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Research Paper

Mapping of QTLs conferring high grain length-breadth relative expansion during cooking in rice cultivar Paw San Hmwe

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Paw San Hmwe (PSH) is a high-quality rice cultivar from Myanmar. PSH has short and broad grains, but the grains become slender after cooking. This desirable feature can be described as a high value of grain length-breadth relative expansion index (GREI). To understand the genetic basis of high GREI in PSH, we crossed PSH with Guang 8B (G8B), a rice cultivar from China with low GREI, to develop an F_2 population and a subsequent $F_{2:3}$ population. Based on the phenotypes of these two populations measured in two years and using the method of sequencing-based bulked segregant analysis followed by verification with conventional linkage-based QTL mapping method, we mapped three QTLs for GREI. The three QTLs were located on chromosomes 3, 5 and 12, respectively, with the trait-increasing alleles all from PSH, and could explain a total of 62.5% of the phenotypic variance and 84.1% of the additive genetic variance. The results suggest that the three QTLs would be useful for the genetic improvement of GREI in rice, and the linked markers will facilitate the selection of the favorable alleles from PSH in breeding.

Key Words: rice, cooking quality, grain expansion, QTL mapping.

Introduction

Rice grain quality is a totality of features that meets the demand of consumers. Therefore, it receives great attention in rice breeding. The concept of grain quality is the sum of a number of component traits such as grain appearance, cooking and eating quality, aroma, and nutritional quality (Ge *et al.* 2005). Cooking quality, which can be measured as water uptake ratio, cooking time, grain elongation during cooking, length-breadth ratio after cooking etc. (Oko *et al.* 2012, Rather *et al.* 2016), is critical for the economic value of rice. It is suggested that the most valuable quality characters of rice for export are strong pleasant aroma, long slender grain and high linear grain elongation after cooking (Senapati *et al.* 2011).

When a rice grain is cooked, both the grain length (GL) and the grain breadth (GB) will expand due to the swelling of starch granules by water absorption (Juliano 1979). Several indexes have been defined to describe the rice grain expansion caused by cooking, but the names of the indexes are not unified. For clarity, we shall use the following terms: grain length expansion index (GLEI), grain breadth expansion index (GBEI), grain length expansion rate (GLER), grain breadth expansion rate (GBER), grain length-breadth relative expansion index (GREI), and grain length-breadth relative expansion rate (GRER). The definitions of these terms are: $GLEI = L_1/L_0$ (Fofana *et al.* 2011, Golam and Prodhan 2013, Juliano and Perez 1984, Pilaiyar 1988), $GBEI = B_1/B_0$ (Govindaraj *et al.* 2009, Jiang *et al.* 2008), $GLER = (L_1 - L_0)/L_0 = GLEI - 1$ (Ge *et al.* 2005, Tian *et al.* 2005), $GBER = (B_1 - B_0)/B_0 = GBEI - 1$ (Ge *et al.* 2005), $GREI = (L_1/B_1)/(L_0/B_0) = (L_1/L_0)/(B_1/B_0)$ (Danbaba *et al.* 2011, Juliano and Perez 1984), and $GRER = (L_1/B_1 - L_0/B_0)/(L_0/B_0) = GREI - 1$ (Sood and Siddiq 1980), where L_0 and B_0, and L_1 and B_1 are the length and breadth of uncooked grains and cooked grains, respectively. Obviously, GLEI/GLER and GBEI/GBER reflect grain expansion in length and in breadth, respectively, while GREI/GRER reflects the relative expansion between grain length and grain breadth, which can indicate

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the change of grain shape after cooking.

