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拟南芥和水稻金属蛋白酶 *ftsH* 基因家族的基因组比较分析

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摘 要: FtsH (Filamentation temperature-sensitive H)是一种广泛存在于原核生物和真核生物中的 ATP 依赖型金属蛋白酶。同源性分析表明, 在拟南芥和水稻基因组中分别有 12 个和 9 个 *ftsH* 基因。*ftsH* 基因在染色体上的分布有明显的偏爱性, 如拟南芥的 1、2、5 号染色体和水稻的 1、5 号染色体。亚细胞定位分析表明, 所有 FtsH 蛋白均定位于叶绿体或线粒体中。系统进化分析表明, 21 个 FtsH 蛋白成员可分为 8 个类群, 其中 AtFtsH12 在水稻中没有发现种间同源物。每个类群成员的蛋白序列高度保守, 种内同源物显示出大于 80%的相似性, 而种间同源物的相似性也大于 70%。类群内的同源基因并非平行进化产生的, 拟南芥基因组中进化出 *AtftsH1/5*、*AtftsH2/8*、*AtftsH3/10* 和 *AtftsH7/9* 共 4 个同源基因对, 而水稻基因组中只有 *OsftsH3/8* 和 *OsftsH4/5* 两个同源基因对。每一类群中的成员在基因外显子-内含子边界分布上表现出高度保守性, 在蛋白功能结构域的可变残基上具有偏爱性, 而内含子在碱基组成和序列长度上表现出广泛的变异。拟南芥和水稻 *ftsH* 基因家族的比较分析为其他物种 *ftsH* 基因的特性和功能研究奠定了基础。

关键词: *ftsH* 基因, 拟南芥, 水稻, 基因组, 系统进化分析

Genome-wide comparative analysis of the metalloprotease *ftsH* gene families between *Arabidopsis thaliana* and rice

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Abstract: Filamentation temperature-sensitive H (FtsH) is an ATP-dependent metalloprotease in prokaryotes and eukaryotes. Homology-based analysis was applied to determine 12 *ftsH* genes in *Arabidopsis* genome and 9 members in rice genome. Distribution of these *ftsH* genes on each chromosome displayed a clear preference for some chromosomes such as chromosome 1, 2, 5 of *Arabidopsis* and chromosome 1, 5 of rice. All 21 FtsH proteins were subcellularly targeted to chloroplast or mitochondria. These members could be phylogenetically assorted as eight groups, of which no ortholog of AtFtsH12 in rice was detected. Paralogs in each group shared similarity higher than 80% and orthologs higher than 70%. This strongly indicated that the members from single group were descended from a common ancestral gene. Four pairs of paralogs, *AtftsH1/5*, *AtftsH2/8*, *AtftsH7/9* and *AtftsH3/10* were found in *Arabidopsis* genome. However, only two pairs of *ftsH* paralogs, *OsftsH3/8* and *OsftsH4/5*, resided in rice genome. The highly homologous members in each group performed striking conservation of exon-intron boundaries and preference for the variable

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residues in function domains. By contrast, there was significant difference in base composition and sequence length of introns. The comparative analysis of the *ftsH* gene families of *Arabidopsis* and rice provided the basis for characteristic and function research of *ftsH* genes in other plants.

Keywords: *ftsH* gene, *Arabidopsis thaliana*, rice, genome, phylogenetic analysis

