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Full Length Research Paper

Twenty putative palmitoyl-acyl transferase genes with distinct expression patterns in *Arabidopsis thaliana*

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Palmitoylation is a reversible posttranslational addition of palmitate to cysteine residues in proteins through a thioester bond by a family of DHHC (Asp-His-His-Cys) palmitoyltransferases (PATs) involved in cellular signaling, membrane trafficking, and synaptic transmission. There are 20 genes containing DHHC domain predicted to encode putative palmitoyltransferase in *Arabidopsis thaliana* genome. However, little is known about their characteristics such as genetic relationship and expression profile. Here, we present an overview of the putative PAT genes in *A. thaliana* focusing on their phylogeny , gene structure and expression profiles in different tissues and under different stresses. Besides conserved DHHC domain, the identity of their cDNA sequences was from 30 to 60%. Temprospatial expression profile of each putative gene of the entire PAT family showed that nineteen of twenty putative PAT members differently expressed in flowers, leaves, stems, roots, seedlings, young and old siliques except At2g40990. Among these nineteen expressed putative PATs, some members expressed at very high levels in certain tissue and some exhibited more even distribution in different tissues. This is the first report on the expression patterns of all these putative PAT genes, which will provide important fundamental data for further identification of their biological functions.

Key words: Palmitoylation, palmitoyltransferase, *Arabidopsis thaliana*, expression pattern.

INTRODUCTION

S-acylation (commonly known as palmitoylation) referred to as a widespread post-translational modification that consists of the addition of a lipid molecule to cysteine residues of a protein through a thioester bond. Lipid molecules of different chain lengths, not only palmitate, could serve as anchors to attach soluble proteins to membranes. S-acylation is often combined with either prenylation or N-myristoylation (Sorek et al., 2009). However, besides soluble proteins, many transmembrane proteins are also modified by palmitate (Valdez-Taubas and Pelham, 2005). Among the proteins that rely on palmitoylation for localized function are many of the key players in cellular signaling, membrane trafficking, and synaptic transmission, including many G proteins such as Ras- and Rho-like proteins as well as the α and γ subunits of many hererotrimeric G proteins; many nonreceptor tyrosine kinases; and members of the SNARE family of membrane fusion proteins (Roth et al., 2002; Rothman, 1994; Sollner et al., 1993). Palmitoylation is a reversible process which could be used as a switch to activate or terminate signaling cascades (Sorek et al., 2009). The study of posttranslational lipid modification has implications far beyond molecular and cell biology. The protein lipid modification is known to associate with many types of cancer, genetic blindness and premature aging (Perez-Sala, 2007).

Although, palmitoylation of proteins have been known for many years, only a few palmitoyltransferases have been identified. In the yeast *Saccharomyces cerevisiae*, Akr1 has been reported to modify Yck2 type I casein

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Abbreviations: PAT, palmitoyl-acyl transferase; **CRD,** cysteine-rich domain; **Col,** Columbia-0.

kinase (Roth et al., 2002), Erf2 in association with an additional subunit Erf4 that modifies Ras2 (Bartels et al., 1999; Jung et al., 1995; Lobo et al., 2002), and Swf1 modifies the SNARE Tlg1 (Valdez-Taubas and Pelham, 2005). In mammalian cells, GODZ was shown to palmitoylate the γ^2 subunit of the $GABA_A$ receptor (Keller et al., 2004), and HIP14 was found to modify the cytosolic neuronal protein PSD-95 (Fukata et al., 2004; Huang et al., 2004). All these palmitoyltransferases belong to a family of proteins sharing a 50-residue-long DHCC cysteine-rich domain (CRD), which is a variant of the zinc-finger domain C2H2 (Putilina et al., 1999). Members of this family have been suggested to own a general function in palmitoylation (Roth et al., 2002). There are at least twenty three distinct family members in the human genome and seven in yeast genome (Linder and Deschenes, 2004). BLAST searches within *Arabidopsis* genome have identified twenty genes containing a DHHC domain. Little information is known about all *Arabidopsis* putative PAT genes, except Tip1 that has been shown to regulate root hair growth by acting as an S-acyl transferase (Hemsley et al., 2005). Given the prevalence and importance of protein palmitoylation, it is surprisingly how poorly understood PATs in plants remained. Here, we report expression profiles of all these 20 *Arabidopsis* genes encoding putative PATs in different tissues to suggest PATs that might play an S-acyl transferase role in individual developmental tissue.

MATERIALS AND METHODS

Plant materials and growth conditions

Arabidopsis thaliana ecotypes Columbia-0 (Col) was used in this experiment. Seeds of *A. thaliana* were stratified for 3 days at 4℃ on AT-agar medium (Somerville and Ogren, 1982), then germinated at 20℃ for 7 to 10 days. After germination, seedlings are transplanted into the soil. Plants were generally grown at a density of 12 to15 per pot (Diameter 10 cm), and were grown in continuous light (90 to120 µEin/m2sec PAR) at 20℃.

RNA and cDNA preparation

Total RNA of rossette seedlings, roots, stems, leaves, flowers, young and old siliques were respectively extracted using Trizol (Invitrogen Life Technologies) according to the manufacturer's protocol. Total RNA free of DNA was used for cDNA synthesis by M-MLV Reverse Transcriptase (Promega).

