RESEARCH ARTICLE

QTL mapping and correlation analysis for 1000-grain weight and percentage of grains with chalkiness in rice

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Abstract

The study of 1000-grain weight (TGW) and percentage of grains with chalkiness (PGWC) is very important in rice. In this study, a set of introgression lines (ILs), derived from Sasanishiki/Habataki with Sasanishiki as the recurrent parent, were used to detect correlations and quantitative trait loci (QTL) on TGW and PGWC in two different environments. Phenotypic correlation analysis showed that there was no significant correlation between TGW and PGWC in both environments, which indicated that the linkage of TGW and PGWC traits could be broken via suitable population. A total of 20 QTL were detected in both environments, nine QTL for 1000-paddy-grain weight (PTGW), five QTL for 1000-brown-grain weight (BTGW) and six QTL for percentage of grains with chalkiness (PGWC). Moreover, five QTL, *qPTGW3*, *qPTGW8.2*, *qPTGW11.1* for PTGW and *qPGWC1.1*, *qPGWC1.2* for PGWC, were stably expressed in both environments. Phenotypic values were significantly different ($P < 0.01$) between the introgression lines carrying these five QTL alleles and the genetic background parent, Sasanishiki. The introgression lines carrying these QTL also represent a useful genetic resource in the context of rice yield and quality improvement via a design-breeding approach.

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Introduction

Rice is staple food for more than half of the world's population (Marathi *et al.* 2012). Along with improvements in the standard of living, the demand for superior grain quality with high grain yield is increasingly becoming a priority issue in many rice producing areas of the world (Juliano *et al.* 1990; Hao *et al.* 2009; Nelson *et al.* 2011). As one of the most important yield components, grain weight plays an important role in the formation of rice yield; an increase in 1000-grain weight (TGW) will increase the rice yield (Bai *et al.* 2011). Percentage of grains with chalkiness (PGWC) is an important quality component of rice, as it has a profound influence on eating and milling qualities (Cheng *et al.* 2005; Yamakawa *et al.* 2007). High chalkiness is a major problem in many rice producing areas of the world, especially in hybrid rice production countries. How to improve TGW and decrease PGWC simultaneously is a big challenge for researchers. Some studies have begun to analyse TGW and PGWC, and showed that TGW is related to PGWC (Kang *et al.* 2005; Fujita *et al.* 2007). Although these studies present useful information in understanding of TGW and PGWC, it is difficult to understand the relationship between TGW and PGWC thoroughly. This is because these QTL and relationship analysis of TGW and PGWC were all based on single gene (QTL) level, which limited the understanding of the two important traits. Therefore, the analysis of TGW and PGWC at whole genome level is necessary.

As a permanent mapping population, inbred lines (ILs) are ideally suited for QTL identification (Kubo *et al.* 2002; Bian *et al.* 2013) and widely used for QTL detection, including grain weight or rice chalkiness (Bian *et al.* 2010; Guo *et al.* 2011). However, comprehensive studies of relationship between TGW and PGWC using ILs are lacking. Here, we selected ILs from the backcross progeny of *indica* cultivar, Habataki, as the donor parent, and a *japonica* cultivar, Sasanishiki, as the recurrent parent. By using these plant materials, we mapped QTL controlling TGW and PGWC and analysed the relationship between TGW and PGWC at whole genome level. The objectives of this study were to detect nonenvironment-specific QTL for TGW and PGWC and to elucidate the relationship between the grain weight and

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Keywords. rice; 1000-grain weight; percentage of grains with chalkiness; correlations; quantitative trait loci.

Table 1. Variation of PTGW, BTGW and PGWC between two parents and among the ILs population.

Trait[a]	Environment[b]	Parents		ILs population		
		Sasanishiki	Habataki	Mean	Min.	Max.
PTGW (g)	2011HN	24.70	25.10	24.54	21.20	27.00
	2012NC	21.80	21.90	22.26	20.50	23.90
BTGW (g)	2011HN	20.10	18.90*	19.18	16.80	21.90
	2012NC	17.90	14.70**	18.10	16.10	19.70
PGWC	2011HN	0.23	0.78**	0.59	0.28	1.00
	2012NC	0.30	0.27	0.47	0.16	0.99

[a]PTGW, 1000-paddy-grain weight; BTGW, 1000-brown-grain weight; PGWC, percentage of grains with chalkiness; [b]2011HN, 2011Hainan; 2012NC, 2012Nanchang; *, ** indicate 5% and 1% significant level, respectively.

chalkiness, which would be helpful in marker-assisted selection (MAS) of high yield and low chalkiness rice varieties and map-based cloning of desirable QTL.

