Fine mapping and candidate gene analysis of a major QTL for panicle structure in rice

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Abstract

Key message A gene not only control tiller and plant height, but also regulate panicle structure by QTL dissection in rice.

Abstract An ideal panicle structure is important for improvement of plant architecture and rice yield. In this study, using recombinant inbred lines (RILs) of PA64s and 93-11, we identified a quantitative trait locus (QTL), designated qPPB3 for primary panicle branch number. With a BC3F2 population derived from a backcross between a resequenced RIL carrying PA64s allele and 93-11, qPPB3 was fine mapped to a 34.6-kb genomic region. Gene prediction analysis identified four putative genes, among which Os03g0203200, a previously reported gene for plant height and tiller number, Dwarf 88 (D88)/Dwarf 14 (D14), had three nucleotide substitutions in 93-11 compared with PA64s. The T to G substitution resulted in one amino acid change from valine in 93-11 to glycine in PA64s. Real-time PCR analysis showed expression level of D88 was higher in 93-11 than PA64s. The expression of APO1 and IPA1 increased, while GN1a and DST decreased in 93-11 compared with PA64s. Therefore, D88/D14 is not only a key regulator for branching, but also affects panicle structure.

Keywords Rice · Quantitative trait loci · Primary panicle branch number · Fine mapping · Panicle structure

Abbreviations

APO1 Aberrant panicle organization 1
BAC Bacterial artificial chromosome
BR Brassinosteroid
CK Cytokinin
CSSL Chromosome segment substitution line
DEP1 Dense erect panicle 1
DST Drought and salt tolerance
GFP Green fluorescence protein
GN1a Grain number 1 a
IPA1 Ideal plant architecture 1
LAX1, LAX2 Lax panicle 1, lax panicle 2
LYP9 Liang-you-pei-jiu
MAS Marker-assisted selection
Moc1 Mono-culm 1
ORF Open reading frame
OsCKX2 Cytokinin oxidase 2
OsSPL14 Squamosa promoter binding protein-like 14
PPB Primary panicle branch number
qPCR Quantitative PCR
QTL Quantitative trait locus
RIL Recombinant inbred line
Introduction

Plant architecture is very important for improving rice yield, grain quality, resistance to multiple biotic and abiotic stresses, and nutrient utilization efficiency. Panicle structure, belonging to plant architecture, is one of the important factors for rice yield. It includes four components: panicle length, primary panicle branch number, secondary panicle branch number, and spikelet number. Several genes that regulate the development of rice panicle branches have been cloned, such as \textit{MOC1} (Li et al. 2003), \textit{LAX1} (Komatsu et al. 2003), \textit{LAX2} (Tabuchi et al. 2011), \textit{GN1a/OsCKX2} (Ashikari et al. 2005), \textit{DST} (Li et al. 2013), \textit{DEP1} (Huang et al. 2009), \textit{SP1} (Li et al. 2009), and \textit{APO1} (Ikeda et al. 2007).

Panicle branches are lateral organs emerged at reproductive stage, and their number affects spikelet number. In some cases, panicle branches are regulated by common mechanisms shared with tiller formation and elongation. \textit{MOC1} and \textit{LAX1} were genes that regulate both tillers and panicle branches. Reduction in tiller number and panicle branch number was discovered in both mutants. Mutation in \textit{LAX2} led to decrease in tiller number. However, the primary panicle branch number remained unchanged (Tabuchi et al. 2011). The near isogenic lines (NILs) carrying \textit{ipa1} displayed reduced tillers and increased panicle branches (Jiao et al. 2010). \textit{DEP1} (Huang et al. 2009) was a major dominant QTL that control panicle branches. The NIL-\textit{dep1} showed more panicle branches, which may result from cell proliferation through \textit{GN1a} (Huang et al. 2009). \textit{APO1}, a pivotal gene to regulate primary panicle branch, controlled the vascular bundle formation and could increase the harvest index and grain yield in rice (Terao et al. 2010).