Introduction

Proteolysis is poorly understood in plant biology. Responding to changes in environment conditions, senescence and cell death, proteases play crucial roles in proteolysis during many important processes [1]. There is very little information known on the functions of these proteases such as substrate specificity and physiological roles. FtsH, initially described in a temperature-sensitive and cell-division-defective *E. coli* mutant, also called HflB in bacteriophage λ, is an ATP-dependent metalloprotease that is ubiquitous among prokaryotes and eukaryotes [2-3]. Different number of *ftsH* genes was found in genomes of bacteria, yeast, plants and human [4-10]. Almost all the *ftsH* homologs reported in higher plants were encoded by nuclear DNA. The prokaryotic FtsH proteins are usually bound to the plasma membrane, and the eukaryotic FtsH proteins are targeted to the membranes of chloroplasts or mitochondria [11-12]. At the N terminus of FtsH protein, two transmembrane α-helices anchor the protein to the membrane of mitochondria or thylakoid. The hydrophobic domains are followed by the ATPase domain, which relates this protein to the AAA^+ superfamily of proteins. The proteolytic domain is found in the C terminus, which contains the zinc binding motif [13]. The crystal structure suggested that FtsH protein forms ringlike hexamers, with the ATP binding motifs facing the center of the ring [14-15].

Most *ftsH* mutants do not have visible phenotypes. This makes it difficult to know their biological functions. In *Arabidopsis*, only four chloroplast proteins encoded by the closely related *ftsH* gene pairs (*AtftsH1* and *AtftsH5*, *AtftsH2* and *AtftsH8*) are known to be involved in complex formation, photosystem II repair and chloroplast biogenesis [13].

The genome sequencing of *Arabidopsis* and rice (*Oryza sativa*) had been completed. This makes it possible to find all of the *ftsH* genes in both genomes of *Arabidopsis* and rice. We have undertaken a comprehensive bioinformatics-based analysis of *ftsH* genes across two genomes. This reveals the distribution pattern, homology and organization characteristics and functional relativity of the FtsH members from two species. In this article, we focused on phylogenetic relation of *ftsH* genes between the dicots and monocots.

1 Materials and methods

Our collection of non-redundant FtsH proteins of *Arabidopsis* was gathered from the Institute for Genomic Research (At TIGR database, http://www.tigr.org/). Rice *ftsH* genes were collected by TIGR Rice Genome Annotation-Release 5. Information regarding the gene structure of *Arabidopsis* and rice was obtained from the TIGR. Other *ftsH* homologs were obtained from NCBI database on the basis of blastp.

The isoelectric points and molecular weights of FtsH proteins were obtained with the help of Proteomics and sequence analysis tools on the ExPASy Proteomics Server (http://expasy.org/). Protein subcellular localization prediction was performed at the WoLF PSORT (http://wolfpsort.cbrc.jp/). Prediction of transmembrane regions and orientation was obtained with the aid of TMpred software of database of membrane spanning protein segments (http://www.ch.embnet.org/software/TMPRED_form.html).

Multiple alignments of protein sequences by the CLUSTALW were performed at the DNA Data Bank of Japan (http://www.ddbj.nig.ac.jp/Welcome-e.html). The phylogenetic relationship analysis was conducted using MEGA4.0 by the neighbor-joining method. Bootstrap analysis with 1000 replicates was performed to evaluate the significances of the nodes. Rice and *Arabidopsis* conserved motif analysis within the determined FtsH families was performed by means of the RiceGAAS (Rice Genome Automated Annotation System, http://RiceGAAS.dna.affrc.go.jp/), the computer program MEME (Multiple EM for Motive Elicitation, http:// meme.sdsc.edu/meme/) and BLOCKS (http:// blocks. fhcrc. org/).

2 Results

2.1 Genomic-wide profile of *ftsH* gene family of *Arabidopsis* and rice

Based on the sequence alignments, twelve *ftsH* gene members were found in genome of *Arabidopsis thaliana* (*AtftsH1–AtftsH12*). With a much larger genome, however, only nine *ftsH* members (*OsftsH1–OsftsH9*) were detected in rice genome. Among the five chromosomes of *Arabidopsis* genome, no *ftsH* gene distributes on the chromosome 4. Most of the *ftsH* members were located on the chromosome 1 (four members), chromosome 2 (three members) and chromosome 5 (four members), except for one member on the chromosome 3. For the nine *OsftsH* genes, seven members were located on the chromosome 1 and chromosome 6. No *ftsH* gene can be found on chromosome 3, 4, 7, 8, 9 and 10. This indicates that the location of *ftsH* genes on the chromosomes may

be preferential.

