The Analysis of the Structure and Expression of *OsTB*1 Gene in Rice

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Abstract: *TCP* genes, including *Teosinte Branched* 1 (*TB*1) in maize, *Cyclodiea* (*Cyc*) in snapdragon and *PCF*1 and *PCF*2 in rice etc., constitute a newly discovered gene family which encode transcription regulators in plants. *TB*1 controls the apical dominance in maize and is involved in the maize tiller development. Both rice and maize belong to the *Gramineae* and can produce tillers. By screening a rice genomic library, we isolated a *TB*1-like gene—*Oryza sativa Teosinte Branched* (*OsTB*1) in rice. We also isolated the cDNA of *OsTB*1 by RT-PCR. The *OsTB*1 gene, with no intron, encodes a polypeptide consisting of 388 amino acids. OsTB1 shows 70% amino acid sequence similarity with TB1 and has the conserved TCP and R regions. This gene is a newly discovered gene of the *TCP* gene family in rice. RT-PCR and mRNA *in situ* hybridization showed that *OsTB*1 strongly expressed in rice axillary buds and weakly in inflorescence. *OsTB*1 is suggested to be related to axillary bud and inflorescence development in rice.

Key words: rice; development; axillary bud; *OsTB*1; apical dominance

The studies in modern molecular biology and genetics of the model plants, such as snapdragon (*Antirrhinum*) and *Arabidopsis*, make us learn more about plant development. The comparative study between the homologous genes from different species can give us more information about their biological roles in the phylogenesis. Recently, some members of the *TCP* gene family, putative transcriptional regulators, have been isolated and studied, including *Teosinte Branched* 1 (*TB*1) from maize (*Zea mays*), *Cyclodiea* (*Cyc*) from snapdragon and *PCF*1, *PCF*2 from rice (*Oryza sativa*). The *TCP* gene family members encode putative basic helix-loop-helix DNA-binding proteins that play very important roles in plant development (Cubas *et al*. 1999). In maize, *TB*1 controls the apical dominance in maize and has been very important during the evolution of modern maize. The apical dominance in modern maize is very strong resulting in the outgrowth of only a few of axillary branches at upper nodes. But in *tb*1 mutants, axillary buds of lower nodes grow out to give tillers and axillary buds of upper nodes grow out to give branches which form tassels (male inflorescences) at their tips, a phenotype like that of teosinte, the ancestor of maize. In the wild type maize, the *TB*1 gene prevents the outgrowth of axillary buds of lower nodes and promotes the development of axillary buds of upper nodes that grow into ears (female inflorescences), indicating that the *TB*1 gene affects the fate of maize axillary meristems (Doebley *et al*. 1997, Doebley and Lukens 1998, Wang *et al*. 1999). *Cyc*, together with *Dichomota* (*Dich*), determine the floral asymmetry in snapdragon (Luo *et al*. 1996, 1999), and *PCF*1 and *PCF*2 have close relationship with cell division and proliferation (Kosugi and Ohashi 1997). All these suggest that the *TCP* family may play very important roles in plant development and evolution. Analysis shows that these genes might function in plant by regulating the transcription activity of other genes. Study of these genes enable us to understand how the process of plant development is regulated by genes at the molecular level.

Rice is one of the most important crops for the world and has been studied as a model monocot for a long time. Both rice and maize belong to *Gramineae* and both of them can produce tillers (axillary buds). Rice tiller not only contributes largely to the yield, but also is a very crucial morphological trait. Since *TB*1 in

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maize affects the outgrowth of tillers (axillary buds), we proposed that among the *TB*1 homologue genes in rice, at least one member might be related to rice tiller development. By studying the *TB*1-like genes in rice, we hope to learn and comprehend the process of axillary bud development and the mechanism controlling the formation of rice axillary buds in rice.

Here is reported the isolation of a *TB*1-like gene (referred to as *OsTB*1 below) in rice through the screening of a rice DNA library with the ORF of *TB*1 as the probe. We also obtained its cDNA containing full ORF and 3′UTR by RT-PCR. Expression pattern of *OsTB*1 was analyzed with RT-PCR and mRNA *in situ* hybridization. Our results showed that *OsTB*1 strongly expressed in the formation of rice axillary buds and weakly in inflorescence, suggesting that it is related to the formation of rice architecture.

