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QTL analysis of rice yield components at two different environmental circumstances

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Abstract

The 190 recombinant inbred lines were created by the single-seed descent method using 93-11 and Nippinbare rice varieties as parents. A genetic linkage map was made employing 202 SSR, CAPs, and STS markers. Applying composite interval mapping, we carried out quantitative trait loci (QTL) analysis at two different ecological sites (Sanya and Hefei) on 6 rice yield traits. The traits included panicle number per seed (PNP), total grains per plant (TGP), filled grain per plant (FGP), blighted grains per plant (BGP), seed rate per plant (SRP), as well as 1000-grains weigh per plant (TGW). A total of 33 QTLs were identified. The single trait QTLs ranged from 2 to 9, indicating the yield-related traits are controlled by multiple genes. 4 QTLs were detected in both sites, in which two of them (*qBGP-3* and *qTGP-10a*) detected twice with the contribution rate of 35.85% and 27.33%, respectively. 11 QTLs were pleiotropic, controlling up to 4 yield traits. As example, RM5493-RM458 on chromosome 8 control BGP, TGP, SRP and TGW.

Keywords: rice, yield components, quantitative traits loci, QTL stability, QTL pleiotropy.
Abbreviations: BGP_blighted grains per plant, Caps_cleaved amplified polymorphic sequence, CIM_composite interval mappings, DNA_deoxyribonucleic acid, DPS_data processing system, DUS_distinctness uniformity stability, FGP_filled grain per plant, G×E_genotype × environment interaction, LOD_logarithm of odds, PCR_polymerase chain reaction, PNP_panicle number per seed, QTL_quantitative trait loci, SRP_seed rate per plant, SSR_simple sequence repeat, STS_sequence-tagged site, TGW_1000-grains weigh per plant, TGP_total grains per plant.

Introduction

Rice yield and its relevant component factors are important agronomic traits that are controlled by multiple genes. Breeding researchers also concern the crop growing environment that can put the influent on the genotype. With the development of molecular markers and genetic linkage mapping, great convenience has been achieved for the agronomic traits studies such as the crop yield related QTL mappings. Numerous studies have showed that QTL mappings can reveal crop inheritance of yield traits. One way is to split a number of complex traits into a single genetic element, making it easy to find its location on certain chromosome or further to clone the gene to study its function related with improved crop yields and qualities. With rice genome mapping and sequencing being completed, researchers are still working hard on finding these genes for enhancing rice yield. Apart from major gene regulation, the rice yield-related traits can be affected by minor gene adjustment, while the environmental factors could also be a great impact on it.

Studies by some researchers (Xiao et al., 1996; Zhuang et al., 2002; Ma et al., 2004; Xu et al., 2008) were conducted using QTL analysis for yield-related traits in recombinant inbred lines. Nevertheless, most of these studies were done in the same site or environment. In this study, we conducted a QTL analysis for rice yield traits at two different ecological sites (Sanya and Hefei). Two varieties were chosen, 93-11 and Nipponbare as parental lines. These two recombinant inbred lines have both been completely sequenced and their production rates are quite contrasting. By constructing SSR molecular markers and composite interval mapping analysis, we expected to find an applicable yield component QTL to better learn the mechanism of rice yield-related traits.

Results

Construction of genetic linkage maps

By checking 693 pairs of primer set (659 pairs of SSR primers, and 34 pairs of STS and CAPs markers), 225 pairs of polymorphism primers were chosen. The selected primers were used to screen the parents 93-11 and Nipponbare, as well as 190 recombinant inbred lines for genotyping. Among them, 202 pairs of primers constantly revealed clear PCR products. These genotyping results were used to make a linkage map for polymorphic marker loci using Joinmap3.0 software. As shown in Fig 1, each chromosome contains about 17 markers. The linkage map covers 1640.25cM of an entire rice genome. The average genetic distance for these markers was 8.12 cM that meets the requirements of QTL mapping.

Correlation analysis for yield-related traits in the parents and their progenies

The results of measured yield-related traits from both sites of Sanya and Hefei showed a continuous distribution of RIL population among the 6 rice yield-related traits (PNP, TGP, FGP, BGP, SRP, TGW). Only spike (SRP) in Sanya showed unidirectional segregation. The rest of characters in both sites clearly showed the transgressive segregation, suggesting that rice yield-related traits act as a quantitative trait controlled by multiple genes.

