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ORIGINAL PAPER

Identification and QTL mapping of important agronomic traits based on rice short-wide grain CSSL-Z752 with restorer line Xihui 18 as background

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Abstract
Rice restorer line is one of the important parents for the utilization of rice heterosis. An excellent restorer line is the basis for breeding super hybrid rice. Rice chromosome segment substitution line (CSSL) based on excellent restorer lines is an ideal material for both genetic research and breeding practice due to its consistent genetic backgrounds besides few substitution segments from donor. Here, a short-wide grain rice CSSL-Z752 was developed using the excellent line Xihui 18 as the recipient parent and Huhan 3 as the donor parent by advanced backcrossing and self-polling combined with simple sequence repeat (SSR) marker-assisted selection. Z752 contained 13 substitution segments from Huhan 3 with 3.69 Mb of average substitution length. Compared with the recipient Xihui 18, the number of effective panicles per plant, grain width, 100-grain weight and yield per plant in Z752 increased significantly, and grain length of Z752 was decreased significantly than that of Xihui 18. The other traits showed no significant difference. Then, the secondary F_2 population crossed by Xihui 18 and Z752 was used to map 10 QTLs for the important agronomic traits, which were distributed on the chromosome 2, 3, 4, 5, 6, 7, 10, 11, and 12. Among them, there were two QTLs for effective panicle number per plant, plant height and grain width, respectively, including *QPN*3, *QPN*5 and *QPH*2, *QPH*6, *QGW*2, *QGW*5, and one QTL for grain number per panicle, seed-setting rate, grain length, ratio of grain length to width, respectively, including *QGP*2, *QSSR*2, *QGL*3 and *QRLW*5. The results will be of great significance for development of single-segment substitution lines carrying target QTL sand breeding of hybrid rice.

Keywords Rice · Chromosome segment substitution lines · QTL mapping · Restorer lines

Introduction

Chromosome segment substitution lines (CSSLs) are genetic stocks representing the complete genome of any genotype in the background of a recipient cultivar as overlapping segments (Balakrishnan et al. 2018). Each CSSL only harbored only a few substitution fragments from donor parent. Due to its high purity of the genetic background with the recipient parent, the phenotypic difference between each CSSL and the recipient parent is caused by the difference of the introduced fragment, and thus, the interference of the genetic background in the secondary F_2 segregating population developed by the recipient parent and according CSSL is greatly reduced. Therefore, it is the ideal genetic research material for QTL mapping and cloning. Many important traits such as rice grain shape belong to complex quantitative traits. It is important to dissect these QTLs and further

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unveil their molecular mechanisms. At present, some pathways that regulate rice grain size have been analyzed in rice. WTG1, which is homologous to human OTUB1 protein (Huang et al. 2017), regulates rice grain size through ubiquitination. *D*1(Tanabe 2005), *DEP*1 (Sun et al. 2018) and *GS*3(Liu et al. 2018) regulate grain size through g-protein signaling pathway. Loss of function of *GW*2 leads to increased gluteal cell division and thus increases the width of grains (Song et al. 2007). *GS*5 positively increases the grain size by increasing the proliferation of lemma (Li et al. 2011). *OsMKKK*10, *OsMKK*4 and *OsMPK*6 are MKK cascade pathways mediating grain size of rice (Guo et al. 2018). In addition, Zhang et al. (2020) identified two QTLs of grain length, QGL-5 and QGL-6 using a CSSL Z1392, in which *OsARF*19 is the possible candidate gene of qGL6. Wang et al. (2020) identified two QTLs for grain length (*qKL*3 and *qKL*7), and OsPPKL1 is considered as a possible candidate gene of qKL3 through DNA sequencing. Liang et al. (2021) detected *qGL*3-1, *qGL*3-2 and *qGL*7 for grain length using CSSL-Z563, and fine-mapped *qGL*3-2 to a 696 Kb region of chromosome 3 containing five candidate genes. Although some rice grain shape-related genes have been reported, the molecular mechanism of rice grain regulation is very complex, it is still necessary to further explore more QTLs to clarify its molecular mechanisms.