According to the prediction, the full length of most FtsH proteins ranges from 676 to 822 amino acids, except that the AtFtsH12 is 1008 amino acids in length, which is much larger than others. The isoelectric points of FtsH proteins targeted to mitochondria entirely exhibit alkalinity, and most of the FtsH proteins in chloroplasts were shown to be acidic (Table 1). It was adaptable to the pH values within the matrix of chloroplasts and mitochondria.

2.2 Phylogenetic analysis of *ftsH* gene family in *Arabidopsis* and rice

Sequence alignments of FtsH proteins from *Arabidopsis* and rice suggested that FtsH family members shared high homology in their interior regions especially in the functional domains and high variability at the N or C terminus. Fig.1 showed the phylogenetic tree of FtsH proteins obtained by Nj (neighbor joining). According to the assay, many of the FtsH proteins have their paralogs in *Arabidopsis* and twenty one FtsH proteins are assorted as eight groups. All of FtsH proteins in any group are exclusively localized in the same organelle and share high similarity. All of the group members in *Arabidopsis* have orthologs in other organism, although some could not be found in rice genome, such as that of AtFtsH12. Most of the homologous members of group 3 and 4 (Table 2), subcellularly targeted to mitochondria, are phylogenetically close to the FtsH proteins of *Saccharomyces cerevisiae*. Most of other group members targeted to chloroplast are phylogenetically close to the FtsH proteins of *Synechocystis* sp. PCC 6803. While group7 and group8 members, also targeted to chloroplast, show to be more phylogenetically close to those of *Saccharomyces cerevisiae*.

Among these FtsH proteins from *Arabidopsis* and rice genome, paralogs in any group share similarity higher than 80%, and orthologs between *Arabidopsis* and rice in single group share similarity higher than 70% (Fig. 2). Although with the characteristic function domains, AtFtsH12 share similarity lower than 30% with any other

Table 1 *ftsH* gene family in *Arabidopsis* and rice genome

Species	Gene name	GenBank Accession No.	Chromosome localization	Subcellular localization	Protein size (aa)	Molecular weight	Isoelectric point
Arabidopsis thaliana	*AtftsH1*	NM103909	1	Chloroplast	716	76760	5.54
	AtftsH2	NM147357	2	Chloroplast	695	74158	6.24
	AtftsH3	NM128465	2	Mitochondrion	809	89354	7.29
	AtftsH4	NM128172	2	Mitochondrion	717	77276	9.00
	AtftsH5	NM123592	5	Chloroplast	704	75233	5.13
	AtftsH6	NM121529	5	Chloroplast	688	74516	7.71
	AtftsH7	NM114573	3	Chloroplast	802	87803	8.40
	AtftsH8	NM100523	1	Chloroplast	685	73199	5.68
	AtftsH9	NM125277	5	Chloroplast	806	87839	8.00
	AtftsH10	NM100625	1	Mitochondrion	813	89556	8.65
	AtftsH11	NM124696	5	Chloroplast	806	88718	6.01
	AtftsH12	NM106604	1	Chloroplast	1008	115106	6.92
Oryza sativa	*OsftsH1*	AP003685	6	Chloroplast	686	72703	5.51
	OsftsH2	AP003635	6	Chloroplast	676	72538	5.54
	OsftsH3	AP003240	1	Mitochondrion	802	88144	8.00
	OsftsH4	AP003413	1	Mitochondrion	709	76785	9.24
	OsftsH5	AP003413	1	Mitochondrion	715	77434	8.08
	OsftsH6	AP003569	6	Chloroplast	681	72624	6.06
	OsftsH7	AP004868	2	Chloroplast	822	87919	7.11
	OsftsH8	AC105770	5	Chloroplast	822	52375	5.39
	OsftsH9	AP003328	1	Chloroplast	769	89152	6.00