1 Materials and Methods

1.1 Plant materials

Oryza sativa L. *indica* cv. Guanglu′ai 4, *Oryza sativa* L. *indica* cv. IR36, *Zea mays* L. Nongda 60, were grew in the test fields from June to October or in the greenhouse at 27℃ and day length of 12 h. Tissues were collected for DNA and RNA extraction and *in situ* hybridization or stored at −70℃ for future usage.

1.2 Screening of a rice phage genomic library

The ORF of *TB*1 from maize was obtained by PCR with maize genomic DNA as the template, forward primer SL034 (5′-gga gtc cca tca gta aag ca-3′) and reverse primer SL035 (5′-tca gta gaa gcg tga gtt gtg-3′) was designed basing on the *TB*1 DNA sequence. The probe for screening the library, containing the conserved TCP and R region, was a fragment of 510 bp from *TB*1 ORF obtained by *Bam*H/*Hin*d Ⅲ double digestion.

The rice line used for the genomic library construction was *O. sativa* L. *indica* cv. IR36. The titer was 10^9 pfu/ml, and the vector was Lamdba EMBL3/4, and the host was *E. coli* K802. About 1.8×10^5 clones were screened in the first round, the screening hybridization was done at low stringency (55℃). Finally, two independent clones were obtained and the analysis showed that one of them was *OsTB*1.

1.3 Isolation of *OsTB*1 cDNA

Total RNA was extracted from rice young tillers and was digested with RNaseA-free DNaseI (Promega) to eliminate the trace DNA before being reverse-transcribed to cDNA and then used for RT-PCR to isolate the cDNA with the full ORF and 3′-UTR. Reverse transcription was carried out according to the manufacture′s instructions (Promega). The 3′ end adaptor was B26[5′-gac tcg agt cga cat cga $(t)_{17}$-3′]. Specific primers were designed basing on the DNA sequence from rice genomic library screening: forward primer SL201(5′-caa gca tca acc aag cta gct agc-3′), reverse primer SL202(5′-agc tgc agg agt tcg atc tta g-3′, forward primer SL203(5′-act tct ctc tcc cac aca agc-3′), reverse primer SL204(5′-gta ccg ttc gtt cgt tcg ttc g-3′), forward primer SL209(5′-tgc acc cct tca tgg act tgg ag-3′) and reverse primer SL210(5′-agg acc ggc aca gca aga taa gc-3′). In order to isolate the complete ORF of the gene, primers SL201/SL202 were used in the first round RT-PCR and its product was used as the template of the second round PCR with primers SL203/SL204. In order to isolate the gene′s full 3′-UTR, forward primer SL209 and reverse primer B25 (5′-gac tcg agt cga cat cg-3′) were used in the first round RT-PCR and its product was used as the template of the nest-PCR with primers SL210/B25.

1.4 Southern blot of rice genome

Total genomic DNA was isolated from two-week-old rice cv. Guanglu′ai 4 seedlings. Eight micrograms of genomic DNA were digested and eletrophoresed. The probes *OsTB*1 were labeled by α-[^{32}P] dCTP according to the manufacture′s instructions (Promega). Hybridization and washing were performed at 55℃. The membrane was exposed to the phosphor screen, and the phosphor screen was scanned with STORM 840 for 6 or 12 h after exposure.

1.5 RT-PCR

Total RNA was extracted from various rice tissues and reverse-transcribed to cDNA 1st strand before PCR as described above. Gene expression was studied with RT-PCR, primers SL209/B25 were first used in the first round PCR, and its product was used as the template of nest-PCR with primers SL210/B25. The PCR product was transferred to nylon membrane (Hybond$^+$) and hybridized with *OsTB*1 ORF. Forward primer SL222 (5′-cca aat cca ccg caa gag aaa gcc aag-3′) and reverse primer B25 were used to amplify the rice gene *Histone H*3 (GenBank Accession number

AF093633) as the internal standard in RT-PCR.

