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Identification, phylogenetic analysis, and expression patterns of the *SAUR* gene family in loquat (*Eriobotrya japonica*)

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Abstract: Small auxin-up RNAs (*SAUR*s) are the most frequent and primary auxin responsive genes, and they are commonly used as early auxin-responsive markers. Until now, no *SAUR* gene has been identified in *Eriobotrya* plants. In this study, we used *Arabidopsis SAUR* sequences as a query to search against the loquat genome sequence. In total, we obtained 57 *SAUR* genes in loquat, hereafter referred to as *Eriobotrya japonica SAUR* (*EjSAUR*) genes, which ranged from 267 to 735 bp in the coding sequence with predicted proteins of 88–244 aa. A total of 47 *EjSAUR* genes were distributed on 11 chromosomes of the loquat genome. Based on their physical positions, 80.9% (38 of 47) of the *EjSAUR* genes were clustered together on the loquat chromosomes, suggesting that tandem duplicate genes might be the major mechanism for the expansion of this family. The expression analysis displayed high expression divergence among the different organs, which suggested that *EjSAUR* genes may play an important role in different organs. These results laid a foundation for the functional validation of *EjSAUR* genes in *Eriobotrya* plants.

Key words: Auxin, *SAUR*, phylogenetic analysis, expression analysis, loquat (*Eriobotrya japonica*)

1. Introduction

Auxins, a class of phytohormones, exert pleiotropic effects on various aspects of plant growth and development, including cell elongation, cell division, differentiation, root initiation, apical dominance, and tropic responses. Hundreds of gene expressions are regulated by auxins, including early auxin response gene families, Aux/IAA, Gretchen Hagen3 (*GH3*), and small auxin-up RNAs (*SAURs*) (Abel and Theologis, 1996; Guilfoyle et al., 1998; Liscum and Reed, 2002). Among them, *SAUR* genes are rapidly induced by auxin, so they are commonly used as early auxin-responsive markers in soybean, *Arabidopsis*, and tobacco (McClure et al., 1989; Gil et al., 1994; Roux et al., 1998). The first *SAUR* gene was isolated in soybean (McClure and Guilfoyle, 1987). To date, *SAUR* genes have been reported in many horticultural plants, such as apple (Watillon et al., 1998), pepper (Marois et al., 2002), litchi (Kuang et al., 2012), potato (Wu et al., 2012), citrus (Licciardello et al., 2013), and peach (Tatsuki et al., 2013). Although many *SAUR* genes have been identified or predicted in different species, only a small number were functionally characterized. Most studies on the functions of *SAUR* genes were about *Arabidopsis*, and their functions mainly concentrated on cell expansion (Qiu et al., 2013; Spartz et al., 2014) and cell elongation (Chae et al., 2012; Stamm and Kumar, 2013). Similar conclusions were also drawn for soybean and maize (Gee et al., 1991; Knauss et al., 2003). In rice, the upregulation of *SAUR39* negatively regulated auxin biosynthesis and transport (Kant et al., 2009). With the advent of modern sequencing technology, the whole genomes of many plants have been sequenced, which enabled us to identify important genes; hence, a genome-wide analysis of *SAUR* genes became easier and many *SAUR* genes were identified in maize, Urticales plants, and *Brassica rapa* (Zhao et al., 2012; Chen et al., 2014; Huang et al., 2016; Nadeem et al., 2018).

Loquat belongs to the genus *Eriobotrya* Lindl. of Rosaceae, subfamily Maloideae, and originated in China. It is the only species of the genus that was cultivated for food and it is now being cultivated in more than 10 countries. China has the biggest cultivated area and production of loquat. Compared with other fruits, the molecular basis

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of loquat still remains low, even with the availability of bioinformation (Wang et al., 2017; Yang et al., 2017). From 2013 to 2016, the loquat genome sequence was completed by our research group and BGI-Shenzhen, and this project made it possible to understand the functions and evolution of *SAUR* genes in loquat, although the data are still unpublished. In the present study, a genome-wide search for *Eriobotrya japonica SAUR* genes (*EjSAUR* genes) was carried out and the putative members of the *EjSAUR* genes were identified. Detailed information on the genomic structures and chromosomal locations of the *EjSAUR* genes are presented here. A phylogenetic analysis of *SAUR* genes in *Arabidopsis* and loquat was performed. Moreover, the expression levels of the *EjSAUR* genes were analyzed using the previous transcriptome data. The results provided an overview for loquat *SAUR* genes and will serve as a guideline for future studies.