Table 1. Yield component traits in multiple locations.

Trait	Parents				RIL population			
	Nipponbare		93-11		Average		Range	
	Sanya	Hefei	Sanya	Hefei	Sanya	Hefei	Sanya	Hefei
PNP	19.33±3.28	13.00±0.88	4.00±0.00	8.00±1.73	7.14±0.19	6.37±0.13	3.33-18.00	3.50-13.00
FGNP	72.67±19.93	294.67±20.67	459.5±3.50	1045.67±251.86	577.96±19.66	624.94±21.24	18.67-1540.00	83.00-1872.00
BGP	789.33±54.78	120.67±21.73	21.5±8.50	152.33±36.86	259.04±21.43	364.74±14.21	175.00-1903.00	42.00-1278.00
TGP	862±72.30	415.33±42.31	481±5.00	1198±265.97	837.01±25.07	989.67±25.84	328.00-2285.00	332.67-2426.33
SRP	8.43±1.62	71.41±2.32	95.53±1.72	86.89±3.04	71.06±1.64	62.87±1.13	2.13-96.75	9.73-93.56
TGW	23.74±0.34	25.37±0.80	31.32±0.04	31.6±0.20	26.52±0.28	25.94±0.23	14.04-34.87	17.93-33.53

Date were reported as means ± SD.

Table 2. The correlation analysis of yield component traits.

Site	Trait	PNP	FGP	BGP	TGP	SRP	TGW
Sanya	PNP	1.00					
	FGP	0.31*	1.00				
	BGP	0.47*	-0.26*	1.00			
	TGP	0.64**	0.56**	0.65**	1.00		
	SRP	-0.19	0.57**	-0.82**	-0.25*	1.00	
	TGW	0.03	-0.14	0.08	-0.04	-0.12	1.00
Hefei	PNP	1.00					
	FGP	0.35*	1.00				
	BGP	0.37*	0.02	1.00			
	TGP	0.48*	0.84**	0.57**	1.00		
	SRP	-0.04	0.57**	-0.72**	0.07	1.00	
	TGW	-0.08	-0.06	-0.01	-0.05	-0.05	1.00

Significance levels: *$P \leqslant 0.05$, ** $P \leqslant 0.01$.