Materials and methods

Plant materials

We selected Sasanishiki, an elite *japonica* variety, as the recipient, and Habataki, an *indica* elite variety, as donor. The development of ILs was described previously by Ando *et al.* (2008). Thirty-seven lines (SL401–SL437) were selected out of all the 39 ILs, and renumbered as IL01-IL37 in this research. Each contains a major segment inherited from Habataki, along with a variable number of minor segments in Sasanishiki genetic background, and the selected ILs population covered most of the genome, only one small region at the middle of chromosome 4 (defined by Bb38P21a), one small region at the middle of chromosome 8 (defined by RM1148), one small region at the distal end of the long arm of chromosome 10 (defined by RM7492), and one segment of chromosome 12 (between RM6998 and RM2197) are not represented.

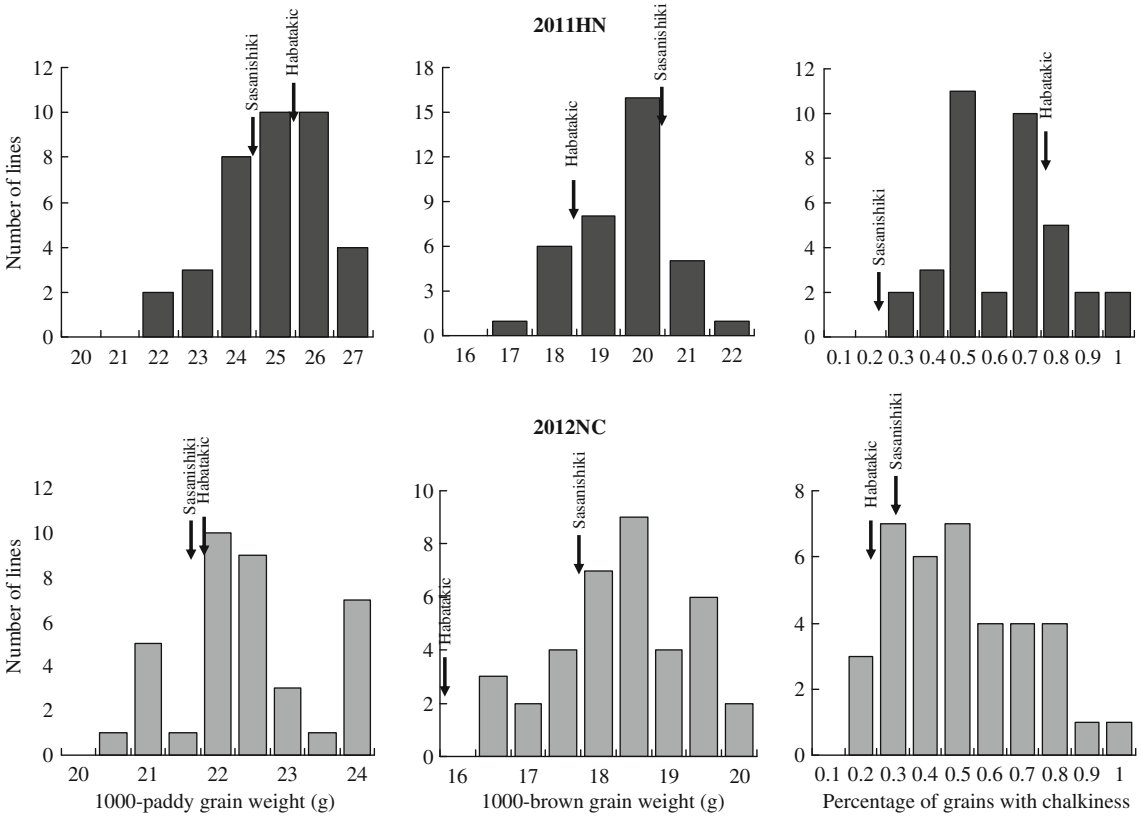

Figure 1. Distribution of 1000-paddy grain weight (PTGW), 1000-brown grain weight (BTGW), and percentage of grains with chalkiness (PGWC) in the ILs population.