In this study, Xihui 18 was used as a recipient parent and Huhan 3 as a donor parent, a short-wide grain rice chromosome segment substitution line Z752 with 13 substitution segments was identified. Then, we constructed a secondary F_2 population from Xihui 18/Z752 to map QTLs for important agronomic traits. The results are important for further developing single-segment substitution lines carrying target QTLs and further cloning these QTLs.

Materials and methods

Materials

The rice CSSL Z752 were developed from Xihui 18 as the recipient parent and Huhan 3 as the donor parent. Xihui 18 is an excellent rice restorer line bred by Southwest University, Chongqing, China. It has the characteristics of high combining ability, long panicle and many grains and long-thin grains. Huhan 3 is a cultivar with short-wide grain and resistance to drought.

Development of Z752 and identification of substitution segments

At first, 429 SSR (single sequence repeat) markers uniformly distributed in the whole genome of rice were used to analysis of polymorphism between Xihui 18 and Huhan 3. Then, 241 polymorphic markers were screened. Starting from BC_2F_1 generation for DNA analysis, 20 individuals each generation, these polymorphic markers were used for molecular marker-assisted selection (MAS), until in BC_3F_6 a stable short-wide chromosome segment substitution line Z752 carried 13 substitution segments were generated. The identification of substitution segment was referred to the method described by Ma et al. (2019), and the estimated length of substitution fragment was calculated referring to the method of Paterson et al. (1991).

Material planting

In July 2018, Xihui 18 was crossed with Z752 to generate hybrid seeds in at the experimental station of Southwest University in Chongqing, China, and the hybrid seeds were harvested and planted in Linshui, Hainan province, and the F_1 grains were harvested in September of the same year. Then, we harvested the F_1 seeds in January 2018. On March 8, 2019, the seedlings were raised in greenhouse of the experimental station of Southwest University. On April 15, Thirteen seedlings for Xihui 18 and Z752, together with 102 F_2 individuals, were transplanted in each plot of the experiment field 40 days after sowing with a spacing of 16.67 cm between hills and 26.67 cm between rows, with conventional field cultivation management.

Phenotypic analysis and agronomic traits investigation

After maturity, ten individuals of Xihui 18 and Z752 and 102 individuals of F_2 population were harvested. 11 traits, including plant height, effective panicle number per plant, panicle length, primary branches per panicle, secondary branches per panicle, grain length, grain width, grain number per panicle, spikelets number per panicle, 1000-grain weight and yield per plant, were investigated. The seed-setting rate was calculated as the percentage of the number of grains per panicle to spikelets number per panicle. The ratio of grain length to grain width was calculated by the ratio of grain length to grain width. The specific measurement was referred to the method described by Ma et al (2019).

Scanning electron microscope analysis of glumes in Z752 and Xihui 18

Before heading, the inner and outer epidermal cells of 5 glume glumes were investigated from Xihui 18 and Z752, respectively, using Hitachi SU3500 scanning electron microscope under the condition of − 20 °C.

QTL mapping

The population of QTL mapping was a secondary F_2 population from recipient Xihui 18 crossed by Z725. The DNA of two parents and 102 F_2 plants was extracted by CTAB method. The procedures for PCR amplification, 10% native polyacrylamide gel electrophoresis, and rapid silver staining followed Zhao et al (2016). The lanes of Xihui 18 were marked by "− 1," and those of the heterozygotes were marked by "0", and the lanes of Huhan 3 were marked by "1." Missing values were replaced by "." Lanes of each marker located on the substitution segments, together with the phenotypic values of each individual of the F_2 population, were used to identify the putative QTLs using the restricted maximum likelihood (REML) method implemented in the HPMIXED procedure in SAS (Zhao et al. 2016); p value of 0.05 was used as the threshold to decide whether a QTL is linked with these markers in the substitution segments.

