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Identification of serine acetyltransferase (SAT) gene family in peach (*Prunus persica*) and study on the function of *PpSAT1* gene regulating adventitious root formation

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Abstract

Background Serine acetyltransferase (SAT), an enzyme that catalyzes the formation of O-acetyl-serine (OAS), is integral to sulfur assimilation, cysteine (Cys) synthesis, and adventitious root development. However, it remains unclear how the SAT gene in *Prunus persica* regulates adventitious root (AR) formation.

Methods Based on transcriptome data and SAT gene family identification, the physicochemical properties, evolutionary relationships, and *cis*-acting elements of the family genes were analyzed. Subsequently, the *PpSAT1* gene was transformed into *Prunus domestica* and *Arabidopsis thaliana* by agrobacterium-mediated method to obtain the transgenic material, and its role in AR formation was characterized by a series of rooting index and enzyme activity experiments.

Results In this study, based on transcriptome data, the cysteine metabolism pathway was significantly enriched during *P. persica* AR growth. After combining the FPKM value of transcriptome data with real-time fluorescence quantitative qRT-PCR, it was found that SAT1/4 showed high expression level, which may be a key gene in peach advection root growth. Based on this, SAT family members were identified from *P. persica*, and further shown by qRT-PCR, *PpSAT1* gene exhibits a notable expression response during AR formation. Therefore, the *PpSAT1* (Prupe.4G239400.1) gene was cloned from *P. persica* and performed genetic transformation on a related *P. domestica* as well as *A. thaliana*. The transgenic *P. domestica* and *A. thaliana* displayed more robust growth, and more developed root system compared to wild-type counterparts. In addition, peroxidase (POD) and superoxide dismutase (SOD) activities were also substantially elevated.

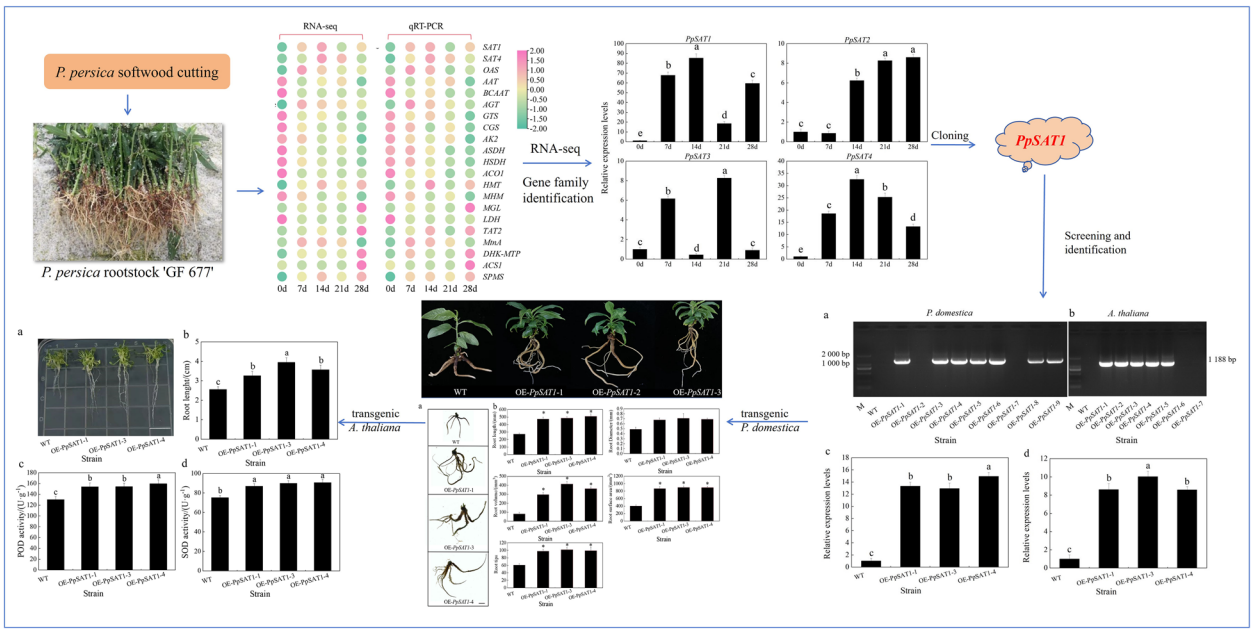
Conclusions In summary, these findings suggest that *PpSAT1* gene can facilitate AR development.

Keywords *Prunus persica*, SAT gene family, Gene cloning, Adventitious root, Genetic transformation

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Graphical Abstract



Background

Serine acetyltransferase (SAT) is involved in many plant growth, development, and adaptation processes to environmental stress [1, 2]. Although the expression of the family members is almost constitutive and tends to be expressed in the phloem of vascular bundles, there are significant differences in expression intensity. Serine acetyltransferase 1 (SAT1), serine acetyltransferase 3 (SAT3), and serine acetyltransferase 5 (SAT5) isoenzymes are mainly expressed in the early stages of *A. thaliana* development, while serine acetyltransferase 2 (SAT2) and serine acetyltransferase 4 (SAT4) are mainly expressed during plant reproduction and under sulfur or cadmium stress [3]. In *S. lycopersicum*, studies have shown that chloroplast localized SISATs are the main responders under abiotic stress conditions, and SISATs adopt different strategies to cope with osmotic, ionotoxic, and other stresses [2]. Tavares et al. [4] revealed isoform-specific induction of *VvSAT2;1* in grape leaves upon drought, whereas high or temperature stress hardly trigger *VvSAT2;1* transcription. It has been found in *Brassica napus* that the *NtSAT4* transgenic strain may excessively produce high levels of cysteine and glutathione to enhance stress resistance, especially tolerance to heavy metals [5]. In the identification of the SAT gene family in tea plants, it was found that under drought stress, the expression level of *CssSAT1* increased significantly at 12 h, indicating its potential enhanced sensitivity to drought at this specific time point. On the contrary, *CssSAT2* showed significant upregulation as early as 8 h, indicating a faster response [6]. Meanwhile, the expression level of *CssSAT3* significantly increased at 48 h, indicating its potential role in long-term drought adaptation. Under salt stress conditions, the expression level of *CssSAT1* was significantly upregulated at 48 h, indicating that it may be involved in later adaptation mechanisms to salt stress. In addition, SAT has also been identified in species such as *A. thaliana* [7], Chinese chives (*A. tuberosum)* [8], rice (*O. sativa*) [9], tomato (*S. lycopersicum*) [10], bean (*P. vulgaris*) [11] and watermelon (*C. lanatus*) [12]. So far, SAT research has mainly focused on abiotic stress and metal stress [13, 14], and there are few reports on the formation of AR in plants.