Real-time PCR conditions

The primers specific for each gene of the entire family were designed using Primer Premier 5.0 software, and validated by to generate a single polymerase chain reaction (PCR) product with expected size with each set of primers. The sequences of these gene specific primers are listed in supplemental Table S1.

Each of cDNA samples prepared above was normalized to get equal amount by using House keeping gene *ACT2* as control gene. The normalized cDNA was used as template to perform Real-time PCR. For each analyzed gene, a standard curve was established, and PCR efficiency ranged from 95 to 105%. All standard and experimental samples were assayed in triplicate wells. Real-time PCR was performed on an iCycler™ (Bio-Rad, Hercules, CA, USA). Samples were amplified in a 20 µl reaction containing 1×SYBR Green Master Mix (Takara) and 300 nM of each primer. The thermal profile consisted of 1 cycle at 95℃ for 1 min followed by 40 cycles at 95℃ for 0.05 s and at 60℃ for 30 s. For each run, data acquisition and analysis was done using the iCycler™ iQ software (version 3.0a, Bio-Rad).

Data analysis

The relative abundance of each transcript was determined by interpolating the Ct values of the unknown samples to each standard curves. The relative abundance of *ACT2* mRNAs in each sample was determined and used to normalize for differences of total RNA amount. Microarray data of expression patterns of *Arabidopsis* putative PATs under stresses was downloaded from Genevestigiator (http://www.genevestigator.ethz.ch/at). Statistic was conducted using Excel software. Cluster analysis of the putative PAT genes in *Arabidopsis* was conducted based on their spatial expression data with Cosine similarity, between-groups distance cluster method by SPSS 10.0 for windows package (SPSS Inc., Chicago, USA. 1999; http://www.spss.com/spss).

RESULTS

The putative PAT gene family in *A. thaliana*

20 putative PAT genes were identified by BLAST in the *A. thaliana* genome using yeast *Swf1* and mammalian GODZ and HIP14 sequences. Phylogenic analysis of all the family members was conducted by neighbor joining analysis based on their cDNA sequences (Figure 1 Left). The degree of identity of seven pairs of paralogous in the terminal nodes is between 30% and 60%, indicated in the phylogenic tree. These aforementioned paralogous showed relatively high identity with cDNAs of other putative PATs in the same subclass in the phylogenic tree respectively (between 40 and 65%). Exon-intron organization indicates that genomic structures of *Arabidopsis* putative PAT genes are complicated (Figure 1 Right). Genomic length of the longest PAT is around twice than length of the shortest one. 20 putative PAT genes vary in exon number as well as lengths of exons. Ten genes contain 4 to 6 exons, six genes contain 7 to 9 exons and four genes contain 10 to13 exons. The length of individual exon is usually shorter if the gene has more exons.

Temprospatial expression profiles of twenty putative PAT genes

Temprospatial expression profile of each member of all 20 putative PAT genes was examined by real time PCR on flowers, leaves, stems, roots, seedlings, young and old siliques in *A. thaliana*. Figure 2A shows the relative

Supplemental Table S1. The sequences of primers specific for each of all 20 putative palmitoyl-acyl transferases genes used for real time PCR in this investigation.

Gene name	Primer sequence (5'-3')
At2g14255	CTACCGAATCACCAACCATC AAGAGCGTAGAAGCCATTATC
At3g60800	AGAAACCCATCACGCTCAAC TAGAGACGACCCTTGTGACT
At4g00840	CTGAAGTAGTGTTGGATGAGAG GTTGGATGTTATTGTCTTGCTTC
At3g18620	ATCACGAATCAGAATCCAGTC AGAATAAATGTTGAGAGCGTTG
At3g26935	CGGATGTAAGCAGCAGAAGAAT TCAGGGAAGGTTTGTATTTGGG
At3g09320	TACCTCAAATCTCCTCCCTTC GTTCAGCCTCACTTCGTCTC
At3g51390	GTAACTTCTGGCTCTTCACCT TAACAACAACGCTCTCACTTTTT
At4g22750	TATCACCATCTCCATCGCTG CCTCGTTCTCACCATTGTTC
At4g24630	GATGGAAGACAAACACCGAG CAATGAGAGCAGCGAGGAG
At3g56930	GAGGAGGAAGGATTGTTGATGA GATGGTGATGGTGGTGGTGAT
At3g56920	GTCTTCCACTTCTACCTTATC CAACCTCCACATCGTCTTCT
At5g50020	CTCCCGTTTGTTTCTTTTCTGT CATAGTTCTTCCTCTGGCGG
At2g40990	GCAGATGAGGTAGAGATGGA AACAAGTGGAAACAGGTAAGC
At5g41060	CCTTGTTGCTGTTGTCTTCAC ACTTCTGGTTCTGGAGGATGA
At3g04970	CCAACACAACAACTAATGAGG CTATCAGAAAGTAAACAAACCC
At1g69420	CAGTAGCAAGAGTCCGTGAAA CTGAAGAGGATGGTATGGAAG
At5g04270	TATTGTGTGTGATGAGGTAGAT AGTGTTGCTGGTTTGCTGTG
At5g05070	GAGAGAATGAGCAAGAAGAAGA CCAATCAAGAAGGAGGTTAGG
At3g48760	CGTCTTGCTCATACTCCTCA ACTATCCATTATCCGCTTGAC

expression level of each PAT gene of the entire family. Of the twenty putative *PAT* genes analyzed, all were found expression with different levels and tissue distributions, but one exception, that is, At2g40990, which was barely