As a complex trait, grain expansion (during cooking) must be controlled by multiple genes. So far, at least 43 quantitative trait loci (QTLs) underlying grain length expansion have been reported in rice, with 14 mapped based on GLEI (Ahn *et al.* 1993, Amarawathi *et al.* 2008, Arikit *et al.* 2019, Govindaraj *et al.* 2009, Li *et al.* 2004, Liu *et al.* 2008, Swamy *et al.* 2012) and 29 based on GLER (Ge *et al.* 2005, Li *et al.* 2015, Shen *et al.* 2005, 2011, Tian *et al.* 2005, Wang *et al.* 2007, Yang *et al.* 2013, Zhang *et al.* 2004). In addition, 10 QTLs underlying the change of rice grain shape measured with GREI have also been reported (He *et al.* 2003, Jiang *et al.* 2008, Li *et al.* 2015, Liu *et al.* 2008). These QTLs are distributed on all chromosomes, with the most on chromosome 6 (16 QTLs), followed by chromosome 3 (8 QTLs), and the fewest on chromosome 12 (1 QTL only).

Paw San Hmwe (PSH) is a popular high-quality rice cultivar in Myanmar. Its grains are short and broad, but become long and slender after cooking. This feature is very desirable because short and broad grains can reduce grain breakage during the milling process, while the slender shape of cooked grains is loved by many consumers. To reveal the genetic basis of this special property in PSH, we carried out a QTL mapping study using the strategy of sequencing-based bulked segregant analysis (BSA-seq) followed by a validation with individual segregant analysis (ISA) based on two generations. We mapped three QTLs for GREI on chromosomes 3, 5 and 12, respectively, which together explained 62.5% phenotypic variance and 84.1% additive genetic variance. The results will promote deep research of the genetic basis of cooking-related rice grain elongation and facilitate the genetic improvement of the trait.

Materials and Methods

Mapping populations and field experiments

An F_2 population and corresponding $F_{2:3}$ population were constructed from a cross between Paw San Hmwe (PSH), a good-taste tropical *japonica* rice variety from Myanmar with short broad grains showing strong aroma and dramatic elongation during cooking, and Guang 8B (G8B), an good-taste *indica* rice variety from China with transparent small slender grains. In 2017, the F_2 population was grown in our rice breeding base at Shuiji, Jianyang (E118.354352°, N27.421165°) during the normal growing season (from Apirl to October). Seeds were sown on seedbed after pregermination and the seedlings were transplanted onto the paddy field 25 days later with a 20-cm spacing between plants and between rows. Field managements followed the normal agronomic procedure. Mature grains were harvested from individual F_2 plants separately. After dried in the sun, the grains were used to measure the GREI of each F_2 plant. A total of 913 F_2 plants were investigated, from which 150 highest and 150 lowest F_2 plants in GREI were identified and the corresponding $F_{2:3}$ lines were grown in the farm of Fujian Agriculture and Forestry at Yangzhong, Youxi (E118.485841°, N26.287161°) during the normal growing season (from Apirl to October) in 2018. Twenty-four seedlings were grown for each line. The operation of field experiment was the same as that in 2017. Mature grains were harvested from individual lines separately for GREI analysis. In both years, the parental lines PSH and G8B were grown and investigated as controls.

Measure of GREI

To measure the GREI of an F_2 plant or an $F_{2:3}$ line, 30 intact white (polished) rice grains from the F_2 plant or $F_{2:3}$ line were scattered on a black plane surface and photographed. Then, the grains were socked in 1 ml distilled water under room temperature for 30 min, cooked in boiled water for 45 min, and removed from the water. From the cooked grains, 15 straight and unbroken ones were selected and placed on a black plane surface and photographed. Three replicates were set for each F_2 plant or $F_{2:3}$ line. The length and breadth of individual uncooked and cooked grains of each F_2 plant or $F_{2:3}$ line were measured from the photos, respectively, using the software SmartGrain (Tanabata *et al.* 2012), and then the corresponding GREI was calculated.