Results

Identification of substitution segments of Z752

15 polymorphic SSR markers in substitution segments of Z752, together with 24 polymorphic SSR markers outside the substitution segments, were used to detect the substitution fragment and assess the purity of the genetic backgrounds of Z752 using ten plants of Z752. The results showed that Z752 was homozygous, and no additional residual segment was detected. Z752 contained 13 substitution segments from the donor parent Huhan 3, distributed on chromosomes 2, 3, 4, 5, 6, 7, 10, 11 and 12. Among them, chromosome 2 harbored 3 substitution fragments; chromosomes 5 and 12 each contained 2 substitution fragments. There was only one substitution segment on chromosomes 3, 4, 6, 7, 10 and 11. The total length of the substitution fragments was 48.00 Mb, the longest substitution length was 7.40 Mb, the shortest one was 2.25 Mb, and the average length was 3.69 Mb. The inbreeding level (background recovery rate) of Z752 from Xihui 18 was 87.66% (Fig. 1).

Agronomic traits analysis of Z752 and its recipient Xihui 18

Compared with Xihui 18, Z752 displayed significant increase in grain width, 1000-grain weight, effective panicle number per plant and yield per plant, which increased by 8.3%, 12.46%, 33.33% and 24.70%, respectively. Grain length (9.96 mm) of Z752 was decreased significantly than that (10.18 mm) of Xihui 18. In addition, there were no significant differences in plant height, panicle length, number of primary branches per panicle, number of secondary branches per panicle, grain number per panicle, spikelets number per panicle, seed-setting rate and grain length (Fig. 2 and Table 1).

Cytological analysis of glume in Z752 and Xihui 18

To examine the cytological reason for the increase grain width of Z752, scanning electron microscopy was used to observe the cell morphology of glumes in Xihui 18 and Z752. The cell width in the inner epidermis of glumes of Z752 was significantly wider than that of Xihui 18, and the cell length in Z752 was significantly shorter than that of Xihui 18. In addition, the cell number in the outside epidermis of glume of Z752 was also significantly more than that of Xihui 18. The results suggest that the short-wide grain of Z752 was caused by increase in both cell width and number as well as decrease in cell length (Fig. 3).

QTL for important agronomic traits carried by substitution fragments of Z752

Using the secondary F_2 population from crosses of Xihui 18 with Z752, we identified 10 QTLs for seven rice agronomic traits, which were distributed on 6 substitution fragments of Z752. These QTLs included two for effective panicle number per plant, plant height and grain width, one for grain number per panicle, seed-setting rate, grain length and ratio of grain length to width, respectively. They explained phenotypic variance from 7.68 to 65.41%. Among them, eight belonged to major effect QTLs (*qPH2*, *qPH6*, *qGP2*, *qSSR2*, *qGL3*, *qGW2*, *qGW5* and *qRLW5*), whose contribution rate for according phenotypic variation was more than 10% (Table 2).

The wide grain of Z752 was responsible for *qGW2* and *qGW5* from donor Huhan 3, whose additive effects increased grain width by 0.11 mm and 0.11 mm, respectively. The short grain of Z752 was harbored by *qGL3* with additive effect of − 0.18 mm. The increased number of effective panicle per plant of Z752 was controlled by two QTLs from donor Huhan 3, *qPN3* and *qPN5*, whose additive effects increased effective panicle by 1.08 and 1.05 per plant, respectively. The plant height of Z752 was responsible for *qPH2* and *qPH6*, while *qPH2* increased the plant height by 6.39 cm and *qPH6* decreased the trait by 7.72 cm, which was consistent with the phenotype that there was no difference in plant height between Z752 and Xihui 18. The additive effects of the alleles (*qGP2* and *qSSR2*) from donor Huhan 3 increased the number of grains per panicle and seed-setting rate by 27.51 and 9.00 percentage point.