With respect to *P. persica*, in terms of seedling cultivation, it has become a trend to use asexual rootstocks instead of solid rootstocks. Thus, the survival rate of cuttings mainly depends on the formation of AR [15]. However, the formation of AR in woody plants such as *P. persica* is relatively difficult, and the rooting process of cuttings is regulated by multiple factors, such as hormones, nutrients, phenolic substances, enzyme activity, and genes [16]. In recent years, the formation of AR in cuttings has encountered bottlenecks that cannot be solved solely from a physiological perspective. Therefore,

studying the characteristics and functions of related genes in the process of AR in *P. persica* trees can not only explain the rooting mechanism, but also improve the molecular mechanism of AR formation in *P. persica* trees. At present, many scholars have studied the mechanism of plant AR formation in gene regulatory networks and other aspects. During the process of AR formation in *A. thaliana* explants, damage induced auxin activates the expression of WOX11 and WOX12, thereby upregulating LBD16 and LBD29, and directly activating WOX5 and WOX7 to promote the AR formation [17, 18]. Transferring the walnut *JrWOX11* gene into poplar trees revealed that overexpression of *JrWOX11* promoted root initiation and significantly increased the number of AR, lateral roots, and root hair length [19]. Some research reports suggest that WOX11 can regulate the growth and development of AR in response to abiotic stress [20]. In apple, Tahir et al. [21] found that nitrogen signaling and *MdWOX11* expression affect the accumulation of cytokinins and response to cytokinins by regulating gene expression related to cytokinin synthesis and transduction pathways, ultimately affecting the formation of AR. Likewise, Wang et al. [22] reported that the overexpression of *PoARRO-1* in peony test tube plants significantly increased rooting rate and average AR number, as well as increased activities of peroxidase (POD), superoxide dismutase (SOD), and indole-3-acetic acid oxidase (IAAO). Further analysis indicates that *PoARRO-1* interacts with *PoIAA7b* to promote the formation of AR. Therefore, screening the key genes in response to AR growth can provide a new gene resource for further genetic improvement of plants advective root molecules. In this study, through omics and fluorescence quantitative analysis, it was found that SAT significantly induced AR in *P. persica* trees, and exploring the role of SAT in AR formation has important practical significance for accelerating clonal breeding of peach trees.

Based on the transcriptome sequencing data from the previous stage of the research group (the transcriptome data was processed for BGI Genomics Co., Ltd. to conduct transcriptome sequencing, and data analysis of the five key stages of adventitious root formation in *P. persica* rootstock 'GF677' using high-throughput sequencing technology) and the qRT-PCR identification of SAT gene family, the AR formation-related gene *PpSAT1* was screened and cloned, and its function was identified. In addition, recent studies have linked serine acetyltransferase to the rooting of model plants such as *A. thaliana*, with one of the most common model plants for studying gene function, it has also been selected for transformation. *P. persica*, as a woody plant, is not easy to genetic transformation, and *P. domestica*, as a *P. persica*-related species, has a close relationship. Thus, this experiment genetically transformed *P. domestica* to investigate the function of *PpSAT1* in AR formation. The phenotype and characterization of *P. domestica* and *A. thaliana* were analyzed to provide a theoretical basis for the development of *P. persica* AR by molecular means.

Materials and methods

Plant materials and treatments

In June 2021, disease-free and well-growing current-year twigs of the *P. persica* rootstock 'GF677' were selected as test materials from the peach garden at the Gansu Academy of Agricultural Sciences. The twigs were cut into sections of 10–15 cm in length, with 3–4 leaves remaining on each cutting. Following a 10 s treatment with a solution of 200 mg/L indole-3-butyric acid (IBA) and 120 mg/L naphthaleneacetic acid (NAA), the cuttings were inserted into perlite to a depth of 5–8 cm. The cuttings were then covered with a shade net to protect them from sunlight, and an automatic spray device was used for watering. The phloem samples near the base of the cuttings were collected at 0, 7, 14, 21, and 28 day post-treatment, with three replicates for each period. All samples were quickly frozen in liquid nitrogen and stored at − 80 °C for further analysis.

Bioinformatics analysis of the SAT gene family

The protein sequence of *A. thaliana* SAT gene family was downloaded from *A. thaliana* genome database (http://www.arabidopsis.org/). Subsequently, it was used as a template to construct a library to identify candidate members of the SAT family from the *P. persica* genome library. Then, Pfam (https://pfam.xfam.org/) was used to verify whether the candidates had common motifs for SATase_N domain (PF06426) and Hexapep_C (PF00132). Remove the genes that do not contain the specific structural domains PF06426 and PF00132, and ultimately obtain members of the *P. persica* SAT family.

The physicochemical properties were analyzed using the ExPASy online tool (http://web.expasy.org/protparam/). Subcellular localization was predicted with WoLF PSORT (https://wolfpsort.hgc.jp/). The secondary structure of the encoded protein was predicted using the NPS@ online tool (https://npsa-prabi.ibcp. fr/cgi-bin/npsa_automat.pl? page=/NPSA/npsa_hnn. html). The tertiary structure of the protein was predicted using the Phyre2.2 online software (http://www.sbg.bio.ic.ac.uk/phyre2/html/page.cgi). DNAMAN software was employed for protein amino acid sequence alignment. The phylogenetic tree was constructed using the Neighbor-Joining method. Gene structures were visualized with TBtools software. The MEME suite (https://meme-suite.org/meme/tools/meme) was used to analyze conserved protein motifs. *Cis*-regulatory elements of family

members were analyzed using PlantCARE (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/). Chromosome mapping was visualized using TBtools, based on the location of the SAT gene in the *P. persica* genome database.

PpSAT1 gene cloning

Primers were designed using Premier 6.0 software (Table 1). The cDNA from *P. persica* 'GF677' leaves was used as the template for PCR amplification. The PCR reaction system (40 μL) consisted of 20 μL of 2×P515 enzyme, 1 μL of forward and reverse primers, 3 μL of cDNA, and 15 μL of ultra-pure H_2O. The reaction procedure was as follows: 95 °C for 10 min, 95 °C for 30 s, 56 °C for 30 s, and 72 °C for 60 s per kilobase, followed by 33 cycles, with a final extension at 72 °C for 10 min.

Construction of plant expression vector and agrobacterium transformation

Plasmid CAM-FLAG was digested using *EcoRI* and *XhoI* enzymes. The target gene fragment was ligated to the vector and transformed into *E. coli* to obtain the recombinant plasmid. Subsequently, Agrobacterium GV3101 was transformed through freeze–thaw and incubated at 28 °C. Once a single colony emerged, it was verified by PCR.

Genetic transformation of *P. domestica* hypocotyl

Mature seed hypocotyl slices from the cultivar *P. domestica* L.cv. 'Victoria' were used as explants. Specifically, seeds with fully mature and disinfect were selected, sterilize them with 100 times 84 disinfectant for 10 min, and then remove the inner skin with a walnut clip.

Then, the seeds were sterilized with 1% sodium hypochlorite solution (approximately 20 μL of surfactant Tween-20 per 100 mL) for 30 min, along with intermittent shaking during the sterilization process. After washing 2–3 times, leave the seed coat overnight in sterile water at room temperature. Then, a surgical knife was used to remove the seed coat, discard the embryonic root and hypocotyl, and cut the hypocotyl into three cross sections (0.5–1 mm), which were used for regeneration/transformation. The media used in this study were: (1) sprout regeneration medium (SRM) containing 3/4-strength MS salt, 7.5 μM thidiazuron (TDZ), 0.25 μM indole butyric acid (IBA) and 9.05 μM 2,4-dichlorophenoxy-acetic acid (2,4-D), pH 5.8; (2) Sprout growth medium (SGM) containing strength MS salt, 3.0 μM benzylaminopurine (BAP), pH 5.8; (3) Rooting medium (RM) containing 1/2-strength MS salt, 0.1 μM kinetin (K), and 5.0 l μM α-naphthaleneacetic acid (NAA), pH 5.8.