Table 2 Groups classification of FtsH proteins from *Arabidopsis* and rice

Group number	Gene member	Number of exon	Protein subcellular localization
1	*AtftsH1*, *AtftsH5*, *OsftsH1*	5, 5, 5	C
2	*AtftsH2*, *AtftsH8*, *OsftsH2*	4, 4, 4	C
3	*AtftsH3*, *AtftsH10*, *OsftsH3*, *OsftsH8*	8, 8, 8, 8	M
4	*AtftsH4*, *OsftsH4*, *OsftsH5*	7, 7, 7	M
5	*AtftsH6*, *OsftsH6*	5, 2	C
6	*AtftsH7*, *AtftsH9*, *OsftsH7*	13, 13, 13	C
7	*AtftsH11*, *OsftsH9*	17, 17	C
8	*AtftsH12*	19	C

C: chloroplast; M: mitochondrion.

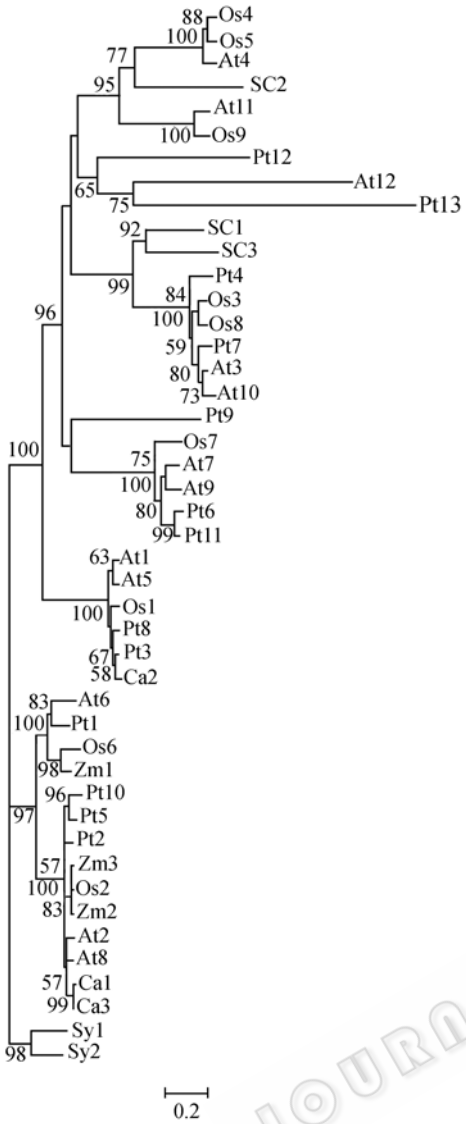

Fig. 1 Phylogenetic tree of FtsH proteins from *Arabidopsis*, rice and their homologs. Phylogenetic tree was inferred using the neighbour-joining method and is based on an alignment of the 21 *Arabidopsis* and rice FtsH proteins and their homologs in other genomes. Bootstrap analysis with 1000 replicates was performed with the FtsH proteins of *Synechocystis* sp. as the outgroup. At1−At12 and Os1−Os9, the FtsH1−FtsH12 of *Arabidopsis* and FtsH1−FtsH9 of rice as presented in Fig.1. Sy1, Sy2, FtsH homologs of *Synechocystis* sp. PCC 6803 (BAA17205 and BAA10230). Sc1−Sc3, FtsH homologs of *Saccharomyces cerevisiae* (CAA56953, AAA02883 and CAA56955). Ca1−Ca3, FtsH homologs of *Capsicum annum* (CAA09935, CAA62084 and X80755). Zm1−Zm3, the FtsH homologs of *Zea mays* (ACG28886, ABY82591 and ABY82592). Pt1−Pt13, FtsH homolog of *Populus trichocarpal* (EEF04193, EEE98711, EEE81200, EEF05269, EEE72861, EEE88077, EEE87381, EEE93966, EEE86485, EEE82098, EEE84631, EEE84268 and ABO36749).