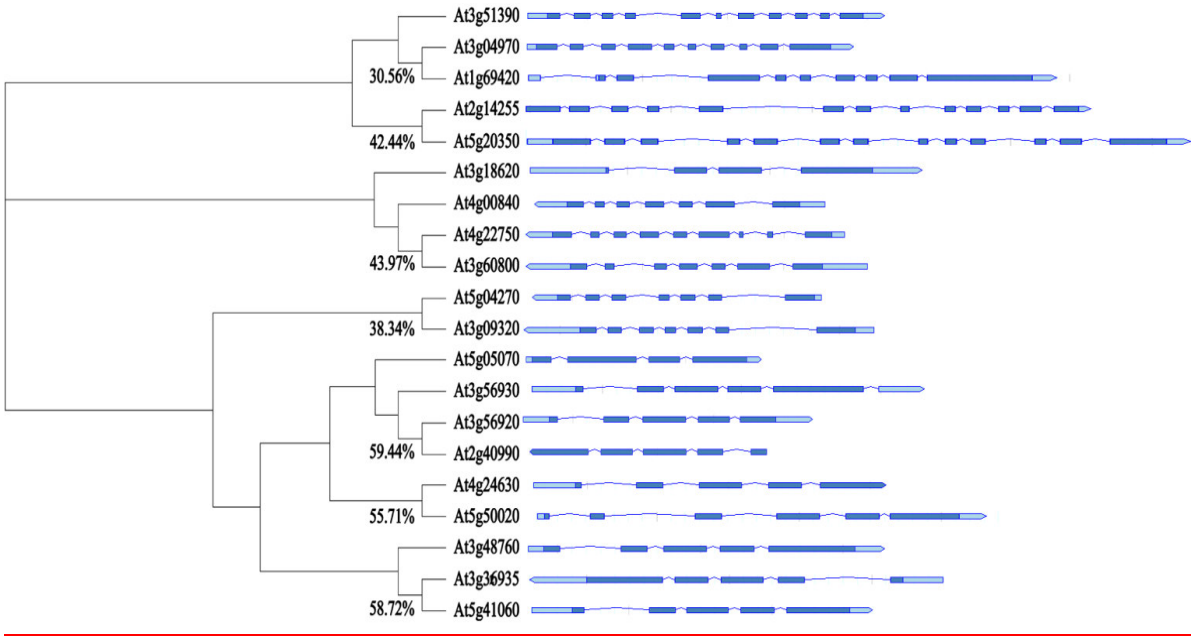


Figure 1. Phylogenic analysis of the *Arabidopsis* putative PAT cDNA sequences and exon-intron organization of *Arabidopsis* putative PATs. Left, the neighbor-joining phylogenetic tree. The degree of identity of seven pairs of paralogous in the terminal nodes is indicated in brackets. Right, deep blue rectangles and thin lines represent exons and inrons, recpectively. The light blue boxes represent 5'-UTR or 3'-UTR.

expressed in any tissues. Fifteen of these genes are expressed in flowers, 10 in roots, 11 in seedlings, 12 in young siliques, 14 in old siliques, 8 in leaves and 10 in stems. Some members are highly expressed in flowers, roots, seedlings, young or old siliques with different patterns. For example, At3g56920 is only highly expressed in flowers whose transcript level is about twelve times than that of housekeeping gene *ACT2*; At3g09320 is only expressed at high levels in seedlings, while At3g60800 is expressed not only in flowers but also in seedlings, young and old siliques with comparably even distribution in the aforementioned tissues. Moreover, PAT family members are expressed relatively lower in leaves and stems compared with expression in other examined tissues.

The putative PAT genes in *Arabidopsis* were further clustered according to their temprospatial expression profile (Figure 2B). Figure 2B shows that in rescaled distance ten, all twenty *Arabidopsis* putative PAT genes could be classified into five groups. Group 1 enclosed seven members that show a relative high expression in flowers. Among these, At3g56920, At5g05070 and At3g26935 were only expressed in flowers and the transcript levels of At3g56920 and At5g05070 were the highest and weakest respectively, while At3g51390, At3g18620 and At5g20350 were also expressed in other tissues with lower level. Group 2 consisted of At4g24630 and At3g56930 which was preferentially expressed in old siliques, while At4g24630 was also expressed at lower level in flowers. Group 3 included At3g04970, At2g14255, At3g09320, At3g60800 and At4g00840 that showed a similar pattern of expression, high in seedlings and young siliques. At3g04970 and At2g14255 exhibited predominantly high expression in seedlings and weaker expression in flowers, roots, young and old siliques, At3g60800 and At4g00840 were preferentially expressed in both seedlings and young siliques, but At3g09320 displayed specific high expression only in seedlings. Group 4 had five members of At5g41060, At1g69420, At5g04270, At4g22750 and At3g48760, all of which did not show tissue preference at the transcription level. At5g41060 and At1g69420 were expressed ubiquitously in flowers, seedlings, young and old siliques rather than leaves, roots and stems. At5g04270 and At4g22750 were highly expressed in young siliques, while At5g04270 showed additional weaker expression in seedlings and At4g22750 expression was also in abundance in flowers and stems. At3g48760 displayed a weaker expression in flowers, roots and young siliques. Group 5 had only one member At2g40990 whose transcript level could not be detected in any tissue. The expression patterns of these putative PAT genes suggest that each member of the PAT family might have very different biological function in various tissues and developmental stages in *A. thaliana.*

