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RESEARCH ARTICLE

Fine mapping and grain yield analysis of a major QTL controlling primary branch number in rice (*Oryza sativa* L.)

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Abstract Panicle size is one of the most important agronomic traits highly associated with grain yield in rice. For quantitative trait locus (QTL) analysis and breeding utilization of panicle size in rice, a large panicle rice line YR1 was used as a donor to cross and backcross with a commercial cultivar Ningjing 1 (NJ1), and developed backcross populations. In a BC_2F_2 population, a total of 3 QTL associated with panicle size were found on chromosome 1 and 8. Two of the QTLs, *qPBN1* and *qGNP1*, were mapped to an interval on chromosome 1, where a previously cloned gene *GN1a* was located. *qPBN8*, a major QTL for primary branch number on chromosome 8, was finally narrowed to a 51.8 kb region, containing reported gene *OsSPL14* regulating branch number and plant architecture. Through sequence and expression comparison, the *qPBN8* was considered to be the allele of *OsSPL14*. The investigation of yield structure in six pairs of near-isogenic lines revealed that the effects of *qPBN8* on grain yield were related to the length of vegetative period. The *qPBN8* allele of large panicle was suitable for late-maturing varieties to improve yield.

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Introduction

Grain yield is one of the most valuable traits in crop production. Increasing rice yield per unit area is particularly important in the global situation that crop yields on limited arable land are provided to a growing population (Takai et al. 2018). Therefore, cultivating high-yield varieties is one of the most economical and effective approach to solve rice yield. Different environments and cultivation methods require different varieties to achieve high yield. In the high humidity environment where most rice grows, large-panicle varieties can effectively improve field climate, reduce disease and lodging incidence (Peng et al. 2008). Moreover, direct-seeded rice is becoming a global tendency of labor-saving rice production (Kumar and Ladha 2011), and claim suitable varieties that has the characteristics of large-panicle, thick stem, less tillers or panicles and rapid seedling (Liu et al. 2015).

It has been recognized that panicle size is the major factors for rice yield. Panicle traits includes four factors: panicle length (PL), primary branch number (PBN), secondary branch number (SBN), and spikelet number per panicle/grain number per panicle (SPP/GNP) (Peng et al. 2014). Primary and secondary

branches bear spikelets. The number of spikelets is an important determinant of grain yield (Bai et al. 2016). SBN and GNP are positively correlated (Luo et al. 2009; Mei et al. 2006). During panicle development, the inflorescence meristem is an important regulator of grain number formation (Li et al. 2013; Sasaki et al. 2017). The inflorescence meristem initiates primary branch meristems. The primary panicle branches also produce a certain number of secondary branch meristems, which generate secondary panicle branches or differentiate into spikelets. Ultimately, the primary and secondary branch meristems differentiate into terminal spikelets (Tabuchi et al. 2011; Xing and Zhang 2010).

In recent years, many quantitative trait loci (QTLs) for grain number have been identified. Some genes or loci related grain number in rice have been cloned. Such as, *Gn1a* which encodes a cytokinin oxidase/dehydrogenase (CKX), was the first isolated QTL for grain number (Ashikari et al. 2005). *APO1* positively controls spikelet number by suppressing the precocious conversion of inflorescence meristems to spikelet meristems (Ikeda et al. 2007). *Ghd7* was reported to function in rice growth, development and environmental response, thus regulating rice grain yield, plant height and heading date (Weng et al. 2014; Xue et al. 2008). Artificial selection for the PROSTRATE GROWTH 1 (*PROG1*) mutant during rice domestication led to the transition from the plant architecture of wild rice to that of domesticated rice, resulting in erect growth, greater grain number and higher grain yield (Jin et al. 2008; Tan et al. 2008). *DEP1* enhanced meristematic activity, increased number of grains per panicle and a consequent increased in grain yield (Huang et al. 2009). *WFP/IPA1* regulates primary branch number and ideal plant architecture (Jiao et al. 2010; Miura et al. 2010). *SPIKE/NAL1* can increase spikelet number without changing grain quality or growth period (Fujita et al. 2013). *PAY1* affects plant architecture and grain yield in rice (Zhao et al. 2015). *NOG1*, which encodes an enoyl-CoA hydratase/isomerase, increases the grain yield of rice by enhancing grain number per panicle without a negative effect on the number of panicles per plant or grain weight (Huo et al. 2017). Molecular characterization of genes controlling rice grain yield will not only strengthen our understanding of regulatory mechanisms of these traits, but also be valuable for high-yield breeding in rice.

In this study, QTL analysis was carried out in BC_2F_2 population. A major QTL (*qPBN8*) was detected on chromosome 8. The target region was narrowed by map-based cloning strategy with BC_2F_4 population. Based on sequencing and expression analysis, the predicted ORF3 for *qPBN8* encoding the plant-specific transcription factor *OsSPL14*, was proved to be not only responsible for branch number (Miura et al. 2010), but also for ideal plant architecture (Jiao et al. 2010).