2. Materials and methods

2.1. Searching for EjSAUR genes

Loquat genome sequencing data (unpublished) from BGI-Shenzhen, in Guangdong, China, were used for the identification of putative *SAURs* in loquat. The amino acid sequences of *Arabidopsis* SAUR proteins were downloaded from the National Center for Biotechnology Information (NCBI) (http://www.ncbi.nlm.nih.gov). The BLAST search tool BLASTP (Altschul et al., 1997) was used to identify putative *EjSAUR* genes in loquat using 72 *Arabidopsis* SAUR protein sequences as queries. The hits with an optimized cutoff value of identity of more than 50%, coverage of more than 50%, and expect value of less than $1e^{-5}$, without any filter, were used for further analysis. The Pfam database (http://www.sanger.ac.uk/Software/Pfam/search.shtml) was used to confirm each predicted *EjSAUR* protein sequence.

2.2 Mapping of the EjSAUR genes on the chromosomes

To determine the location of the *EjSAUR* genes on the chromosomes, we converted the coordinates of the *SAUR* genes on the scaffold to the coordinates of corresponding chromosome. Finally, the locations of the 47 *EjSAUR* genes in the loquat genome were identified. Finally, the locations of the 47 *EjSAUR* genes in the loquat genome were identified.

2.3. Phylogenetic analysis and subcellular localization prediction

Multiple-sequence alignments for all of the available SAUR protein sequences of *Arabidopsis* and loquat were generated using ClustalX (Thompson et al., 1997). The phylogenetic analysis was performed using the MEGA 5.0 program and neighbor-joining (NJ) method, and the bootstrap test was carried out with 1000 replicates based on the full-length protein sequences. Subcellular localization prediction of each of these family genes was carried out using ProtComp 9.0 software (http://www.softberry.com/berry.phtml?topic=protcompan&group=programs&subgroup=proloc).

2.4. Expression profiling of the EjSAUR genes

To further investigate the *EjSAUR* gene expressions in different organs, previous transcriptome data were used. The total RNA of each sample was isolated using the QuickRNA isolation kit (Bioteke Corporation, Beijing, China) according to the manufacturer's protocols and treated with DNase I (TaKaRa, Japan) for 4 h. The integrity of the RNA samples was examined with an Agilent 2100 bioanalyzer (Agilent Technologies, Palo Alto, USA). The cDNA library preparation and sequencing reactions were conducted by BGI-Shenzhen. The cDNA library was sequenced on the Illumina sequencing platform (HiSeqTM2500).

3. Results

3.1. Identification and subcellular localization of the EjSAUR genes

After removing the redundant sequences, 57 *SAUR* sequences were separately retrieved from the unpublished loquat genome, which were named *EjSAUR1* to *EjSAUR57* (Table). These genes ranged from 267 to 735 bp in the coding sequence (CDS) with predicted proteins of 88–244 aa. The predicted protein localization was conducted online by a subcellular localization predictor (ProtComp 9.0, http://www.softberry.com/berry.phtml?topic=protcompan&group=programs&subgroup=proloc). We found that 26, 8, and 7 *EjSAUR* genes were more likely to be located in the mitochondrial, cytoplasmic, and membrane-bound organelles, respectively. Only 6 *EjSAUR* genes were located in the plasma membrane. Moreover, the other 10 *EjSAUR* genes were distributed in extracellular, Golgi, nuclear, and membrane-bound extracellular regions (Table).

3.2. Chromosomal locations of the EjSAUR genes

The chromosomal locations and transcription directions of the 57 *EjSAUR* genes were determined and demonstrated. However, only 47 *EjSAUR* genes were found in the loquat chromosomes and we failed to localize 10 *EjSAUR* genes on the chromosomes. The *EjSAUR* genes were randomly distributed over all 11 of the loquat chromosomes (Figure 1) and the number of *EjSAUR* genes per chromosome ranged from 1 (Chr14) to 17 (Chr7). Seventeen genes were located on chromosome 7; 5 on chromosome 15; 4 on chromosomes 16 and 17; 3 on chromosomes 4, 5, 11, and 12; and 2 on chromosomes 6 and 13, respectively. Only 1 gene was located on chromosome 14. Based on their physical positions, 80.9% (38 of the 47) of the

Table. *SAUR* gene family in loquat.

