice tillering and 1000-grain weight have been carried out. Functional mapping of QTLs for rice tillering in 129 doubled haploid lines derived from a cross between IR64 and Azucena was carried out, and 27 QTLs that account for 2.49-8.54% of the total phenotypic variance were probed (Liu *et al*., 2010). Multi-marker joint analysis and composite-interval mapping (CIM) indicated that nine common QTLs showed high stability across various samples, whereas one QTL was environment-specific and three were epistatic. Furthermore a QTL for tiller number on chromosome 1, 5 and 7 of recombinant inbred lines (RILs) derived from a combination of Zhenshan 97 and SLG was detected (Wu *et al*., 2002). In addition, using Lemont/Teqing RILs as the plant material, Xu *et al*., (2001) also found some QTLs for the number of tiller per plant and number of grain per panicle by restriction fragment length polymorphism (RFLP), simple sequence repeat (SSR) and random amplified polymorphic DNA (RAPD) markers. Till now more than 200 QTLs for 1000-grain weight have been located in 12 chromosomes of rice, in which the main QTL affecting the grain weight is likely to be found (Ghafoor *et al*., 2005).

Panicle architecture is of vital significance to rice yield. Thirty-nine chromosome-segment substitution lines (CSSLs) were development from a cross between an average-yielding japonica cultivar and a high-yielding indica cultivar and used for searching for QTLs for five morphological components of panicle architecture, and as a result 38 QTLs distributed on 11 chromosomes were found. Wherever the additive effect of each QTL was relatively small(Ando *et al*., 2008).

QTLs associated with nitrogen–utilizing efficiency have been reported. Sixteen QTLs for nitrogen–utilizing efficiency were detected using a set of 82 double-haploid lines derived from IR64/Azucena (Senthilvel *et al*., 2008) . Among these, 11 QTLs showed significant QTL × environment interactions. Seven QTLs for nitrogen–utilizing efficiency and yield-related traits were located on chromosome 3, and a QTL region between markers RZ678, RZ574 and RZ284 was also associated with nitrogen–utilizing and yield (Masood *et al*., 2004).

In general, because of the differences between the genetic backgrounds, the types of molecular markers tested and test environment, the obtained results, such as the number of QTLs, chromosomal regions, the nature of the additive effect and so on, could also be different. It is hence necessary to select new test materials and further identify the QTLs associated with yield and its components in rice. In this study, an RIL population derived from a cross between Guanghui 116 (a restorer line in hybrid rice from south China) and LaGrue (an American rice variety) was used for QTL analysis of five yield-related traits (such as the grain yield per plant, number of tiller per plant, number of grain per panicle, 1000-grain weight and seed-setting rate) to obtain more genetic information about yield-related traits. LaGrue has the merits of high photosynthetic efficiency, lodging resistance, high quality and transparency of seeds, while Guanghui 116 is significantly different in genetic background with LaGrue. Therefore, a rice recombinant inbred line population derived from a cross between Guanghui 116 and LaGrue is beneficial both to basic research and rice genetic improvement.

Materials and Methods

Plant materials: An F7 RIL population, consisting of 307 lines derived from a cross between rice Guanghui 116 and LaGrue by single-seed descent was developed by the Rice Institute, Guangdong Academy of Agricultural Sciences, China, and was used to construct a molecular map and identify QTLs for traits associated with yield.

In 2009, 307 lines and 2 parent materials were planted in the Dafeng Experimental Base of the Guangdong Academy of Agricultural Sciences, China. Seeds were sown on July 24 and transplanted on August 11 with a randomised block design and three replications. Each plot contained four rows with 8 plants per row and the planting density was 16.6 × 26.6 cm, with regular fertilization and water management. Upon harvest, 5 plants from each plot were used for analysis of various features, including the number of tiller per plant, number of grain per panicle, 1000-grain weight, grain yield per plant, seed-setting rate and other important yield traits. Among these, the analyses of number of grain per panicle and seed-setting rate were carried out by conventional methods, wherever grain yield per plant was the average of the values from28 plants from each plot. The number of tiller was recorded as the average of values from 5 plants in the middle line of the plot. QTL positioning was based on the average value of each trait in three replications.