Materials and methods

Plant materials

YR1 is an F_8 line with erected large panicles, and selected from the selfing of a hybrid rice Yongyou 11. Ningjing 1 (NJ1) is a commercial japonica cultivar that is widely planted in the Lower Yangtze River of China. YR1 was crossed with NJ1, and F_2 plants with large panicles were continuously backcrossed with NJ1, so that the beneficial trait of large panicle was introduced into NJ1 background. A BC_2F_2 population of 164 plants was used for preliminary QTL mapping of panicle size. Subsequently, the heterozygotes from BC_2F_2 population were selected by marker assisted selection (MAS) to generate segregating BC_2F_3 populations for QTL confirmation. A total of 1374 BC_2F_4 plants were used for fine mapping. In addition, heterozygous plants from F_2 and BC_1F_2 with different other agronomic traits were successively self-pollinated and keep residual heterozygous *qPBN8* by MAS to F_6 and BC_1F_5. At last each residual heterozygote was formed a pair of pure lines (near-isogenic line, NIL) in F_8 and BC_1F_7, whose *qPBN8* come from two different parents, and each pair of NIL has its own genetic background. These NILs were used to evaluate the *qPBN8* effects on grain yield.

Field experiments and trait evaluation

Rice materials were grown in the field at the Experimental Station of Nanjing Agricultural University (Jiangsu Province, China). Field management was carried out in keeping with the local standard methods (Cheng et al. 2014). At maturity, panicles on the main stems were harvested, and then dried naturally after harvesting and stored at 45 °C for 3 days before

testing (Zhu et al. 2011). Panicle length (PL), primary branch number (PBN), secondary branch number (SNB), spikelets number per panicle (SPP) and seed setting rate (SSR) were evaluated as the mean measurement from the three main-stem panicles. Heading date is described by the number of days from seeding to initial heading, and initial heading is 10% of the panicles in population extracted from the sheathes.

Molecular marker development

Simple sequence repeat (SSR) markers were designed as described on the Gramene database (http://www.gramene.org/). Insert and deletion (InDel) markers were newly designed on the RiceVarMap v2.0 database (http://ricevarmap.ncpgr.cn/v2/).

Linkage and QTL analysis

A total of 119 polymorphic SSR markers and InDel markers evenly distributed on 12 chromosomes were used to identify the genotypes of 164 BC_2F_2 individuals in this study. The genomic DNA of each plant was extracted from fresh rice leaves according to a modified CTAB protocol. PCR was performed as following: 95 °C for 3–5 min, followed by 32–35 cycles of 95 °C for 15 s, 55–60 °C for 20 s, 72 °C for 40 s, and a final elongation step at 72 °C for 5 min. The PCR products were analyzed on 6–8% agarose gels, which depend on PCR product length. The genetic map construction and QTL analysis were conducted by the composite interval mapping method using the IciMapping4.1.0 (www.isbreeding.net/) software. We selected the LOD threshold of 3 and walking speed of 1.0 cM for QTL identification (Fang et al. 2016).

Fine mapping

To further narrow down *qPBN8* locus, new polymorphic molecular markers were developed (Table 1). For the convenience of scoring the phenotype, numbers of primary branch were selected as the target trait for fine mapping. BC_2F_4 individuals were used to screen recombinant events between InDel markers S98 and S21, flanking *qPBN8*. Nucleotide sequence alignment of candidate genes were performed between YR1 and NJ1.

RNA extraction and expression analysis

Total RNA was extracted from young panicles with the RNA extraction kit (Bioteke). The complementary DNA (cDNA) was synthesized with random oligo nucleotides utilizing a reverse transcription system (vazyme). Quantitative real-time PCR (20 µl reaction volume) was conducted using 1 µl of cDNA, 0.5 µl of each primer and 10 µl of AceQ qPCR SYBR Green Master Mix (vazyme, http://www.vazyme.com/) in a Roche480 real-time PCR detection system. The rice *Actin* gene (Os03g0718100) was used as the internal control. Each sample was performed in triplicate. A relative gene expression level was calculated using the comparative Ct method (Livak and Schmittgen 2001). The gene-specific primers were shown on Table 1.

Grain yield evaluation of *qPBN8* NILs

Six pairs of *qPBN8* NILs with different heading date were seeded in nursery trays containing nutrient matrix. After 30 days, the NILs were transplanted to experimental plot in randomized complete block design with three replications. Each replication had forty plants in a density of 25 cm (4 lines) × 13.3 cm (10 plants). Twenty plants, excluding marginal effects, were collected to evaluated yield structure, when the grain matured. The agronomy traits were surveyed included heading date, panicle number per plant, spikelet number per panicle, seed setting rate, thousand grain weight and grain yield per plant.

