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Sequence Variation and Phylogenetic Relationship Analysis of *Starch Branching Enzyme I* Gene (*SBEI*) in Rice Varieties from China, Laos and Thailand

S. Talamphai[1], X.L. Tan[1,2]* and C. Jantasuriyarat[3,4]*

[1]Crop Genetics and Breeding, Faculty of Agriculture and Biological Technology, Yunnan Agricultural University, Kunming 650201, China
[2]Rice Research Institute, Yunnan Agricultural University, Kunming 650201, China
[3]Department of Genetics, Faculty of Science, Kasetsart University, Chatuchak, Bangkok 10900, Thailand
[4]Center for Advanced Studies in Tropical Natural Resources, National Research University-Kasetsart (CASNAR, NRU-KU) Kasetsart University, Chatuchak, Bangkok 10900, Thailand

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The coding sequence of *starch branching enzyme I* gene (*SBEI*) of 30 rice varieties from China, Laos and Thailand were cloned. All thirty sequences contain 2,463 bp and 14 exons and encode for 820 amino acids. Three sites of Single Nucleotide Polymorphisms (SNPs) A>C, T>C, and T>C were found at positions 1,107, 2,156 and 2,271 in Exon with 6, 13 and 14 respectively. The SNPs at position 1,107 A>C and position 2,271 T>C were silent mutations. The SNP at position 2,156 T>C was a missense mutation and induced a mutation from valine (GTG) to alanine (GCG). Three haplotypes A/T/T, C/T/C and C/C/C were observed. The phylogenetic analysis of 81 SBEI CDS sequences, out of which 30 are from this study and 51 are from previous, classifies them into 2 major groups using 4 sequences as outgroup. The group of monocot comprised of rice, barley, wheat, sorghum whereas maize and the group of dicot comprised of potato, cassava, poplar, Chinese chestnut, bean, legumes and apple. The group of rice *SBEI* CDS was a major clade in monocot group with high bootstrap value. *SBEI* gene of rice from China, Laos and Thailand, wheat, apple and poplar contain 14 exons while *SBEI* gene of rice from Japan and Korea contained only 12 exons. The GC content of *SBEI* gene of rice varieties was lower than that of wheat and apple but higher than that of poplar.

Keywords: starch branching enzyme I (SBEI), single nucleotide polymorphisms (SNPs)

Introduction

Rice (*Oryza sativa* L.) is significant crop among all the world crops and it becomes more important due to growing population of the world as it feeds more than half of the world's population as a (source of) staple food (Khush 1997). Starch is the major component of yield (James et al. 2003). Starch is composed of two polymers of glucose, amylose and amylopectin (Zeeman et al. 2010). Amylose is a linear molecule of 1/4 linked a-D-glu-