FtsH member. This strongly suggested that the members from single group maybe descend from a common ancestral gene. However, the seven groups were not from parallel evolution. The FtsH homologs of group 2 were more closely related to those of group 5, and both of these two groups were found in chloroplasts. The group 4 and group 7 were also great relative, while they resided in mitochondria and chloroplasts, respectively. Therefore, not only sequence shuffling but also subfunctionalization occurred during the evolution.

As apparent results of more frequent genetic duplication, the *Arabidopsis ftsH* gene family was larger than that of rice. Four pairs of paralogs from *Arabidopsis* genome are highly conservative, of which three protein pairs, AtFtsH1/5, AtFtsH2/8, AtFtsH7/9, are localized in chloroplasts and only one protein pair, AtFtsH3/10, are located in mitochondria (Table 2). This homology implicates that *ftsH* genes in one group might play the same or relative roles in different plants. It has been known that the members within the pair of *AtftsH1/5* (subunit type A) or *AtftsH2/8* (subunit type B) is functionally redundant [13]. However, only two pairs of *ftsH* paralogs from *OsftsH 3/8* and *OsftsH4/5*, reside in rice genome, which were targeted to mitochondria. As shown in Table 1, all the members of the *ftsH* gene pairs in *Arabidopsis* and the *OsftsH3/8* pair in rice distribute on different chromosomes except that *OsftsH4* and *OsftsH5* are tandemly arrayed on the chromosome 1 with only four kilobase distances (Table 1). The results showed that the duplication of *ftsH* genes companied with gene rearrangement on the chromosome.

2.3 Conservation of *ftsH* gene family in *Arabidopsis* and rice

As an independent member of AAA proteases superfamily, FtsH proteins own their sequence specificity in the functional domains. Usually there are two transmembrane domains at the N terminus anchoring the FtsH protein to the membranes of thylakoids or mitochondria; exceptionally AtFtsH11 contains only one transmembrane domain. The ATP binding domains, including motifs of Walker A and Walker B, can be represented as $GX_1LLX_2GX_3PGTGKT$ and $PX_1X_2VFX_3DE$ IDA (X is variable residue, the same as follows, Fig. 3). The characteristic SRH (the second region of homology) domain of FtsH can be represented as $TNX_1X_2X_3X_4LDX_5X_6X_7X_8RX_9GRX_{10}DR$. This domain distinguishes the FtsH proteins from other AAA proteases. The zinc binding motif HEX_1X_2H in FtsH protein serves as the active site of protease, of which only the residue X_1 of the *Arabidopsis* and rice FtsH proteins performed to be variant, the residue X_2 is conservative as G. Surprisingly, another region of high homology ($TX_1GFX_2GADX_3X_4NX_5X_6NX_7AA$) in FtsH proteins is found between the SRH domain and zinc binding motif. By the NCBI conserved domain search, the non-named region of homology is predicted as the choline kinase domain, but its function remains unclear.

Of the variable region of the function domains, the FtsH members of the same group usually tend to select the same residue. This conservation of some residues in the variable region can be regarded as the characteristics for one group. For instance, group 1 select the residue X_1 in Walker A domain as O and the residue X_4 in the non-named