Results

Phenotypic variation

The two parents, YR1 and NJ1, displayed significant differences in the panicle traits examined (Fig. 1, Table 2). The main panicle of the commercial cultivar NJ1 has approximately 16.7 cm in length, 164.3 spikelets, 13.3 primary branches, 21.7 secondary branches, and 93.1% seed setting rate. However, that of YR1 has approximately 19.3 cm in length, 421.0 spikelets, 23.0 primary branches and, 76.0 secondary branches, and 89.3% seed setting rate. Moreover, YR1 heading date is about 30 days earlier than NJ1 (Table 2). A great differences existed between two parents in panicle traits, which provided an abundance

Table 1 Primers for fine mapping *qPBN8* and Real-time PCR

Markers	Forward primer	Reverse primer	Product size (bp)	Intention
S10	CAGCGTGCTTAGGATGCAAA	CGCTCTAACGGTGGTTTTCA	126	Fine mapping
S15	CCGACAAATCTGATAATGACTG	CGACCAAATGCCAATGTAAG	193	
S21	ACTCTTTGGTGCCAAGTTGC	TTCGTGGTAAACTTGGTTGAATC	124	
S28	CCTACCTTTGAACACTCACTGA	GCAGGACGACAGATTGAGAA	96	
S30	GGAGGAAGCAAATCATTAGTG	CTGAGTAAAATGAATCGTCGAA	197	
S36	GAGTAGTCTTGACTTTGACCA	GATGCCTGGTTGATTTAGT	95	
S45	ATCTTGGGGCTTGTGCTT	TGAACTTGGTCTGAGAGGTTTC	211	
S98	CCAACCTGCTTTCCTTTGCT	GCTGCACATAAAAGAGGAGGG	127	
IPA	CACCTATGTTGCAGCTGTGGTA	CTGAATCTTCTGTGGTAAGGAC	4496	Gene cloning
Action	AGGAAGGCTGGAAGAGGACC	CGGGAAATTGTGAGGGACAT	181	Real-time PCR
qIPA1	GGATATGGTGCCAACACATACAG	GACATGGCTGCAGCCTGGTTGTG	209	

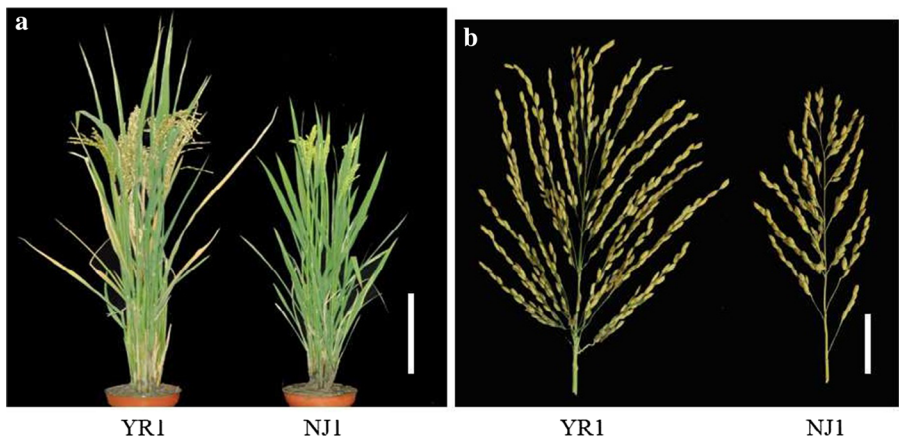

Fig. 1 Phenotype of two parents. **a** Morphology of NJ1 and YR1. Scale bar, 30 cm; **b** panicle feature of NJ1 and YR1. Scale bar, 4 cm

Table 2 Data collection of panicle traits in parents and BC_2F_2 population

Traits	YR1	NJ1	BC_2F_2		
			Average	Range	SD
PL	19.3 ± 0.57	16.7 ± 0.57	15.8	12.7–19.2	− 0.60
PBN	23.0 ± 1.52	13.3 ± 1.15	19.0	10.0–29.0	4.14
SBN	76.0 ± 3.05	21.7 ± 2.50	32.1	6.3–100.0	14.98
SPP	421.0 ± 15.62	164.3 ± 8.40	203.6	77.5–450.0	60.25
SSR (%)	89.3 ± 4.60	93.1 ± 3.20	86.4	36.3–97.7	11.46
HD	74.4 ± 1.60	104.0 ± 2.40	94.5	86.2–131.0	2.24

of trait variation for population development and QTL mapping. The frequency distribution of PL, PBN, SBN, SPP and SSR in BC_2F_2 population are shown in Fig. 2. The panicle length and the primary branch are close to a normal distribution, and the positive super-parent individuals of primary branch are relatively more. The variation of the number of secondary branches and spikelets per panicle is large, showing a skew distribution, and the number of positive super-parents is small. The seed setting rate is skewed, and most individuals have a high seed setting rate.