BSA-seq

Fifty $F_{2:3}$ lines with the highest GREI values and 50 $F_{2:3}$ lines with lowest GREI values were selected and bulked respectively into two opposite groups. For each group, equal amount of leaves from all the $F_{2:3}$ lines belonging to the same group was mixed for DNA extraction so as to make a pair of opposite DNA pools: the high-GREI (H) pool and the low-GREI (L) pool. The leaves of each $F_{2:3}$ line were from 20 seedlings at three-leaf stage. DNA extraction was conducted using the Plant Genomic DNA Kit (TianGen, China). DNAs of the two parental lines were also extracted. The two DNA pools and the parental DNAs were sent to Xiamen Jointgene Technologies Corporation for deep sequencing using Illumina Hiseq 2000 platform.

The raw reads of the sequenced DNA samples were subjected to quality control using the program BBTool v1.0 (https://sourceforge.net/projects/bbmap/). The cleaned reads were mapped to the public reference genome (Nipponbare: IRGSP1.0, http://rice.plantbiology.msu.edu/) using the program BWA v1.0 (Li and Durbin 2009). Uniquely mapped reads were kept to call single nucleotide polymorphisms (SNPs) and short insertions/deletions (InDels) using the program FreeBayes v1.0 (https://arxiv.org/abs/1207.3907). The SNPs and short InDels with a sequencing depth between 10 and 500 in both of the parental DNA samples were used as markers for QTL mapping. QTL mapping was performed using the block regression mapping (BRM) method (Huang *et al.* 2020). The block size used was 20-kb.

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ISA

To validate the QTLs detected by BSA-seq, 130 $F_{2:3}$ lines were randomly selected from those derived from the 300 extreme (150 highest + 150 lowest) GREI F_2 plants as the mapping population, and the genome DNA of each line was extracted using the same method as above. A set of InDel markers were developed in the predicted QTL regions according to the parental genome sequencing data. The primers for the InDel markers were designed using the program Prime3 (http://bioinfo.ut.ee/primer3-0.4.0/) and synthesized by Shanghai Sangon Biological Engineering & Technology Company. These InDel markers were used to genotype the 130 $F_{2:3}$ lines. PCR was performed following Xu *et al.* (2002) with minor modification. The marker data were analyzed to construct a regional genetic map using the program MAPMAKER/EXP 3.0 (Lander *et al.* 1987). Based on the regional genetic map and the marker data, and taking the $F_{2:3}$ lines and their corresponding F_2 plants as the same population grown under two different environments (years), the trait data of the F_2 plants ($F_{2:3}$ seeds) and those of the $F_{2:3}$ lines ($F_{2:4}$ seeds) were jointly analyzed for QTL mapping using the software QTLNetwork 2.0 (http://ibi.zju.edu.cn/software/qtlnetwork/), from which the additive and dominance effects of each QTL and their interactions with the environment could be estimated. Significance threshold for judging QTLs was estimated by permutation tests. Default settings were adopted. In addition, to evaluate the relative contribution of each QTL to the genetic variation, the broad-sense heritability and the narrow-sense heritability of GREI in the mapping population (the 130 F_2 plants and $F_{2:3}$ lines) were estimated through two-way analysis of variance (ANOVA) and linear regression analysis of $F_{2:3}$ against F_2, respectively.

Results

Trait performance

The parent G8B had slender grains with a large grain length-breadth ratio (GLBR, mean ± standard deviation = 3.38 ± 0.05, **Fig. 1A**). After cooking, the GLBR of G8B was reduced (2.58 ± 0.14, **Fig. 1C**). So, G8B had a very low GREI (0.76 ± 0.03). In contrast, the parent PSH had short broad grains with a small GLBR (1.99 ± 0.02, **Fig. 1B**), but the grains became slender (**Fig. 1D**) and the GLBR greatly increased (3.57 ± 0.09) after cooking. Hence, PSH had a very high GREI (1.79 ± 0.06). In both of the F_2 population of PSH × G8B and the $F_{2:3}$ population derived from the 150 highest (GREI > 1.17) and the 150 lowest (GREI < 0.93) F_2 plants, GREI varied continuously, following a unimodal distribution slightly skew to the low value side, with a mean and standard deviation of 1.05 and 0.12 and of 1.06 and 0.19, respectively (**Fig. 2**). This clearly suggests that GREI is a quantitative trait controlled by multiple genes. No F_2 plants and $F_{2:3}$ lines exceeded the higher-value parent PSH (**Fig. 2**), implying that all the alleles increasing GREI were from PSH. The GREI values of the $F_{2:3}$ lines from the 150 highest F_2 plants were higher as a whole than those from the 150 lowest F_2 plants (**Fig. 2B**), indicating the genetic difference between the two groups. Therefore, the 50 highest $F_{2:3}$ lines (GREI > 1.12) and 50 lowest $F_{2:3}$ lines (GREI < 0.87) selected for BSA-seq were actually from the highest F_2 group and the lowest F_2 group, respectively (**Fig. 2B**).