Gene code	Gene	CDS (bp)	Predicted protein (aa)	ProtComp localization	Chromosome number	Location
Eri015342.1	*EjSAUR1*	456	151	Membrane-bound mitochondrial	16	2415751-2416619
Eri017132.2	*EjSAUR2*	735	244	Nuclear	15	18915802-18917012
Eri037237.1	*EjSAUR3*	531	176	Mitochondrial	11	30071829-30072712
Eri020301.1	*EjSAUR4*	303	100	Plasma membrane	7	5046494-5046796
Eri006245.1	*EjSAUR5*	375	124	Plasma membrane	17	10855116-10855490
Eri006286.1	*EjSAUR6*	300	99	Plasma membrane	17	11728804-11729103
Eri020294.1	*EjSAUR7*	276	91	Mitochondrial	7	4973483-4974455
Eri005825.1	*EjSAUR8*	447	148	Mitochondrial	12	17413361-17414596
Eri011283.1	*EjSAUR9*	387	128	Mitochondrial	–	141198205-141199185
Eri012400.1	*EjSAUR10*	306	101	Mitochondrial	16	1036844-1037679
Eri022983.1	*EjSAUR11*	267	88	Mitochondrial	–	38404574-38404840
Eri039660.1	*EjSAUR12*	450	149	Golgi	–	30323853-30324878
Eri004860.1	*EjSAUR13*	507	168	Cytoplasmic	4	7999513-8000019
Eri016135.1	*EjSAUR14*	576	191	Cytoplasmic	14	24876941-24877782
Eri004500.1	*EjSAUR15*	552	183	Mitochondrial	5	7745685-7747982
Eri016849.1	*EjSAUR16*	306	101	Mitochondrial	7	4891019-4891753
Eri017126.1	*EjSAUR17*	360	119	Extracellular	15	18816209-18816568
Eri020302.2	*EjSAUR18*	603	200	Membrane-bound mitochondrial	7	5056005-5059403
Eri039636.1	*EjSAUR19*	384	127	Extracellular	–	30008574-30008957
Eri029663.1	*EjSAUR20*	372	123	Plasma membrane	–	10738381-10739630
Eri036160.1	*EjSAUR21*	516	171	Mitochondrial	17	20858288-20859740
Eri020300.1	*EjSAUR22*	297	98	Mitochondrial	7	5043902-5044839
Eri020290.1	*EjSAUR23*	306	101	Mitochondrial	7	4939641-4939946
Eri017127.1	*EjSAUR24*	360	119	Extracellular	15	18822467-18822826
Eri005415.1	*EjSAUR25*	354	117	Membrane-bound mitochondrial	–	203402802-203403155
Eri037933.1	*EjSAUR26*	321	106	Mitochondrial	11	39354054-39354513
Eri006244.1	*EjSAUR27*	375	124	Plasma membrane	17	10853491-10853865
Eri019186.1	*EjSAUR28*	360	119	Mitochondrial	12	16587904-16588263
Eri020299.1	*EjSAUR29*	276	91	Mitochondrial	7	5036320-5037238
Eri015126.2	*EjSAUR30*	480	159	Membrane-bound extracellular	13	2452306-2454985
Eri015123.1	*EjSAUR31*	318	105	Mitochondrial	13	2412135-2413354
Eri037239.1	*EjSAUR32*	366	121	Golgi	11	30088767-30089527
Eri020297.1	*EjSAUR33*	306	101	Mitochondrial	7	4985478-4985783
Eri015341.2	*EjSAUR34*	324	107	Plasma membrane	16	2353952-2354859
Eri022980.1	*EjSAUR35*	285	94	Membrane-bound mitochondrial	–	38351371-38352167
Eri020477.1	*EjSAUR36*	402	133	Extracellular	–	15936363-15936764
Eri020295.1	*EjSAUR37*	276	91	Cytoplasmic	7	4976010-4977120
Eri020293.1	*EjSAUR38*	306	101	Mitochondrial	7	4971427-4972718
Eri016848.1	*EjSAUR39*	318	105	Mitochondrial	7	4888279-4889318
Eri004501.1	*EjSAUR40*	363	120	Golgi	5	7806084-7806919

Table. Continued.