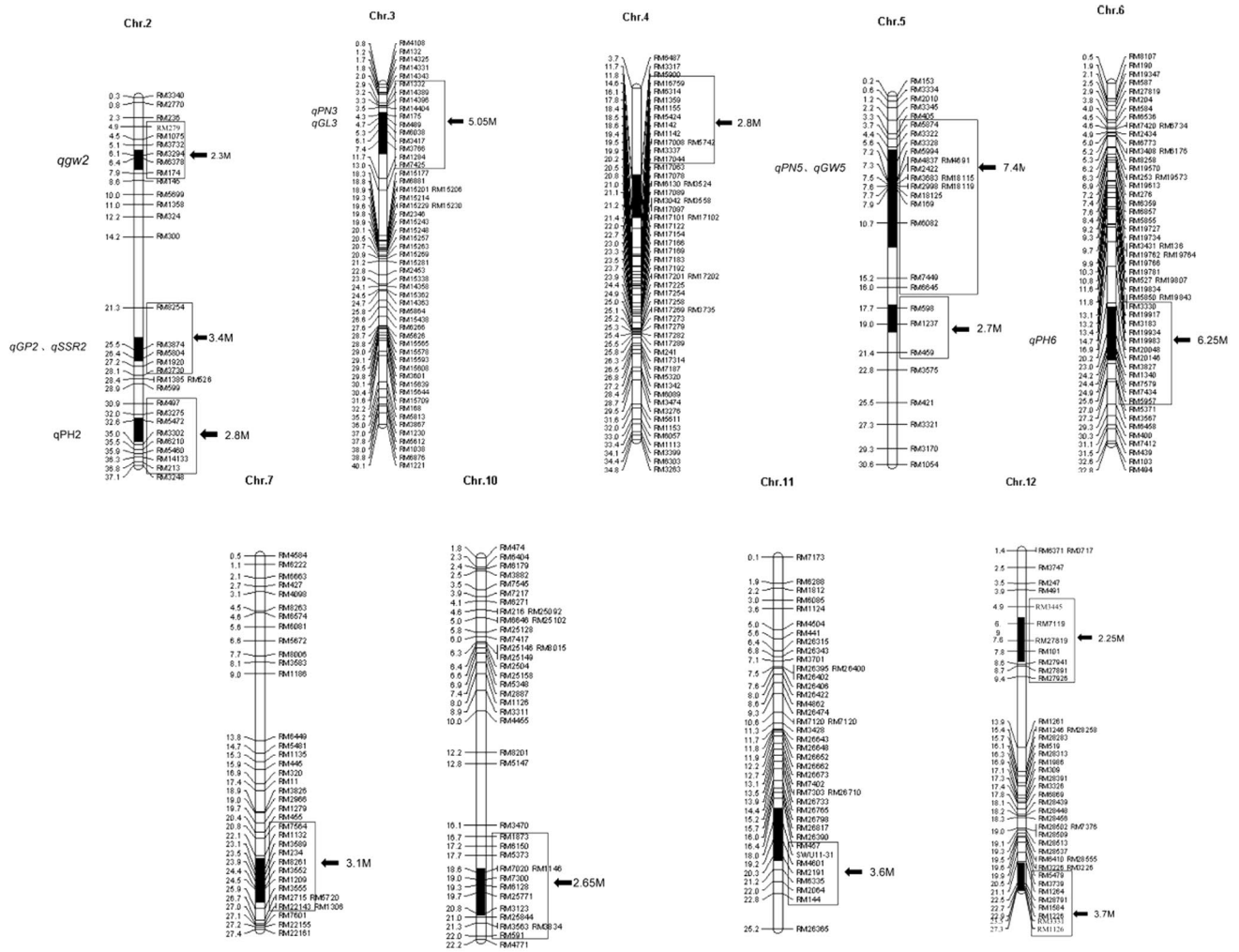

Fig. 1 Substitution segments and detected QTL of Z752. The left side of each chromosome is the QTL of physical distance (Mb) and location. On the right are the tag name, the substitution interval (the tag in the box), and the substitution length (the black arrow points to). PH: plant height, PL: panicle length, GP: grain number per panicle, SPP: total grain number per panicle, SSR: seed-setting rate, GL: grain length, GW: grain width, RLW: ratio of grain length to width