Table 2. Correlation coefficients between PTGW, BTGW and PGWC in 2011HN and 2012NC.

Traits[a]	PTGW (g)		BTGW (g)	
	2011HN[b]	2012NC	2011HN	2012NC
PGWC	0.203	0.039	−0.067	−0.066

[a]PTGW, 1000-paddy-grain weight; BTGW, 1000-brown-grain weight; PGWC, percentage of grains with chalkiness; [b]2011HN, 2011Hainan; 2012NC, 2012Nanchang.

Field trials

The ILs population and the two parents, Sasanishiki and Habataki, were sown at Tengqiao, Hainan province, China, in autumn 2011 (2011HN) in a completely randomized block design with two replications. Each plot consisted two rows separated by 30 cm, with each row consisting of 10 plants, each separated from its neighbour by 20 cm. Crop management followed normal procedures for rice.

The same materials were also sown on 19 May at Jiangxi Agricultural University, Nanchang, China in 2012 (2012NC). Their seedlings were transplanted on 20 June and were grown under natural conditions in a completely randomized block design with two replications. Each plot consisted four rows separated by 30 cm, with each row consisting of 10 plants, each separated from its neighbour by 20 cm. Crop management followed normal procedures for rice.

Data collection

In 2011HN, the grains of eight plants from the middle of each plot were bulked and air-dried at maturity, and from these, a sample of fully filled grains was dried in an oven at 30°C for 24 h, after which they were dehulled to determine PGWC. The weight of three samples of 100 paddy and brown rice grains per entry was used to estimate 1000-paddy-grain weight (PTGW) and 1000-brown-grain weight (BTGW), and the values were averaged and used as the measurements for introgression lines and their parents. The