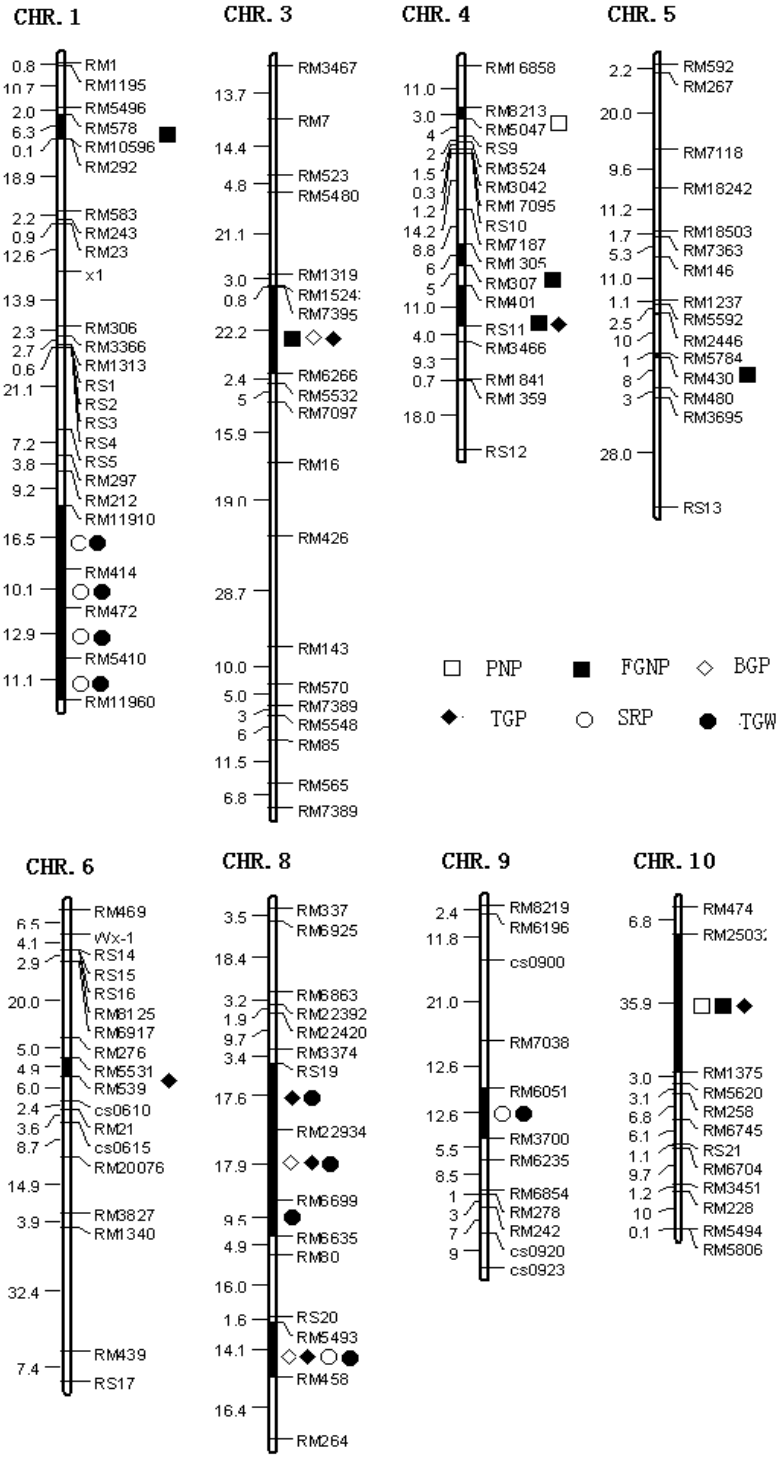

Fig 1. The QTL localization on chromosome of yield component traits.

Table 3. The QTL analysis of yield component traits

Trait and QTL	Chromosome	Interval	Site	LOD Value	Variation explained/%	Additive effect	Positive allele
PNP							
qPNP-4	4	RM8213-RM5047	Sanya	2.58	10.33	0.98	j
qPNP-10	10	RM25032-RM1375	Sanya	2.54	14.95	-2.23	i
			Hefei	2.86	20.77	-1.59	i
FGP							
qFGNP-1	1	RM578-RM10596	Sanya	2.67	8.13	-74.78	j
qFGNP-3	3	RM7395-RM6266	Hefei	5.41	18.89	335.26	i
qFGNP-4a	4	RM1305-RM307	Hefei	2.54	7.17	-79.77	j
qFGNP-4b	4	RM401-RS11	Hefei	2.55	8.66	-86.55	j
qFGNP-5	5	RM5784-RM430	Hefei	2.93	7.2	-100.41	j
qFGNP-10	10	RM25032-RM1375	Hefei	4.37	24.41	-290.06	j
BGP							
qBGP-3	3	RM7395-RM6266	Sanya	9.05	35.85	664.81	j
			Hefei	2.58	19.94	219.15	i
qBGP-8a	8	RM22934-RM6699	Hefei	4.24	20.02	222.06	i
qBGP-8b	8	RM5493-RM458	Hefei	2.7	19.55	319.3	i
TGP							
qTGP-3	3	RM7395-RM6266	Sanya	3.41	22.43	359.12	j
			Hefei	3.4	19.83	401.98	i
qTGP-4	4	RM401-RS11	Hefei	2.56	9.78	-111.79	j
qTGP-6	6	RM5531-RM539	Sanya	2.83	13.7	178.6	j
qTGP-8a	8	RS19-RM22934	Sanya	3.23	23.86	401.94	j
qTGP-8b	8	RM22934-RM6699	Sanya	3.54	22.89	427.07	j
qTGP-8c	8	RM5493-RM458	Sanya	3.94	23.49	419.29	j
qTGP-10	10	RM25032-RM1375	Sanya	5.09	27.33	-366.64	i
			Hefei	3.64	24.13	-344.62	j
SRP							
qSRP-1a	1	RM11910-RM414	Sanya	2.53	10.15	-7.22	j
qSRP-1b	1	RM414-RM472	Sanya	2.88	11.83	-7.65	j
qSRP-1c	1	RM472-RM5410	Sanya	2.59	12.07	-7.58	j
qSRP-1d	1	RM5410-RM11960	Sanya	2.52	9.9	-6.63	j
qSRP-8	8	RM5493-RM458	Sanya	5.64	29.52	-26.8	j
qSRP-9	9	RM6051-RM3700	Sanya	3.11	28.55	-23.76	j
TGW							
qTGW-1a	1	RM11910-RM414	Hefei	2.57	9.79	-0.07	j
qTGW-1b	1	RM414-RM472	Hefei	2.77	12.28	-0.08	j
qTGW-1c	1	RM472-RM5410	Hefei	2.63	11.66	-0.07	j
qTGW-1d	1	RM5410-RM11960	Hefei	2.54	10.37	-0.07	j
qTGW-8a	8	RS19-RM22934	Sanya	3.02	15.77	-2.23	j
qTGW-8b	8	RM22934-RM6699	Sanya	4.01	19.08	-2.8	j
qTGW-8c	8	RM6699-RM6635	Sanya	3.53	17.51	-2.61	j
qTGW-8d	8	RM5493-RM458	Hefei	5.6	29.01	-0.27	j
qTGW-9	9	RM6051-RM3700	Hefei	3.11	28.01	-0.24	j