*Corresponding author; E-mails: fscicwj@ku.ac.th; tanxuelin2008@163.com

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copyranosyl units. Amylopectin is the highly branched component of starch. It is formed through chains of a-D-glucopyranosyl residues linked together by 1/4 linkages but with 1/6 bonds at the branch points (Buléon et al. 1998). Over 20 genes involved in the starch synthesis pathway have been identified so far with six genes playing a major role in rice endosperm starch synthesis: ADP-glucose pyrophosphorylase large subunit 2 (*AGPL2*), ADP-glucose pyrophosphorylase small subunit 2b (*AGPS2b*), granule-bound starch synthase I (*GBSSI*), starch synthase IIa (*SSIIa*), starch branching enzyme IIb (*SBEIIb*), and isoamylase1 (*ISA1*) (Myers et al. 2000; Tanaka et al. 2004; Nakamura et al. 2005; Lee et al. 2007; Pico et al. 2008). Starch branching enzymes (SBEs) play important roles in the synthesis of amylopectin. Multiple SBE isoforms occur in plants such as barley (*Hordeum vulgare*) (Sun et al. 1998), wheat (*Triticum aestivum*) (Morell et al. 1997), maize (*Zea mays*) (Gao et al. 1997), rice (*Oryza sativa*) (Mizuno et al. 1992), pea (*Pisum sativum*) (Denyer et al. 1993), potato (*Solanum tuberosum*) (Kossmann et al. 1991; Poulsen and Kreiberg 1993), and *Arabidopsis thaliana* (Fisher et al. 1996). Starch branching enzymes can be classified into two classes, class I and class II (sometimes defined as B and A, respectively), based on amino acid sequence similarity (Burton et al. 1995). *SBEI* and *SBEII* differ in substrate specificity and expression patterns. Class II differs from class I by having an acidic amino terminal extension and a shorter carboxy terminus. The studies with maize endosperm indicated that *SBE* isoforms differ in their action on starch polymers: *SBEI* has the highest activity in branching amylose, whereas *SBEII* has higher rates of branching amylopectin than *SBEI* (Guan et al. 1993). Furthermore, *SBEI* predominantly transfers longer chains and produces a few shorter chains, *SBEII* preferentially transfers smaller chains and produces longer chains (Guan et al. 1997). The relative expression levels of *SBEI* gene were significantly different among different plant species. *SBEI* gene is expressed abundantly and specifically in developing seed and maximally at the middle stages of seed development (Kawasaki et al. 1993). In maize, *SBEI* gene was expressed moderately during middle stage and strongly during the later stage of kernel development (Gao et al. 1996). In wheat endosperm, *SBEI* play a central role for SBE activity at later stages in development of amyloplast (Wang et al. 2011). Sequence changes of *SBEI* gene may result in different SBE activity and can be used to develop a biomarker for starch synthesizing gene markers (Liu et al. 2004). The molecular information of *SBEI* rice gene is a basis for understanding the mechanism of starch biosynthesis and starch quality improvement and helpful for the breeder to generate novel desired starch. In this study, our aim was to examine the coding sequence of *SBEI* gene, to identify single nucleotide polymorphisms (SNPs) and to analyze phylogenetic relationship of *SBEI* sequences in 30 rice varieties from China, Laos and Thailand.

Materials and Methods

Plant materials

A total of 30 rice varieties from China, Laos and Thailand including, 10 rice varieties from China (Duantun502, Chujing27, Funingnuo, Linxian21, Yixiang1919, Yixiang101, Gangyou900, Yiyou1988, Fuliangyou366 and Luxiang658), 12 rice varieties from Laos

(VTS-165-5, VTS-250-1, VTS-250-2, VTS-250-3, VTN-289-1, VTN-324, VTS-483-1, VTS-483-3, VTS-620-1, VTS-620-2, VTS-640-1 and VTS-640-2) and 8 rice varieties from Thailand (KDML105-1, KDML105-2, KDML105-3, Mali Gomain1, Mali Gomain2, Mali NilSurin, Chinat1 and RD6) (Table 1).

Table 1. Primer sequence, region covering and size of *SBE1* gene

Primer	5'-3' Sequence	Region covering	Size
F1	AGAAAAGGAAGGAGAGACACG	Exon 1 and 2	778 bp
R1	GCATCAGCGGCTTGGGAAC		
F2	TTGGTGGAGTAGCAATCTTT	Exon 3 and 4	791 bp
R2	CTCAAAACATCTCTATTACC		
F3	TTCTGAACTTGTGAGGCTGT	Exon 5	476 bp
R3	CTTTGCGTCTTTATGCTTCC		
F4	GTTGATCGTATTCCCGCAT	Exon 6	1,271 bp
R4	ATCAAAAAATAGAGTAGCAAT		
F5	AGGTTCCTTTTTTCACTATG	Exon 7 and 8	655 bp
R5	ATGCTTCAGTTTATGTATGT		
F6	GATGTGTTCTGTTATTCCTGG	Exon 9 and 10	1,129 bp
R7	TTGAAAACAAAAACCAAATCT		
F8	CTTGTATGTCCTATGTATTCA	Exon 11, 12, 13 and 14	1,040 bp
R8	ATCACTGCTTATTCTTTCTT		