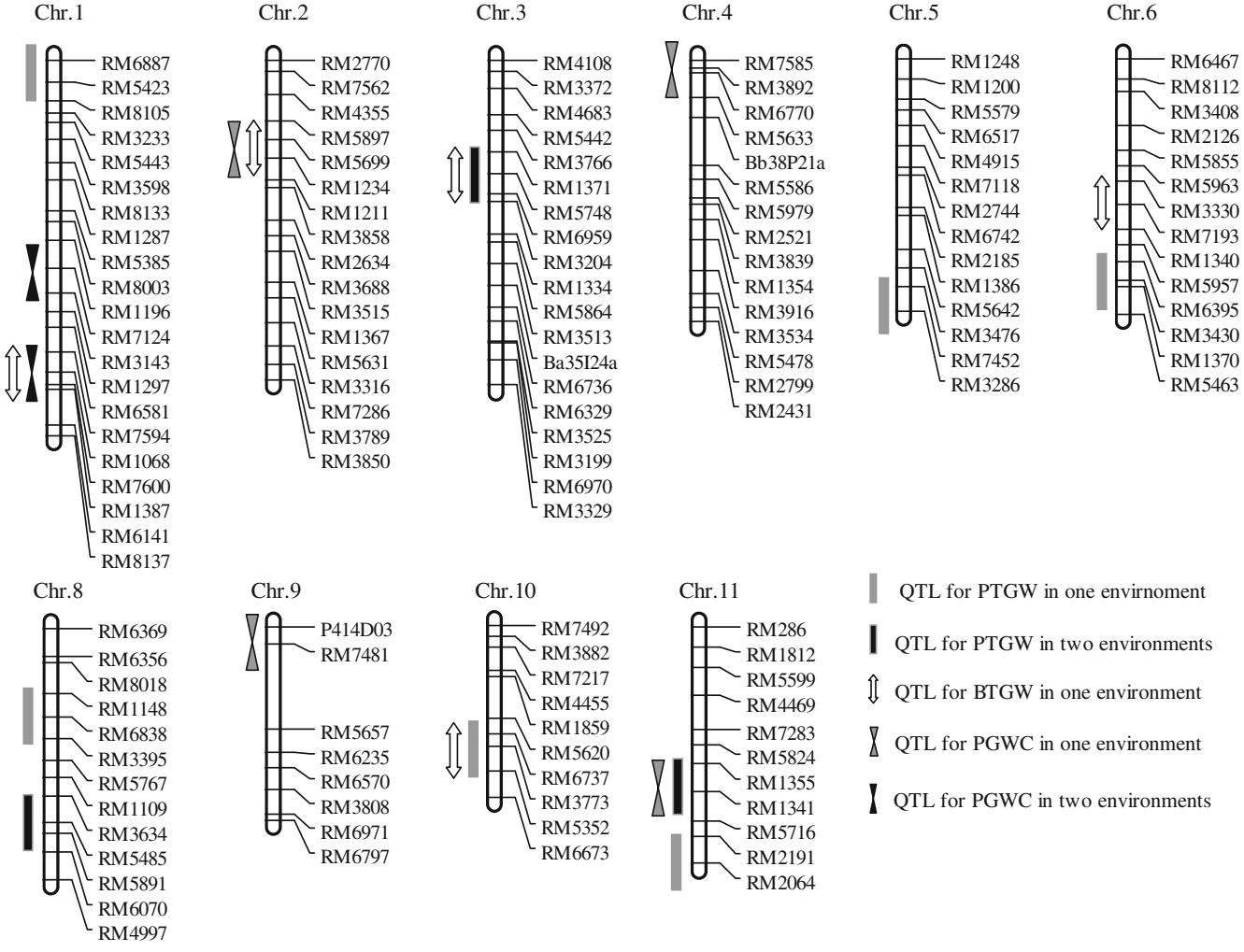

Figure 2. Chromosomal locations of QTL detected for 1000-paddy-grain weight (PTGW), 1000-brown-grain weight (BTGW), and percentage of grains with chalkiness (PGWC).

measurement of PGWC was carried out as follows: one hundred brown rice grains of each entry were randomly selected, the chalky grains, including those with a white belly, white core and white back, were counted by visual assessment. All measurements were replicated twice. The same evaluation of PGWC, PTGW and BTGW was calculated as above in 2012NC.

Data analysis

To explore PTGW, BTGW and PGWC gene expression in different environments, a QTL analysis was carried out using QTL IciMapping ver. 2.2 Mapping software (Li *et al.* 2008), applying a threshold LOD of 3.0, which was used for non-ideal or ideal ILs population QTL detection (Li *et al.* 2007; Wang 2009). QTL nomenclature followed the recommendations of McCouch and CGSNL (Rice Genetics Cooperative 2008). The criterion to select a stable QTL under study is as follow: if both the 2011HN and 2012NC predict the presence of a QTL at a similar location (located near the same maker), it can be considered to harbour one QTL. Correlation analysis was performed to detect association between PTGW, BTGW and PGWC based on the data of ILs population using SPSS software.

Results

Phenotypic variation

Table 1 shows the phenotypic variation of the ILs and their parents for PTGW, BTGW and PGWC across the two environments. Sasanishiki and Habataki showed differences for BTGW and phenotypic values of Sasanishiki for BTGW were much higher than those of Habataki in both environments. The PTGW trait of the two parents showed no significant differences in both environments. However, PGWC of Habataki was higher than that of Sasanishiki in 2011HN, but lower in 2012NC, indicating that rice chalkiness is readily influenced by environment (table 1).

The PTGW, BTGW and PGWC in ILs population segregated continuously and fit a normal distribution in both environments (figure 1), suggesting that the characters studied were quantitative inheritance. Transgressive segregants, with a higher or lower value than those of the parents, were also observed for all the traits (table 1), which suggested that the set of ILs was suitable for QTL analysis.

Correlations between PTGW, BTGW and PGWC

Correlations between PGWC and PTGW, BTGW are shown in table 2. The results suggested that, the ILs population used in present study, PGWC was positively correlated with PTGW, negatively correlated with BTGW in both environments, but the correlation does not reach significant level ($P = 0.01$ or 0.05), the levels of correlation were very low (table 2).