Both Variation explained and Addtive effect were estimated from means trait values of individual RILs in the individual location.
i 93-11 allele, j Nipponbare allele.

Table 4. The QTLs detected by multiple frequency.

	QTL detected in two sites
PNP	*qPNP-10*
BGP	*qBGP-3*
TGP	*qTGP-3*、*qTGP-10*

Table 5. The QTLs with pleiotropic.

Chromosome	Pleiotropic Locus	Character
1	RM11910-RM414	SRP 、TGW
1	RM414-RM472	SRP 、TGW
1	RM472-RM5410	SRP 、TGW
1	RM5410-RM11960	SRP 、TGW
3	RM7395-RM6266	PNP 、FGNP 、BGP
4	RM401-RS11	FGNP 、TGP
8	RS19-RM22934	TGP 、TGW
8	RM22934-RM6699	BGP 、TGP 、TGW
8	RM5493-RM458	BGP 、TGP 、SRP 、TGW
9	RM6051-RM3700	SRP 、TGW
10	RM25032-RM1375	PNP 、FNGP 、TGP

The gene recombination can generate positive, or negative transgressive segregation (Table 1).

The 93-11 parent revealed a higher value than Nipponbare for PNP, FGP, BGP, TGP (in Hefei), and for SRP (in Sanya). Nipponbare exhibited a higher value than 93-11 for FGP, BGP, TGP (in Hefei) and for PNP, SRP (in Sanya). It was noticed that the number given for SRP was extremely small in Sanya. TGW for both varieties revealed similar value at both sites, although Nipponbare grown in Hefei was 10% more that in Sanya. Comparing the results in these two locations in Table 1, it clearly showed that the numbers given for these yield-related traits are quite different both from parental and from this recombinant inbred, suggesting that environmental factors such as light and temperature may play a big impact on rice yield.

Correlation analysis showed that yield-related trait TGP has relative significant positive correlation to PNP in Hefei, and extremely significant positive correlation with PNP in Sanya. It also shows extremely significant positive correlation with FGP and BGP at both sites. The result might suggest that these three yield-related traits are less affected by the environment. Meanwhile, SRP at both locations also has significant positive correlation with FGP, and BGP.

The yield-related QTL positioning and analysis

Based on the phenotypic values, the genotypes and the completed linkage map, the yield-related trait QTLs for these inbred lines were analyzed in both sites using the method for composite interval mappings. 33 QTLs were localized, for which single trait QTL varies from 2 to 9 (Table 3 and Fig 1).