AtFtsH1	100%												
AtFtsH2	48.5%	100%											
AtFtsH3	36.6%	36.3%	100%										
AtFtsH4	37.8%	38.7%	32.5%	100%									
AtFtsH5	88.6%	49.3%	37.5%	38.5%	100%								
AtFtsH6	45.6%	68.8%	36.5%	38.0%	46.9%	100%							
AtFtsH7	39.6%	37.3%	31.8%	33.5%	39.0%	37.8%	100%						
AtFtsH8	47.8%	91.3%	36.4%	38.2%	48.7%	68.4%	37.4%	100%					
AtFtsH9	38.2%	37.4%	31.5%	32.9%	38.0%	37.7%	85.0%	37.5%	100%				
AtFtsH10	36.1%	34.7%	84.8%	31.4%	36.3%	36.1%	31.1%	35.5%	30.7%	100%			
AtFtsH11	36.7%	36.9%	32.8%	50.3%	36.3%	37.6%	29.7%	37.5%	29.6%	31.6%	100%		
AtFtsH12	26.8%	24.6%	22.2%	22.2%	27.4%	24.7%	21.5%	24.7%	21.1%	22.3%	20.1%	100%	
OsFsH1	82.3%	48.4%	37.0%	38.3%	83.9%	46.6%	40.5%	47.9%	39.5%	36.8%	87.5%	28.4%	100%
OsFsH2	48.2%	85.0%	36.5%	39.0%	48.2%	69.9%	37.3%	85.6%	37.5%	35.4%	37.9%	26.0%	47.8% 100%
OsFsH3	36.4%	37.7%	72.5%	34.2%	36.7%	36.8%	30.6%	38.3%	30.3%	72.1%	33.2%	21.0%	37.3% 37.3% 100%
OsFsH4	37.6%	37.4%	33.9%	76.5%	37.8%	36.7%	33.4%	37.5%	32.8%	32.3%	48.7%	23.0%	37.6% 38.5% 33.4% 100%
OsFsH5	38.0%	87.6%	33.9%	79.1%	38.4%	38.3%	33.8%	37.7%	32.7%	32.2%	50.3%	22.4%	38.4% 39.1% 33.8% 87.3% 100%
OsFsH6	46.0%	66.4%	35.8%	36.6%	47.4%	71.1%	37.8%	66.6%	37.6%	35.1%	36.5%	25.6%	47.4% 68.6% 36.3% 35.9% 37.9% 100%
OsFsH7	38.1%	37.2%	30.1%	34.6%	38.8%	38.1%	73.3%	38.0%	71.8%	29.3%	29.7%	21.2%	39.3% 39.7% 29.5% 33.6% 33.9% 38.1% 100%
OsFsH8	37.8%	36.5%	76.9%	32.4%	38.2%	36.2%	31.2%	37.0%	30.5%	76.7%	32.5%	21.0%	38.4% 36.9% 83.0% 33.4% 33.0% 36.5% 30.0% 100%
OsFsH9	37.5%	37.3%	32.5%	50.8%	37.2%	37.8%	29.9%	37.8%	28.8%	31.5%	75.3%	20.0%	38.3% 38.6% 31.7% 49.4% 50.7% 36.9% 29.2% 31.9% 100%

Fig. 2 Sequence similarity of FtsH proteins from *Arabidopsis* and rice.

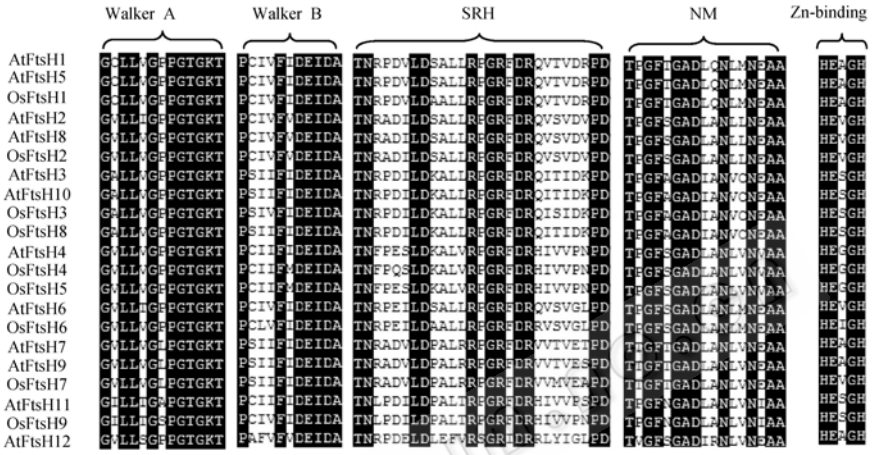

Fig. 3 Amino acid sequence conservation of the FtsH domains from *Arabidopsis* and rice. NM: non-named region of homology.

region as Q, while group 7 select the residue X1 in Walker A domain as I and the residue X2 in the non-named region as N. The majority of the variable residues in AtFtsH12 differ from other group, it also implicated that AtFtsH12 was origined from independent evolutionary incident. These conservative sequences provided the criterion for the isolation and identification of the *ftsH* gene from other plant genome.