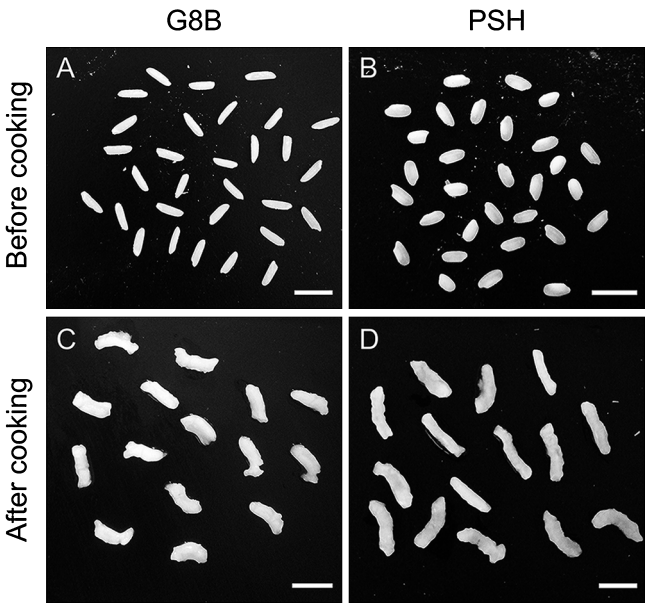

Fig. 1. Rice grains of Guang 8B (G8B) and Paw San Hmwe (PSH) before and after cooking. Scale bar = 1 cm.

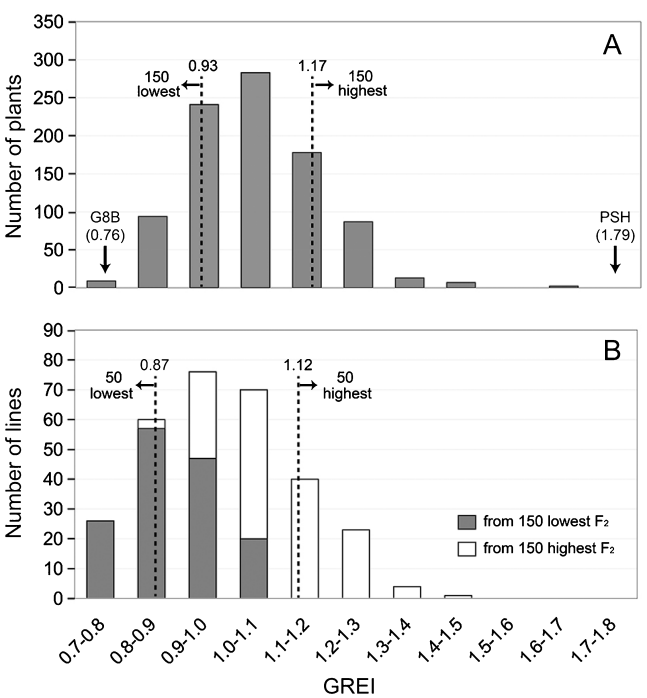

Fig. 2. Frequency distributions of grain length-breadth relative expansion index (GREI) in the F_2 (A) and $F_{2:3}$ (B) populations of G8B × PSH.