DNA extraction and polymerase chain reaction analysis: DNA extraction was carried out using an improvement of the simple cetyl tri-methyl ammonium bromide (CTAB) extraction method (Mccouch & Doerge 1995). The leaf sample (1.0g) was ground into powder immediator after being frozen in liquid nitrogen. Then 750µl of CTAB extraction solution (200 mM Tris-HCl, 250 mM NaCl, 25 mM EDTA, 0.5% SDS, pH 7.5) were added to the tube and placed in a water bath at 65°C for 30 min with shaking. Subsequently, 750 µl of a chloroform/isoamyl alcohol mixture (chloroform: isoamyl alcohol = 24: 1) were added and mixed lightly. This mixture was centrifuged for 5 min at 14,000 rpm after incubating for 10-20 min at room temperature to separate the liquid phase from solid phase. The supernatant was transferred to another clean centrifuge tube and twice volume of frozen ethanol was added to precipitate genomic DNA. Next, centrifugation was carried out for 3 min at 13,000 rpm, the supernatant was discarded and the precipitate was washed with 75% ethanol, rinsed with ethanol and air-dried. Finally, the precipitate was dissolved at room temperature with sterile deionized water. The DNA concentration was determined using a DNA fluorimeter (Hitachi Co. Ltd., Japan) and diluted to 50 ng/µl. The DNA sample was stored at -20°C.

For QTLs mapping, 389 pairs of SSR markers were uniformly extracted from the 12 rice chromosomes, and their synthesis was carried out by the Shanghai Health Bioengineering Co., Ltd, Shanghai, China. Polymerase chain reaction (PCR) reaction was further carried out as follows: the reaction mix (20µl) consisted of 1×PCR buffer [10 mM Tris–HCl (pH 8.8), 50 mM KCl], 1.5 mM $MgCl_2$, 0.2 mol M of each primer, 0.1 mM dNTPs, .05 U of Taq DNA polymerase (Promega, Mannheim, Germany) and 50 ng of DNA template. The amplification was carried out in a Perkin Elmer 9600 cycler (PE Applied Biosystems, Weiterstadt, Germany). After a denaturation step (94°C for 5 min), 30 cycles of amplification (94°C for 30 s, 55°C for 30 s and 72°C for 30 s) a final extension for 7 min at 72°C were performed. The PCR products were subjected to 8% poly-acrylamide gel electrophoresis in a DYY-6B electrophoresis apparatus (Beijing Liuyi Instrument Factory, Beijing), followed by rinsing with water twice, staining in 1% $AgNO_3$ for 10 min and development of the image in the developing solution composed of formaldehyde, NaOH and anhydrous Na_2CO_3 in a certain proportion (40g NaOH/L, 0.38g Na_2CO_3/L). Clear bands were observed and the results were recorded. The recording method was as follows: parent Guanghui 116 was recorded as type 1, parent LaGrue was recorded as type 3, heterozygous band pattern was denoted as type 2, and missing was assigned to 0 with a note.

Construction of linkage map and QTL localisation: MAPMAKER/EXP3.0 software was used for constructing the genetic linkage map (Wu & Huang 1992). The results of electrophoresis were converted into original data and the software-running program was applied according to the instructions of the manufacturer. Linkage analysis and grouping was carried out by using the "Group" command "LOD>-2.0, Recombination rate < 0.50". The linked markers were optimised using the "compare" command when their number was less than 8. Otherwise, the "Ripple" command was used. The error detection rate was 1%. The recombination rate was transformed into a genetic map (distance, cM) using the Kosambi function. The located SSR markers (Temnykh *et al*., 2001)were considered anchor tags to determine the appropriate linkage groups. A 2101-cM-long linkage map containing 119 pairs of SSR primers was constructed. WinQTLCartographer2.5 was used for CIM analysis, and the trait values from various investigations were converted into original data and translated into Kosambi function to be analysed at an interval of 2 cM with permutation testing for 1000,

significance level of 0.05 and LOD threshold value of 2.0. The yield of the RILs was analysed using QTL localisation-related traits. Then, these values were plotted in the corresponding genetic linkage map according to the positioning of the above traits with the QTLs named following McCouch's methods.