After 20 min of *Agrobacterium* infection, the infected hypocotyl slices were placed on SRM without antibiotics for 3 days of dark culture, and then transferred to SRM containing 250 mg/L cephalosporin and 30 mg/L kanamycin for cultivation. After 6–8 weeks of emergence of new shoots, the explants were cultured on antibiotic containing SGM. After about 3 weeks of cultivation, green and vibrant bud clusters were isolated, labeled, and placed on antibiotic containing fresh SGM medium for subculture every 3 weeks. When the buds reach 3–4 cm in length, transfer them to RM supplemented with antibiotics for cultivation. DNA and RNA was extracted from the leaves of transgenic *P. domestica* plants obtained through transformation and detect whether they were false positive plant lines.

Acquisition of genetically modified *A. thaliana*

To obtain T3 homozygous transgenic plants, T0 seeds were treated with 75% ethanol for 5 min, followed by 26% NaClO for 10 min. After treatment, the seeds were rinsed 3–4 times with deionized water and sown on culture medium containing 30 mg/L kanamycin. Following three consecutive screenings, T3 generation homozygous transgenic plants were obtained. On the one hand, RNA was extracted and qRT-PCR was performed to verify whether the obtained material had successfully genetically cycled. Meanwhile, the DNA is extracted and verified by RT-PCR.

Quantitative real-time PCR (qRT-PCR) analysis

The specific primer sequence for the SATs family gene were designed and synthesized by Shanghai Sangong Bioengineering Technology Service Co., Ltd. (Table 1).

Table 1 qRT-PCR and clone primers for expression analysis of SATs in peach

Usage	Accession no	Gene	Forward primer(5′ → 3′)	Reverse primer(5′ → 3′)
Quantitative real-time PCR	Prupe.4G239400.1	*PpSAT1*	TTGCCTACCCATTTGCCAGAATCG	GCCCATCGCCCTTGTCTTCATC
	Prupe.4G239500.1	*PpSAT2*	AGGATTGGTGAAGGTGCTAAGATTG	ACATGGTTAAGTGCTTGGACTGTG
	Prupe.7G179500.1	*PpSAT3*	TCTCGGAACGCTTGGCTCTG	CGGGTCGGAGTCGGGTTTC
	Prupe.7G212700.1	*PpSAT4*	CGTCGTTGAAGCGATCCCTGTC	GGTCATAGAGGAGCGTGGAGAGG
Gene clone	Prupe.4G239400.1	*PpSAT1*	TGGAGAGGACACGCTCGAGATGAAAGG TCTGGCCGTAGC	CATCCTTGTAGTCGAATTCAATAA CATAATCAGACCACTCAGACATG
Internal reference gene		*Actin*	GATTCCGGTGCCCAGAAGT	CCAGCAGCTTCCATTCCAA

cDNA was synthesized using the PrimeScript RT Reagent Kit (Perfect RealTime) from TaKaRa, following the manufacturer's instructions. Actin was used as the internal reference gene for specific expression analysis. The reaction system consisted of 10 μL TB Green II, 2 μL mixed upstream and downstream primers, 6 μL ultra pure H_2O, and 2 μL cDNA, with a total volume of 20 μL. The PCR program included an initial denaturation at 95 °C for 30 s, followed by 40 cycles of denaturation at 95 °C for 10 s, annealing at 60 °C for 30 s, and extension at 72 °C for 30 s. The experiment was repeated 3 times.

Determination of transgenic root morphology and enzyme activity

Root seedlings from three overexpressing (OE) strains and one wild-type (WT) strain of transgenic *P. domestica* and *A. thaliana* were collected. The roots were excised, washed with running water, and scanned using a ScanMaker i800 Plus root scanner to record root configuration parameters, including root length, surface area, root diameter, root volume, and root tip count. *A. thaliana* measured its root length with a ruler. The phenotypic characteristics of the strains were then photographed.

The SOD and POD activities were measured on a spectrophotometer using kits from Shanghai Enzyme Linked Biotechnology Co., Ltd. Three replicates were tested for each line.

Statistical analysis

Treatment effects were tested by analysis of variance and comparisons of means were conducted with the Duncan's test ($P < 0.05$). SPSS version 22.0 (IBM, Armonk, NY, USA) were used for statistical analyses, and Origin 8.0 software (OriginLab, Hampton, MA, USA) were used to process figures.

Result and analysis

Analysis of cysteine metabolic pathway

Based on the transcriptome sequencing data from the previous stage of the research group, it was discovered that the cysteine metabolic pathway is significantly enriched during AR formation. As shown in Fig. 1, serine acetyltransferase (SAT1/4) showed significant upregulation at 14 days (from callus tissue to AR formation), especially SAT1 was significantly induced at 7, 14, and 28 days, and also significantly expressed at 21 days, indicating its potential role in inducing AR formation. In addition, *O*-acetylserine(thio)lyase (OAS) demonstrated significant expression at 7 days (the activation phase of AR), indicating its likely involvement in the induction of AR. Methyline gamma-lyase (MGL), homocysteine S-methyltransferase 3 (HMT), and 1,2-dihydroxy-3-keto-5-methylthiopentene dioxygenase (DHK-MTP) were

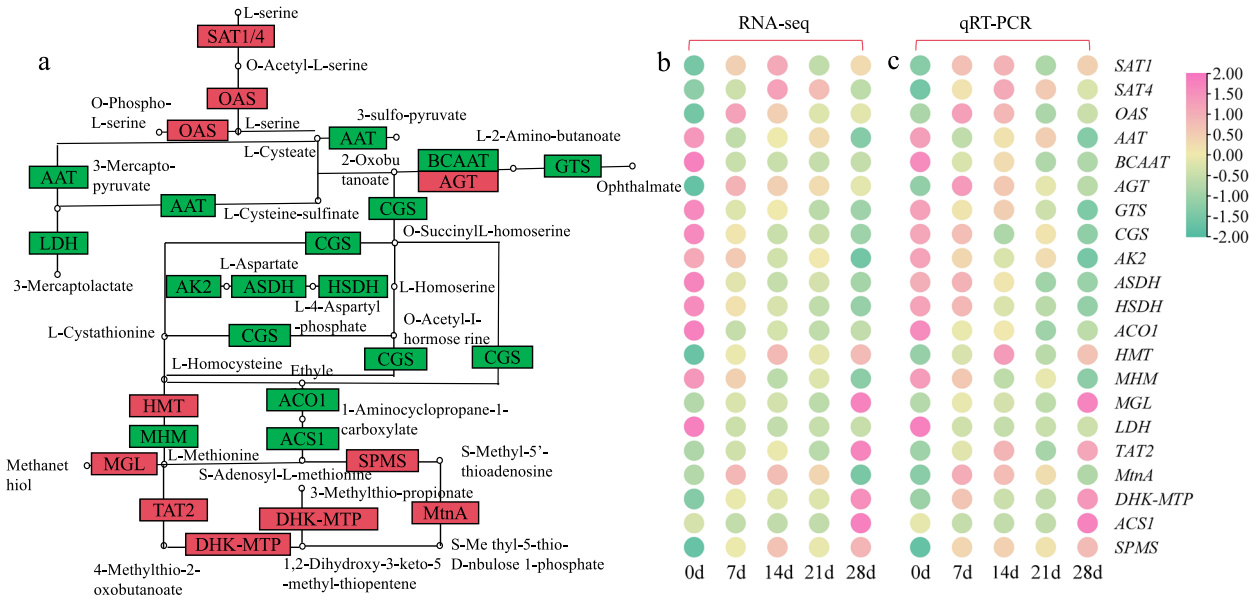


Fig. 1 Cysteine metabolic pathway during AR formation. **a** The cysteine metabolic pathway. Red boxes upregulated and green boxes downregulated. **b** The FPKM value based on transcriptome sequencing, shows a cysteine metabolism pathway analysis based on transcriptome sequencing. Log2 based FPKM value was used to create the heat map with clustering. The color scale representing the relative expression values is shown on the upper right, the closer the color is to pink, the higher the level of expression. **c** The qRT-PCR analysis of key genes of cysteine metabolism pathway