Discussion

Chromosome segment substitution lines (CSSLs) are ideal materials for studying quantitative traits. Each CSSL has one or several specific marker-defined chromosome segment from the donor with a maximum recipient parent genome recovered in the background (Balakrishnan et al. 2018). Thus, all the genetic differences between the recipient parent and a CSSL only occur in the few chromosome substitution segments from donor parent. Due to its reduced interference from genetic backgrounds in the secondary F_2 segregation population developed from crosses of the recipient parent a CSSL with only a few substitution segments from donor and consistence with its recipient parent in the other genome regions, unlike traditional F_2 primary populations, it is more accurate for CSSLs to be used in mapping quantitative trait loci (QTLs) or causal genes (Ashikari and Matsuoka 2006; Qiu et al. 2012; Yang et al. 2021). Furthermore, CSSLs are valuable prebreeding tools for broadening the genetic base of existing cultivars and harnessing the genetic diversity from the wild-type and distant-related species (Balakrishnan et al. 2018). In this study, a rice CSSL, Z752, was identified from advanced backcross progeny of the recipient parent *Indica* Xihui 18 and the donor parent *Japonica* Huhan 3. Z752 contained 13 substitution segments with an average length of 3.69 Mb and displayed short-wide grain and significant increased number of effective panicle per plant and yield per plant. In particular, *Rf*-1(Akagi et al. 2004), *Rf*2(Cai et al. 2013), *Rf*3(Etsuko et al. 2010) were all not in these substitution regions. However, *Rf*4 (Tomohiko and Kinya 2014) was replaced in substitution segment

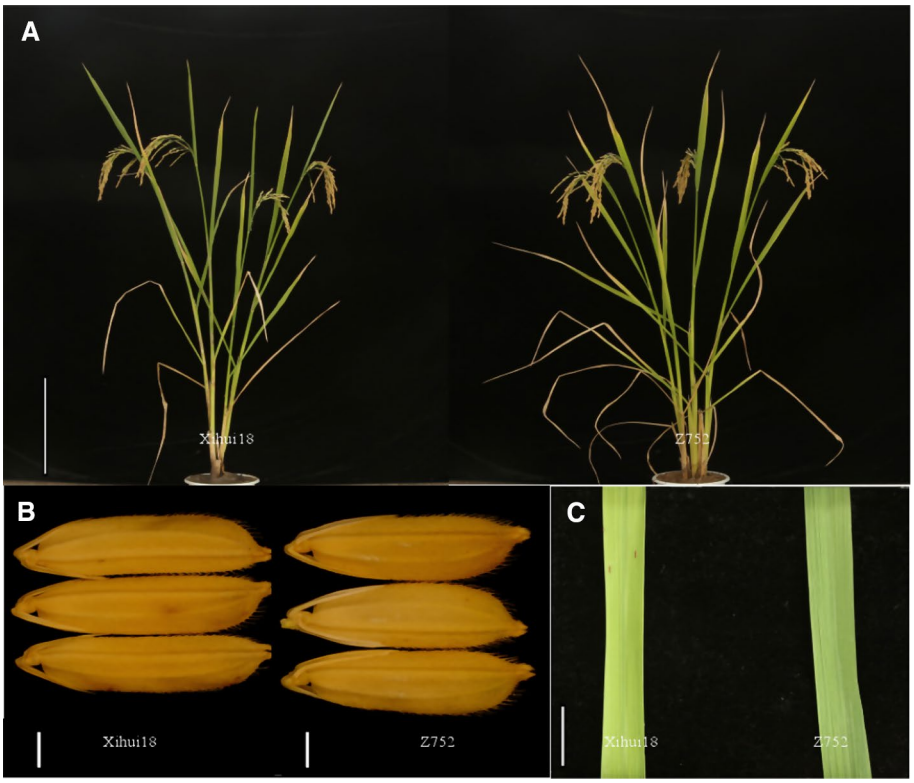

Fig. 2 Phenotype of Xihui 18 and Z752. **a**: Photos of plants of Xihui 18 and Z752 in the mature stage; bar = 25 cm. **b**: Photos of seeds of Xihui 18 and Z752; bar = 500um. **c**: Photos of leaves at heading stage of Xihui 18 and Z752; bar = 1 cm