Results

Variation of traits associated with yield in the parents and RIL populations: The grain yield and number of tiller per plant of the parent Guanghui 116 is 34.50 g and 12 t respectively, which is higher than those of the other parent LaGrue. On the contrary, LaGrue has higher 1000-grain weight, number of grain per panicle and seed-setting rate compared to Guanghui 116, with the number of grain per panicle reaching up to 302.57. Both positive and negative over-parent characteristics were found in each group, with a significant fluctuation. Except the seed-setting rate, the skewness and kurtosis of the other four traits were smaller than type 1, indicating their suitability for further QTL analysis (Table 1).

Distribution of yield-related traits in the RIL population: Yield-related traits including the grain yield per plant (Fig. 1a), number of tiller per plant (Fig. 1b), number of grain per panicle (Fig. 1c) and 1000-grain weight (Fig. 1d) showed a typical normal distribution, indicating that these traits were quantitative traits controlled by multiple genes. The seed-setting rate in the RIL groups also showed a continuous distribution, indicating that it also was quantitative traits controlled by multiple genes. However, the seed-setting rate appears skewed, which may be caused by the partial segregation in the population (Fig. 1e).

QTL markers of yield and related trait: CIM was used in the RILs of rice and 15 traits related to the yield-QTL were detected (Table 2, Fig. 2). For the trait of grain yield per plant, three QTLs located on chromosomes 5 and 8 were found. Among them, two QTLs, *qGY-8-1* and *qGY-8-2*, controlling the grain yield per plant were located on chromosome 8. The additive effect of these three QTLs was positive, indicating that the allele came from the parent Guanghui 116, and explained 23.64% of the phenotypic variation.

Five QTLs for the tiller number per plant were located on chromosomes 3, 4, 6, 9, and 12, respectively. The additive effects were all positive, explaining the phenotype by 7.21%, 10.52%, 4.46%, 8.07%, and 3.54%, respectively, with the total contribution of 33.81%, in which *qTL-4* contributed the most, up to 10.52%, indicating that the number of tiller per plant was controlled by multiple quantitative trait genes.

Three QTLs for the number of grain per panicle were located on chromosomes 1, 4, and 6, respectively. The additive effect of the QTL on chromosome 4 had the value of -16.48, and explains 10.66% of the phenotypic variation, indicating that this QTL's positive allele was from the paternal parent LaGrue.