Eri020307.1	*EjSAUR41*	441	146	Membrane-bound mitochondrial	7	5138897-5139337
Eri020298.1	*EjSAUR42*	306	101	Cytoplasmic	7	5023844-5024149
Eri029408.1	*EjSAUR43*	321	106	Mitochondrial	5	13063957-13064976
Eri020292.1	*EjSAUR44*	303	100	Mitochondrial	7	4963982-4964284
Eri005824.1	*EjSAUR45*	561	186	Cytoplasmic	12	17405170-17406238
Eri012398.1	*EjSAUR46*	306	101	Mitochondrial	16	1017792-1018576
Eri022979.3	*EjSAUR47*	237	78	Mitochondrial	–	38349005-38349241
Eri022982.1	*EjSAUR48*	309	102	Mitochondrial	–	38378887-38379935
Eri020291.1	*EjSAUR49*	306	101	Mitochondrial	7	4943664-4943969
Eri034938.1	*EjSAUR50*	429	142	Cytoplasmic	6	9364503-9364931
Eri033824.1	*EjSAUR51*	318	105	Mitochondrial	4	3825641-3827146
Eri020296.1	*EjSAUR52*	306	101	Mitochondrial	7	4982893-4983810
Eri033822.1	*EjSAUR53*	453	150	Membrane-bound mitochondrial	4	3789261-3789713
Eri034937.1	*EjSAUR54*	429	142	Cytoplasmic	6	9361451-9361879
Eri020304.1	*EjSAUR55*	315	104	Cytoplasmic	7	5083735-5084784
Eri018004.1	*EjSAUR56*	459	152	Membrane-bound mitochondrial	15	12654513-12655426
Eri008583.1	*EjSAUR57*	297	98	Nuclear	15	20398931-20399575

EjSAUR genes were clustered together on the loquat chromosomes (Figure 1). It was worth noting that 17 members were localized on chromosome 7 and all 17 of the *EjSAUR* genes were clustered in the same region with different transcriptional orientations. In addition, further investigation showed that the distribution of each class of *EjSAUR* genes was significantly irregular and most of the *EjSAUR* genes located on the same chromosome belonged to different classes, except for *EjSAUR16* and *EjSAUR49* on chromosome 7 and *EjSAUR50* and *EjSAUR54* on chromosome 6, which constituted a pair of sister paralogs that belonged to Class I and Class VIII in the phylogenetic tree of *EjSAUR* genes, respectively (Figure 1). We speculate that the functions of the *EjSAUR* genes on the same chromosome are complementary.

3.3. Phylogenetic analysis

To study the phylogenetic relationships between the members of the *EjSAUR* gene family, an unrooted tree was constructed from an alignment of their protein sequences and viewed using the MEGA 5 program and the NJ method. It showed that all of the *EjSAUR* genes fell into 10 broad groups (Figure 2). All 57 *EjSAUR* genes were distributed into 13 sister pairs of paralogous *EjSAUR*s (*EjSAUR38/52*, *EjSAUR16/49*, *EjSAUR44/42*, *EjSAUR26/43*, *EjSAUR31/51*, *EjSAUR34/55*, *EjSAUR19/57*, E*jSAUR14/45*, *EjSAUR30/53*, *EjSAUR1/41*, *EjSAUR50/54*, *EjSAUR3/15*, and *EjSAUR32/40*), and 10 of them had very strong bootstrap support (>95%), while the remaining *EjSAUR* genes were not matched.

A phylogenetic relationship between *Arabidopsis* and loquat was further investigated by aligning the protein sequences of the 72 *AtSAUR*s and 57 *EjSAUR* genes. Hence, 129 *SAUR*s were divided into 10 groups named Classes I, II, III, IV, V, VI, VII, VIII, IX, and X (Figure 3). In total, 12 sister pairs, containing 6 *EjSAUR* genes and 6 *AtSAUR*s, were confirmed based on the bootstrap values (above 90%) in the phylogenetic tree. It was noteworthy that Classes II and IV included only *EjSAUR* genes, while Class III had only *AtSAUR*s without *EjSAUR* genes. The other classes comprised both *EjSAUR* genes and *AtSAUR*s.