1.6 *In situ* Hybridization

Forward primer SL249 (5′-acc aag gag aag aac cgg atg-3′) and reverse primer SL251 (5′-cga tca gac gat agt gct agc-3′) were designed basing on the *OsTB*1 cDNA sequence to amplify a fragment of 630 bp as the template of the probe in the *in situ* hybridization. The template, excluding the conserved TCP and R regions of *OsTB*1, consisted partly of *OsTB*1 ORF and partly of 3′UTR fragment and was subcloned into the vector pBluescript II KS. The plasmid was transcribed into antisense probe with T7 promoter after digestion with *Hin*d III and transcribed into sense probe with T3 promoter after digestion with *Bam*H Ⅰ.

Primers SL222 (5′-cca aat cca ccg caa gag aaa gcc aag-3′) and B25 were used to amplify the cDNA of rice Histone H3. The RT-PCR product was digested with *Sac* Ⅱ and the 3′ poly A was deleted. The 5′ terminal of 440 bp was cloned into the vector pGEMT-Easy (Promega). Then the plasmid was transcribed into antisense probe with T7 promoter after digestion with *Spe* Ⅰ and transcribed into sense probe with SP6 promoter after digestion with *Nco* Ⅰ.

Plant materials were fixed in 4% (*W/V*) paraformaldehyde and 0.25% glutaraldehyde in 0.1 mol/L sodium phosphate buffer, pH 7.4, overnight at 4℃, dehydrated through graded ethanol series and xylene series, and finally embedded in Paraplast Plus (Sigma) (Sentoku *et al*. 1999). Microtome sections (8 μm thick) were applied to glass slides treated with polylysine. *In situ* hybridization with digoxigenin-labeled sense or antisense RNA was conducted according to the method of Coen *et al*. (1990).

2 Results

2.1 Structure of *OsTB*1 in rice

A rice phage genomic library was screened with *TB*1 from maize as the probe, and a *TB*1-like gene of rice was obtained. We named it as *OsTB*1, after *Oryza sativa Teosinte Branched* 1. And we also cloned its cDNA containing full ORF and 3′-UTR by means of RT-PCR from young rice tillers. The Southern blotting of rice genome with *OsTB*1 as probe under low stringency conditions showed that there were at least two copies of *TB*1-like genes in rice genome (Fig. 1). Sequence analysis showed that, like *TB*1, *OsTB*1 had no intron, its full ORF was 1 164 bp, encoding a 388-amino acids protein with the common conserved TCP and R regions among the TCP proteins. Its 3′-UTR is 285 bp (Fig. 2). The OsTB1 shows 70%, 41%, 38%, 38%, 32% and 31% similarity with TB1, CYC, DICH, LCYC, PCF1 and PCF2, respectively. The conserved TCP region of OsTB1 had 93%, 80%, 78%, 76%, 49% and 46% similarity with TB1, CYC, DICH, LCYC, PCF1 and PCF2, respectively (Fig. 3A). Moreover, the R conserved regions among TB1, CYC, DICH, OsTB1 and LCYC are nearly identical (Fig. 3B).

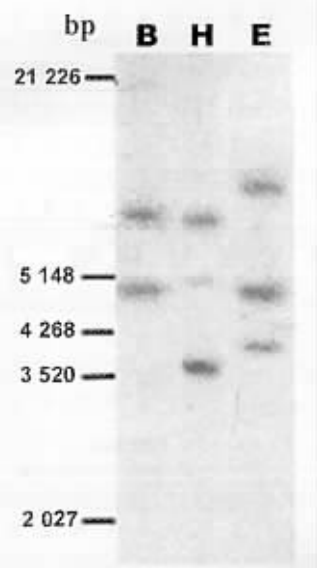

Fig. 1 Southern blot of rice genome with *OsTB*1 as the probe B: *Bam*H; H: *Hind* Ⅲ; E: *Eco*R Ⅰ.

2.2 The expression pattern of *OsTB*1

Total RNA was extracted from various rice tissues, including young leaves and young roots of 10-day-old rice, the vegetative apical meristems (including a few leaf primordia), the developed spikelets and tillers (less than 1 – 2 mm). And the RNA was transcribed to cDNA and used for PCR study. The results showed that the expression of *OsTB*1 was detected in vegetative apical meristems, young roots and tillers of rice, and it seemed that there was weak expression in developed spikelets, but no expression in young leaves. The expression of *OsTB*1 in tillers was stronger than in other tissues (Fig. 4).