2.4 Organization of exon-intron in *ftsH* genes from *Arabidopsis* and rice genome

Comparison of the predicted gene structure of the *AtftsH* genes with the annotated pseudomolecule sequences with the sequences of cDNAs and ESTs revealed that the TIGR annotation of exon-intron is largely correct. As for the nine *OsftsH* gene captured from rice genome, some with incomplete information of gene structures were complimented and corrected by comparison of the reported protein sequences with the predicted open reading frames. The rectified exon-intron organization of twenty-one *ftsH* genes was shown in Fig.4. The last intron in *OsftsH1* (4381 bp in length) and the first intron in *OsftsH9* (11089 bp in length) marked with dot lines seem unreasonable, which maybe derive from the overlapping error in sequencing.

All of the *ftsH* genes of *Arabidopsis* and rice are splicing genes. Consistent with the sequence alignments, *ftsH* genes with high homology confirmed a striking conservation of the exon-intron borders. Among the *ftsH* gene family, the number of exons in each member ranges from two to nineteen. The homologous *ftsH* genes usually own the same number of exons except for the orthologs of *AtftsH6/OsftsH6* (Table 2). Every exon of the gene member in any group exhibits the high similarity and even the same size and base composition. Comparing with the high conservative exons of homologs among the different groups in Fig.1, the introns are more various in the base composition and sequence length. This result suggested that introns were evolutionarily more instable than exons, which accorded with the traditional evolution. Exceptionally, *OsftsH6* owns exons much lower than that of *AtftsH6*, which maybe come from the intragenic rearrangement resulting in the deletion or insertion of intron.

There are four *ftsH* gene pairs in *Arabidopsis*, and only two gene pairs reside in rice genome. The homologous gene pairs in the group 3, *OsftsH3/8* and *AtftsH3/10*, indicated the similar duplication during the evolution occurred after chloroplasts had diverged from their prokaryotic progenitors. However, in many cases, duplications seem to occur independently. The gene pairs

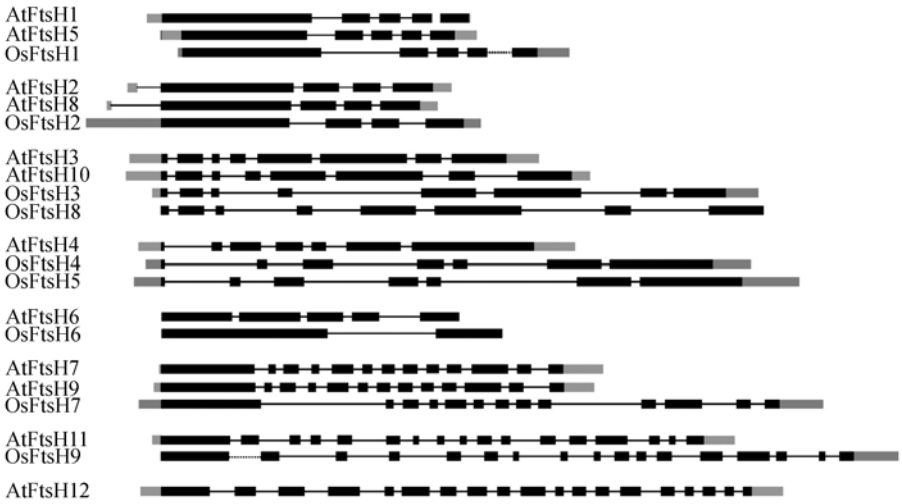

Fig. 4 Structure of *Arabidopsis* and rice *ftsH* genes. Black boxes indicate exons and lines represent introns. Bilateral grey boxes indicate the 5′-UTRs and 3′-UTRs. The size of the boxes and lines are proportionally mapped.

corresponding to *AtftsH1/5*, *AtftsH2/8* and *AtftsH7/9* can not be found in rice, just like that the corresponding gene pair to *OsftsH4/5* can not be detected in *Arabidopsis*. Ultimately, gene duplications under different genetic background indicate the similarity and independence in evolution.