DNA extraction

All rice varieties were grown in a light and temperature controlled greenhouse until the tillering stage. Only young and healthy leaves were harvested and collected for DNA extraction. Genomic DNA was extracted by using the modified cetyl trimethylammonium bromide (CTAB) method (Agrawal et al. 1992). The quality of DNA was estimated using NanoDrop2000 on 260/280 and 260/230 wave length ratios. The DNA was migrated on 1% agarose and stained in ethidium bromide, then visualized on UV transilluminator.

Primer design for amplification of SBEI gene exons

For *SBEI* CDS cloning, 7 primer pairs were designed based on *SBEI* gene sequences of *Oryza sativa* Japonica Group cultivar Tainung 78 and *Oryza sativa* Indica Group cultivar Kasalath from NCBI database (https://www.ncbi.nlm.nih.gov/) (GenBank accession number KF984385.1 and GQ150908.1, respectively). Primers are located on introns that flank the targeted exon (Table 1).

PCR amplification of SBEI gene

PCR amplifications were performed using *Taq* polymerase (Apslagen, Thailand) and ingredients shown in Table S1* by using the following PCR condition: initial denaturation at 94 °C for 4 min; then 35 cycles of 94 °C for 30 s, Annealing step (Annealing temperature follow Table S1) for 30 s and 72 °C for 1 min; and a final extension step of 72 °C for 5 min. PCR products were examined by agarose gel electrophoresis and purified by using The GF-1 AmbiClean Kit (Gel & PCR) (Vivantis, USA). Sequence analysis of purified fragments was done by BGI tech in Hong Kong.

Structure and sequence comparison of the SBEI gene

The full length *SBEI* CDS of 30 rice varieties from China, Laos and Thailand were compared with *SBEI* CDS from several plant species including 19 rice varieties from China, 8 rice varieties from Korea, one rice variety from Japan, wheat, apple and poplar (Table 2). Number and size of exons were reported and percent GC content was

Table 2. The comparisons of exon size and %GC content of rice *SBE I* coding sequence from rice, wheat, apple and poplar

Exon No.	Exon size (bp)					
	Rice Group A China, Laos, Thailand	Rice Group B Korea and Japan	Wheat (*Ta*)	Wheat (*Tm*)	Apple	Poplar
1	84		90	87	117	72
2	63		69	69	114	123
3	208	160	208	208	211	208
4	70	70	70	70	70	70
5	270	270	269	270	270	270
6	907	907	904	907	907	907
7	117	117	117	117	117	117
8	63	63	63	63	63	63
9	108	108	108	108	108	108
10	102	102	102	102	102	102
11	68	68	68	68	68	68
12	82	82	82	82	82	82
13	117	117	117	117	117	117
14	204	204	222	222	171	210
%GC	45.40	44.46	46.06	47.21	47.11	42.71

Wheat (*Ta*) = bread wheat (*Triticum aestivum*), wheat (*Tm*) = wheat (*Triticum monococcum*).

*Further details about the Electronic Supplementary Material (ESM) can be found at the end of the article.

calculated by using DNA/RNA GC Content Calculator (http://www.endmemo.com/bio/gc.php).

Phylogenetic analysis of SBEI sequence

A total of 81 *SBEI* sequences were used to construct phylogenetic tree by using MEGA7 program (Kumar et al. 2016) (Table 3). There were 30 *SBEI* sequences obtained from this study and 51 *SBE1* sequences, which were downloaded from NCBI database including *SBEI* sequences from rice, maize, wheat, barley, Chinese chestnut, sorghum, apple, sweet potato, cassava, legumes, black cottonwood, green bean, mung bean, plankton, red algal, protozoa and cyanobacteria (Table S2). Phylogenetic trees were separately constructed from 5 models (including Maximum likelihood (ML), Neighbor-joining (NJ), UPGMA, Minimum evolution (ME) and Maximum parsimony (MP)) with 1,000 bootstrap replicate.