3.4. Expression profiles of the EjSAUR genes

The expression profiles of the *EjSAUR* genes in the flowers, fruits, leaves, pollen, roots, and seeds are shown in Figure 4. Forty-seven *EjSAUR* genes were actively expressed in at least in 1 organ. Among them, 11 *EjSAUR* genes were expressed in all of the organs, and 6 *EjSAUR* genes were expressed in only 2 organs. In addition, *EjSAUR14* was only expressed in the roots, while *EjSAUR25* was only expressed in the flowers. Different *EjSAUR* genes had different expression levels in the same organ; for example, *EjSAUR3*, *EjSAUR12*, and *EjSAUR15* displayed much higher expression levels than the other *EjSAUR* genes in the flowers. However, *EjSAUR3* and *EjSAUR15* also exhibited higher expression levels in the pollen. The same situation

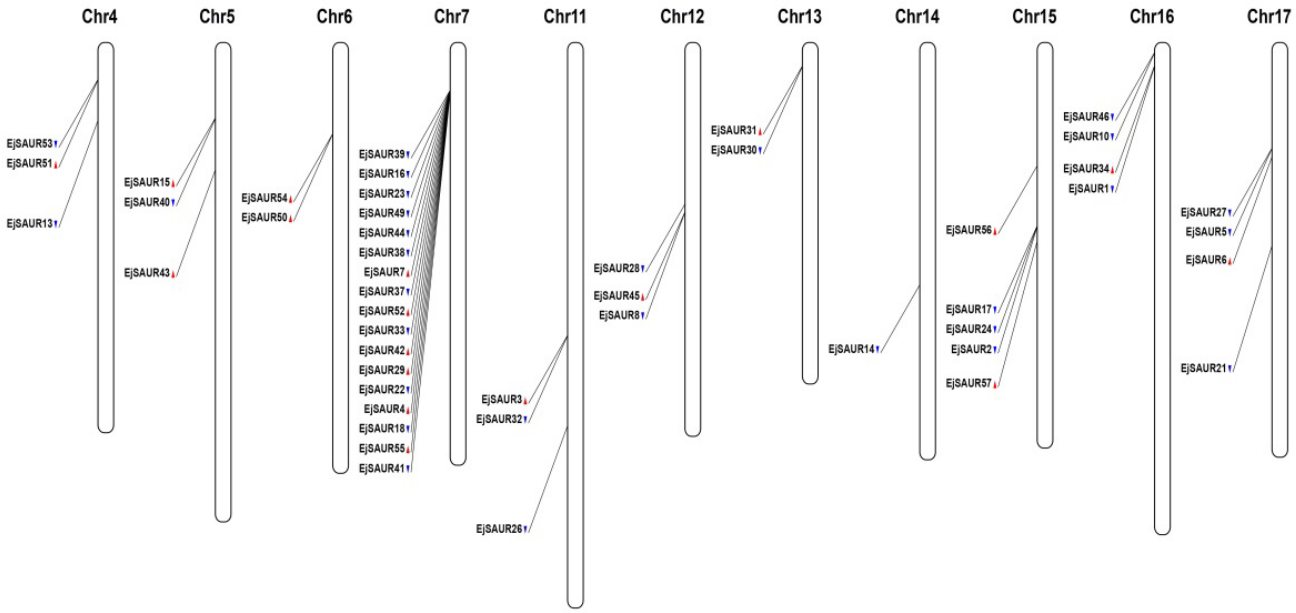

Figure 1. Distribution of the *EjSAUR* genes on loquat chromosomes. The chromosome number is indicated at the top of each chromosome. The numbers beside the chromosomes represent the corresponding *EjSAUR* genes. The arrows show the direction of transcription.