In this study, QTL analysis of panicle branches was performed with a RIL population derived from an \textit{indica/javanica} cross, and a major QTL (\textit{qPPB3}) for primary panicle branch number was detected on chromosome 3. The region of \textit{qPPB3} was narrowed by map-based cloning strategy with BC\textsubscript{3}F\textsubscript{2} population derived from a chromosome segment substitution line (CSSL). Based on sequencing and expression analysis, the predicted ORF for \textit{qPPB3} encoding a protein of the \(\alpha/\beta\)-fold hydrolase superfamily (D88/D14), was proved to be not only a key regulator for plant shoot branching (Jiang et al. 2013; Arite et al. 2009; Gao et al. 2009), but also effected primary panicle branching.

Materials and methods

Mapping population and phenotyping

The core mapping population of 132 LYP9 RILs was randomly chosen from 1,841 RILs derived by single-seed descend from a cross between an elite paternal inbred \textit{Oryza sativa, indica} cv. 93-11 and the maternal inbred \textit{Oryza sativa ssp. javanica} cv. PA64s, a photo-thermo-sensitive male sterile line with a mixed genetic background of \textit{indica}, \textit{javanica}, and \textit{japonica}. The population was developed in the experimental fields at China National Rice Research Institute in Hangzhou, Zhejiang Province, and in Sanya, Hainan Province, China. After 12 generations of self-fertilization, genomic DNA samples of the F\textsubscript{13} RILs were isolated for genotyping (Gao et al. 2013). Phenotyping was conducted according to Gao et al. (2013).

Data analysis and QTL detection

All statistical analyses were completed using the SAS (Statistical Analysis System) V8.01. QTL analysis was performed with the MultiQTL1.6 package (http://www.multiqtl.com) using maximum likelihood interval mapping (MIM) based on a permutation test (1,000 permutation, \(P = 0.05\)) for each dataset to confirm the LOD threshold. It was considered as a major effect QTL when its LOD was larger than 2.5. QTLs were named according to McCouch et al. (1997).

Acquisition of CSSL involving \textit{qPPB3}

To develop a CSSL containing \textit{qPPB3}, a line of RILs with PA64s’ genotype in the \textit{qPPB3} region was selected to backcross with recurrent parent 93-11. Two STS markers P1 and P2 (Table 1) were used for marker-assisted selection (MAS) of each generation in the segregating progenies. As a result, a BC\textsubscript{3}F\textsubscript{1} line GH18, with 93-11 genetic background exhibiting heterozygous across the entire \textit{qPPB3} region, was constructed. After self-crossing, we acquired a BC\textsubscript{3}F\textsubscript{2} population for fine mapping of \textit{qPPB3}.

Design of fine mapping markers

Primers were designed around \textit{qPPB3} on chromosome 3 using insertions/deletions (InDels) identified between 93-11 and PA64s (Gao et al. 2013) by two software, Primer Premier 5.0 and Oligo 7 (Table 1).
RNA extraction and real-time PCR analysis

Total RNA was isolated from panicles before booting stage with the micro RNA extraction kit (Axygen). DNase treatment, cDNA synthesis, primer design and SYBR Green I Real-time PCR were carried out as described (Vandesompele et al. 2002) using a ReverTra Ace qPCR-RT kit (TOYOBA, Japan). Real-time PCR amplification mixtures (10 μl) contained 50 ng template cDNA, 2 × SYBR Green PCR Master Mix (10 μl) (Applied Biosystems), and 200 nM forward and reverse primers. Reactions were run on an ABI PRISM 7900HT Sequence Detector (Applied Biosystems). The relative expression level of each transcript was obtained by comparing to the expression of the OsACTIN1 gene. Primers for D88, APO1, IPAI, GN1a, DST, and Actin are listed in Table 1.

Subcellular localization of D88

Full-length cDNA of D88 was isolated from Nipponbare and sequenced. Then it was inserted into the vector pCAMBIA1302. The D88::GFP fusion was made by inframe fusion of the full-length D88 cDNA with GFP. Rice transformation was performed by an Agrobacterium-mediated method (Hiei et al. 1994). The root tips of transgenic plants expressing the GFP fusions were observed directly with a microscope (Nikon 90i).