Table 1 Statistical parameters of different traits in Xihui 18, Z752, and the F_2 population

Trait	Mean ± SD (parents)		Average ± SD (parents) SD (F_2 population)	Range	Skewness	Kurtosis
	Xihui 18	Z752				
Effective panicle number	4.20 ± 0.63	6.30 ± 1.16**	10.65 ± 5.63	3.00–27.00	0.52	−0.50
Panicle length (cm)	27.04 ± 1.04	27.60 ± 1.96	23.65 ± 3.81	17.56–31.87	0.43	−1.11
Number of primary branch	16.61 ± 0.69	15.67 ± 2.12	11.89 ± 3.31	6.89–23.29	0.64	−0.10
Number of secondary branch	42.73 ± 5.96	42.89 ± 14.58	26.89 ± 13.37	7.00–59.67	0.77	−0.59
Grain number per panicle	201.46 ± 24.21	215.98 ± 22.66	130.41 ± 85.67	2.38–323.25	0.78	−0.99
Spikelet number per panicle	228.82 ± 25.83	239.95 ± 25.46	155.25 ± 84.56	23.18–353.50	0.72	−0.98
Seed-setting rate (%)	87.99 ± 0.02	90.09 ± 0.02	0.80 ± 0.19	9.00–95.00	−2.08	4.14
Grain length (mm)	10.18 ± 0.14	9.96 ± 0.15 *	8.67 ± 1.04	7.00–10.40	0.03	−1.35
Grain width (mm)	2.76 ± 0.08	3.01 ± 0.02**	2.94 ± 0.23	2.40–3.50	0.34	−0.33
100-grain weight (g)	2.53 ± 011	2.89 ± 0.08**	2.63 ± 0.28	1.99–3.42	0.11	−0.17
Yield per plant (*g*)	24.82 ± 4.82	32.96 ± 2.15**	29.76 ± 12.11	4.92–57.49	0.26	−0.3
Plant height (cm)	132.96 ± 4.38	134.93 ± 4.16	110.57 ± 17.57	83.00–150.00	0.18	−1.38

*and **indicate significant difference between traits of Xihui 18 and Z752 at $P < 0.05$ and $P < 0.01$, respectively

on chromosome 10. Nevertheless, Z752 will also have application potential for rice molecular design breeding of Xihui 18 series.

Furthermore, the secondary F_2 population constructed by crossing Xihui 18 and Z752 was used to identify 10 QTLs for important agronomic traits, which were distributed on 6 substitution fragments of Z752. Due to *OsGS*1 encoding, a glutamine synthetase (Tabuchi et al. 2005) was located in the substitution region of *qPH*2, lacking *OsGS*1 causes severe reduction in rice growth rate, we suspected that *OsGS*1 might be with the *qPH*2. Also, *qPH*6 may be allele with *D*35. *D*35 encodes a ent-kaurene oxidase enzyme (KO) that catalyzes the early steps of gibberellin biosynthesis (Itoh et al. 2004). *qGP*2 and *qSSR*2 maybe belonged to pleiotropy, linked with the same marker Rm3874, where *Ghd*2 (Liu et al. 2016) was located. *Ghd*2 is a multifunctional gene that controls plant height and the number of spikelets per panicle(Liu