QTL mapping by BSA-seq

In total, ~0.5 G clean (trimmed and filtered) reads were obtained in the four samples (two parents and two pools), of which ~96% were mapped to the reference genome and ~80% were uniquely mapped (**Supplemental Table 1**). The average sequencing depth in each sample varied 33.78–43.87. Based on the uniquely mapped reads, a total of ~1 M markers meeting the requirement for QTL mapping were obtained, including 921,577 (88.1%) SNPs, 111,287 (10.6%) short InDels and 13,394 (1.3%) others. The average depth of these markers was 17.09 in the H pool and 19.08 in the L pool, respectively.

Under the overall significance level of 0.05, significant AFD (allele frequency difference) peaks were detected on chromosomes 3, 5, 7 and 12 (**Fig. 3**). The peak on chromosome 3 was the highest and covered a very wide region with many fluctuations, suggesting that there might be one or more QTLs in that region and the QTL(s) might have the largest effect(s). Chromosome 12 had two obvious significant AFD peaks second to the peak on chromosome 3, suggesting that there might be two QTLs on this chromosome. The peak on chromosome 5 only a little bit exceeded the threshold and the peak on chromosome 7 only just reach the threshold. Therefore, these two chromosomes might have a QTL with small effect each.

QTL validation by ISA

To validate the possible QTLs identified by BSA-seq, we constructed a regional genetic map of chromosomes 3, 5, 7 and 12, consisting of 33 InDel markers (**Fig. 4**, **Supplemental Table 2**). Under the overall significance level of 0.05, three significant *F* peaks were detected on chromosomes 3, 5 and 12 (**Fig. 4**), which were consistent with the AFD peaks on chromosome 3 and 5 and the right AFD peak on chromosome 12, respectively (**Fig. 5**). So, these three AFD peaks were validated, while the AFD peak on chromosome 7 and the left AFD peak on chromosome 12 might be false positives. In light of the results of ISA, these three AFD peaks represented a QTL each, although the AFD peak on chromosome 3 spanned a wide range. We named these three QTLs as *qGREI3*, *qGREI5* and *qGREI12*, respectively.

According to the directions of AFD peaks (**Fig. 4**) and the additive effects estimated by ISA, the GREI-increasing

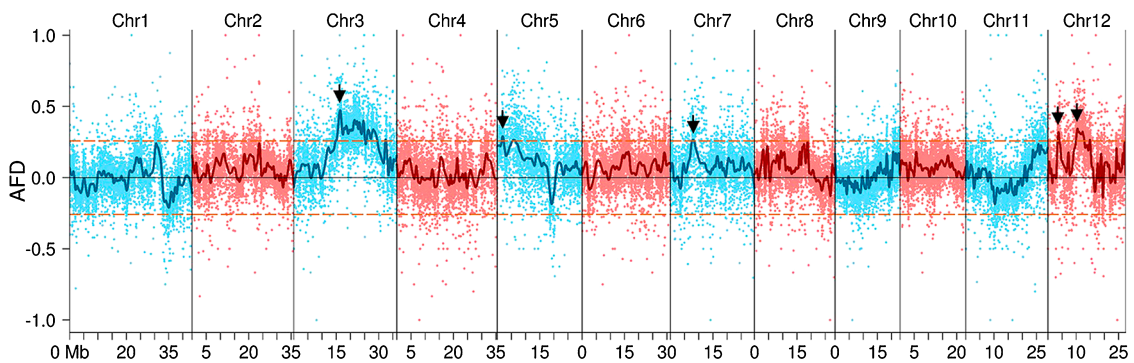

Fig. 3. QTL mapping results for GREI obtained by BSA-seq using BRM. The lower and upper horizontal dashed lines are thresholds at the overall significance level of 0.05. The arrows indicate the significant AFD (allele frequency difference) peaks.