DISCUSSION

In this study, we present phylogenic analysis of *Arabidopsis* putative *PAT* sequences and expression con-

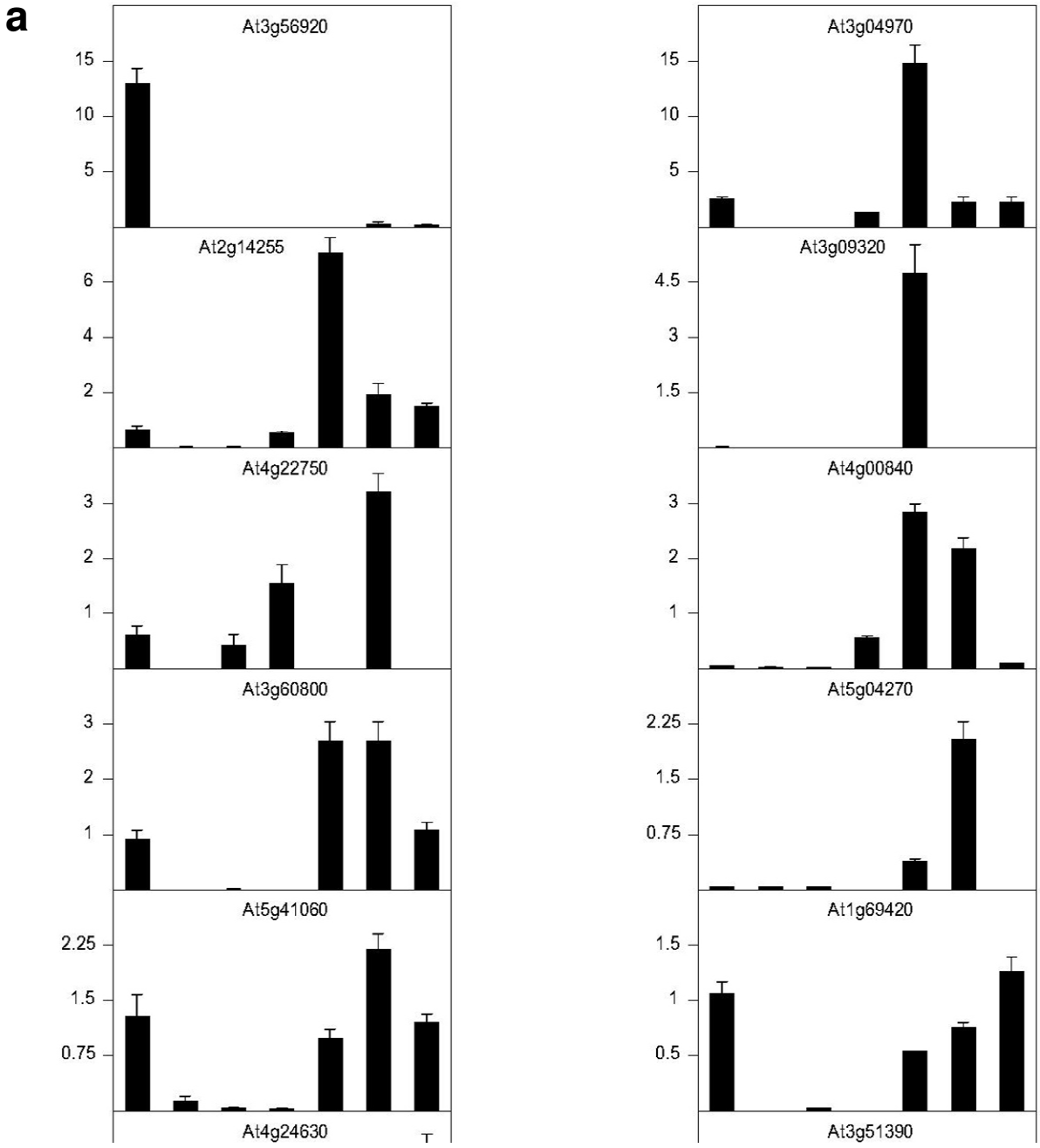


Figure 2a. The expression patterns of putative PAT genes in various tissues of *Arabidopsis*. The gene expression level was determined by real-time PCR analysis. The relative transcript abundance of ACT2 in each sample was determined and used to normalize the differences of total RNA amount. The data represent the means ±SD of three replicates. Y axis values presented ratio of putative PAT transcript abundance to ACT2 transcript abundance. X axis presented tissues total RNA isolated from flowers (F), leaves (L), stems (St), roots (R), 15-day-old seedlings (S), young siliques (YSi) and old siliques (OSi).

served in all yeast and mammalian PAT proteins and is required for palmitoyl acyl transferase activity (Tian et al., 2010). We found all twenty *Arabidopsis* putative PATs had DHHC domain after blasting with yeast Swf1 and mammalian GODZ and HIP14 whose palmitoyl-transferase activity and biological functions had been illustrated (Supplemental Figure 1) (Huang et al., 2004; Tian et al., 2010; Valdez-Taubas and Pelham, 2005). But we could not find any other conserved domains between *Arabidopsis* twenty putative PATs except highly the conserved DHHC domain, consistent with conclusion proposed previously that the DHHC- family proteins