Table 2 Physical and chemical properties of *P. persica* SAT family

Gene	Protein length (aa)	Molecular weight (ku)	PI	Subcellular localization
PpSAT1	395	43.04	8.30	Chlo:11, mito:2.5, cyto_mito:2
PpSAT2	356	39.00	6.89	Chlo:13
PpSAT3	344	37.34	6.00	Cyto:9, chlo:2, nucl:2
PpSAT4	287	30.49	6.70	Cyto:7, chlo:2, cysk:2, mito:1, plas:1

Table 3 Prediction of secondary structure of *P. persica* SAT family

Gene	Extended strand (Ee)	Random coil (Cc)
PpSAT1	14.68%	53.67%
PpSAT2	16.85%	46.35%
PpSAT3	12.21%	39.83%
PpSAT4	14.63%	44.25%

upregulated at 28 days (AR extension period), suggesting their potential regulation of genes related to AR extension. The genes encoding aspartate aminotransferase (AAT), glutathione synthase (GTS), and aspartate-semialdehyde dehydrogenase (ASDH) were significantly downregulated, potentially influencing the expression of genes related to AR formation through this pathway. Furthermore, combined with qRT-PCR validation, identification of differentially expressed genes within the cysteine metabolism pathway indicated a certain level of reliability for the transcriptome data. Notably, serine acetyltransferase (SAT) displayed significant expression throughout the entire process of AR formation, hence further research will be conducted on SAT.

Basic physical and chemical properties and secondary and tertiary structure analysis of protein

The physical and chemical properties of the four SAT genes were analyzed using the ExPASY database. As shown in Table 2, the amino acid sequence lengths indicated that all four SAT proteins were within 1000 amino acids, with significant differences in length across different subgroups. The shortest protein was *PpSAT4* (287 amino acids), while the longest was *PpSAT1* (395 amino acids). The predicted molecular weights ranged from 30.49 kD (*PpSAT4*) to 43.04 kD (*PpSAT1*), and the isoelectric points (pI) varied from 6.00 (*PpSAT3*) to 8.30 (*PpSAT1*). The subcellular localization prediction indicated that the SAT genes were primarily distributed in the chloroplast and cytoplasm.

Secondary structure analysis revealed that the secondary structure of *P. persica* SAT proteins comprises alpha helix (Hh), extended strand (Ee), and random coil (Cc) (Table 3). The alpha helix distribution ranged from 31.65 to 47.97%, while the random coil distribution ranged from 39.83 to 53.67%. These two configurations were prevalent throughout the protein sequence, accounting for a significant proportion. The extended strand distribution in the protein sequence was relatively minor, ranging from 12.21 to 16.85%. The Swiss Model was used to analyze the tertiary structure of the SAT gene family protein sequence, and the results showed that the tertiary structure of the protein was highly similar in spatial structure, which was consistent with the prediction of the secondary structure. All four genes included Hh, Ee, and Cc structures (Fig. 2).

Chromosome localization and collinearity analysis of the *P. persica* SAT family

The genomic positions of *P. persica* SAT genes was determined based on their localization coordinates. The four PpSAT genes are evenly distributed on two chromosomes of the *P. persica* genome, namely chromosome 4 and chromosome 7. Among them, *PpSAT1* and *PpSAT2* are distributed on chromosome 4, while *PpSAT3* and *PpSAT4* are distributed on chromosome 7 (Fig. 3a).

The phylogenetic relationship between the *P. persica* SAT gene family and those of other species can be further elucidated through interspecific collinearity analysis maps of *P. persica*, *A. thaliana*, and apple. As illustrated in Fig. 3c, there are multiple pairs of collinear relationships between *P. persica*, rice, and apple. Specifically, three collinear relationships between the *P. persica* and

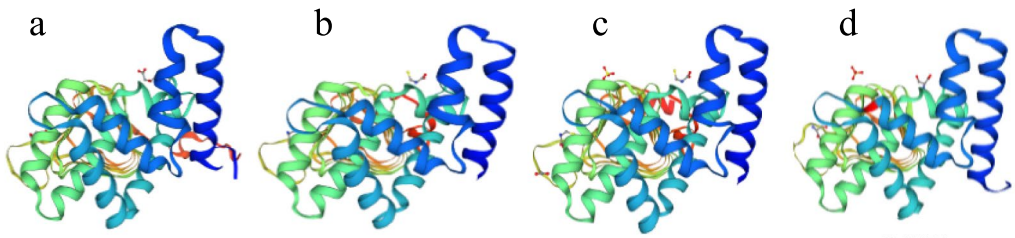


Fig. 2 Prediction of tertiary structure of *P. persica* SAT family. **a** *PpSAT1*. **b** *PpSAT2*. **c** *PpSAT3*. **d** *PpSAT4*

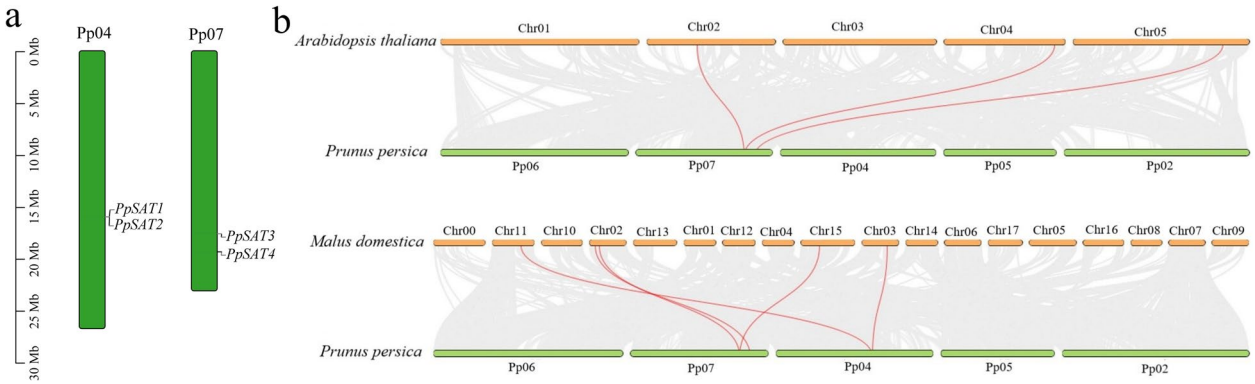


Fig. 3 Chromosome localization of four *P. persica* SAT genes. **a** Constrictions on the chromosomes (vertical bar) indicate the position of centromeres. The chromosome numbers are indicated at the top of each chromosome image. Scale is in megabases (Mb). **b** Synthesis analysis of SAT genes in *P. persica*, *A. thaliana*, and apple. Gray lines in the background indicate the collinear blocks between the *P. persica*, *A. thaliana* and apple genomes, and the red lines highlight the syntenic SAT gene pairs

A. thaliana genomes are located on chromosome Pp07 of *P. persica*, while five collinear relationships between the *P. persica* and apple genomes are distributed on chromosomes Chr11, Chr02, Chr15, and Chr03 of peach and Pp04 of apple. These results indicate the homology of the SAT gene family among *P. persica*, *A. thaliana*, and apple.