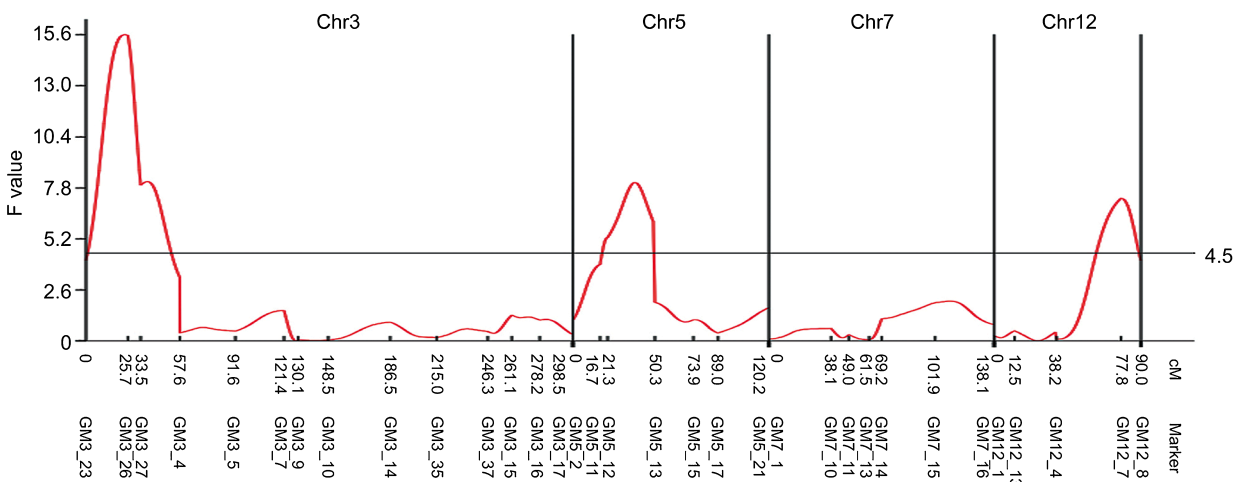

Fig. 4. QTL mapping results for GREI obtained by individual segregant analysis (ISA) using QTLNetwork 2.0. The horizontal line indicates threshold at the overall significance level of 0.05.

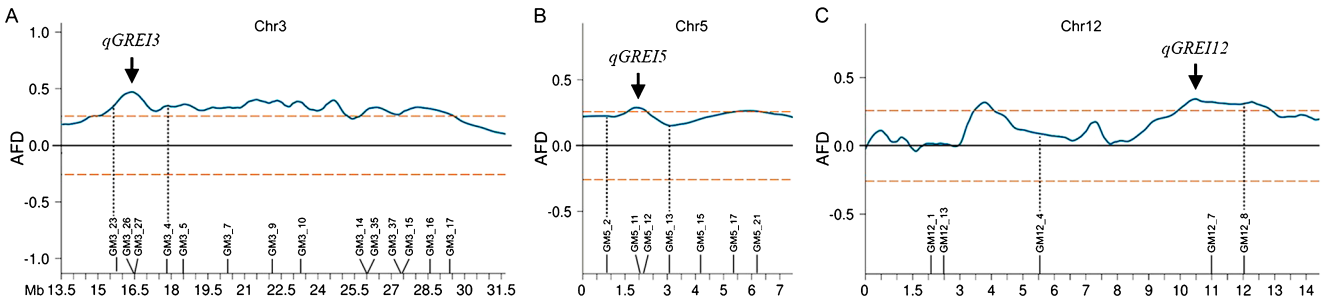

Fig. 5. Comparison of QTL mapping results obtained by BSA-seq and ISA. The arrows indicate the AFD peaks (QTL positions) detected by BSA-seq. The vertical dotted lines indicate the marker intervals of QTLs identified by ISA.