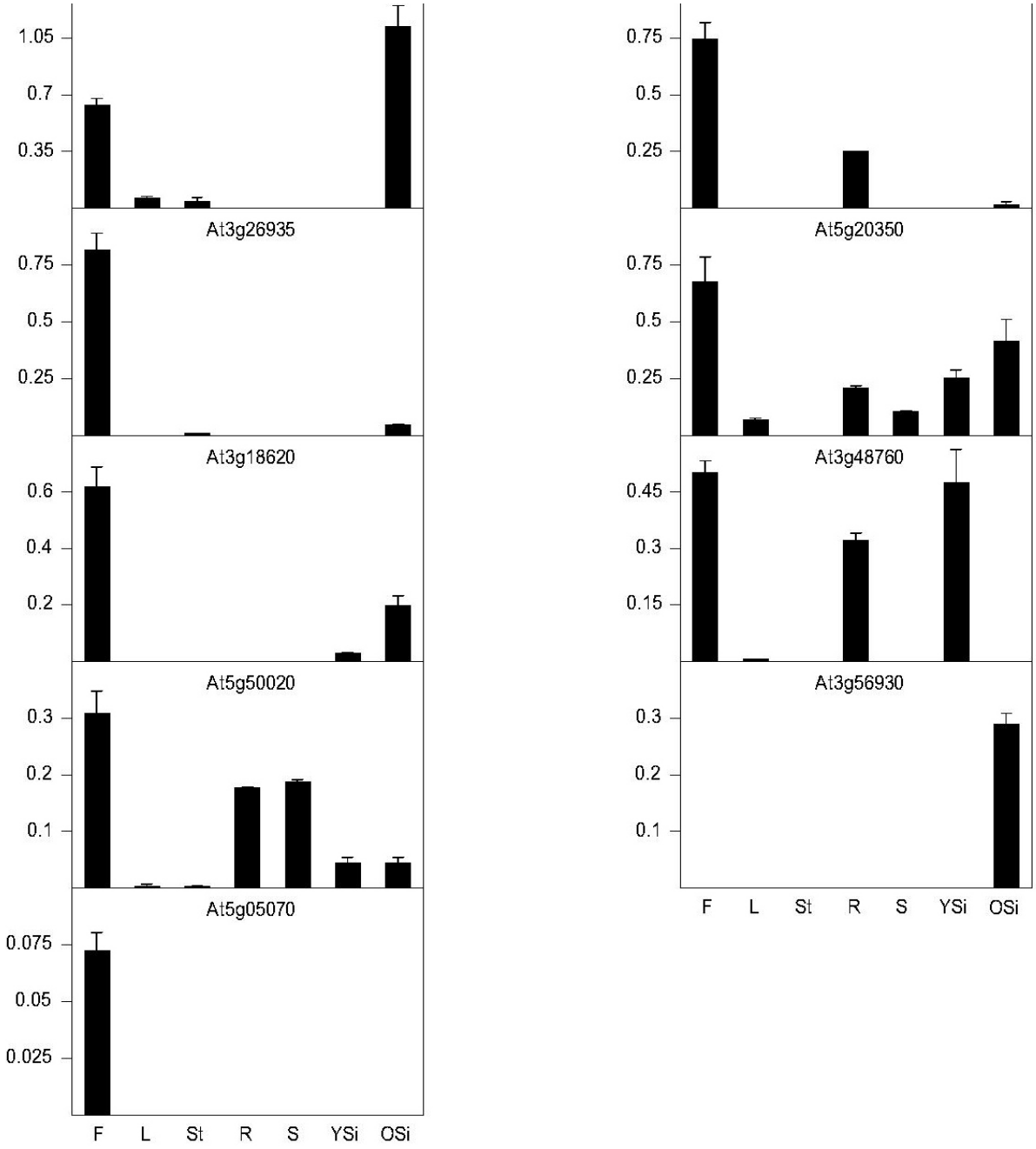


Figure 2a. Contd.

pattern of *Arabidopsis* putative *PAT* genes in various organs of Arabidopsis. The zinc finger DHHC domain is typically share little or no homology beyond their defining DHHC domain (Roth et al., 2006).

In order to check biological processes *Arabidopsis* putative PAT genes are involved in, we mined all expression data under various stresses from Gene-vestigiator website shown in Supplemental Figure 2. There is expression data of seventeen putative PATs and absence of the rest three putative PATs (At3g18620, At3g56920 and At2g14255) is caused by unavailable probes of these genes according to the given explanation from website. We found expression of different putative PATs was up-regulated, down-regulated or unchanged respectively under each individual stress, suggesting all seventeen putative PAT genes might be involved in each stress, and play positive roles under some stresses and negative roles under some stresses.