Table 3. Cultivar name, country, GenBank accession number and SNPs site of 57 rice *SBE1* CDS sequences

Cultivar name	Country	GenBank accession No.	SNPs site			Source
			1107 A>C	2156 T>C	2271 T>C	
KDML105-1	Thailand	MF678446	A	T	T	This study
KDML105-2	Thailand	MF678447	A	T	T	This study
KDML105-3	Thailand	MF678448	A	T	T	This study
Mali Gomain1	Thailand	MF678449	A	T	T	This study
Mali Gomain2	Thailand	MF678450	A	T	T	This study
Mali NilSurin	Thailand	MF678451	A	T	T	This study
Chinat1	Thailand	MF678452	A	T	T	This study
RD6	Thailand	MF678453	A	T	T	This study
Duantun502	China	MF678454	A	T	T	This study
Chujing27	China	MF678455	C	T	C	This study
Funingnuo	China	MF678456	C	C	C	This study
Linxian21	China	MF678457	A	T	T	This study
Yixiang1919	China	MF678458	A	T	T	This study
Yixiang101	China	MF678459	A	T	T	This study
Gangyou900	China	MF678460	A	T	T	This study
Yiyou1988	China	MF678461	A	T	T	This study
Fuliangyou366	China	MF678462	A	T	T	This study
Luxiang658	China	MF678463	A	T	T	This study
VTS-165-5	Laos	MF678464	A	T	T	This study
VTS-250-1	Laos	MF678465	A	T	T	This study
VTS-250-2	Laos	MF678466	A	T	T	This study
VTS-250-3	Laos	MF678467	A	T	T	This study
VTN-289-1	Laos	MF678468	C	C	C	This study

Cultivar name	Country	GenBank accession No.	SNPs site			Source
			1107 A>C	2156 T>C	2271 T>C	
VTN-324	Laos	MF678469	C	C	C	This study
VTS-483-1	Laos	MF678470	A	T	T	This study
VTS-483-3	Laos	MF678471	A	T	T	This study
VTS-620-1	Laos	MF678472	A	T	T	This study
VTS-620-2	Laos	MF678473	A	T	T	This study
VTS-640-1	Laos	MF678474	A	T	T	This study
VTS-640-2	Laos	MF678475	A	T	T	This study
9308	China	GQ150906.1	A	T	T	NCBI database
LongtefuB	China	GQ150909.1	A	T	T	NCBI database
Minghui63	China	GQ150910.1	A	T	T	NCBI database
TaichungNative1	China	GQ150911.1	A	T	T	NCBI database
Taichungsen17	China	KF984390.1	A	T	T	NCBI database
Zhenshan97B	China	GQ150912.1	A	T	T	NCBI database
Guichao2	China	GQ150907.1	A	T	T	NCBI database
Guixiangsinuo	China	GQ150905.1	A	T	T	NCBI database
OsSBE1_Kasalath	China	GQ150908.1	A	T	T	NCBI database
clone KCS171F10	China	EF122471.1	C	T	C	NCBI database
clone KCS318A05	China	EF122470.1	C	T	C	NCBI database
Dobong	Korea	HQ712133.1	C	T	C	NCBI database
Gopum	Korea	HQ712126.1	C	T	C	NCBI database
Ilpum	Korea	HQ712127.1	C	T	C	NCBI database
Koshihikari	Japan	HQ712129.1	C	T	C	NCBI database
Palgong	Korea	HQ712130.1	C	T	C	NCBI database
Samgwang	Korea	HQ712128.1	C	T	C	NCBI database
Samnam	Korea	HQ712131.1	C	T	C	NCBI database
Singeumo	Korea	HQ712132.1	C	T	C	NCBI database
Tainung78	China	KF984385.1	C	T	C	NCBI database
Wuyunjing7	China	GQ150900.1	C	T	C	NCBI database
Zhonghan3	China	GQ150901.1	A	T	T	NCBI database
Chunjiang06	China	GQ150899.1	C	T	C	NCBI database
Jiangzhouxiangnuo	China	GQ150902.1	C	T	C	NCBI database
SuYuNuo	China	GQ150903.1	C	T	C	NCBI database
Taihunuo	China	GQ150904.1	C	T	C	NCBI database
OsSBE1	China	D10752.1	C	T	C	NCBI database