QTL detection

QTL for PTGW: A total of nine QTL were identified on seven linkage groups for PTGW across the two environments (figure 2). The QTL *qPTGW3*, *qPTGW8.2* and *qPTGW11.1* were consistently detected across both 2011HN and 2012NC, whereas the remainder QTL were specific to one environment or the other. The positive alleles for PTGW came from Habataki for *qPTGW6*, *qPTGW8.1*, *qPTGW8.2*, *qPTGW11.1* and *qPTGW11.2*, except for the *qPTGW1*, *qPTGW3*, *qPTGW5* and *qPTGW10*. The variance explained by individual QTL was 5.50 ∼ 16.00% because of the large number of QTL identified for the trait.

QTL for BTGW: Five chromosomes were associated with BTGW QTL (figure 2). The Sasanishiki alleles were associated with greater BTGW for all loci. For example, the QTL at locus RM7600 on chromosome 1, with allele from its donor parent Sasanishiki, accounted for 9.44% of the phenotypic

Main-effect QTL	SSR loci in the substituted segments	Phenotypic values of grain weight and chalkiness of parents and target ILs across the two environments	
		2011HN	2012NC
qPTGW3	RM5442 RM3766 RM1371 **RM5748** RM6959	1000-paddy grain weight (g)	
IL09	■ ■ ■ ■ ■	22.700**	20.500**
Sasanishiki	□ □ □ □ □	24.700	21.800
qPTGW8.2	RM3634 RM5485 **RM5891** RM6070 RM4997	1000-paddy grain weight (g)	
IL27	■ ■ ■ □ □	27.000**	23.900**
Sasanishiki	□ □ □ □ □	24.700	21.800
qPTGW11.1	RM1355 **RM1341** RM5716 RM2191 RM2064	1000-paddy grain weight (g)	
IL35	■ ■ ■ ■ □	26.800**	23.900**
Sasanishiki	□ □ □ □ □	24.700	21.800
qPGWC1.1	RM8003 RM1196 **RM7124** RM3143 RM1297	Percentage of grains with chalkiness	
IL02	■ ■ ■ ■ ■	1.000**	0.990**
Sasanishiki	□ □ □ □ □	0.230	0.300
qPGWC1.2	RM7594 RM1068 **RM7600** RM1387 RM6141	Percentage of grains with chalkiness	
IL03	■ ■ ■ □ □	0.975**	0.850**
Sasanishiki	□ □ □ □ □	0.230	0.300

Figure 3. Phenotype analyses between the recurrent parent Sasanishiki and target ILs carrying each of five main-effect QTLs alleles in 2011HN and 2012NC. The *t*-test was conducted between Sasanishiki and the target IL; 2011HN, 2011Hainan; 2012NC, 2012Nanchang; ** indicated 1% significant level.

variation. All of the five QTL were detected in only one environment, The variance explained by individual QTL was 6.90 ~ 14.59%.

QTL for PGWC: Six QTL *qPGWC1.1, qPGWC1.2, qPGWC2, qPGWC4, qPGWC9* and *qPGWC11* were identified for PGWC in the ILs population. The phenotypic variation explained by each QTL ranged from 6.49 to 18.04%. The Habataki alleles contributed higher PGWC value at all loci. Of these QTL, *qPGWC1.1* and *qPGWC1.2* were constantly detected in both environments.

Stable QTL analysis

Of the 20 QTL underlying PTGW, BTGW and PGWC traits, five QTL, *qPTGW3*, *qPTGW8.2*, *qPTGW11.1* for PTGW and *qPGWC1.1*, *qPGWC1.2* for PGWC, were stably expressed in both environments. To confirm gene action of the five main-effect QTL identified in this study, the ILs carrying these QTL (genes) were used to investigate the target traits. In IL35, the Habataki chromosomal segment carrying *qPTGW11.1* (defined by markers RM1355 and RM2191) was substituted in the genetic background of Sasanishiki. The *t*-test analysis showed that the IL35 increased PTGW significantly compared to Sasanishiki across two environments (figure 3). A similar situation pertains for *qPTGW8.2* (IL27), *qPGWC1.1* (IL02) and *qPGWC1.2* (IL03), where the presence of the Habataki alleles increased PTGW, PGWC and PGWC respectively in both environments.