Results

Phenotypic performance of panicle branches in parents and RILs

Rice panicle branch traits include primary panicle branch number (PPB) and secondary panicle branch number (SPB). And they directly affect spikelet number per panicle (SN), a crucial factor for rice grain yield. Our study showed PPB was significantly related to SPB and SN, with correlation coefficient 0.5204 and 0.4062, respectively. SPB was significantly related to SN (r = 0.8568) (Table 2). The relationships of PPB, SPB, and SN were positive to each other. Therefore, increase in PPB help improve rice grain yield. In parents, spikelet number per panicle, primary panicle branch number and secondary panicle branch number of 93-11 are larger than PA64s. Significant difference existed between parents in spikelet number per panicle and secondary panicle branch number. On the contrary tiller number exhibits less in 93-11 than PA64s. (Fig. 1).

QTL analysis for PPB, SPB, and SN

SNP markers, covered all 12 chromosomes, were used to construct a high-resolution genetic linkage map with total genetic distance of 1,382 cM and an average distance of 0.53 cM between two adjacent SNP markers, as described in Gao et al. (2013).

QTL analysis was performed with MultiQTL1.6 using the maximum likelihood interval mapping approach with an LOD threshold 2.5. We detected two QTLs for PPB on chromosomes 3 and 8, named qPPB3 and qPPB8. The qPPB3 explained 9.4 % phenotypic variation with additive

### Table 1 Primers for fine mapping of qPPB3 and real time PCR

| Primer | Forward | Reverse | Experiment |
|--------|---------|---------|------------|
| P1     | TCGTCATATACTCTTTATG | AACCGCACTCTAGATTG | Mapping |
| P2     | ACCATGAACTCTAGCTGC | TGGCTTAAGACCGTCTCCT | Mapping |
| P3     | TCTCAACAACTGCACGGTTG | TGTGTTCAGCACATGTGC | Mapping |
| P4     | ACCTTAGATATTAGATCCAG | TGGTAAATAGCTAAATGTTG | Mapping |
| P5     | TGTCGATATCATACTACAC | AACGTCATGCCCTCAACTCTC | Mapping |
| P6     | TGGCCAATCAAGTCGACATTC | TCTCTGCTACTTCATGAC | Mapping |
| P7     | TCTTTATCGCTCCCATCGTT | TCGATTGACACCCCTCCTGTC | Mapping |
| Actin  | CATATTGGCTCGAGCGTTT | CCGAGCTTCTCATCTTCATGAA | Real-time PCR |
| D88    | CGCTCTCGCTCGCCACTC | TCGAACCCCGCTCTGTAGTC | Real-time PCR |
| APO1   | GTCATCTGAGTGTTGGTTGTCG | CAACAGATCTCATGGCAAG | Real-time PCR |
| IPAI   | GGATAGTGGCTGCAACACTACAG | GACATGGCTGCGCCCTGGTTG | Real-time PCR |
| GN1a   | TGTCTCCCTTACAAATGGTCG | CATCCTGACCTGCTTCTTCT | Real-time PCR |
| DST    | GCTAATGCTGGCGTTG | GAGATGGTGCTGGGTGGG | Real-time PCR |

### Table 2 Correlation coefficient of branch in RIL population

|          | PPB | SN |
|----------|-----|----|
| SN       | 0.5204* |
| SPB      | 0.4062* | 0.8568* |

* Significant at the level of 1 %
effect came from PA64s. And qPPB8 explained 15.3 % phenotypic variation came from 93-11. Two QTLs for SPB were identified. The qSPB1 was mapped on chromosome 1 and explained 10 % phenotypic variation with additive effect came from 93-11. The positive effect of qSPB9 was from 93-11, explained 9.6 % phenotypic variation. PPB and SPB are two key factors for SN determined by panicle architecture. Two QTLs, qSN8 and qSN9 for SN were mapped on chromosomes 8 and 9 with additive effects of 35.5 and 33.2, respectively (Table 3; Fig. 2a). They totally explained 25.4 % phenotypic variation.