Table 1. QTLs for GREI Mapped by BSA-seq and validated by ISA

QTL	Chr.	Pos. (Mb)[a]	Marker interval	PVE (%)[b]			GVE (%)[c]	
				Add.	Dom.	Total	Add.	Total
qGREI3	3	16.4	GM3_23–GM3_4	28.6	3.5	32.1	43.2	36.0
qGREI5	5	1.9	GM5_2–GM5_13	10.1	3.0	13.1	15.2	14.7
qGREI12	12	10.5	GM12_4–GM12_8	17.0	0.3	17.3	25.7	19.4
Total				55.7	6.8	62.5	84.1	70.1

[a] Physical position of the QTL estimated by BSA-seq. [b] Proportions of phenotypic variance explained by the additive effect (Add.) and dominance effect (Dom.) of the QTL estimated by ISA. [c] Proportions of additive genetic variance and total genetic variance explained by the QTL. Add. GVE = Add. PVE ÷ Narrow-sense heritability; Total GVE = Total PVE ÷ Broad-sense heritability.

alleles of the three QTLs were all from the parent PSH. This was consistent with the result that no F_2 plants and $F_{2:3}$ lines had as high GREI as that of PSH (**Fig. 2**). The three QTLs explained 62.5% of phenotypic variance in total (**Table 1**). Among them, *qGREI3* explained the most (32.1%), followed by *qGREI12* (17.3%), while *qGREI5* explained the least (13.1%). This was consistent with the relative heights of their AFD peaks (**Fig. 3**). All the three QTLs displayed mainly additive effect (**Table 1**). None of them showed significant interactions with the environment. Regression analysis and ANOVA showed that the narrow-sense heritability and broad-sense heritability of GREI in the mapping population were estimated to be 66.2% and 89.2%, respectively. Thus, it could be estimated that the proportions of additive genetic variance and total genetic variance explained by the three QTLs together were 84.1% and 70.1%, respectively (**Table 1**). The results indicated that the three QTLs had explained most of the additive genetic variance and a large proportion of the total genetic variance in this experiment.

Discussion

In this study, the continuous phenotypic variation (**Fig. 2**) clearly indicated that rice GREI was a complex trait. However, the trait showed very high broad-sense heritability (89.2%) and over medium narrow-sense heritability (66.2%), suggesting that selection on GREI could be effective in breeding. This was demonstrated by the obvious difference between the two groups of $F_{2:3}$ lines derived from the 150 highest-GREI and the 150 lowest-GREI F_2 plants, respectively (**Fig. 2**). Using two generations and two mapping methods, we mapped three QTLs for GREI, which could explain most of the genetic variance (especially the additive component) in the mapping population (**Table 1**). The results suggested that the high GREI of PSH was mainly attributed to these three QTLs, although there could be many minor QTLs with small effects involved. Therefore, these three QTLs will be useful for the genetic improvement of GREI in rice.

As mentioned above, at least 10 QTLs for rice GREI have been reported, which are distributed on chromosomes 1, 2, 3, 5, 6 and 9 (He *et al.* 2003, Jiang *et al.* 2008, Li *et al.* 2015, Liu *et al.* 2008). Among them, one QTL on chromosome 5 overlaps with *qGREI5*, suggesting that they are probably the same QTL (**Supplemental Table 3**; He *et al.* 2003). There are no reported GREI QTLs located inside or overlapping with *qGREI3* or *qGREI12*, suggesting that these two QTLs are novel.

According to the definition, the length and breadth of both cooked and uncooked grains and their combinations (e.g. GLBR, GLEI and GBEI) are all components of GREI. It is possible that GREI is correlated with them. Using analysis of variance and covariance, we estimated the genetic correlations of GREI with GL, GB, GLBR, GLEI and GBEI in the population used for ISA. As expected, GREI had high genetic correlation (ranging 0.674–0.889 in absolute value) with these component traits either positively (with GB and GLEI) or negatively (with GL, GLBR and GBEI, **Supplemental Table 4**). To examine whether these component traits share the same genetic basis with GREI, we performed QTL mapping for them based on the regional