Comparison of our expression results based on real time PCR with the published Microarray data, we found

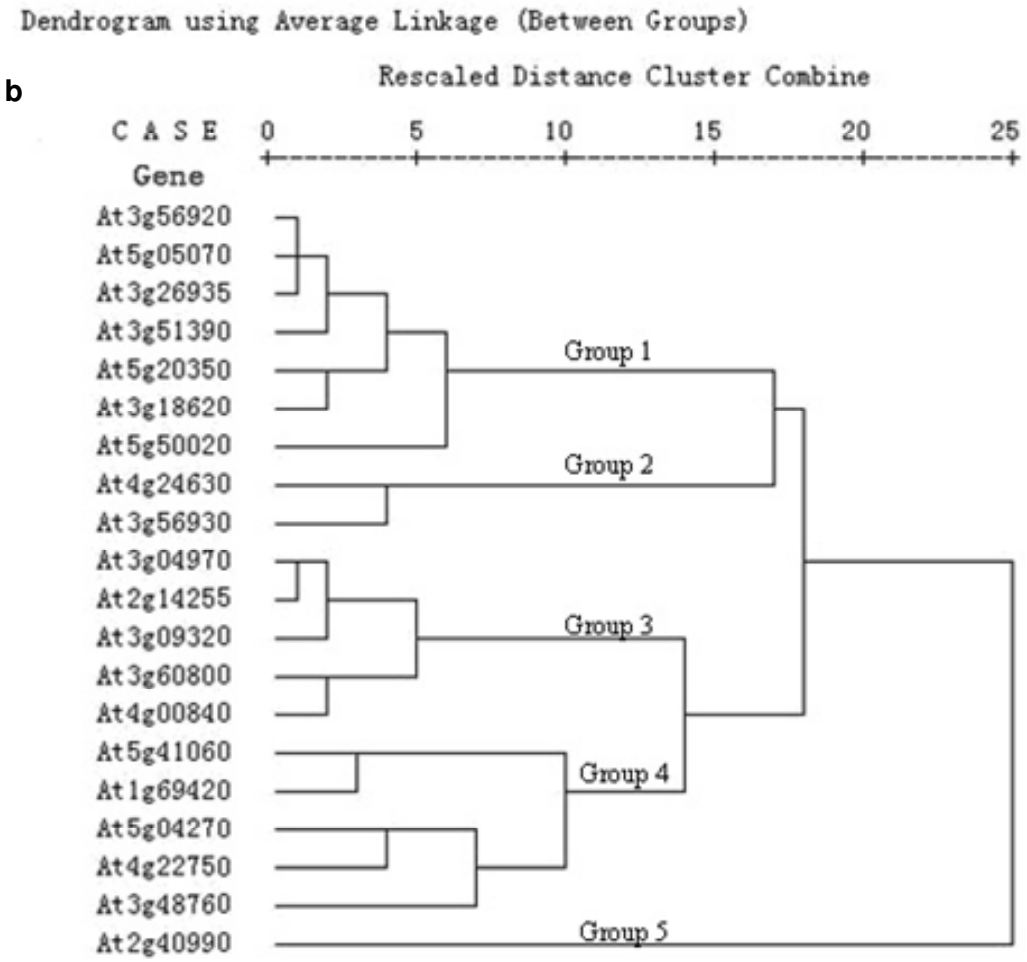
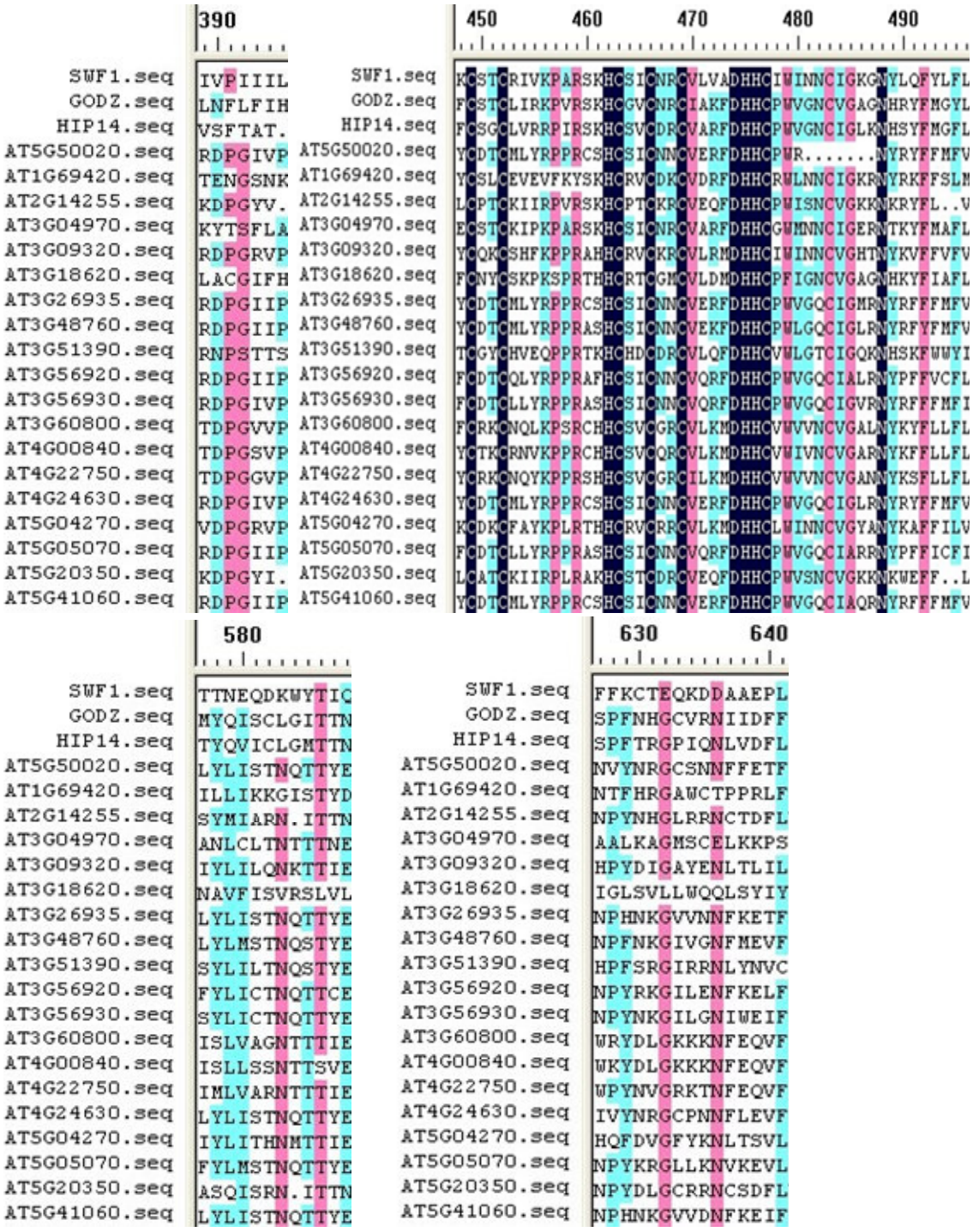