*OsTB*1 expression was also studied with *in situ* mRNA hybridization. Our results showed that *OsTB*1

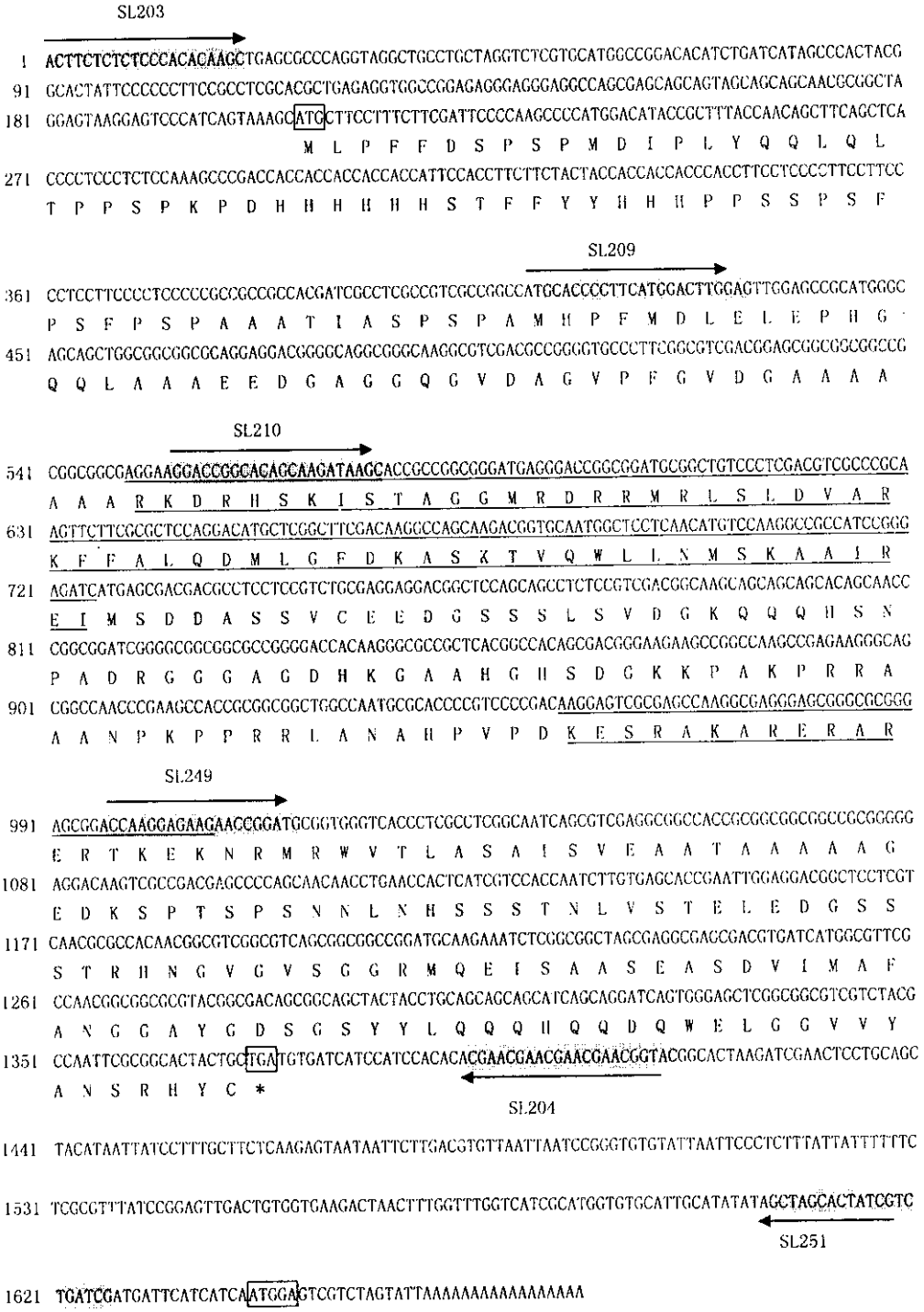

Fig. 2 The sequence of *OsTB*1 and the deduced amino acids

Some primers are shaded, the TCP and R regions are underlined (This nucleotide sequence has been deposited in GenBank database with accession number AY043215). The rice for the genomic library construction was *O. sativa* L. *indica* cv. IR36, and the rice line for the cDNA isolation was *O. sativa* L. *indica* cv. Guanglu'ai 4. *OsTB*1 sequence from *O. sativa* L. *indica* cv. Guanglu'ai 4 was amplified by PCR and compared with *O. sativa* L. *indica* cv. IR36, but no polymorphism was found between the two rice lines used.

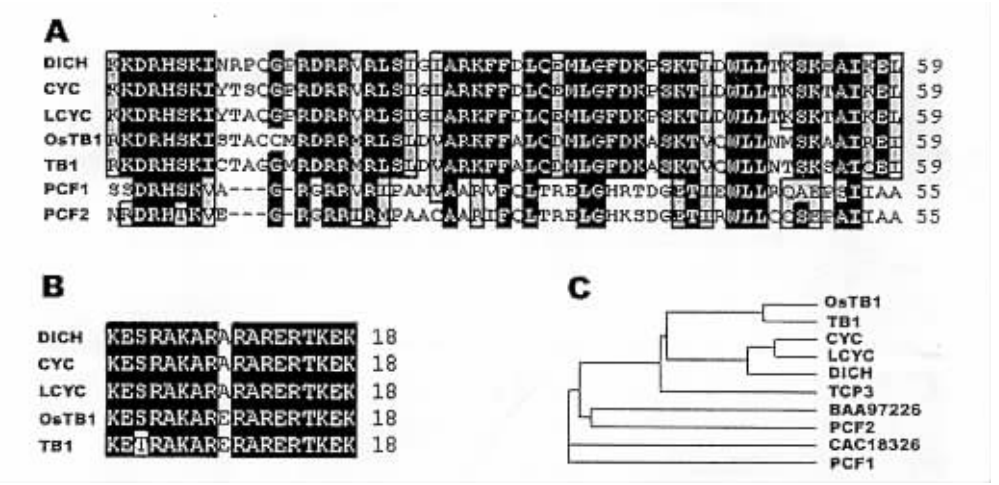

Fig. 3　Alignment of TCP and R conserved regions and the phylogenetic tree in the TCP protein family

A: The similarity comparison of TCP conserved regions in the TCP protein family. The accession numbers of these genes in the GenBank are: DICH, AF199465; CYC, Y16313; LCYC, AF161252; OsTB1, AY043215; TB1, U94494; PCF1, D87260; PCF2, D87261. B: The similarity comparison of R conserved regions in the TCP protein family. C: The phylogenetic tree of *OsTB1* and other TCP members.