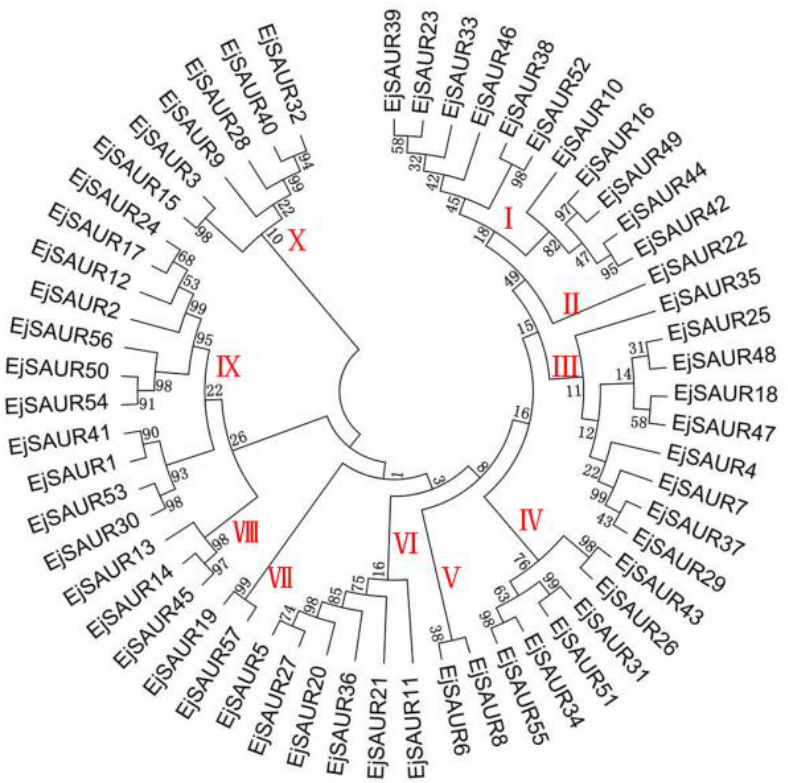

Figure 2. Phylogenetic relationship among the loquat SAUR proteins. The tree was generated using the MEGA 5.0 program by neighbor-joining method. Bootstrap values from 1000 replicates are indicated at each branch.