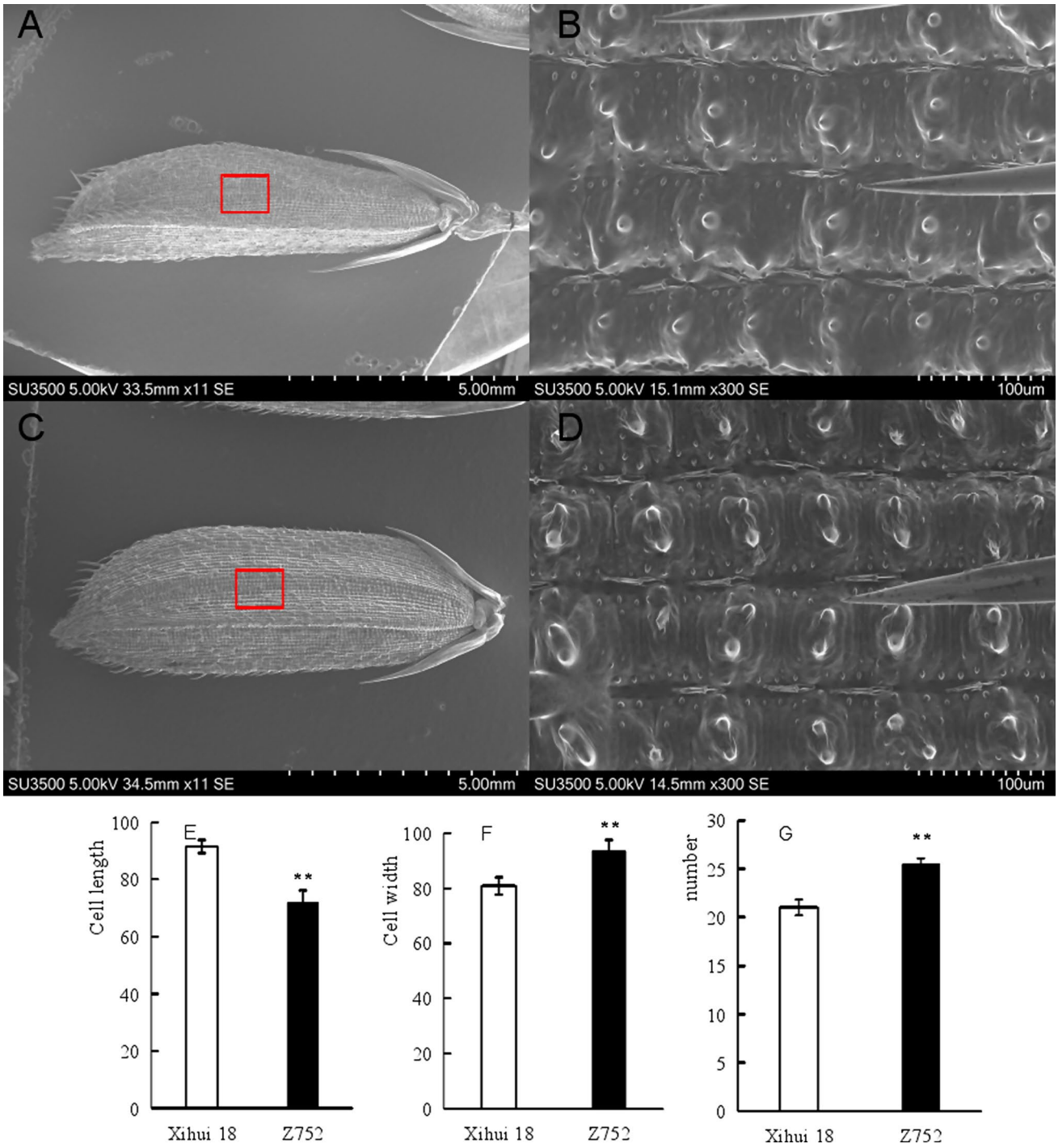

Fig. 3 Scanning electron microscopic observation and analysis of the glume **a**, **b**: scanning electron microscopy of the glume of Xihui 18; **c**, **d**: scanning electron microscopy of Z752 glume; **e**, **f**, **g**: statistics of the length, width and number of cells per unit area of the epidermal cells of the glume

et al. 2016). Overexpression of *Ghd*2 resulted significantly increased the number of grains per panicle and plant height under normal conditions. *qGW*5 and *qRLW*5 are also linked at the same marker, which also should be pleiotropic. In this substitution interval, *GW*5 has been cloned. *GW*5 is a novel positive regulator of BR signaling and a viable target for genetic manipulation to improve grain yield in rice and perhaps in other cereal crops as well (Liu et al. 2017). In addition, we found that *GW*2, *AFG*1, *OsmiR*396*c*, *OsMKK*4, *OsNf-YB*1 and *GS*2 were all