Results

Sequencing and deposition at genbank of SBEI gene coding sequences

The *SBEI* coding sequences of 30 rice varieties from China, Laos and Thailand were sequenced and submitted to NCBI database (GenBank accession numbers are shown in Table 3). The thirty sequences showed the same size and exon number, which were 2,463 bp long and consist of 14 exons, encoding 820 amino acids.

Single Nucleotide Polymorphisms (SNPs) in rice SBEI gene

Three SNPs were found in *SBEI* CDS. The first SNP was located at position 1,107 in exon 6, which changes from adenine (A) to cytosine (C). Twenty-six rice varieties have A allele and four varieties have C allele. The second SNP was located at position 2,156 in exon 13, which changes from thymine (T) to cytosine (C). Twenty-seven rice varieties have T allele and three rice varieties have C allele. The third SNP was located at position 2,271 in exon 14, which changes from thymine (T) to cytosine (C). Twenty-six rice varieties have T allele and four varieties have C allele. The SNP at position 1,107 A>C and 2,271 T>C were silent mutation. The SNP at position 2,156 T>C was missense mutation and induced a mutation from valine (GTG) to alanine (GCG) (Table 4). The 3 SNPs from 30 rice varieties were present as 3 haplotypes (A/T/T, C/T/C and C/C/C). The haplotype A/T/T was the dominant haplotype with 26 of 30 rice varieties and all rice varieties from Thailand have this haplotype (A/T/T). Three rice varieties, one from China (Funingnuo) and two from Laos (VTN-289-1 and VTN-324) have C/C/C haplotype. Only one rice variety from China has C/T/C haplotype, which has not been reported before. In order to compare *SBEI* CDS of our study to others, 27 rice *SBEI* CDS from China, Korea and Japan from previous studies were downloaded from NCBI database and sequence analysis showed that *SBEI* CDS from other studies can be classified into 2 haplotypes (A/T/T, C/T/C), with rice from China containing both haplotypes but rice from Korea and Japan containing C/T/C haplotype only (Table 3).

Phylogenetic relationship of SBEI sequences

Thirty *SBEI* CDS from China, Laos and Thailand from this study, and 47 *SBEI* CDS of other plant species and 4 sequences used as outgroup from NCBI database were used to construct a phylogenetic tree (sequence data are shown in Table S2). Phylogenetic tree from Maximum likelihood, Neighbor-joining, Minimum evolution, UPGMA and Maximum parsimony showed the similar results (only tree from Neighbor-joining is showed in Figure 1). The phylogenetic tree could clearly separate 81 samples into 2 major groups and 4 outgroup sequences. Two major groups were the group of monocot and the group of dicot species and the outgroup sequences used were plankton, red algal, protozoa and cyanobacteria. The monocot group composed of rice, barley, wheat, sorghum and maize and the dicot group composed of potato, cassava, poplar, Chinese chestnut, bean, legumes and apple. The group of rice *SBEI* CDS was a major clade in monocot group with high

bootstrap value, which could separate haplotype C/C/C from the other three haplotypes, C/T/C and A/T/T.