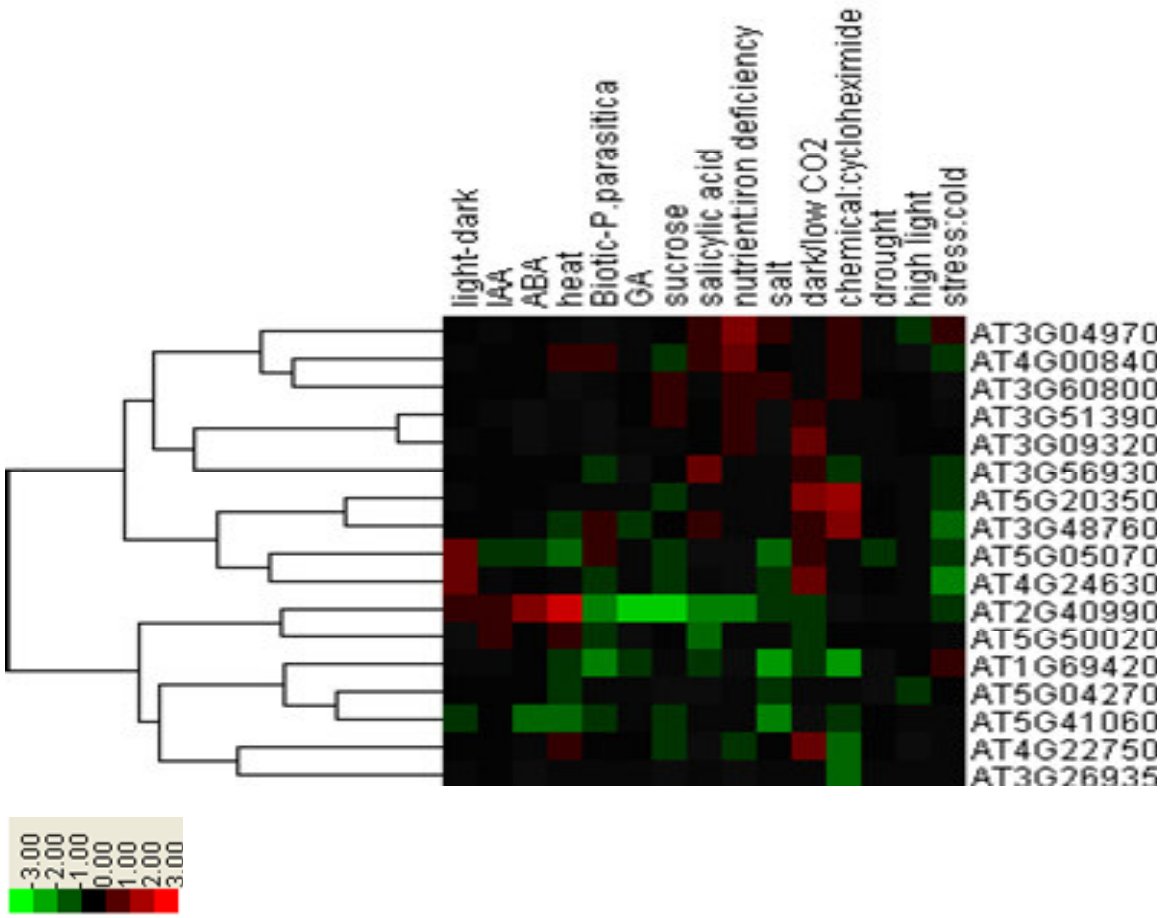
Figure 2b. Hierachical clustering of putative PAT genes in *Arabidopsis* according to their expression profiles in different development stage and tissues.