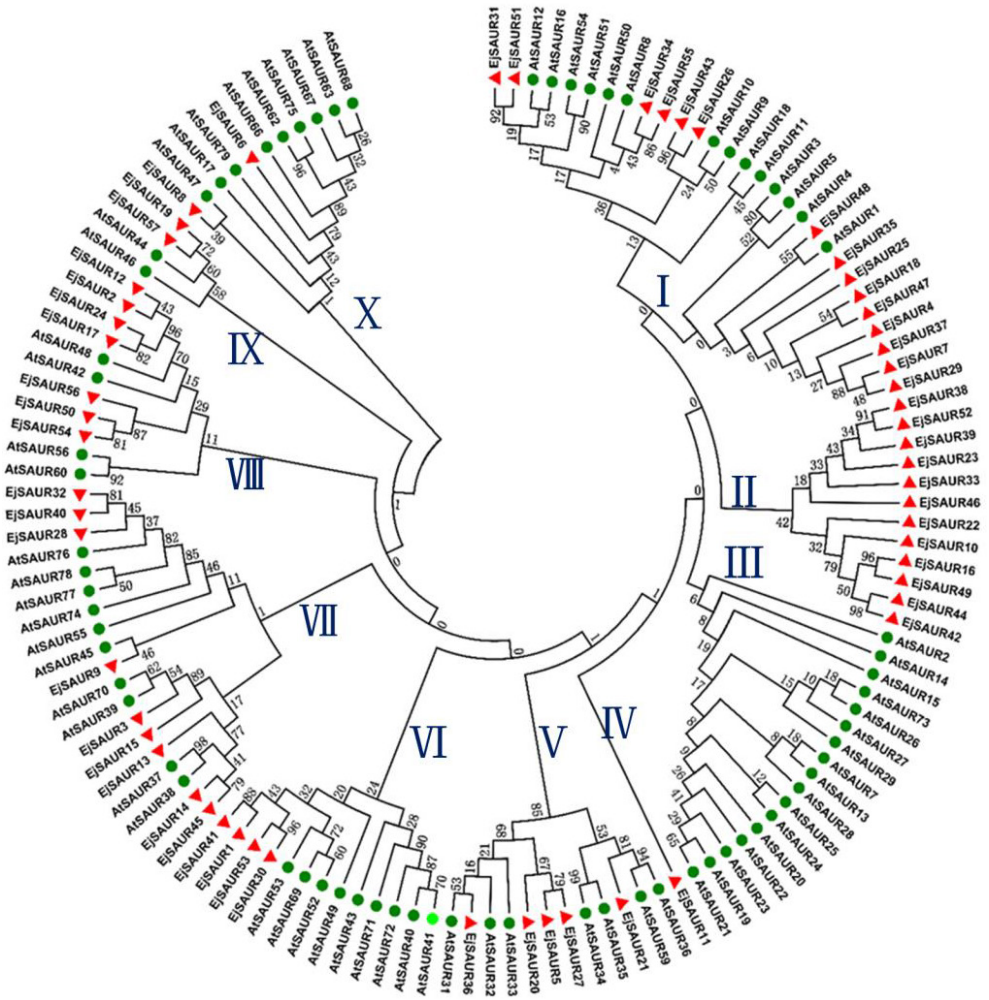

Figure 3. Phylogenetic analysis of the SAUR proteins in *Arabidopsis* and loquat. The phylogenetic inference was conducted using MEGA 5.0. The branch width corresponds to the support values. Green and red indicate *Arabidopsis* and loquat proteins, respectively.

was found in the other organs, such as the expression levels of *EjSAUR23* and *EjSAUR31* in the fruits, *EjSAUR28* and *EjSAUR53* in the seeds, and *EjSAUR31* and *EjSAUR36* in the roots being higher than in the other tissues. On the other hand, there was a distinct difference in the number of expressed *EjSAUR* genes in the different organs. Among the flowers, fruits, leaves, pollen, seeds and roots, the number of expressed *EjSAUR* genes was the highest (39) in the flowers, followed by the fruits (37), while the lowest number of *EjSAUR* genes (26) was detected in the roots.

4. Discussion

4.1. Identification of SAUR genes in loquat

Different numbers of *SAUR* genes in plants have been detected in several studies, such as 72 in *Arabidopsis*, 71 in sorghum, 134 in potato, and 75 in maize (Hagen and Guilfoyle, 2002; Wang et al., 2010; Wu et al., 2012; Chen et al., 2014). In this study, 57 *EjSAUR* genes were identified and characterized from the current version of the SGN database. All of the members were predicted to encode the *SAUR* domains. Compared with the *SAUR* gene family in other species, a lower number of genes was identified in loquat. The small scale of the *SAUR* family might be correlated with whole-genome duplication (Jaillon et al., 2009) and incomplete sequencing. The phylogenetic analysis revealed 13 sister pairs in the EjSAUR proteins (Figure 3). However, only *EjSAUR16/48*, *EjSAUR38/52*, and *EjSAUR42/44* were found to be genetically linked based on their corresponding chromosomal locations (Figure 1), and all 3 sister pairs were localized on chromosome 7. These results were consistent with previous studies, which also found clusters in *Arabidopsis*, rice, soybean,