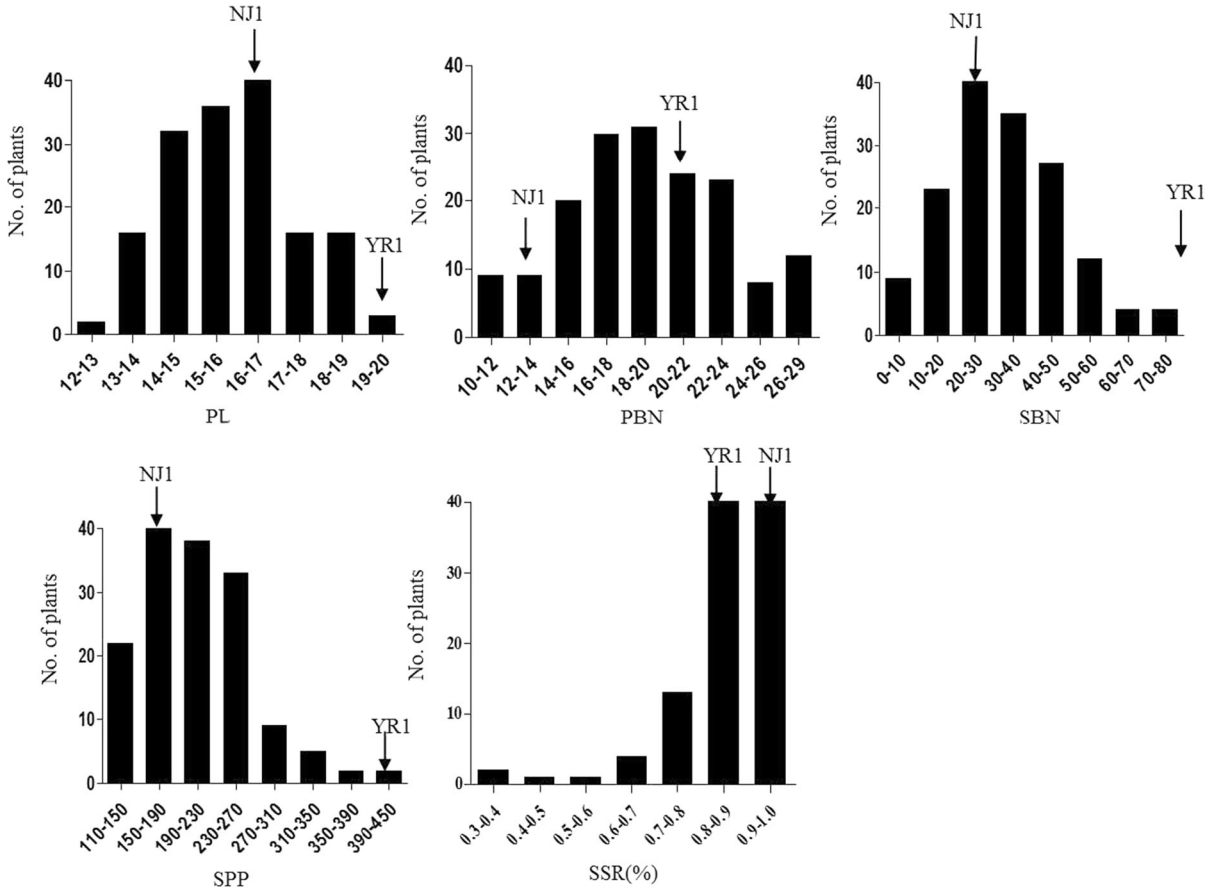

Fig. 2 Frequency distribution of panicle traits in the BC_2F_2 population

Quantitative trait loci mapping

To uncover the genetic factors of panicle size, QTL analysis was performed in a BC_2F_2 population of 164 individuals. 119 Polymorphic markers distributed on 12 chromosomes were used to identify the genotypes of BC_2F_2 individuals (Fig. 3). For five panicle traits as mentioned above, only three major QTL were identified on chromosomes 1 and 8 (Table 3, Fig. 3). *qSBN1* and *qGNP1* controlling secondary branch number (SBN) and spikelets per panicle (SPP) respectively, shared the same interval between markers RM8105 and RM1220 on chromosome 1, explaining 30.6% and 25.4% of phenotypic variance with an additive effect of 11.0 secondary branches and 34.7 spikelets, respectively. In this interval, a reported grain number locus *Gn1a* was located (Ashikari et al. 2005). *qPBN8*, a QTL for primary branch number (PBN), was located between InDel markers S4 and S21 on chromosome 8. This QTL explained 39.6% of phenotypic variance with an additive effect of 3.6 primary branches in the BC_2F_2 population. YR1 allele had dominant and positive effects on primary branches. No QTL was identified controlling PL and SSR. In addition, one QTL of heading date was located on chromosome 10, explaining 7.3% of phenotypic variance with an additive effect of 5.4 heading date.