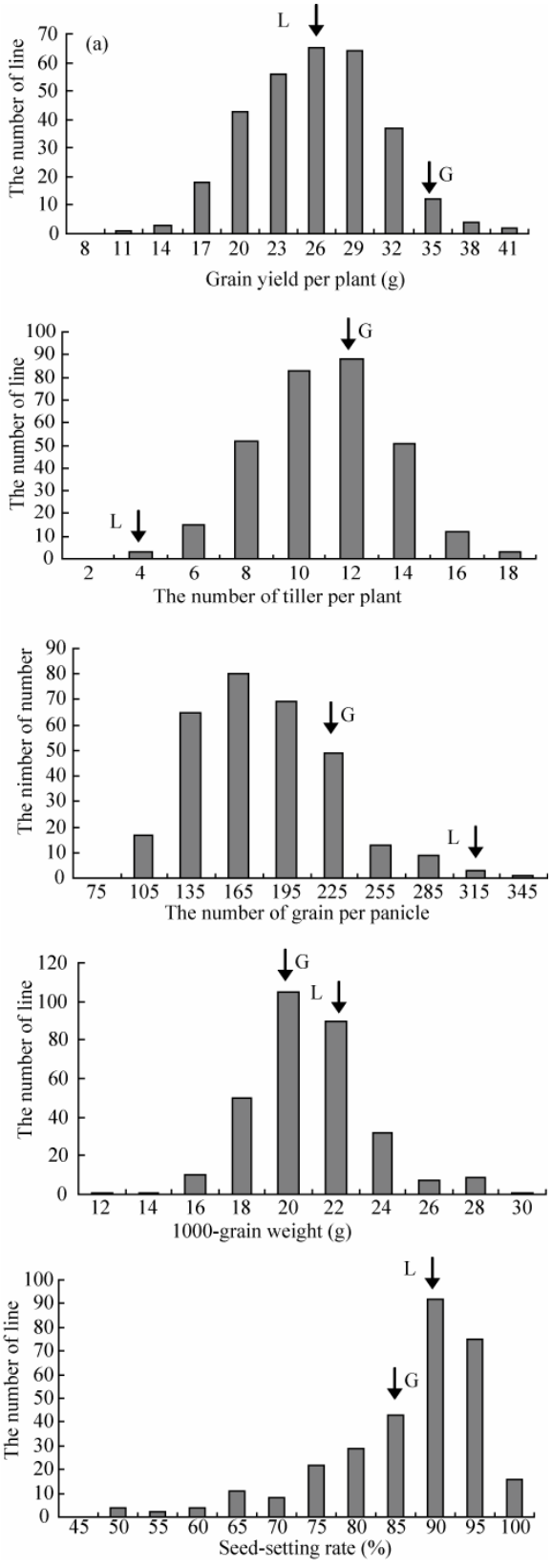

Fig. 1. Distribution of yield and its components in RILs
L, indicates LaGrue; G, indicates Guanghui116. (a) grain yield per plant; (b) the number of tiller per plant; (c) the number of grain per panicle; (d) 1000-grain weight; (e) seed-setting rate.

Table 1. Variation of yield and its components among the two parents and the RIL lines.

Traits	Parents		RIL population					
	Guanghui 116	LaGrue	Mean	Maximum	Minimum	SD	Kurtosis	Skewness
GYPP(g)	34.50	26.41	24.16	38.56	8.825	5.51	1.64	–0.490
NTPH	10.60	3.50	10.038	17.20	3.20	2.465	–0.139	0.070
GNPP	201.83	302.58	165.4	325.38	75.89	44.81	0.656	0.402
GW (g)	18.33	20.52	19.86	28.77	10.54	2.730631	0.033	–0.780
SR (%)	82.56	86.58	83.77	99.93	46.69	10.95	11.39	–2.380

Note: GYPP, NTPH, GNPP, GW and SR represent grain yield per plant, number of tillers per hill, grain number per panicle, 1000-grain weight and seed-setting rate