that our real time PCR data is in general consistent with published Microarray data. However, our data is more comprehensive on the complete set of genes. First, expression patterns of *Arabidopsis* putative PATs in flowers, leaves, seedlings, young and old siliques were examined in both of our experiments and website Microarray data but we also checked in roots and stems. Second, we have examined the expression of all twenty *Arabidopsis* putative PATs but Microarray data from website only contains seventeen *Arabidopsis* putative PATs and information of the other three putative PATs is absent from Microarray data. Third, expression pattern of fourteen putative PATs from website Microarray data is consistent with that from our real time PCR data, but three putative PATs display different expression pattern. For example, in the website Microarray data, At3g04970 showed even relatively low expression in flowers, leaves, seedlings, young and old siliques, but in our experiment, we found At3g04970 was preferentially expressed at high levels in seedlings with twelve times more than the control gene actin. It is possible some data are not correct by Microarray analysis and need to be further confirmed by real time PCR. Fourth, Microarray data show signals of At2g40990 are extremely low-expressed. We found all putative PAT genes except At2g40990 were expressed with different distributions in *Arabidopsis* tissues. We could not detect any transcript level of At2g40990 in individual tissues although, after trying different sets of primers which could be employed to amplify PCR products using *Arabidopsis* genomic genome as templates, but their transcript level could not be detected when using cDNA as templates, which worked very well using *ACTIN 2* and primers for amplifying other PAT genes. This indicated that the gene At2g40990 keep silencing and no functions in *A. thaliana* in normal growth condition. However, Microarray data of expression pattern under stresses showed that the transcript levels of At2g40990 were up-regulated dramatically by treatment of light-dark and heat as well as application of IAA and ABA, and were down-regulated from strikingly to subtly depending on other different stresses indicating At2g40990 was likely to play roles



Supplemental Figure S1. Sequences of one yeast and two mammalian PATs and twenty *Arabidopsis* putative PATs were aligned using the DNAMAN software. Identical amino acids were marked by black, red showed high similarity and green showed lower similarity than red ones.

under stresses. In addition, when leaves and stems are attacked by pathogens or affected by other environmental external factors, cell signaling cascades works where the expression of putative PATs would also be increased. Recent study demonstrated that the expression levels of some putative PATs, such as At4g22750 and At3g60800, were altered when impacting pathogen response and cell cycle during geminivirus infection indicating palmitoyl



Supplemental Figure S2. Expression patterns of Arabidopsis putative PAT genes under stresses. Red and green boxes indicate up-and down-regulation, respectively.

modification may take part in pathogen-plant interaction (Ascencio-Ibanez et al., 2008).

Although, we found quite a few putative PAT genes are expressed especially highly in some tissues, the functions they play in posttranslational lipid modification and broad biological roles in plants remain poorly known. Only the protein TIP1 encoded by At5g20350 has been identified to possess palmitoyltransferase activity and loss of function mutant displays abnormal growth of root-hairs and pollen tubes (Hemsley et al., 2005). They have reported that northern blot results indicated that At5g20350 was expressed in roots, leaves, inflorescence and flowers, which was consistent with our real time PCR results (Hemsley et al., 2005). However, the substrate proteins to which TIP1 adds palmitate after translation have not been identified until now. A recent study experimentally confirmed that the palmitoylation was not stereoselective and lacks any primary consensus sequences, demonstrating that substrate specificity was not essential for palmitoylation (Rocks et al., 2010). Therefore, it is difficult to predict substrates for PATs according to conserved sequences. In addition, the palmitoyl proteome of the yeast *Saccharomyces cerevisiae* had been characterized and found many SNARE proteins, Rho proteins, amino acid permeases and so on (Roth et al., 2006). However, the detailed ways in which TIP1 regulates growth and development of root and pollen tubes through functioning as a palmitoyl-transferase remain to be understood. Our data show that many PAT genes had much higher relative transcript levels than TIP1, but their biological roles have not been investigated. Furthermore, analysis of mutant yeast strains defective for members of the DHHC protein family revealed PATs to be a family of diverse substrate specificities but to redundantly act with one (or several) of the other PATs to identical substrates. Therefore it could not exclude the possibility that *Arabidopsis* putative PATs whose expression patterns were similar under some certain stress might act the same substrates and own partially overlapping functions. Therefore, it is emerging to examine whether all these highly expressed putative PATs display palmitoyl transferase activity *in vivo* and *in vitro* and to study membrane proteins which are attached to palmitate by individual putative PAT. Work on TIP1 and

related S-acylation transferases have potential implications beyond our understanding of plant cell growth and development. Further detailed characterization in *Aarbidopsis* of putative PATs could shed light on the mechanisms affecting plant-pathogen interaction, Ras-based cancer, Huntington's disease and other valuable biological processes owing to posttranslational lipid modification.

In general, twenty putative PAT genes were identified in the *A. thaliana* genome, phylogenic analysis of all the family members was conducted by neighbor joining analysis based on their cDNA sequences and temprospatial expression profile of each member of the all 20 putative PAT genes was investigated in this study. To our knowledge, this is the first report on the expression patterns of all these putative PAT genes. Although, we found quite a few putative PAT genes are expressed especially highly in some tissues and under some stresses, the functions they play in posttranslational lipid modification and broad biological roles in plants remain poorly known. The information of these temprospatial expression profiles will provide important fundamental data for further identification of their biological functions.

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