Phylogenetic tree and structural analysis of the *P. persica* SAT family

Sequence alignment was conducted on the amino acid sequences encoded by PpSAT, revealing a deduced amino acid sequence homology of 75.06% (Fig. 4a). To investigate the evolutionary relationships among SAT proteins in *P. persica*, *A. thaliana*, apple, and rice, a phylogenetic tree was constructed using MEGA-X based on the SAT protein sequences (Fig. 4b). Phylogenetic analysis indicates that the proteins are divided into three main clades (Groups I, II, and III), containing 8, 6, and 7 members, respectively. In addition, Group I, there are two members, *PpSAT1* and *PpSAT2*. *PpSAT3* exists in Group II, while *PpSAT4* is distributed in Group III. The genes from *P. persica*, *A. thaliana*, apple, and rice are distributed across these three clades, suggesting that the SAT genes from these species exhibit high homology and a close evolutionary relationship within each group.

MEME analysis was employed to examine the distribution of conserved motifs within the *P. persica* SAT gene family. A total of 10 motifs were identified, with the main 6 motifs illustrated in Fig. 4c. Motifs 1, 2, 3, 4, and 6 are present in all family members, indicating that most members of the family share similar motifs, suggesting potential functional similarities. The gene structure analysis of the *P. persica* SAT family (Fig. 4d) reveals that the number of exons in the family genes ranges from 1 to 9, with the *PpSAT3* gene having the maximum number of 9 exons. Each gene in the family contains several introns. In additionally, the length and location of introns and exons vary significantly, which may account for differences in gene function.

cis-acting element analysis of the *P. persica* SAT family

To further investigate the potential regulatory mechanisms of the *P. persica* SAT genes in response to adventitious root formation, PlantCARE software was used to analyze the upstream 2 000 bp promoter region of each SAT gene. The results showed that hormone-related *cis*-elements (salicylic acid, abscisic acid, auxin, gibberellin, and MeJA), plant development-related *cis*-elements (meristematic tissue expression), stress-related *cis*-elements (drought), and light responsive elements were identified (Fig. 5). Among the hormone-related *cis*-elements, the promoter regions of four *P. persica* SAT genes contain abscisic acid and gibberellin responsive elements, three peach SAT genes contain MeJA responsive elements, two *P. persica* SAT genes contain auxin responsive elements, and one *P. persica* SAT gene contains salicylic acid responsive elements, indicating that adventitious root formation is a complex process regulated by hormones. Among the stress-related *cis*-elements, the identified drought responsive elements may be involved in the formation of adventitious roots. All SAT genes contain light signal response elements. Interestingly, *PpSAT1* was the only gene that showed salicylic acid responsiveness, likewise; *PpSAT2* showed meristem responsiveness. This suggests that members of the *PpSAT1* and *PpSAT2* families may have functional differences in physiological responses during plant growth and development.

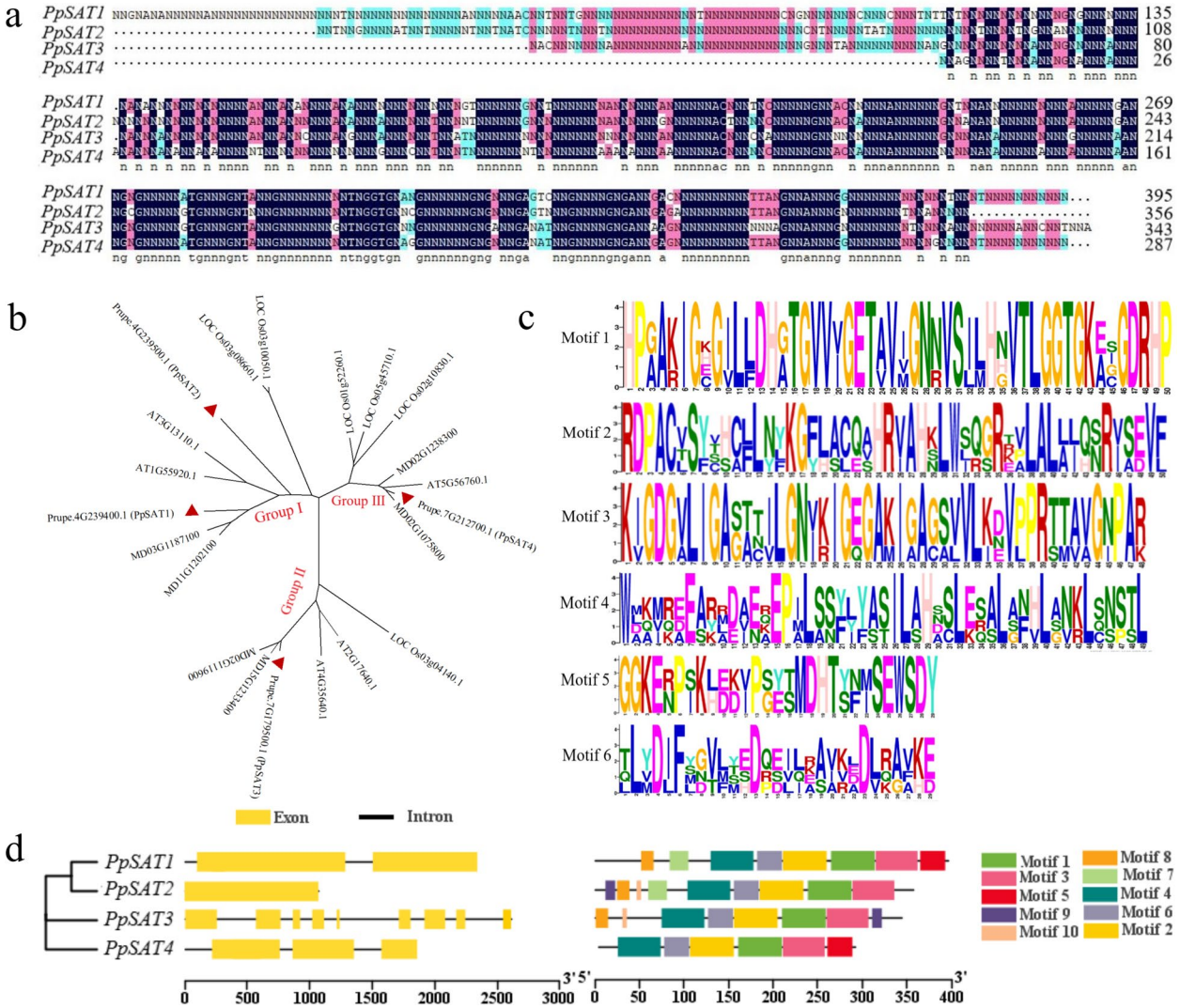
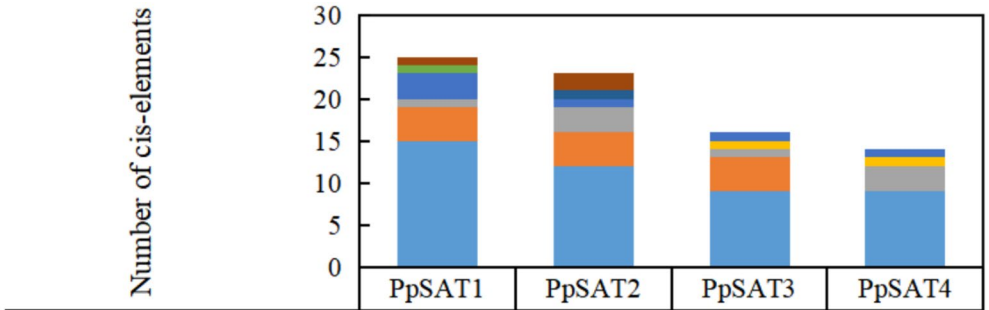