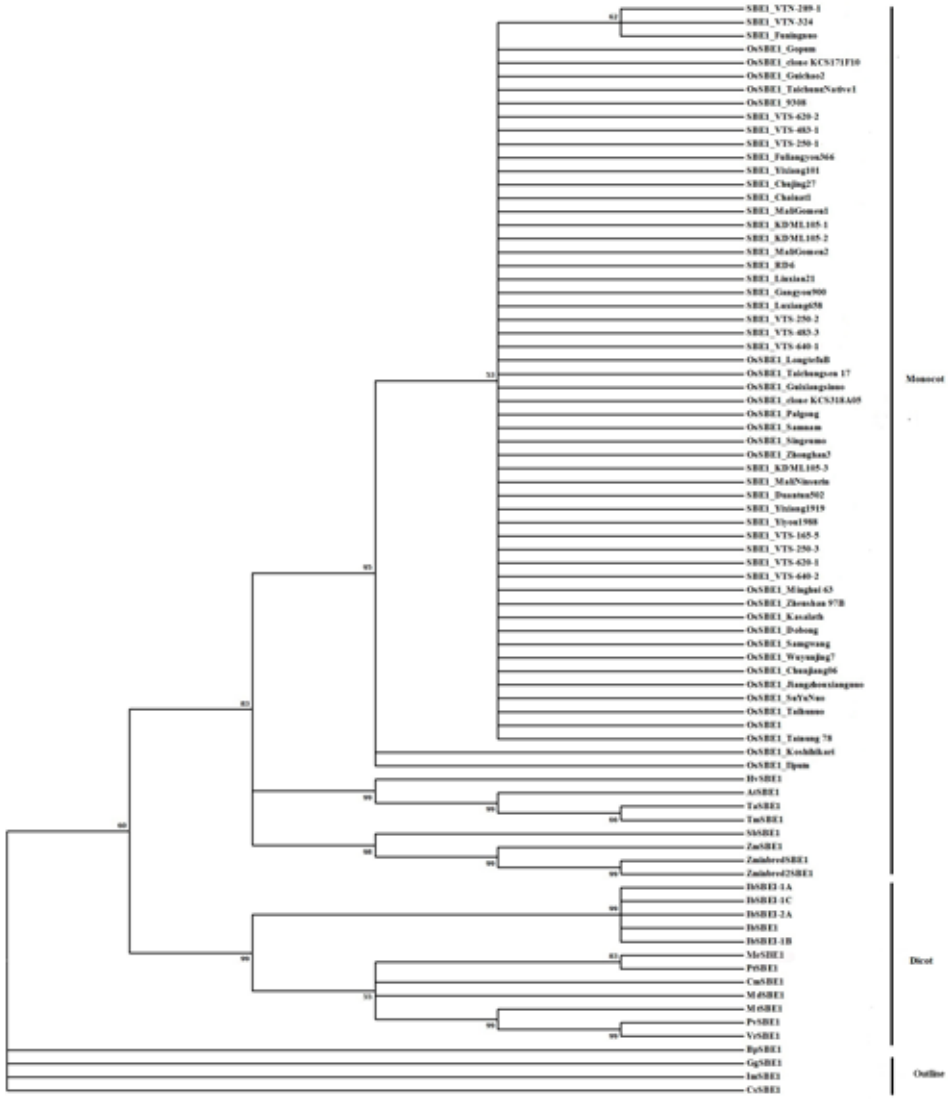

Figure 1. Phylogenetic tree of 81 *SBEI* coding sequences, constructed using; Maximum likelihood (ML) with 1,000 replicates for Bootstrap test using MEGA 7 program

Comparison of SBEI CDS between rice, wheat, apple and poplar

From sequence comparison, *SBEI* CDS showed 2 forms, first form contains 14 exons while second form contains 12 exons. Rice varieties from China, Laos and Thailand, wheat, apple and poplar have 14 exons whereas rice varieties from Japan and Korea have 12 exons. All plant species shared the similar exon size (Table 2). The percent GC content of *SBEI* gene of rice, both with 14 and 12 exons, was lower than that of wheat and apple but higher than that of poplar.