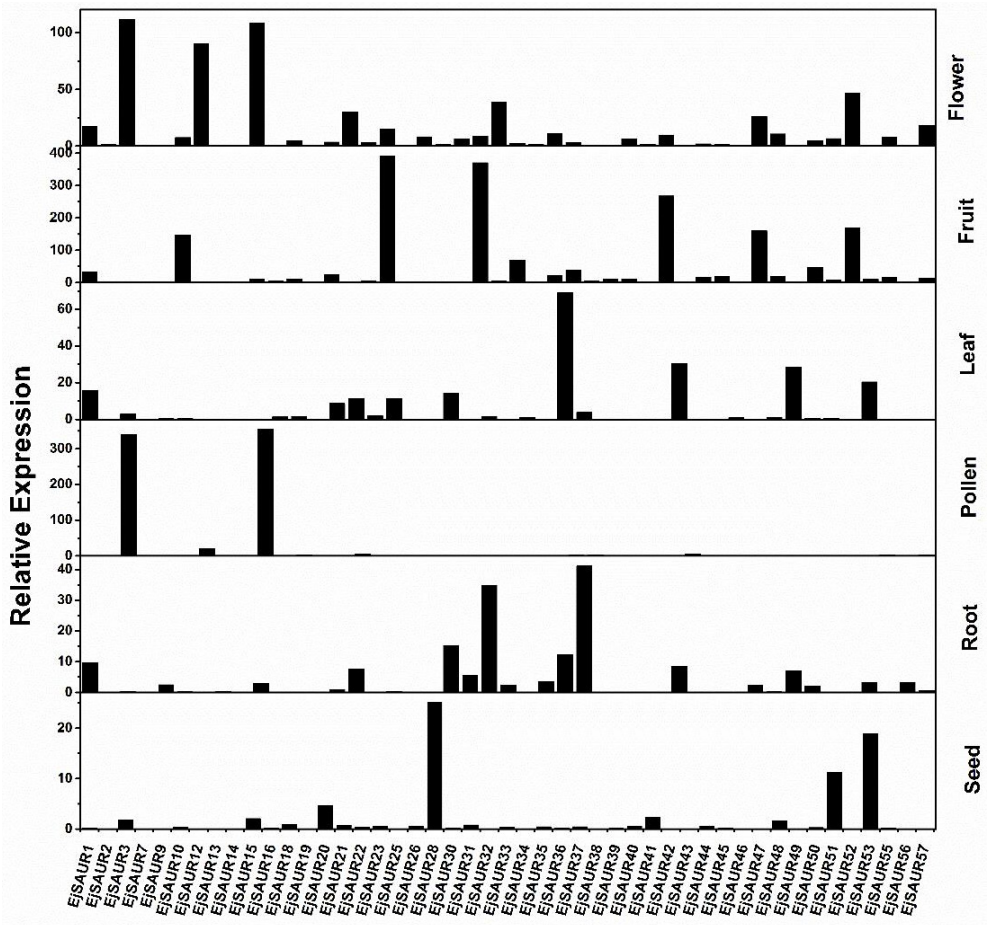

Figure 4. Expression profiles of the *EjSAUR* genes in different loquat organs.

and tomato (Hagen and Guilfoyle, 2002; Wu et al., 2012). Based on their physical positions, 80.9% (38 of the 47) of the *EjSAUR* genes were clustered together on the loquat chromosomes, which suggested that tandem duplicate genes might be the major mechanism for expansion of this family instead of duplicated chromosomal segments. Jain et al. (2006) also linked the expansion of *OsSAUR*s with localized gene duplications. The retaining of a high number of duplicated *SAUR* genes in these plants was very interesting, as they have experienced the same evolutionary mechanism (Wu et al., 2012).

4.2. Expression profiles of loquat EjSAUR genes

The expression profiles of the 57 *EjSAUR* genes were investigated in different organs of loquat; however, only 47 *EjSAUR* genes were found to be expressed in various organs. The expression profiles exhibited remarkable differences in different organs. In *Arabidopsis*, a previous study revealed that Clades I and II of the *SAUR* genes displayed coexpression, and the highest expression levels were detected in the leaves, while the lowest expression patterns were observed in seeds and roots. In contrast, some *SAUR* genes were not clustered into Clades I or II and showed higher expression patterns in the roots and seeds. Auxin responsiveness and remarkable differences in the expression patterns suggested that Clades I and II and the other *SAUR* genes had particular functions in roots and leaves (Paponov et al., 2008). Some *EjSAUR* genes also exhibited tissue-specific expression patterns. For example, *EjSAUR25* may play an important role in flowers due to the specific expression pattern in flowers. *EjSAUR14* showed a root-specific expression, which indicated that it mainly affected root development. In fact, most of the *EjSAUR* genes were found to be differentially expressed in the flowers and fruits, suggesting an important role of *EjSAUR* genes in flower and fruit development in loquat. Notably, some *EjSAUR* genes showed higher expression levels in specific organs, such as *EjSAUR3/12/15* having the highest expression levels in the flowers, *EjSAUR3/15* in pollen, *EjSAUR23/31* in fruits, *EJSAUR28/53* in seeds, and *EjSAUR31/36* in roots. Among these genes, only

EjSAUR3/15 was a sister pair in the phylogenetic analysis and had the same expression pattern in flowers and pollen, while the rest belonged to different groups. The remarkable expression patterns of the *SAUR* genes indicated that the abundance of *SAUR* was not just a matter of redundancy; instead, their existence may play crucial roles in the development of different organs.

In conclusion, this study presents a comprehensive analysis of the *SAUR* gene family in loquat. A total of 57 *EjSAUR* genes were identified in loquat. The phylogenetic relationships among *Arabidopsis* and loquat showed that all of these *SAUR* genes clustered into 10 groups. Their chromosomal distribution analysis suggested that the tandem duplication of the loquat chromosomes mainly contributed to *SAUR* gene family expansion in loquat. Expression analysis revealed that *EjSAUR* genes in loquat had different expression patterns in various organs, while some displayed tissue-specific expression patterns. The results of this study provide a framework for further research on loquat *SAUR* genes.

Acknowledgments

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