genetic map and the marker data. All of the three GREI QTLs were mapped at least in one of the component traits (**Supplemental Fig. 1**). This indicated that the three GREI QTLs all had pleiotropic effects on one or more component traits. Among them, *qGREI3* showed the widest pleiotropy (affecting GL, GB, GLBR and GBEI), followed by *qGREI12* (affecting GB, GLBR and GBEI), while *qGREI5* only affected GBEI. These results suggested that the GREI QTLs might all probably control GREI by affecting some component traits, though different GREI QTLs had different pleiotropy. Indeed, many QTLs (or genes) for the components of GREI have been detected either fully or partially inside the marker intervals of the three GREI QTLs (**Supplemental Table 3**; Fan *et al.* 2006, Govindaraj *et al.* 2009, He *et al.* 2003, Li *et al.* 2003, 2004, Liu *et al.* 2016, Qi *et al.* 2017, Redoña and Mackill 1998, Swamy *et al.* 2012, Wan *et al.* 2005, 2006).

It is noticeable that the three GREI QTLs were all significant for GBEI, but none of them was detected for GLEI (**Supplemental Fig. 1D**, **1E**). The alleles of the three QTLs from PSH all acted to decrease GBEI as expected. This suggests that the three QTLs might probably affect GREI mainly by regulating GBEI instead of GLEI in this population. Interestingly, while *qGREI5* did not affect GB and GLBR, a new QTL for GB and GLBR (named as *qGB5* or *qGLBR5*) was mapped on chromosome 5 (**Supplemental Fig. 1B**, **1C**), which, according to the linked markers, happened to be consistent with the lower and wider AFD peak beside *qGREI5* (**Fig. 5**), suggesting that this AFD peak was probably caused by *qGB5* or *qGLBR5* due to the high genetic correlation of GREI with GB and GLBR. Taken together, it appeared that the GB-related component traits played main roles in GREI in this study. It is possible that PSH exhibits distinctive high GREI mainly due to the ability of suppressing grain breadth expansion.

In addition, since rice grains expand during cooking because of the swelling of starch granules by water absorption (Juliano 1979), it can expected that traits related to starch in rice grains might probably also be correlated with GREI. To investigate their relationship, we analyzed the amylose contents (ACs) of the parents and 100 $F_{2:3}$ lines randomly selected from the population for ISA. The results indicated that the ACs (%) of the parents PSH and G8B were 24.74 ± 0.62 and 17.60 ± 0.19, respectively, and AC was significantly correlated with GREI in the population, although the genetic correlation coefficient (0.359) was not very high in comparison with those of the component traits of GREI (**Supplemental Table 4**). The positive correlation suggested that higher AC would increase GREI. However, no QTLs for AC were detected in the regions harboring the QTLs for GREI (**Supplemental Fig. 1F**). It is known that AC is mainly controlled by a *Wx* gene on chromosome 6 in rice. The BSA-seq results suggested that the *Wx* might not affect GREI in this experiment because no QTLs for GREI were detected on chromosome 6 (**Fig. 3**). To verify this result, we developed an InDel marker (AC6-1) near the *Wx* locus (~44 kb apart; **Supplemental Table 5**) to genotype 70 lines randomly selected from the mapping population and examined the associations of the marker with AC and GREI using analysis of variance (**Supplemental Table 6**). The marker exhibited significant association with AC (*P*-value = 0.000963), indicating that the *Wx* gene contributed to the genetic variation of AC in the population. However, the marker was not significantly associated with GREI ($F = 2.550$ and $2.225 < F_{0.05} = 3.134$ in F_2 and F_3, respectively). This confirmed the result of BSA-seq. These results suggested that AC was not an important factor for GREI in this population.

Author Contribution Statement

WW conceived and designed the experiment; KMT, YZ, EEK, EEN, MHWL, KTO, WWN, MZZT, MMM and SSA performed the experiments; KMT, YZ and WW analyzed the data; WW, YZ and KMT wrote the paper. All authors read and approved the final manuscript.

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