Discussion

Rice quality improving is one of the important goals in rice breeding program. The molecular mechanism of rice quality formation is the prerequisite for efficiently improving the quality of rice. Previous studies showed that the ratio of amylose in total starch is a key factor in determining the starch physicochemical properties and the amylopectin structure is also considered as an important factor for rice quality. The structure of amylopectin is mainly controlled by the *SBE* genes. There are 4 types of SBE found in rice, such as SBEI, SBEII, SBEIII, and SBEIV. SBEI and SBEIII are proven to be the principal factors in the process of endosperm starch synthesis. They are responsible for 70% and 30% of amylopectin synthesis, respectively (Mizuno et al. 1992). *SBEI* and *SBEIII* expression pattern and function are different. *SBEI* was found to be expressed on the third day after flowering and reached peak point during the fifth and seventh day (Mizuno et al. 2001), while SBEIII reached peak point of expression at 5–7 days after flowering (Rahman et al. 2001). In terms of their function, *SBEI* is in charge of long and middle length chain branching, while *SBEIII* is in charge of short chain branching.

The CDS of *SBEI* gene from 30 rice varieties from China, Laos and Thailand showed high similarity with 18 *SBEI* gene sequenes from Chinese rice varieties in NCBI database. All of them shared same exon number and gene size, which were 2,463 bp long and contained 14 exons, encoding 820 amino acids. On the other hand, there was a report of *SBEI* CDS of rice from Japan and Korea, which had only 12 exons (Sun et al. 2011; Puji et al. 2013). The different gene size and exon number indicated the presence of rice genetic variation and can be referred to the source or country origin of the rice variety. Rice varieties from China, Laos and Thailand have conserved 14 exons and rice varieties from Japan and Korea have conserved 12 exons (Sun et al. 2011; Puji et al. 2013). Three sites of SNPs were found. The SNP at position 1,107 A>C and position 2,271 T>C were silent mutations. The SNP at position 2,156 T>C was a missense mutation and induced a mutation from valine (GTG) to alanine (GCG). Three haplotypes A/T/T, C/T/C and C/C/C were observed. Based on *SBEI* CDS genetic variation, 97.7% genetic identity indicated that *SBEI* gene in rice has low genetic diversity or high conservation because its function is very important. Our result was similar to Yawen et al. (2007) which study evaluation of genetic diversity of rice landraces (*Oryza sativa* L.) in Yunnan, China. Interestingly, variation in number of exons in *SBE1* gene does occur as shown in Japanese and Korean rice varieties, which have only 12 exons (absence of exon 1 and 2 from normal *SBEI* gene).

These 12 exons are conserved with exon 3 through exon 14 of the *SBEI* gene that has 14 exons (Sun et al. 2011; Puji and Hel 2013).

Phylogenetic analysis of *SBEI* coding sequences from 81 plant species showed two major groups of monocot and dicot plant species. *SBEI* gene orthologs in both monocots and dicots have evolved from a common ancestor by speciation. The ancestor can be traced back to a remote antiquity prior to the divergence of monocots from dicots (Yuepeng et al. 2007). The rice clade in monocot group of phylogenetic tree can be separated by SNP haplotype. The results from our study clearly indicated that the genetic variation of *SBEI* gene can be used as biomarker and the genetic information of *SBEI* rice gene involved in starch biosynthesis is the basis of understanding the mechanism of starch biosynthesis and starch quality improvement by the application of genetic engineering approach and help for the breeder to generate novel desired starch in the future.

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Electronic Supplementary Material (ESM)

Electronic Supplementary Material (ESM) associated with this article can be found at the website of CRC at https://akademiai.com/loi/0806

Electronic Supplementary *Table S1*. PCR condition used for *SBE1* gene cloning

Electronic Supplementary *Table S2*. 51 *SBE1* CDS used for *SBE1* phylogenetic analysis