For verification of the *qPBN8* loci, the BC_2F_2 plants with heterozygous *qPBN8* and homozygous NJ1 *qSBN1* locus were developed to BC_2F_3 populations. 134 plants of a BC_2F_3 line were used for *qPBN8* remapping. The results showed that the *qPBN8* was narrowed to an interval between markers S98 and S21, explaining 43.4% phenotypic variation with an additive effect of 4.4 primary branches (Fig. 4, Table 3). A QTL for the spikelet number *qSPP8* was detected in this interval, and explained 18.3% of phenotypic variation with an additive effect of 27.4 spikelets. This

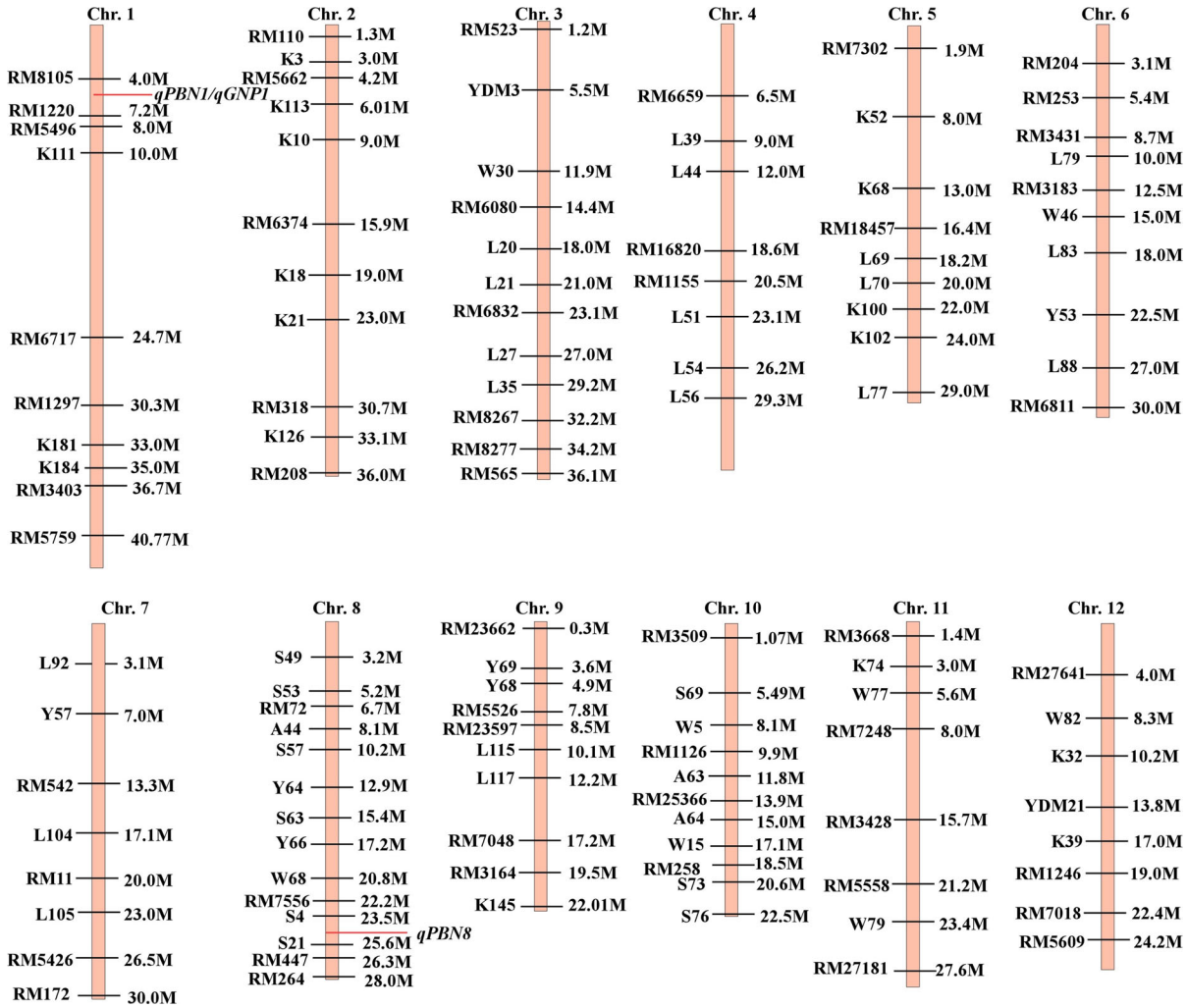

Fig. 3 Distribution of 119 molecular markers on chromosomes and location of the QTL mapped on the chromosome in BC_2F_2 population

Table 3 QTL detected in the BC_2F_2 and BC_2F_3 population

Trait name	Generation	QTL	Chr	Left marker	Right marker	LOD	PVE (%)	Add	Dom
PBN	BC_2F_2	*qPBN8*	8	S4	S21	9.433	39.575	3.567	0.173
SBN		*qSBN1*	1	RM8105	RM1220	6.932	30.601	10.988	4.146
SPP		*qSPP1*	1	RM8105	RM1220	6.141	25.473	34.793	21.408
HD		*qHD10*	10	RM258	S73	8.023	7.252	5.421	− 13.968
PBN	BC_2F_3	*qPBN8*	8	S98	S21	16.604	43.371	4.448	0.775
SPP		*qSPP8*	8	S98	S21	5.926	18.382	27.405	15.917

shows that increasing the number of primary branches can increase the number of spikelets.