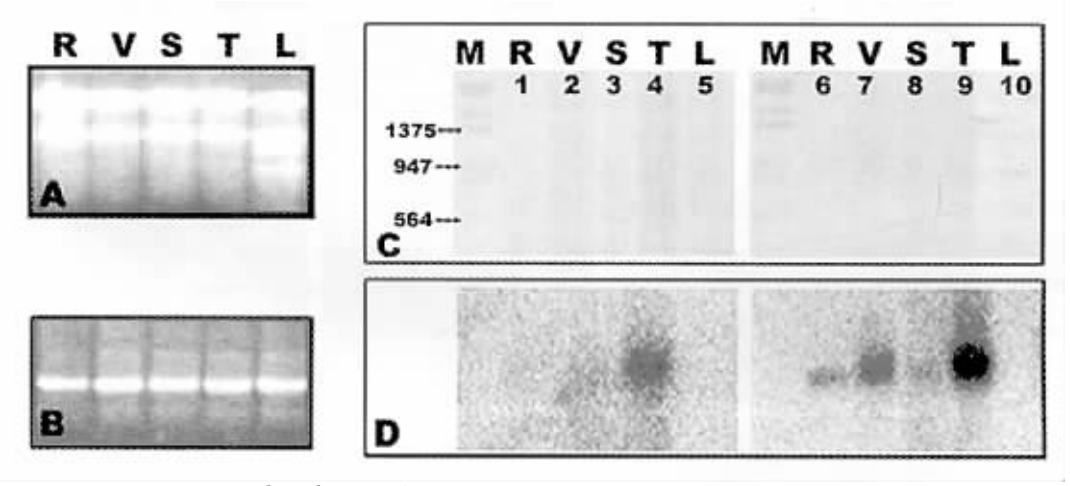

Fig. 4　*OsTB1* expression pattern analysis by RT-PCR

A: total RNA from various tissues. R, root; V, vegetative apical meristem; S, spikelet; T, tillers; L, leaves. B: PCR results of rice *Histone H3* as the inner standard. C: The results of RT-PCR. 1 – 5 were the first-round RT-PCR after electrophoresis and 6 – 10 were the second-round nested-PCR after electrophoresis. M, standard DNA marker. D: The hybridizing results of RT-PCR with *OsTB1* as the probe.

strongly expressed in axillary buds at upper nodes of rice, including axillary shoot meristems and the young leaves around the axillary shoot meristems. *OsTB1* also weakly expressed in inflorescence. No signals were detected in young leaves or SAM (Fig. 5).

3　Discussion

3.1　*OsTB1* is a member of the TCP gene family in rice

Analysis of the sequence shows that the structure of *OsTB1* is similar to *TB1*, the gene, with no intron, has two conserved domains—TCP and R regions. The TCP conserved region of OsTB1 had 93% identity with TB1. The conserved R regions between CYC, TB1, LCYC and DICH were nearly identical. The basic region of TCP domain contained a putative bipartite nuclear localization signal. The R domain is predicted to form a hydrophilic alpha helix (Cubas *et al*. 1999). Phylogenetic alignment analysis indicates that OsTB1 has closer relationship with *TB1* than other