QTL analysis also indicated that *qPTGW3* was another important PTGW QTL, the increasing effect of Sasanishiki allele on PTGW was detected in both environments. The PTGW performance of the IL09 (in which the only major Habataki segment present is the *qPTGW3* segment defined by RM3766 and RM6959) showed that the Habataki *qPTGW3* allele reduced the trait across two environments (figure 3).

Discussion

QTL detection using Sasanishiki/Habataki ILs population

In this study, the two parents Sasanishiki and Habataki did not show significant differences for all the three traits in both contrast environments. However, nine, five and six QTL for PTGW, BTGW and PGWC respectively were successfully detected in both environments, indicating that the ILs population within the same *japonica* Sasanishiki were ideally suited for quantitative traits QTL identification. Among these QTL, most explained only a modest proportion of the phenotypic variance (table 3), confirming that ILs can eliminate the complicated genetic background noise and precisely estimate the location and the size of each individual QTL,

Table 3. QTL for PTGW, BTGW and PGWC in 2011HN and 2012NC.

Traits[a]	QTL	Chromosome	Marker	LOD value	Additive effect[b]	Variance explained (%)	Environment[c]
PTGW (g)	*qPTGW1*	1	RM6887	10.13	−1.61	14.37	2011HN
	qPTGW3	3	RM5748	5.88	−1.06	6.20	2011HN
				3.75	−0.89	8.45	2012NC
	qPTGW5	5	RM3286	6.28	−1.11	6.81	2011HN
	qPTGW6	6	RM1370	3.18	0.81	6.87	2012NC
	qPTGW8.1	8	RM6838	3.18	0.81	6.87	2012NC
	qPTGW8.2	8	RM5891	7.49	1.09	12.94	2011HN
				3.41	0.80	13.23	2012NC
	qPTGW10	10	RM3773	10.78	−1.69	16.00	2011HN
	qPTGW11.1	11	RM1341	5.41	0.99	5.50	2011HN
				3.18	0.81	6.87	2012NC
	qPTGW11.2	11	RM2064	3.13	0.74	11.39	2012NC
BTGW (g)	*qBTGW1*	1	RM7600	3.20	−1.03	9.44	2011HN
	qBTGW2	2	RM5699	3.25	−0.79	6.90	2012NC
	qBTGW3	3	RM5748	4.88	−1.07	12.42	2012NC
	qBTGW6	6	RM7193	4.53	−1.28	14.59	2011HN
	qBTGW10	10	RM3773	5.02	−1.09	12.89	2012NC
PGWC	*qPGWC1.1*	1	RM7124	5.01	0.22	14.65	2011HN
				8.18	0.28	18.04	2012NC
	qPGWC1.2	1	RM7600	4.59	0.21	13.04	2011HN
				5.48	0.21	10.03	2012NC
	qPGWC2	2	RM5699	4.21	0.17	7.09	2012NC
	qPGWC4	4	RM7585	3.93	0.17	6.49	2012NC
	qPGWC9	9	P414D03	4.23	0.12	11.73	2011HN
	qPGWC11	11	RM1341	4.12	0.17	6.89	2012NC

[a]PTGW, 1000-paddy-grain weight; BTGW, 1000-brown-grain weight; PGWC, percentage of grains with chalkiness; [b]additive effect positive value indicated the increasing effects from Habataki; [c]2011HN, 2011Hainan; 2012NC, 2012Nanchang.

particularly small effect QTL. The results also suggested that grain weight and chalkiness traits investigated were polygenic phenomenon, this is according to the view of Mackill and Ni (2001). Therefore, pyramiding multiple genes (QTL) for grain weight and chalkiness is necessary in rice yield and quality molecular design breeding.

Comparison of QTL detected in this population with other researches

In all, 20 QTL for PTGW, BTGW and PGWC located on 10 of the 12 rice chromosomes were uncovered in this study (figure 2). Five major stable QTL were detected in both environments and most of them appeared to coincide with those of loci described in the literature (www.gramene.org). Thus, the chromosome 3 locus *qPTGW3* (between RM3766 and RM6959) maps to a similar location as does *gw3* (Guo *et al.* 2009), *qPTGW8.2* (between RM3634 and RM5891) are probably the same locus as *gw8.1* described by Bai *et al.* (2010), while *qPTGW11.1* (between RM1355 and RM2191) appears to be the same as the chromosome 11 locus *qTGW11.1* detected by Bian *et al.* (2010). However, as *qPGWC1.1* and *qPGWC1.2* have not been previously identified, we chose to detail its map location on chromosome 1, and showed that it cosegregated with RM7124 and RM7600 respectively. We are presently engaged in the identification of candidate genes for this QTL using large segregating population.