Fine mapping of qPPB3

To narrow down the region of qPPB3, we developed seven markers (P1–P7). With 1,522 RIL populations, qPPB3 was fine mapped in the region between markers P1 and P2. Total 1,105 BC3F2 individuals were utilized to further mapping, and 17 lines were selected from BC3F2 progenies derived from the cross between GH18 and 93-11. Parent 93-11 and GH18 were designated as the controls L1 and L2, respectively. Out of ten lines with high PPB similar to L2 (genotype of PA64s), there were five recombinant events between P4 and qPPB3, four between P5 and qPPB3, one between P7 and qPPB3, one between P6 and qPPB3, four between P3 and qPPB3. On the other hand, among seven lines with low PPB similar to L1 (genotype of 93-11), there were two recombinant events between P4 and qPPB3, one between P5 and qPPB3, one between P3 and qPPB3, and P6 and P7 co-segregated with qPPB3. Finally, qPPB3 was delimited to an interval of 34.6-kb region between markers P6 and P7 on the BAC clone AC146702 (Fig. 2b, c).

A candidate gene for qPPB3

To screen candidate genes in the critical 34.6-kb genomic region of Nipponbare genome (http://rapdb.dna.affrc.go.jp/), and four corresponding genes (Os03g0203100, Os03g0203200, Os03g0203700, Os03g0203800) were found. After comparing sequence of the region between parents, only two genes, Os03g0203200 and Os03g0203700,
Table 3 QTL identified for panicle branch in the RIL population

| Trait | QTL   | Chr | Pos (cM) | LOD | P value | PVE  | A   |
|-------|-------|-----|----------|-----|---------|------|-----|
| PPB   | qPPB3 | 3   | 2.55–12.60 | 4.00 | 0.01    | 0.094 | -0.986 |
| PPB   | qPPB8 | 8   | 23.10–28.30 | 6.03 | 0.01    | 0.153 | 1.258 |
| SPB   | qSPB1 | 1   | 115.40–125.75 | 2.70 | 0.01    | 0.100 | 3.489 |
| SPB   | qSPB9 | 9   | 31.01–38.34 | 2.57 | 0.03    | 0.096 | 6.700 |
| SN    | qSN8  | 8   | 23.10–30.45 | 3.97 | 0.01    | 0.136 | 35.500 |
| SN    | qSN9  | 9   | 30.43–38.53 | 3.75 | 0.01    | 0.118 | 33.200 |

A QTLs for panicle traits in the RIL population. SNP markers are shown on the left of chromosomes. QTLs signed on chromosomes were detected in several environments and different years. b QTL peak map of rice chromosome 3. The genetic distances (cM) are shown below the x axis. c Fine mapping of qPPB3. The white, black, and gray bars represent genotypes of PA64s, 93-11, and heterozygote, respectively. All genotypic lines exhibited (G1-G11) were derived from BC3F2 population

had three SNPs and one InDel between two parents, respectively. However, product of Os03g0203700 was similar to Calcium-transporting ATPase 2, which has been found irrelevant to plant branching so far, and its expression showed no significant difference between two parents. Instead, Os03g0203200 (D88) encoded esterase D14/D88 homologous to the α/β-fold hydrolase superfamily protein, which has been reported affecting plant branching and significant difference in its expression level was detected here between 93-11 and PA64s. Only one substitution (T959 to G959) resulted in amino acid change from valine in 93-11 to glycine in PA64s (Fig. 3). Therefore, Os03g0203200 (D88) gene was suggested to be a candidate gene for qPPB3.

Expression comparison of D88 and panicle structure related genes in initial inflorescence of parents

RNA was extracted from inflorescences with length less than 5 mm at the formation stage of panicle primary branch. At the initial formation stage of panicle, the expression level of D88 in PA64s was significantly lower than that in 93-11 (Fig. 4), which is consistent with the previous report
that lower expression of D88 gene led to higher tillers but smaller panicle in the d88 mutant (Gao et al. 2009). With the same material, the expression of APO1 and IPA1, two negative regulators of grain number, enhanced in PA64s significantly.