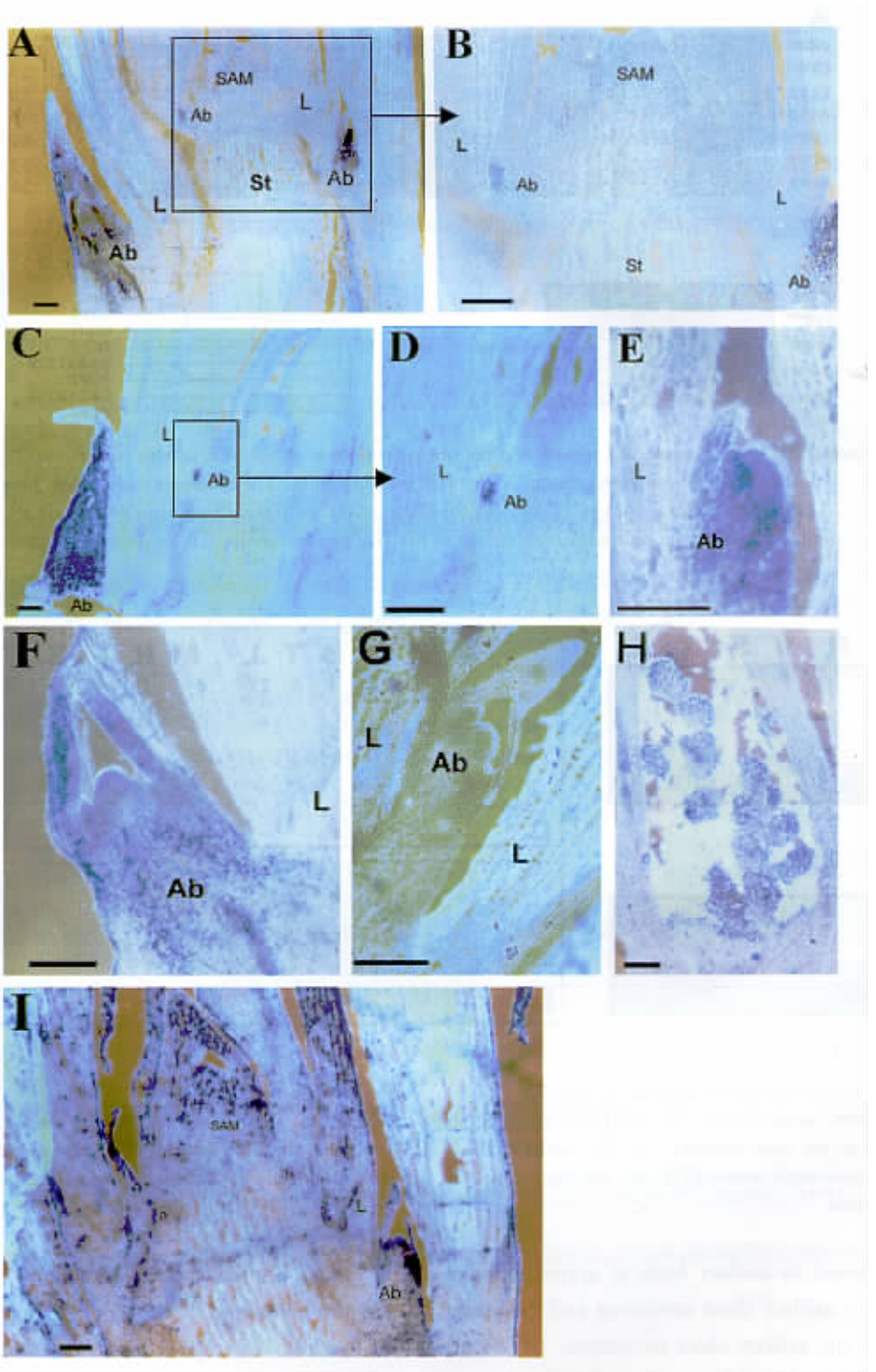

Fig. 5 The *in situ* hybridization of *OsTB*1 and rice *Histone H*3

A – F：Hybridization probed with the *OsTB*1 antisense RNA in rice seedlings. Gene *OsTB*1 expression was detected in rice axillary buds at the upper nodes，including small axillary primordia and big axillary buds. B is the magnified picture magnification of the panel in A. D is a magnified picture of the panel in C. G：*OsTB*1 sense control. No signal was detected. H：Gene *OsTB*1 expression was detected in inflorescence. I：Hybridization probed with the histone *H*3 antisense RNA. Hybridization signals were observed in rice SAM，axillary buds and leaf. Bar = 50 μm. St，stem；L，leaf；Ab，axillary bud；SAM，shoot apical meristem.

TCP members (Fig. 3C). These data show that *OsTB*1 is a member of TCP gene family in rice.

Recently, Takeda *et al*. (2003) reported that they isolated a 3 626-bp genomic fragment encompassing *OsTB*1 by screening a DNA library constructed from a *japonica* rice cultivar, Nipponbare. Comparison between Takeda's and ours data shows that the ORF of the *OsTB*1 they deduced from the 3 626-bp genomic fragment is nearly identical to our *OsTB*1, which was produced by RT-PCR, except that the No. 345 nucleotide in our *OsTB*1 is T while C in Taketa's gene, which leads to an amino acid discrepancy there.

3.2 *OsTB*1 expressed in both rice axillary buds and inflorescence

In maize, *TB*1 expression has been detected in maize axillary inflorescence (ear) primordia, immature internodes below these primordia and the immature husks surrounding these primordia and not detected in other tissues and organs such as leaves, roots, stem, male inflorescence and the like (Doebley *et al*. 1997, Doebley and Lukens 1998).