Fig. 4 PpSAT gene family analysis. **a** Sequence alignment of *P. persica* SAT gene family. Complete protein sequences of plant SAT were aligned using Clustal-X. Dashes indicate gaps in sequence for best alignment. Black shade indicates identical amino acid residue. Red and blue shade indicates similar amino acid residue. **b** Phylogenetic tree and subgroup classifications of SAT proteins in *P. persica*, rice, apple and *A. thaliana*, red triangle represents the SAT proteins in *P. persica*. **c** Sequences of the 6 conserved motifs in the PpSAT proteins. **d** Gene structure composition of the SAT in *P. persica*. The scale represents the length of the gene, yellow lines represent exons and black lines represent introns, in which the conserved motifs are indicated by colored boxes

Real-time fluorescence quantitative qRT-PCR analysis

The qRT-PCR analysis results (Supplementary Material Fig. S1) revealed that the expression of *PpSAT2* gradually increased over time. In contrast, *PpSAT3* exhibited an ascending–descending–ascending–descending pattern expression. The expression levels of *PpSAT1* and *PpSAT4* were significantly higher than those of *PpSAT2* and *PpSAT3*. The expression trends of *PpSAT1* and *PpSAT4* were consistent with the transcriptome data, confirming the reliability of the results, which suggest that *PpSAT1* and *PpSAT4* may play crucial roles in the formation of AR.



	PpSAT1	PpSAT2	PpSAT3	PpSAT4
Drought-inducibility	1	2	0	0
Meristem expression	0	1	0	0
Salicylic acid responsiveness	1	0	0	0
Abscisic acid responsiveness	3	1	1	1
Auxin-responsiveness	0	0	1	1
Gibberellin-responsiveness	1	3	1	3
MeJA-responsiveness	4	4	4	0
Light responsiveness	15	12	9	9

P. persica SAT genes

Fig. 5 Common *cis*-acting elements found in *P. persica SAT* genes

Cloning of *PpSAT1* gene, construction of expression vector, and screening and identification of transgenic *P. domestica* and *A. thaliana*

Based on the FPKM value and the expression level of qRT-PCR, it is decided to select *PpSAT1* gene for cloning. We amplified the CDS region of the *PpSAT1* gene was amplified using cDNA from the phloem of the *P. persica* rootstock 'GF 677'. The amplified band size was consistent with the expected size of 1188 bp, indicating that the *PpSAT1* gene was successfully cloned in *P. persica*. The gene was subsequently ligated into the CAM–FLAG overexpression vector, and a single colony was selected for PCR verification. The fragment size matched the expected size, confirming that the target gene was successfully inserted into the CAM–FLAG vector.

DNA was extracted from *P. domestica* and *A. thaliana* materials obtained through genetic transformation for PCR identification (Fig. 6a, b). The results indicated that OE-*PpSAT1-1*, OE-*PpSAT1-3*, OE-*PpSAT1-4*, OE-*PpSAT1-5*, OE-*PpSAT1-6*, OE-*PpSAT1-8*, and OE-*PpSAT1-9* exhibited bands with the expected size of 1 188 bp in *P. domestica*. The band sizes for OE-*PpSAT1-1*, OE-*PpSAT1-2*, OE-*PpSAT1-3*, OE-*PpSAT1-4*, and OE-*PpSAT1-5* in *A. thaliana* were consistent with the target sizes, indicating successful transformation in *P. domestica* and *A. thaliana*. Subsequently, OE-*PpSAT1-1*, OE-*PpSAT1-3*, and OE-*PpSAT1-4* were selected for further verification. RNA was extracted from these selected transgenic *P. domestica* and *A. thaliana*, and the expression of *PpSAT1* genes was detected by qRT-PCR. As shown in Fig. 6c, d, the expression levels of OE-*PpSAT1-1*, OE-*PpSAT1-3*, and OE-*PpSAT1-4* in the overexpressing lines of *P. domestica* and *A. thaliana* were significantly higher than those in the wild type, confirming that transgenic *P. domestica* and *A. thaliana* overexpressing *PpSAT1* were successfully obtained. In addition, DNA was extracted to confirm that the genetically modified material had been successfully produced.

Functional verification in *P. domestica*

The WT and overexpressing *P. domestica* strains of *PpSAT1*, with similar growth states, were cultured on MS solid medium. After 45 days, robust and consistent strains were selected for comparison. As shown in Fig. 7a, the root index of OE was significantly higher than that of WT, indicating that transgenic *PpSAT1* promotes AR growth. Root scans of *PpSAT1* transgenic plants and WT plants were performed, the root morphological parameters (root length, root surface area, root diameter, root volume, and root tip number) were significantly enhanced in *PpSAT1* overexpressing plants compared to WT, as shown in Fig. 7b, c. These findings suggest that transgenic *PpSAT1* plays a role in AR development. As shown in Fig. 7d, e, the activities of POD and SOD were measured in WT and overexpressing *PpSAT1 P. domestica* strains. The results indicated no significant difference