For controlling the panicle numbers per plant (PNP), two QTLs were detected among the two different sites. These two QTLs are located on separated chromosomes. Their LOD values are 2.54 ~ 2.86. The contribution rates ranged from 10.33% to 20.77%. The additive effects ranged from -2.23 to 0.98. Both QTLs were detected in samples from Sanya, while in the samples from Hefei, only one QTL could be detected. One large detectable position is *qPNP-10* from 93-11, located in the range of RM25032-RM1375 on chromosome 10. The *qPNP-10* gene contribution rate is about 20.77%.

For controlling the filled grains per plant (FGP), two QTLs were detected from two different sites. These two QTLs are located on five chromosomes. Their LOD values are 2.54 ~ 5.41. The contribution rates were ranged from 7.17% to 24.41%. The additive effects ranged from -290.06 to 335.26. Five QTLs were detected in samples from Hefei, while only one was from Sanya. One large detectable position was *qFGNP-10* from Nipponbare, located in the range of RM25032-RM1375 on chromosome 10. The *qFGNP-10* gene contribution rate is about 24.41%.

For controlling the blighted grains per plant (BGP), three QTLs were detected from two different sites. The three QTLs are located on two chromosomes. The LOD values are 2.58 ~ 9.05. The contribution rates are ranged from 19.55% to 35.85%. The additive effects ranged from 219.15 to 664.81. Three QTLs were detected in samples from Hefei, while only one was detected from Sanya. The *qBGP-3* from Nipponbare and *qBGP-8a* from 93-11 are the large detectable sites, located between RM7395-RM6266 of chromosome 3 and RM22934-RM6699 of chromosome 8, respectively. The contribution rate for *qBGP-3* from Nipponbare was about 35.83%, while the contribution rate for *qBGP-8a* from 93-11 was about 20.92%.

For controlling the total grains per plant (TGP), Seven QTLs were detected from two different sites. These seven QTLs are located on five chromosomes. The LOD value are 2.56 ~ 5.09. The contribution rates are ranged from 9.78% to 27.33%. The additive effects ranged from -366.64 to 427.07. Among these seven QTLs, three were detected in samples from Hefei, and six were detected from Sanya. The five large detectable sites were *qTGP-3*, *qTGP-8a*, *qTGP-8b*, *qTGP-8c* and *qTGP-10*. They were located in RM7395-RM6266, RS19-RM22934, RM22934-RM6699, RM5493- RM458 and RM25032-RM137 intervals of chromosome 3, 8 and 10, respectively. Apart from gene *qTGP-10* which originated from 93-11, the rest of genes were all from Nipponbare. The contribution rates were 22.43%, 23.86%, 22.89%, 23.49% and 27.33%, respectively.

For controlling the spikelet fertility (SRP), six QTLs were detected from two different sites. The six QTLs were located on three chromosomes. The LOD values were 2.52 ~ 5.64. The contribution rates ranged from 9.9% to 29.52%. The additive effects ranged from -26.80 to -6.63. Six QTLs were all detected from Sanya. Two large detectable sites are *qSRP-8* and *qSRP-9* both originated from Nipponbare. The *qSRP-8* located in the range of RM5493-RM458 on chromosome 8 and *qSRP-9* located in the range of RM6051-RM3700 on chromosome 9. The contribution rates were 29.52% and 28.55%.

For controlling the grain weight per plant (TGW), nine QTLs were detected from two different sites. The nine QTLs were located on three chromosomes. The LOD values were 2.54 ~ 5.60. The contribution rates ranged from 9.79% to 29.01%. The additive effects ranged from -2.80 to -0.07. Among the nine QTLs, six were detected in samples from Hefei, and three were detected from Sanya. Two large detectable sites *qTGW-8* and *qTGW-9* both originated from Nipponbare. The *qTGW-8* is located between RM5493-RM458 on chromosome 8, and the *qTGW-9* is located between RM6051-RM3700 on chromosome 9, respectively. The contribution rates were 29.01% and 28.01%.

Table 4 shows four yield-related QTLs that were detected at both sites. Among them, *qPNP-10* controls PNP at the contribution rate of 20.77%, *qBGP-3* controls BGP at the contribution rate of 35.85%. Both the *qTGP-3a* and *qTGP-10a* control TGP at the contribution rate of 22.43% and 27.33%, respectively. The high rates suggest that all of them showed a dominant position effect. These three yield-related traits (PNP, BGP, TGP) were stable and consistent both at sites of Hefei and Sanya.