Takeda *et al*. (2003) examined the expression of *OsTB*1 in rice with *OsTB*1 promoter-glucuronidase (GUS) fusion gene. They found that *OsTB*1 expressed in rice axillary buds, which was consistent with our results. Similarly, Li *et al*. (2003) also showed that *OsTB*1 was expressed in rice axillary buds. These works were partly consistent with ours. We investigated the expression of rice *OsTB*1 by means of RT-PCR and *in situ* mRNA hybridization (Fig. 4 and Fig. 5). The RT-PCR results (Fig. 4) showed that *OsTB*1 was expressed in rice roots, vegetative apical meristems and tillers, and very weakly in developed spikelets but not in young leaves. By *in situ* hybridization (Fig. 5), its expression was detected in rice axillary buds and weak expression in inflorescence. *OsTB*1 was strongly expressed in rice axillary buds at all developing stages, from axillary meristem initiation to big axillary buds, including axillary shoot meristems and the young leaves around the axillary shoot meristems. But the expression of *OsTB*1 in SAM was not detected by *in situ* hybridization (Fig. 5). This discrepancy may be due to the fact that the vegetative SAM material used for RT-PCR may be (and very easily) mixed with young leaf primordia and tiller primordia. But our *in situ* results showed that the *OsTB*1 also expressed in rice inflorescence, which has not been reported before so far. Thus, our results showed that *OsTB*1 expressed not only in vegetative axillary buds but also in inflorescence.