3 Discussion

3.1 Phylogenetic relation of *ftsH* genes between the dicots and monocots

The comparative analysis of the FtsH proteins between *Arabidopsis* and rice strongly suggested that FtsH family was highly conservative. The paralogs or orthologs of each FtsH member among these two genomes share high similarity in amino acid sequences, especially in functional domains. Almost all the FtsH proteins in *Arabidopsis* can be found their orthologs in rice. This means that the *ftsH* genes of monocots and dicots origin from the same ancients. While a few members and its homologs were added or cancelled during the evolution, just as the corresponding ortholog of AtFtsH12 can not be found in rice.

After the differentiation of *Arabidopsis* and rice, independent evolutionary duplication occurred, so we detect the characteristic paralog groups in each genome. By comparison of sequence and intron-exon organization between the *Arabidopsis* and rice, some important informations are given for classification and biological prediction of a new *ftsH* gene. First, the new *ftsH* gene shares high similarity with its homolog. Second, according to its homolog, the new *ftsH* gene contains similar, even the same number and size of exons. Third, the new FtsH protein contains the same characteristic residues in the variable region of function domains as that of its homolog. Furthermore, the new one is usually targeted to the same subcellular localization as its homolog.

All of the FtsH proteins in *Arabidopsis* and rice subcellularly located in chloroplasts or mitochondria. This accorded with other FtsH proteins reported from other plants. Yeast FtsH proteins known so far were localized at mitochondria [16]. None of the FtsH proteins in eukaryotes could be found at organelle out of chloroplasts and mitochondria. So the FtsH family maybe play important roles in the protein quality control of the semi-independently genetic organelles.

3.2 FtsH multiplication and its function

The FtsH family in higher plants contains numerous members, many of which are found in chloroplasts[17-19], whereas all bacterial genomes contain a single *ftsH* gene. It appears that multiplication of *ftsH* genes correlates with the evolution of oxygenic photosynthesis. This multiplication of higher plant *ftsH* genes occurred after chloroplasts had diverged from their prokaryotic progenitors [12-13,20].

Functional studies have revealed important roles for FtsH homologs in stress responses [21-22]. The identified FtsH homologs degrade various proteins and are thus involved in diverse biological functions. When plants were subjected to various stress, either chloroplast or mitochondrion protein turnover is disturbed, the energy cycle would be out of order. The membrane-bound FtsH proteases serve to degrade the irreversibly-damaged protein and are involved in the protein quality control.

Of the nine FtsH that resides in the chloroplasts, four chloroplastic FtsH proteins (AtFtsH1/5 and AtFtsH2/8) have been shown to be involved in the degradation of photosynthetic proteins during light acclimation or after high light damage [21,23]. The FtsH proteins within the same pair very likely work in concert, and have overlapping functions. In *Arabidopsis*, FtsH1 and FtsH5 (subunit type A) and FtsH2 and FtsH8 (subunit type B) are redundant. FtsH1 and FtsH5 are interchangeable in

thylakoid membranes. The functional significance of FtsH multiplication in plants is unclear.

Study using the *Arabidopsis* ΔFtsH6 mutant shows that the AtFtsH6 protease degrades both Lhcb3 and Lhcb1, and is involved in both senescence-induced degradation and HL (high light intensity) acclimation [24]. Most recently, a study showed that the *Arabidopsis* FtsH11 is essential to thermotolerance in *Arabidopsis*, which plays an important role in high temperature stress tolerance but not in light stress [25]. We here present a comparative analysis of the gene families encoding for various FtsH proteins of *Arabidopsis* and rice. The high similarity of the gene structure and functional domains of the same group of FtsH homologs means the functional consistency between *Arabidopsis* and rice. This study provided a good theoretical basis for the function research of rice *ftsH* families under various stress conditions.

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