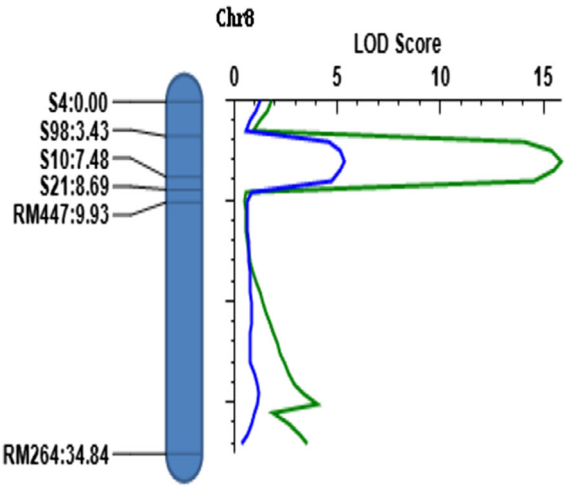

Fig. 4 QTL analysis of target region in BC_2F_3 population

Fine mapping of *qPBN8*

In 1374 BC_2F_4 plants, a total of 56 recombinant events were detected between InDel markers S98 and S21. Through phenotype analysis of the crucial recombination plants and their next generation, *qPBN8* was delimited to a 51.8 kb region between the marker S30 and S10 (Fig. 5). There are six annotated genes in the 51.8 kb region, referring to Rice Genome Annotation Project. ORF1 encodes Os8bglu27-beta-glucosidase. ORF2 encodes G-patch domain containing protein. ORF3 encodes the plant-specific transcription factor *OsSPL14*. ORF4 might encode hypothetical protein. ORF5 and ORF6 might encode retro-transposon protein (Table 4). Previous study demonstrated that ORF3 (*LOC_Os08g39890*) regulates primary branch number and ideal plant architecture (Jiao et al. 2010; Miura et al. 2010). Therefore, ORF3 was selected as the candidate gene for further analysis.

Sequence and expression comparison of *OsSPL14*

Sequence analysis revealed that there was no difference in the coding region of *OsSPL14* between two parents. The expression level of *OsSPL14* at the 1–2 mm panicle stages was about ninefold higher in YR1 than in NJ1. But there is no difference at the 5–10 cm panicle stages (Fig. 6).

The yield effect of *qPBN8*

In six pairs of NILs, all the lines with YR1 *qPBN8* allele had fewer tiller, more spikelets, lower seed setting rate and slightly larger grain, showing the basic

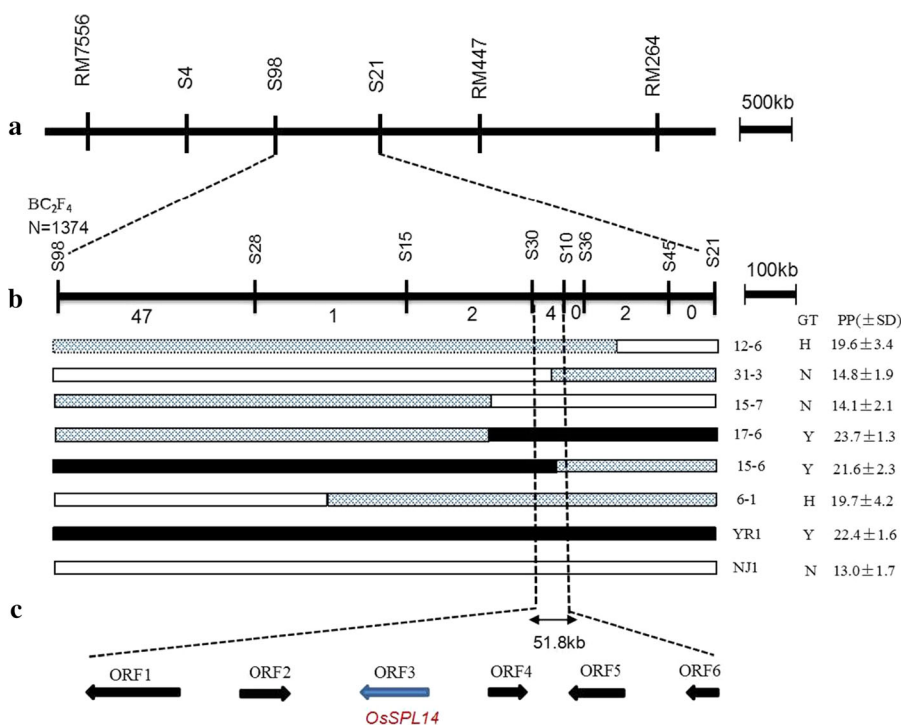

Fig. 5 Fine mapping of *qPBN8*, **a** location of *qPBN8* on rice chromosome 8, **b** high-resolution linkage analysis of *qPBN8* locus. Recombinants numbers are given between markers. The hollow, black and grille bars represent genotypes of NJ1, YR1 and heterozygote, respectively. Serial numbers indicated the key recombinants. GT is the derived genotype of recombinant plant by the phenotype of its progeny line, N (NJ1), Y (YR1), H (heterozygote). PP (± SD) is average value (± standard error) of phenotype of progeny line. **c** Open reading frames (ORFs) within mapped interval of the *qPBN8* on rice genome annotation project