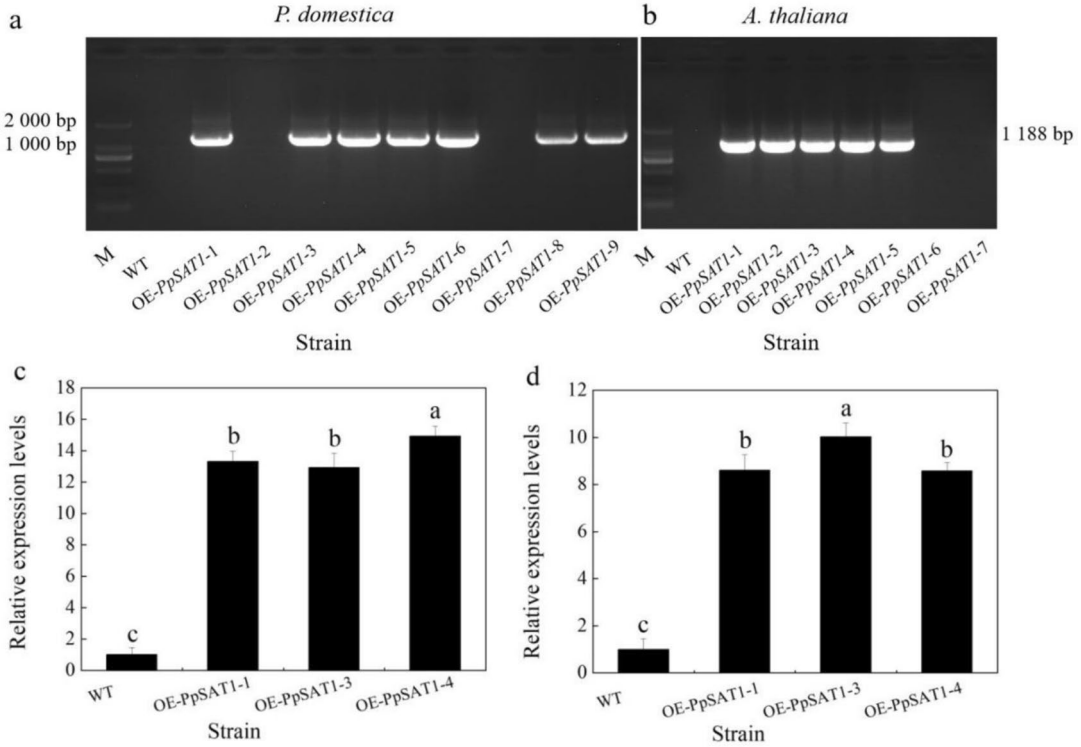


Fig. 6 Identification of transgenic *PpSAT1 P. domestica* and *A. thaliana* at the DNA and RNA Levels. **a** Identification of genetically modified *P. domestica* at the DNA level. **b** Identification of transgenic *A. thaliana* at the DNA level. **c** Identification of genetically modified *P. domestica* at the RNA level. **d** Identification of transgenic *A. thaliana* at the RNA level. M: Marker. WT: Wild-type strain. OE: Transgenic strains. Vertical bars represent the standard errors of the means (three replicates). Lowercase letters indicates there was a significant difference between the transgenic strains and WT ($P < 0.05$)

in the activities among the overexpressing strains OE-*PpSAT1-1*, OE-*PpSAT1-3*, and OE-*PpSAT1-4*, while the overexpression strains exhibited significantly higher activities of both POD, and SOD compared to WT.

Functional verification in *A. thaliana*

WT and transgenic *A. thaliana* were pre-cultured on MS medium for 15 days, after which robust and consistent strains were selected for analysis. As shown in Fig. 8a, b, compared to the WT, *PpSAT1* transgenic *A. thaliana* exhibited better root growth, and the root length of transgenic *PpSAT1* lines ranged from 3 to 4 cm, whereas that of wild-type lines ranged from 2 to 3 cm. It can be concluded that transgenic *PpSAT1* participates in adventitious root development and promotes root elongation.

As shown in Fig. 8c, d, the identification of POD and SOD activities in *A. thaliana* revealed that the root growth of overexpressing *A. thaliana* was significantly better than that of the wild type, which was similar to the results observed in *P. domestica*.

Discussion

SAT in plants is a small family encoded by multiple genes, widely distributed in higher plants [23]. *Prunus persica*, as an economically important woody plants, one of the most widely planted fruit crops in the world [24]. Its genome sequencing has provided a good platform for the identification of families such as Aux/IAA [25], HD Zip [26], MADS box [27], GRAS [28], and WRKY [29, 30]. However, the genome-wide information about the *P. persica* SAT gene remains unknown. In view of this, this study identified serine acetyltransferase in the cysteine metabolic pathway associated with AR formation through transcriptome screening, and characterized its gene family. Four SAT gene family members were identified and located on two different chromosomes, whose members are in single digits compared to previously reported grape (*V. vinifera*) (4) [4], *A. thaliana* (5) [2, 7], rice (*O. sativa*) (6) [9], maize (*Z. mays*) (4) [31], and tomato (*S. lycopersicum*) (4) [10], indicating that there is little difference in the number of SAT members among different species.

The phylogenetic tree divides the proteins encoded by four *P. persica* SAT genes into three subgroups. In each