By comparing the genetic marker locations on chromosome for these yield-related traits, we found 11 intervals that control multiple traits. For example, there are 4 intervals on chromosome 1; 3 intervals on chromosome 8; while only 1 interval locates on each chromosome 3, 4, 9, and 10 (Table 5). Among these locations, RM5493-RM458 interval on chromosome 8 controls BGP, TGP, SRP and TGW; RM7395-RM6266 interval on chromosome 3 controls PNP, FGP and BGP; RM22934-RM6699 interval on chromosome 8 controls BGP, TGP and TGW; RM25032-RM1375 interval on chromosome10 controls PNP, FGP and TGP. It has been noticed that SRP, TGP and TGW were jointly controlled by multiple intervals.

Discussion

Studies by Shen (Shen et al., 2000) showed that interactions of G × E during crop growth were greatly correlated with local temperature, sunshine and rainfall. Therefore, the climate factors are important elements on G × E interaction. In this study, we also found that the climate factors had a significant impact on the yield related traits. Among the six yield-related traits, five (PNP, FGP, BGP, TGP and SRP) exhibited certain degree of variation at these two sites (Table 1). Compared with the Hefei site, rice grown in Sanya has better rates of PNP, SRP and TGW, while it has low rates of FGP, BGP and TGP.

Plant quantitative characters can be affected by surrounding environments and the measuring results for the same trait among the various mapping population (Wei et al., 2009) or the same group at different growing stages (Jansen et al., 1995) can also be variable. Nevertheless, the major QTL factors should be less affected by environments, and can always be detected under different circumstances. To test this hypothesis, we checked all QTLs that are available, and found four yield-related QTLs are detectable at both sites. Loci *qPNP-10*, *qTGP-10* on chromosome 10 were stable markers as they were repeatedly detectable. These loci may be related to gene *OsiICK6* for SRP (Yang et al., 2011). Locus *qBGP-3* controlling BGP and *qTGP-3* controlling TGP were detected at same time. Both of them were located on chromosome 3. Interestingly, Mei (Mei et al., 2006) also detected the main effecting locus qSNP-3 which controls rice spikelet numbers in the vicinity region of chromosome 3.

The QTLs of yield-related traits tends to be located in the adjacent or the identical regions on the same chromosome (Hittalmani et al., 2003; Bao et al., 1999). We localized 11 interval sites of yield-related traits on 6 chromosomes. Among them, each of the interval RM7395-RM6266 on chromosome 3 and the interval RM25032-RM1375 on chromosome10 controlled 3 yield-related traits. We also noted that the QTLs of other yield-related traits, including PNP, BGP and TGP can be easily detected in the same intervals. The intervals RM22934-RM6699 and RM5493-RM458 on chromosome 8 control 3-4 yield-related traits. The correlation coefficients of BGP and TGP, FGP and TGP run up to 0.65 and 0.84, indicating the existence of the gene linkage or a pleiotropic phenomenon.

In this study, 33 QTLs of six yield-related traits were positioned at two environmental circumstances. Comparing with previous high-density genetic maps (Harushima et al., 1998; Causse et al., 1994; Mc-Couch et al., 2002), we found that qTGP-3 with contribution rate at 22.34% was more consistent with previous studies (Xing et al., 2001; Li et al.,1997; Xiao et al.,1995; Yu et al.,1997; Cao et al., 2003). The *qTGP-8a* with contribution rate at 23.86% was also more consistent with the previous reports (Lin et al.,1996; Daisuke et al., 2010); *qSRP-8* with contribution rate at 29.52% was more consistent with Cao (Cao et al., 2003); *qTGW-8d* with contribution rate at 29.01% was more consistent with previous studies (Cui et al., 2003; Xiao et al.,1995; Yu et al., 1997); *qSRP-9* with contribution rate at 28.55% was more consistent (Li et al., 2002); *qTGW-9* with contribution rate at 28.01% was more consistent with previous study (Cui et al., 2003; Xie et al., 2008); *qFGP-10* with contribution rate at 24.41% with was more consistent (Yu et al., 1997); *qTGP-10* with contribution rate at 27.33% was more consistent with these previous studies (Li et al., 1997; Yu et al.,1997; Cao et al., 2003 and Li et al., 2002). Among these, we found multiple intervals on chromosome 8 closely associated with rice yield-related traits that worth to pay more attention in future studies.