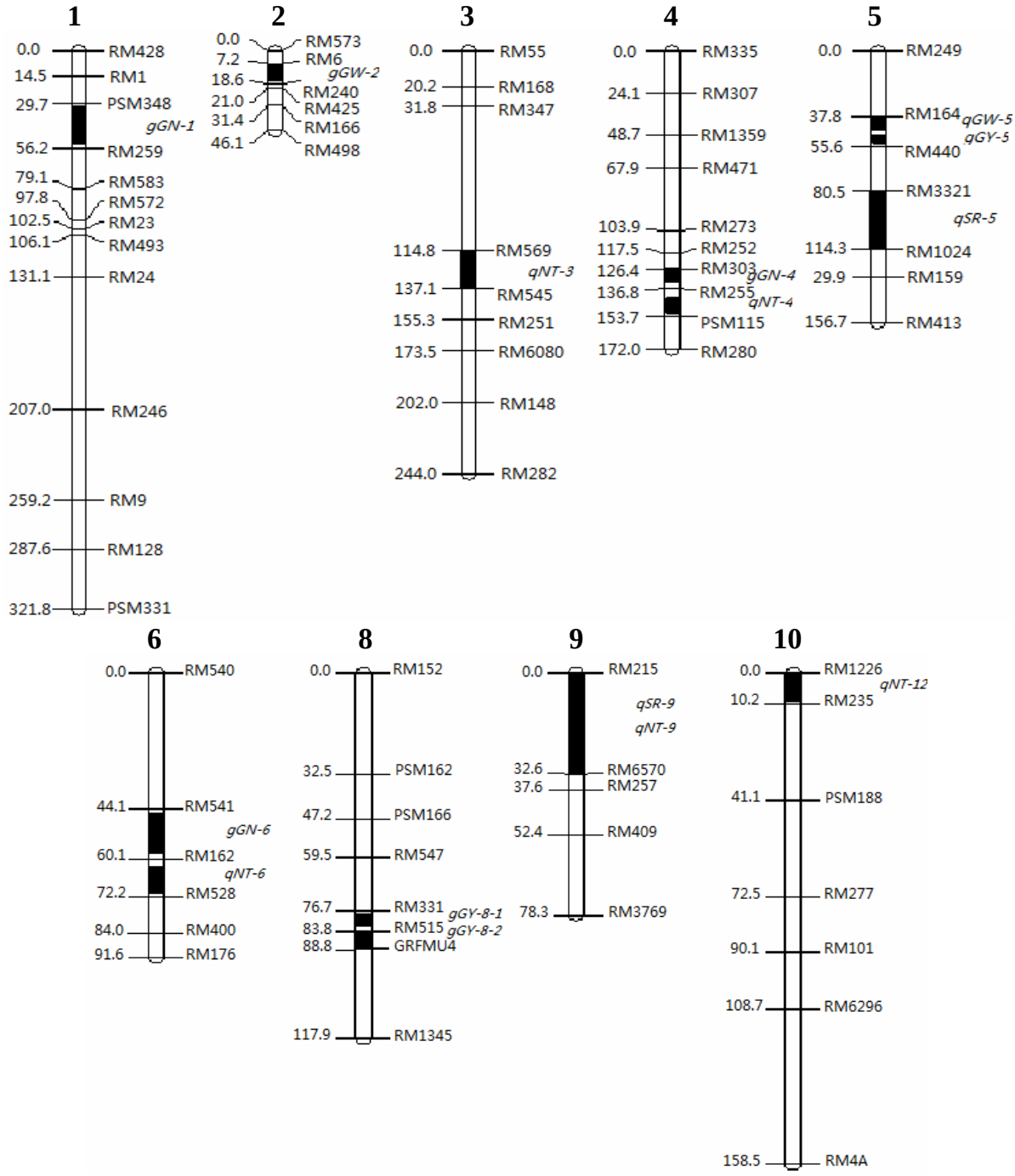

Fig. 2. Locations of the QTLs for the components of yield-related traits in the RIL*sqGY, qNT, qGN, qGW* and *qSR* represent the QTLs for grain yield per plant, the number of tiller per plant, number of grain per panicle, 1000-grain weight and seed-setting rate.

Table 2. QTLs for yield and its components detected in RILs.

Trait	QTL	Chr	Position	LOD score	Marker interval	Additive effect	PVE(%)	Total PVE (%)
NTPH	*qNT-3*	3	111.81	5.55	RM569-RM545	3.38	7.21	33.81%
	qNT-4	4	142.81	7.60	RM255-PSM115	4.38	10.52	
	qNT-6	6	62.11	3.78	RM162-RM528	2.79	4.46	
	qNT-9	9	30.01	6.56	RM215-RM6570	3.75	8.07	
	qNT-12	12	6.01	2.69	RM1226-RM235	2.43	3.54	
GNPP	*qGN-1*	1	51.71	4.07	PSM348-RM259	14.04	8.13	23.70%
	qGN-4	4	130.41	5.96	RM303-RM255	–16.48	10.66	
	qGN-6	6	48.11	2.71	RM541-RM162	10.4	4.91	
GW	*qGW-2*	2	15.21	7.45	RM6-RM240	–0.94	12.33	19.20%
	qGW-5	5	49.81	3.68	RM164-RM440	0.71	6.87	
GYPP	*qGY-5*	5	47.81	4.41	RM164-RM440	1.23	8.00	23.64%
	qGY-8-1	8	78.71	6.58	RM331-RM515	1.32	9.27	
	qGY-8-2	8	87.81	4.8	RM515- GRFM04	1.12	6.37	
SR	*qSR-5*	5	104.51	4.79	RM3321-RM1024	0.05	18.66	28.63%
	qSR-9	9	22.01	3.47	RM215-RM6570	0.03	9.97	

Note: GYPP, MTPH, GNPP, GW and SR represent grain yield per plant, number of tillers per hill, grain number per panicle, 1000-grain weight and seed-setting rate. PVE-Phenotypic variation explained.

Two QTLs for the trait of 1000-grain weight were located on chromosomes 2 and 5. The QTL on chromosome 2, located between RM6 and RM240, had a negative additive effect, and the genetic distance from RM240 was only 3.4 cM. The QTL on chromosome 5, located at 49.81 cM, had a positive additive effect, with a distance of 5.8 cM from RM440. These two QTLs explained 12.33% and 6.87% of the phenotypic variation, respectively. The enhancing alleles are from the maternal parent Guanghui 116.