Subcellular localization of D88

To define the intracellular localization of D88 in rice cells, we introduced D88::GFP into rice by using Agrobacterium transformation. We found that D88::GFP fusion protein was localized to both nucleus and cytoplasm in rice root cells, weakly appeared in the plasma membrane (Fig. 5).

Discussion

Panicle structure is one of the most important factors for rice yield. To date, 54 QTLs for PPB and 33 QTLs for SPB have been reported distributed on 12 chromosomes (Supplemental Fig. 1). Here, two QTLs were mapped for SPB,
Two QTLs, sbr1.1 and qSNB1-1 for SPB on chromosome 1 were mapped to the same interval of qSPB1 (Li et al. 2006; Cui et al. 2002). The qSPB9 was also reported previously (Li et al. 2006), and qSN9 for SN was found in the region of qSPB9. In this study, two QTLs for PPB, qPPB3 and qPPB8 were located on chromosome 3 and chromosome 8, respectively. The region of qPPB8 was also reported to be related to the QTLs for PPB and SN in other studies (Lin et al. 1996; Xu et al. 2001). One QTL (QPbn3a) for PPB and another QTL (QSbn3a) for SPB were detected in the same genomic region of qPPB3 (Xu et al. 2001). The qPPB3 was further mapped to a region of 34.6-kb on a BAC clone AC146702, where four candidate genes (Os03g0203100, Os03g0203200, Os03g0203700, Os03g0203800) existed. The translational product of Os03g0203200 was D88/D14, an esterase that confirmed to control rice tillering, with d88/d14 mutants exhibits high tillers but dwarfism (Arite et al. 2009; Gao et al. 2009).

Panicle primary branches developed from primary branch meristems, which are produced by inflorescence meristem. During reproductive development, inflorescence branching is under genetic control affected by hormones that include brassinosteroid (BR), cytokinin (CK), auxin, and strigolactone (SL) (Beveridge 2006; McSteen and Leyser 2005; Ongaro and Leyser 2008; Dun et al. 2009; Wang et al. 2013). Like strigolactones insensitive mutants, PA64s also exhibited more tillers and less panicle branches than 93-11. In the study, qPPB3 was fine mapped to a region covering the D88 gene, whose product believed to be an important receptor in strigolactone signaling (Jiang et al. 2013). Strigolactones or related compounds were reported to inhibit shoot branching in plants (Gomez-Roldan et al. 2008). At the initial development stage of panicle, the expression level of D88 was significantly higher in 93-11 than PA64s. And the PPB of 93-11 was larger than PA64s. Therefore, strigolactones or their derivants might be the recepible hormone by D88 in cytoplasm or nucleus to affect the PPB, though regulatory mechanism of branching in panicle is different from that in shoot. In contrast to SL, CK directly promote bud growth and cell proliferation. We tested the expression of two CK related genes, GN1a/OsCKX2 and DST. The expression level of GN1a/OsCKX2 was significantly lower in 93-11 with more SN, suggesting CK might be accumulated higher in 93-11 than PA64s. The expression level of DST was also higher in PA64s, which in accord with its direct regulation of GN1a/OsCKX2 to control CK level in the reproductive SAM and, as a result, affects panicle branching and grain number (Li et al. 2013).

The APO1/SCM2, GN1a/OsCKX2 and IPA1/OsSPL14 were cloned QTLs associated with panicle structure. The line contained APO1 ORF and the proximal promoter region controlled only the number of PPB but not the number of grains per panicle. However, the line included only the distal promoter region that could increase the grain number and harvest index (Terao et al. 2010). The present study also confirmed that the higher PPB in 93-11 exhibited higher expression level of APO1. IPA1 was considered important not only for plant architecture but also for panicle structure. Higher expression of IPA1/OsSPL14 at the reproductive stage promoting panicle branching is consistent with our results (Miura et al. 2010; Jiao et al. 2010).

Dense panicle structure has been a major target for improvement of rice grain yield because of its relationship with grain number. The utilization of QTLs panicle...
structure, such as dep1, ipa1, and apol has increased the crop productivity. Therefore, pyramiding of these elite QTLs, including qPPB3 mapped here, will certainly benefit high-yield breeding by marker-assisted selection (MAS) for rice in the future.

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

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