Materials and Methods

Plant materials

The materials used were the recombinant inbred lines produced by F_2 hybrids of *indica* 93-11 (Yang-dao 6 hao) and *japonica* Nipponbare. The recombinant inbred lines (190 lines) of 12 high-generation were generated with the single seed descend method. The late-maturing *indica* variety 93-11, with good leaf shape and grain quality, was bred in Jiangsu Province. The pre-maturing variety *japonica* Nipponbare that also gives good grain quality, was bred in agricultural test stations in Aichi, Japan during 1950s. Both varieties have the completed genome sequence.

Field test and plant traits analysis

The parents of 93-11 and Nipponbare and their 190 recombinant inbred lines were planted on the experimental fields at Anhui Academy of Agricultural Sciences (AAAS), Rice Research Institute in Hefei, China (32.21 N. Lat., 117.25 E. Long.) in May, 2012. Each line was planted for two rows, and each row had 10 grains. The row space was about 13.5 cm × 23.5 cm. All experiments were repeated twice with proper paddy field management. Mature seeds from each plant were harvested separately then the seeds were examined after drying. These seeds were also planted in same setting at AAAS South Rice Breeding Base in Sanya County, Hainan Province, China (18.15 N. Lat, 109.30 E. Long.).

The analysis was done by taking 3 plants each line. Each plant separately assessed for panicles, filled grains, blighted grains, total seeds, seed setting rate and 1000-grains weight. The value was taken by average of 3 plants. The measuring method was following the test guidance of New Varieties of Plants DUS test guidelines in China (2003): rice (*Oryza sativa* L.).

Construction of molecular linkage map

Genomic DNA was extracted from plant leaf with CTAB method (Rogers et al. 1988). Total of 659 pairs of SSR markers and 34 pairs of STS and CAPs markers were selected for parental polymorphism. Some of these markers are routinely been used in this lab. Among them, 202 markers showed stable amplifications. Therefore, these stable markers were selected for genotyping analysis of 190 inbred lines.

PCR with 10μL reaction mixture was used for SSR analysis. The reaction contained 3μL of template DNA (2 ng μL^{-1}), 0.25μL of forward and reverse primers (0.25 μmol L^{-1}), 0.4μL of dNTPs (2.5 mmol L^{-1}), 1μL of 10 × Buffer (with Mg^{2+}), 0.2μL of *Taq* DNA polymerase (5 U μL^{-1}) and 4.9μL of ddH_2O. The cycle setting was 34 cycle at 94ºC for 5 min; 35 cycles at 94 ºC for 1 min, 55 ºC for 1 min, 72 ºC for 1 min, and 1 cycle at 72 ºC for 7 min. The PCR products run on 8.0% w/v polyacrylamide gels or 3% w/v agarose gels. Construction of linkage maps were done with Joinmap 3.0 software.

Data analysis and QTL mapping

The distribution of the target characters in RIL population was analyzed by DPS software, and the correlation between each trait was analyzed by Excel 2007. The related QTL of RVA profile characteristic values were detected by MapQTL5.0 software. The values considered composite interval mappings (CIM) with phenotyping, genotype and linkage map of the recombinant inbred lines. Then, the phenotypic explainable variation of each QTL contribution was calculated. LOD value of 2.5 was set as the threshold. The corresponding QTL was named by Mc-Couch method (Mc-Couch et al., 1997).

Conclusion

In this study, the rice yield QTL was analyzed under two different environments. The main effect QTL (*qBGP-3*) and yield traits pleiotropic loci (RM5493-RM458) have been positioned. The QTL analysis in different environments can mitigate the effects of environmental factors to find a stable, major QTL. The QTL as a broader range could not be directly applied. The near isogenic lines of rice yield-related traits are

currently being constructed. Then, these major QTLs might be cloned. It hoped that the results of this study could provide more of the target gene in rice molecular breeding.

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