Two QTLs or the seed-setting rate, were located on chromosomes 5 and 9. The contribution of the QTL on chromosome 5 was 18.66% and was a major-effect QTL, which located between the markers RM3321 and RM1024, 9.8 cM away from RM1024 while the QTL on chromosome 9 showed a contribution of 9.97%. In general, the two QTLs explained 28.63% of the phenotypic variation.

Discussion

The tagging of QTLs controlling rice yield and its components has already been published in previous reports. Yield-related traits were analysed using the backcross population (Agrama & Eizenga 2007; Moncada *et al*., 2001), and the grain yield per plant and its components by epistasis-QTL location was analysed using RILs (Xing *et al*., 2002). In addition, a rice population comprising 240 RILs was used for detecting QTL for seed dormancy, which is an important traits affecting grain yield and quality in rice (Li *et al*., 2010). Liu *et al*., made a comparison of QTL for 1,000-grain weight and spikelets per panicle across three connected rice populations (Liu, Zhang *et al*., 2010). However, as the number and effects of the QTLs were influenced by the test material, population size, statistical threshold, marker density and so on, the reported results were not consistent.

In this study, RILs based on a cross between Guanghui 116, an indica rice from south China, and LaGrue Javanica rice from America, were used as research materials. In summary, three QTLs were detected for the grain yield per plant. Among them, the QTLs near RM164-RM331 on chromosomes 5 and 8 are located in the same zone as *qYl-5* and *gyp8* detected (Cheng *et al*., 2001). The two QTLs detected in the region of RM515-GRFM04 on chromosome 8 were different from those reported previously and could be a new yield-QTL. For the number of tiller per plant, five QTLs were detected. Among them, two located on chromosomes 4 and 9 were consistent with the previous reports (Cheng *et al*., 2001; Thomson *et al*., 2003; Xing *et al*., 2002). Three new QTLs were detected, namely *qTL-3* in the region of RM569-RM545 on chromosome 3, *qTL-6* in the region of RM162-RM528 on chromosome 6 and *qTL-12* in the region RM1226-RM235 on chromosome 12. For the trait of number of grain per panicle, three QTLs were already

published on the Gramene web site. Furthermore, similar QTLs had been detected in this area (Lu *et al*., 1997; Thomson *et al*., 2003; Xing *et al*., 2002). For grain weight, two QTLs were detected in this study. Among them, QTL s*qGW-5* located on chromosome 5 controls grain weight. In previous studies, RM459 was detected in the same region by using the interlock disequilibrium method (Agrama & Eizenga 2007), and *qGW-2* was detected located on chromosome 2 in the same region using a single-segment substitution method (Zhao *et al*., 2007). For the seed-setting rate, two QTLs on chromosome 2 were found for the first time in this study. Among them, *qSR-5* explains 18.66% of the phenotypic variation and was a main-effect QTL, and the other, *qSR-9*, explains 9.97% of the phenotypic variation.

Among the QTLs obtained in this study, some were consistent as reported previously, indicating that these QTLs were reliable because of the repeatability in different studies with various segregation population; whereas others have been probed for the first time, indicating that more information on QTLs could be found by using populations of different genetic backgrounds. This is important for an in-depth understanding of the genetic control of yield traits in rice and for future rice production by using molecular marker–assisted selection in rice breeding (Iqbal *et al*., 2003).

Many studies showed that the QTLs for yield-related traits were often set in the same or adjacent chromosome regions. Usually a certain chromosomal region is related to the expression of a variety of characters and that the relationship between genes within the same section depends on the traits (Li *et al*., 2005; Tan *et al*., 2008; Zia-ul-Qamar *et al*., 2012). These genes or QTLs in the same section are related to several characters, which might be a pleiotropic effect, or it may be that several genes/QTLs are closely linked in the same section. Meanwhile, QTLs for some traits have been found to show a trend of concentrated distribution on the chromosome, which may help regulation among genes. Besides, the pleiotropic effect or tight linkage that controls the heredity seat of various traits were considered to be the reason for the correlation among the traits (Jiang *et al*., 2004; Zhuang *et al*., 2002).

In conclusion, six QTLs conferring the traits including the number of tiller per plant, seed-setting rate and grain yield per plant have been detected for the first time, indicating that more information on QTLs could be found by using populations with different genetic backgrounds. It is important for an in-depth understanding of the genetic control of yield traits in rice and for future molecular marker assisted selection in rice breeding.

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