The potential use of these QTL

To find the favorable alleles of Habataki in Sasanishiki background, ILs were used to detect QTL controlling grain weight and chalkiness, and some favourable genes were uncovered. The ILs carrying these QTL (genes) represent effective resource in the context of rice yield and quality improvement. For example, the IL35, carrying the Habataki *qPTGW11.1* allele, showed increasing PTGW across two environments (figure 3), thus the introgression line (IL35) carrying this QTL not only provides an opportunity for map-based cloning of this important grain yield QTL but also supplies with useful inbred line to improve TGW for Sasanishiki, then result in yield improvement in future. We have bred a set of progenies from IL35 which contrast for the *qPTGW11.1* allele, and these are well suited for positional cloning of the QTL. A similar situation pertains for *qPTGW8.2* (IL27). Further, *qPTGW3* was an important PTGW QTL, the increasing effect of Sasanishiki allele on PTGW was detected in both environments. The Sasanishiki segment represents a good candidate for marker-assisted selection for PTGW, and hence for grain yield itself. A similar situation pertains for *qPGWC1.1* (IL02) and *qPGWC1.2* (IL03), where the presence of the Sasanishiki allele decreased PGWC respectively in both environments (figure 3); therefore, the Sasanishiki segments represent good candidates for marker-assisted selection for low percentage of grains with chalkiness. The simultaneous manipulation of these three QTL in a marker assisted context is therefore a technical possibility.

However, the other 15 QTL were environment-specificity as their significant effects were only detected in one environment (table 3), for example, *qPTGW1* showed great value in 2011HN, but was not detected in 2012NC. These QTL also represent an interesting genetic resource in the context of rice yield improvement in different environments via a design-breeding approach, as described by Wang *et al.* (2007).

The improvement of grain yield and quality traits

Studies have shown that there is a correlation between TGW and PGWC, increasing grain weight would always increase grain chalkiness. For example, two white-core endosperm mutants, which were affected by the key enzymes *OsPPDKB* and *SSIIa*, also showed decreased TGW (Kang *et al.* 2005; Fujita *et al.* 2007); Song *et al.* (2007) demonstrated that the *GW2* allele, which results in a large grain size, also increased the grain chalkiness; Zhou *et al.* (2009) showed that the TGW was significantly positive correlation with PGWC. The correlation analysis in the present study, however, showed that there is no significant correlation between TGW and PGWC in both environments; moreover, half of the PGWC QTL (three out six) was not located in the same genomic region with TGW QTL. This indicated that the linkage of TGW and PGWC traits could be broken via constructing suitable population, e.g. ILs population. With respect to rice yield and grain quality, a previous study showed that the mapped QTL for yield and grain quality were independent and the two important agronomic traits can be combined together (He *et al.* 1999). This conclusion is in accordance with the results of the present study. Therefore, breeding high grain weight and low chalky rice variety simultaneously is feasible, but it is difficult to achieve the aim by traditional method. The exploitation of closely linked markers that flank the QTL for yield and grain quality, combined with MAS and high generation population, might aid in developing high yield and quality rice varieties.

Conclusion

In this study, we performed QTL and correlations analysis on TGW and PGWC in two different environments using an ILs population for the first time, and 20 QTL were identified. The result demonstrated that the mapping population can be used for detecting yield and quality traits QTL. Moreover, five QTL were detected in both environments and two of them were detected for the first time, the introgression lines carrying these QTL also represent a useful genetic resource for rice yield improvement, which also could serve as candidates for future fine mapping and positional cloning projects. Further, there is no significant correlation between TGW and

PGWC in all environments, which suggested that the linkage of TGW and PGWC traits could be broken via constructing suitable population; therefore, breeding high grain weight and low chalky rice variety simultaneously is feasible in theory.

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