Table 2 QTLs for rice important agronomic traits detected in Z752

Trait	Chr	QTL	Linked marker	Additive effect	Var. (%)	*P* value	Possible alleles
Effective panicle number	3	*qPN3*	RM489	1.08	8.18	0.0463	*HTD2*
	5	*qPN5*	RM169	1.05	7.69	0.0494	
Plant height	2	*qPH2*	RM5472	6.39	46.87	0.0025	*OsGS1*
	6	*qPH6*	RM7434	−7.72	65.41	0.0333	*d35*
Grain number per panicle	2	*qGP2*	RM3874	27.51	24.57	0.0198	*Ghd2*
Seed-setting rate	2	*qSSR2*	RM3874	9.00	29.00	0.0285	*Ghd2*
Grain length	3	*qGL3*	RM489	−0.18	11.93	0.0124	*HTD2*
	2	*qGW2*	RM6378	0.11	45.55	0.0049	
Grain width	5	*qGW5*	RM169	0.11	46.28	< .0001	*GW5*
Rate of length to width	5	*qRLW5*	RM169	−0.16	19.33%	0.0017	*GW5*

in the *qGW2* substitution region. *GW2* encodes a cyclic E3 ubiquitin ligase located in the cytoplasm that negatively regulates cell division by anchoring its substrate to the proteasome for degradation (Yu et al. 2020). *AFG1* is a transcriptional activator, which may regulate grain size of rice by regulating cell proliferation and elongation and regulate rice quality by affecting the expressions of *GluD*, *RM1*, *Prol14*, *RP10* and *OsSSIVa* (Kawakatsu et al. 2009; Yu et al. 2020). In *OsmiR396c* overexpressing transgenic rice, the width, length and weight of grain decreased (Li et al. 2016b). *OsMKK4* regulates the size of rice grains by regulating cell proliferation and may be used as a connection factor between MAPK pathway and BRs in seed growth (Duan et al. 2014). *OsNf-yb1*, through interaction with transcription factor *OsERF,* may form protein complexes containing *OSNF-YB1*, *OSNF-YC* and *ERF*, specifically regulate the transcription of middle and downstream genes in rice endosperm development and regulate grain filling and endosperm development (Li et al. 2016a). *GS2* interacts with transcriptional co-activator *OsGRFs* to regulate cell elongation and cell division, affecting rice grain type and grain weight (Sun et al. 2016). Whether these genes are allelic or not, they need to be validated by genetic complementary experiment. These QTLs are important to both explain the diversity of biological trait phenotypes and rice breed practice.

We identified a short-wide grain chromosomal segment substitution line Z752 in the background of Xihui 18. Z752 contained 13 substitution segments with an average length of 3.69 Mb and displayed short-wide grain and significant increased number of effective panicle per plant and yield per plant. In six substitution segments of Z752, we detected 10 QTLs for 7 rice important agronomic traits. Increase in the effective panicle number per plant of Z752 was controlled by *qPN3* and *qPN5*. The short-wide grain of Z752 was controlled by *qGL3*, *qGW2* and *qGW5*. The results will be important for further functional analysis and rice molecular breeding of these QTLs.

Author contributions CWZ and FMZ conceived and designed the research. LJC, HY, XLZ, DD, XMP, FMZ, JCD and ZLY assisted in the experiments. LJC and HY analyzed the experimental data and wrote the manuscript. All authors discussed the results and commented on the manuscript.

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Data availability All data are fully available without restriction.

Declarations

Conflict of interest Authors have no conflict of interest to declare.

Ethical approval All analyses were based on previously published studies; thus, no ethical approval and patient consent are required.

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