Table 4 Candidate genes for the *qPBN8* in the 51.8 kb region

ORF	Gene	Nucleotides length	CDS length	Predicted protein length	Putative function
ORF1	LOC_Os08g39870	6812	1503	500	Os8bglu27—beta-glucosidase homologue similar to Os4bglu12 exoglucanase, expressed
ORF2	LOC_Os08g39880	3571	744	247	G-patch domain containing protein, expressed
ORF3	LOC_Os08g39890	4248	1254	417	OsSPL14—SBP-box gene family member, expressed
ORF4	LOC_Os08g39900	627	306	101	Hypothetical protein
ORF5	LOC_Os08g39910	2995	2673	890	Retrotransposon protein, putative Ty3-gypsy subclass, expressed
ORF6	LOC_Os08g39920	966	966	321	Retrotransposon protein, putative Ty3-gypsy subclass, expressed

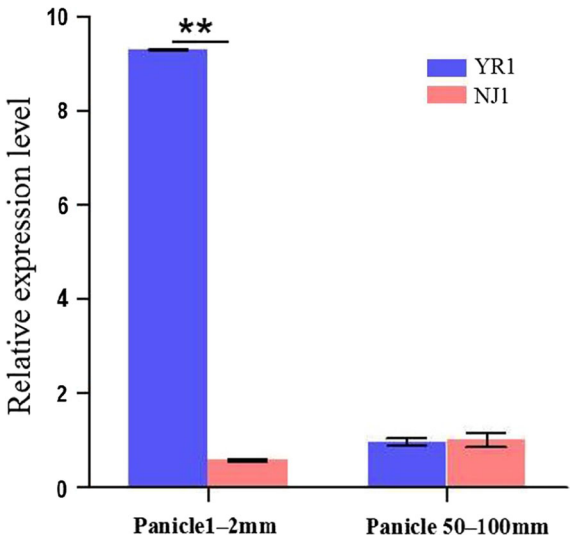

Fig. 6 Expression level of *OsSPL14* by real-time PCR

characteristics of *qPBN8*. NILs of *qPBN8* were derived from different F_2 and BC_1F_2 heterozygotes. Their genetic background were very different especially in vegetative growth. The days from seeding to heading ranged from 69 to 115 days. The yield of NIL was related to the length of vegetative period. Between early-maturing NILs, the grain yield of the NIL with YR1 allele of *qPBN8* was significantly lower than that with NJ1-*qPBN8*. However, between late-maturing NILs, the yield of YR1-*qPBN8* NILs was significantly higher than that of NJ1-*qPBN8* NILs (Table 5).

Discussion

Increasing yield is one of the most important goals in rice breeding. Grain number per panicle is a major component of rice yield that is typically controlled by many quantitative trait loci (QTLs). The identification of QTLs controlling grain number per panicle in rice would be valuable for the breeding of high-yielding rice (Hu et al. 2018; Zhu et al. 2011). Many QTLs for yield related traits have been verified and used for developing high yield rice (Miura et al. 2011). Panicle traits have been the vital factors for rice yield. It includes four factors: panicle length, primary branch number, secondary branch number, and spikelet number (Cheng et al. 2007; Peng et al. 2014). Increasing the value of each panicle characteristic would be an effective method for improving grain yield. To develop varieties with a large number of grain is a major direction in super rice breeding. Most of QTLs controlling GNB/SPP and SBN were located in cluster or closely linked on chromosomes, and the directions of their additive effects were consistent, which explained the genetic basis of significant correlations between their phenotypic characters (Luo et al. 2009). Therefore, one of the methods to increase yield is to pyramid the favorable alleles in the present high-yielding cultivar backgrounds (Takai et al. 2018).

In this study, panicle traits were focused on and genetic analysis was carried out in BC_2 population derived from donor parent YR1 and recurrent parent NJ1. The two QTLs, *qSBN1* and *qGNP1*, were mapped to the same interval of *GN1a* (Ashikari et al. 2005).