3.3 *OsTB*1 may play key roles in rice architecture formation

Takeda *et al*. (2003) studied the possible role of *OsTB*1 using transgenic rice plants. The ectopic overexpression of *OsTB*1 in wild-type rice plants significantly reduced lateral branching, but the formation of tillers were not affected. An *fc*1 mutant, which contains loss-of-function mutation of *OsTB*1 showed enhanced lateral branching. These results indicated that *OsTB*1 might repress the outgrowth of the axillary buds, but did not affect the formation of tillers. Li *et al*. (2003) identified a gene named *Moc*1 (monoculm 1) from a rice mutant, which may be the master regulator of branching rice, for *Moc*1 has critical roles in the initiation, formation and outgrowth of axillary meristems in rice. *OsTB*1 maybe one of the downstream genes regulated by *Moc*1 (Li *et al*. 2003). The development fate of an axillary meristem can be developmentally and environmentally regulated (Sussex and Kerk 2001). The interaction between *OsTB*1 and other genes or auxin that control axillary buds formation and tillering in rice awaits to be elucidated.

Our data here partly agreed with the above reports. Expression of *OsTB*1 investigated by RT-PCR and *in situ* in our experiments showed that *OsTB*1 was expressed not only in axillary buds but also in inflorescence of rice (Fig. 4 and Fig. 5). Since the expression of both *Cyc* and *TB*1 was detected in flower or inflorescence, they repressed the development of the dorsal petal and stamen (*Cyc* in snapdragon) or the lodicules and stamen (*TB*1 in maize). The expression of *OsTB*1 both in axillary buds and inflorescence suggested that, as *TB*1 in maize and *Cyc* in snapdragon, *OsTB*1 might also have similar functions. It can affect rice architecture in both branching and inflorescence development. Of course, there are still more studies that should be carried out with respect to its function in rice flower development.

Combining Southern blot of rice genomic DNA with rice genome sequencing, we get to know that there are more than one copies of *OsTB*1 gene in rice genome (Fig. 1), and sequence comparison also told us that the *OsTB*1 reported in this paper is the most similar to *TB*1. We hope that the study of other members of this *TCP* family in rice could give us more

clear information about their roles in controlling rice architecture.

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水稻 *OsTB*1 基因的结构及其表达分析

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摘要: *TCP* 基因是一类植物中新发现的、可能具有转录因子活性的基因家族,成员包括金鱼草的 *Cyclodiea* (*Cyc*)、玉米的 *Teosinte Branched*1 (*TB*1) 以及水稻中的 *PCF*1、*PCF*2 等。玉米的 *TB*1 基因有维持玉米顶端优势的作用,与分蘖的发生密切相关;水稻和玉米同属禾本科,在发育的过程中都有分蘖的发生。通过筛选水稻的基因组文库,得到了水稻中的一个 *TB*1 同源基因 *Oryza sativa Teosinte Branched*1 (*OsTB*1)。该基因不含内含子,基因编码一个长度为 388 个氨基酸的蛋白,在氨基酸水平上与 TB1 的同源性为 70%,含有保守的 TCP 区和 R 区,是属于 *TCP* 基因家族的一个成员。RT-PCR 和 mRNA 原位杂交分析结果表明,*OsTB*1 在水稻的侧芽中有很强的表达,在花序中有较弱的表达。以上结果显示该基因可能在水稻侧芽和花序的起始和发育过程中起重要作用。

关键词:水稻;发育;侧芽; *OsTB*1 ;顶端优势

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水稻OsTB1基因的结构及其表达分析

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