Table 5 Agronomy traits of six paired near-isogenic lines of *qPBN8*

Heterozygote	NILs		Heading date	No. of panicle	No. of spikelets per panicle	Seed setting rate (%)	1000-grain weight (g)	Yield per plant
$F_{2:6}$	F_8	S	69.67 ± 0.58	5.35 ± 0.06	90.73 ± 2.46	76.63 ± 1.80	25.63 ± 0.21	9.56 ± 0.28
		L	68.67 ± 1.15	3.67 ± 0.12**	111.23 ± 5.12**	72.60 ± 0.53*	26.50 ± 0.17**	7.84 ± 0.11**
$F_{2:6}$	F_8	S	85.00 ± 0.00	5.95 ± 0.07	92.25 ± 2.90	82.90 ± 0.99	26.35 ± 0.07	11.99 ± 0.12
		L	85.50 ± 0.71	4.20 ± 0.14**	110.75 ± 5.30*	76.00 ± 0.14*	27.30 ± 0.28*	9.64 ± 0.22**
$F_{2:6}$	F_8	S	114.33 ± 0.58	7.07 ± 0.12	121.50 ± 3.10	87.83 ± 1.00	25.70 ± 0.10	19.37 ± 0.03
		L	115.00 ± 0.37	6.17 ± 0.00**	138.23 ± 0.00**	88.00 ± 0.81	26.70 ± 0.00**	20.02 ± 0.01**
$BC_1F_{2:5}$	BC_1F_7	S	74.33 ± 1.15	5.17 ± 0.15	100.33 ± 3.36	77.37 ± 1.19	26.20 ± 0.20	10.50 ± 0.21
		L	73.00 ± 0.00	3.60 ± 0.10**	124.77 ± 2.28**	72.23 ± 1.79*	26.83 ± 0.15*	8.71 ± 0.53**
$BC_1F_{2:5}$	BC_1F_7	S	109.33 ± 0.58	6.37 ± 0.06	115.83 ± 3.16	90.97 ± 1.10	26.43 ± 0.25	17.73 ± 0.52
		L	111.33 ± 1.15	5.77 ± 0.15**	135.47 ± 3.01**	87.77 ± 1.18*	26.83 ± 0.15	18.39 ± 0.21
$BC_1F_{2:5}$	BC_1F_7	S	115.00 ± 0.00	6.90 ± 0.14	109.70 ± 1.98	91.25 ± 1.63	26.35 ± 0.07	18.20 ± 0.23
		L	116.33 ± 0.58	5.73 ± 0.12*	140.93 ± 4.69*	88.67 ± 0.93	27.8 ± 0.20**	19.91 ± 0.44*

Values are mean ± standard error. * or ** indicate that large panicle differed significantly from small panicle at the 5% or 1% level, respectively (*t* test). L stand for larger panicle NIL with YR1 *qPBN8*. S stand for smaller panicle NIL with NJ1 *qPBN8*

One QTL (*qPBN8*) for primary branch were fine-mapped and targeted to *IPA1*/*WFP*. The YR1 alleles of QTLs on chromosomes 1 and chromosome 8 increased the number of grain per panicle, primary branch and secondary branch. The additive effect of three QTLs came from YR1. These results suggested that larger panicles can be achieved by pyramiding the favorable alleles of these QTLs. *qPBN8* was finally localized to 51.8 kb interval containing six annotated genes. Of them, ORF3 has been reported not only regulating branch number and plant architecture but also promoting both yield and disease resistance by sustaining a balance between growth and immunity (Jiao et al. 2010; Miura et al. 2010; Wang et al. 2018). There was no difference in nucleotide sequence. The expression level of *OsSPL14* was significantly higher in YR1 than NJ1 at the initial development stage of panicle (Fig. 6). And the primary branch number of YR1 was larger than NJ1. Therefore, it was considered that candidate of *qPBN8* is *OsSPL14* and plays an important role in controlling primary branch number and grain number.

In six paired NILs of *qPBN8*, the large panicle lines showed fewer tiller, more spikelets, lower seed setting rate and slightly larger grain. The yield of NILs was related to the length of vegetative period. The earlier the heading, the lower the yield. Between late-maturing NILs, the yield of YR1-*qPBN8* NILs was significantly higher than that of NJ1-*qPBN8* NILs. Between early-maturing NILs, however, the grain yield of the NIL with YR1-*qPBN8* allele was unexpectedly lower than that with NJ1-*qPBN8*. This means that the yield effect of the large panicle allele of YR1-*qPBN8* depended more on the length of vegetative period. The main reason for the result might be that the yield effect of more spikelets in early-maturing YR1-*qPBN8* NIL was difficult to compensate for its effect of fewer panicles and lower seed setting rate. Therefore, the *qPBN8* large panicle genotype was suitable for late-maturing varieties to increase yield.

Larger panicles have been an important target for improvement of rice grain yield because of its relationship with grain number. The utilization of favorable QTL panicles related, for example, *GN1A*, *IPA1*/*WFP*, *SPIKE*/*NAL1*, has increased the rice yield. Three QTL for the panicle traits were detected, which all were most likely to be *GN1a* and *IPA1*. The additive effect of three QTL all came from YR1. Our study suggest that larger panicles might be possible with the combination of the alleles of these QTLs. Therefore, pyramiding of elite QTLs will certainly benefit for breeding high-yield varieties by marker-assisted selection for rice in the future.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

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