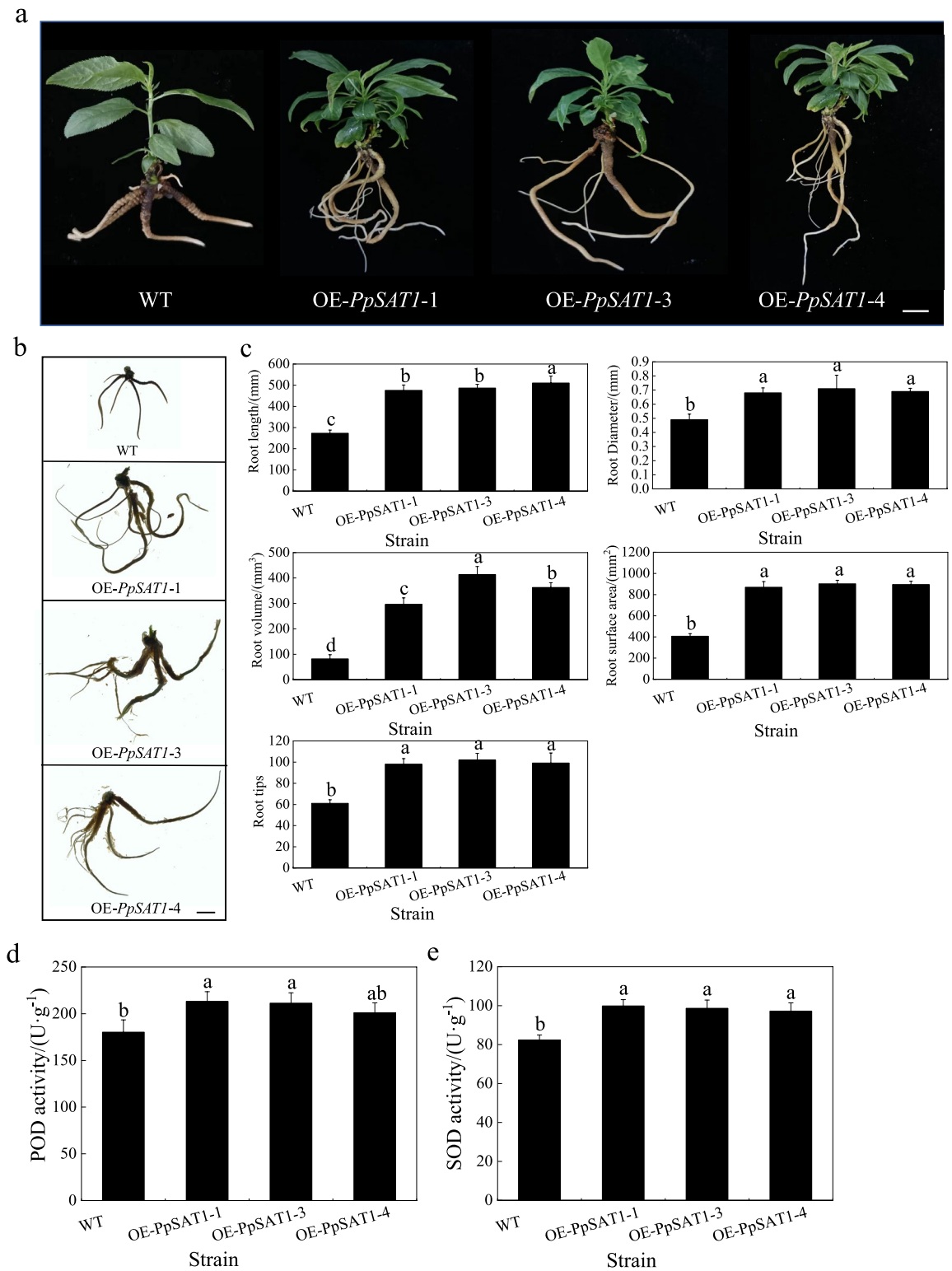


Fig. 7 Determination of phenotypic, morphological indices of transgenic *P. domestica* and enzyme activity in transgenic *P. domestica* roots. **a** Phenotype of *P. domestica* strains; **b** Scanning image of *P. domestica* root system. **c** *P. domestica* root length, root diameter, root volume, root surface are and root tips bar chart. **d** POD activity in *P. domestica*; **e** SOD activity in *P. domestica*. WT: Wild-type strain. OE: Transgenic strains. Vertical bars represent the standard errors of the means (three replicates). Lowercase letters indicates there was a significant difference between the transgenic strains and WT *(P < 0.05)*. Bar, 1 cm

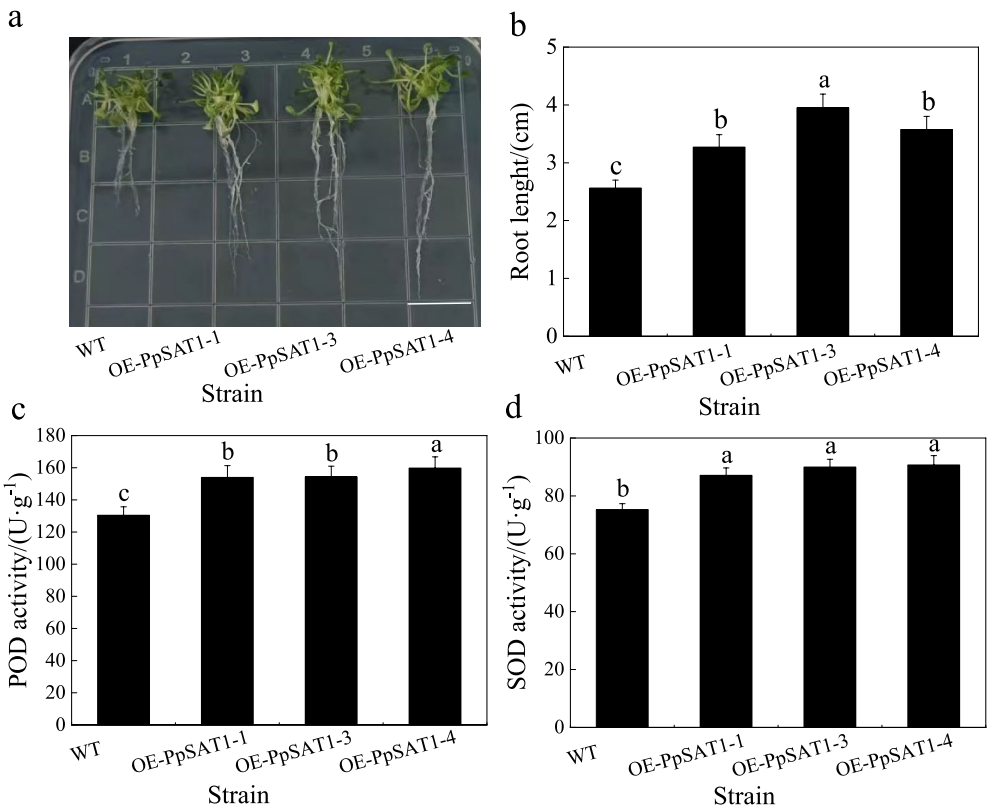


Fig. 8 Phenotype and enzyme activity determination of *A. thaliana* strains. **a** Phenotype of *A. thaliana* strains. **b** Root length of *A. thaliana* strains. **c** POD activity in *A. thaliana*. **d** SOD activity in *A. thaliana*. WT: Wild-type strain. OE: Transgenic strains. Vertical bars represent the standard errors of the means (three replicates). Lowercase letters indicates there was a significant difference between the transgenic strains and WT *(P < 0.05)*. Bar, 1 cm

group, subgroup members have similar gene structures, which is consistent with those reported in other species [2, 4, 10]. In generally, paralogous and orthologous functional relationships can be confirmed by knowing the functions of certain members; it is likely that members within a subgroup have common evolutionary origins and a conserved function [32, 33]. In the study, *PpSAT1* and *PpSAT2* were clustered into a subgroup, suggesting that they may have similar functions. *Cis*-regulatory elements are important molecular switches involved in transcriptional regulation of dynamic gene activity networks that control a variety of biological processes, including abiotic stress response, hormonal response, and developmental processes. *Cis*-acting element analysis showed that the 2000 bp region of *PpSAT1* promoter was present in gibberellin, auxin, salicylic acid, abscisic acid and other hormone-related *cis*-elements, suggesting that this gene may be involved in plant growth and development as well as hormone response processes. Subsequently, we evaluated the expression of four SAT gene family members in the phloem using qRT-PCR, and the results showed a significant upregulation of *PpSAT1*. Based on this, we combined previous transcriptome data to screen and clone *PpSAT1* protein, and studied its function in AR formation.

The expression of SAT gene is regulated by plant hormones, As it has been shown in rice, the expression of *OsSAT1* in different tissues, organs and hormones indicates that jasmonate is the main hormone inducing the expression of *OsSAT1;1*, *OsSAT2;1* and *OsSAT2;2*, while auxin and abscisic acid only trigger the expression of *OsSAT1;1* [10]. Another study has shown that plant hormones can regulate AR growth. Studies on petunia (*P. hybrida*) cuttings revealed early IAA accumulation in the stem base as dependent on Polar auxin transport (PAT) and essential for subsequent AR formation [34]. Transcriptome analysis of Taxus media stem cuttings has demonstrated that auxin promotes AR formation, whereas cytokinin inhibits AR formation [35]. However, it remains to be determined whether plant hormones respond to AR formation by regulating SAT genes. Therefore, in this study, the *PpSAT1* gene related to AR formation was successfully cloned, and the overexpression vector for *PpSAT1* was constructed.

Through agrobacterium-mediated genetic transformation, transgenic *P. persica* relatives *P. domestica* and *A. thaliana* were successfully obtained, with significantly higher expression levels in transgenic plants compared to the wild type. Previous studies on SAT have also shown that after genetic transformation in soybean [36], watermelon [12], spinach [37], and onion [38], SAT overexpression plants significantly promote plant growth compared to wild-type plants. In this experiment, the root morphology index of transgenic *P. domestica* and *A. thaliana PpSAT1* was significantly higher than that of wild-type plants, indicating that overexpression of *PpSAT1* promotes AR formation, enhances plant root index, and promotes later transplantation survival rate. This is consistent with the results of Wei et al. [39] in *Populus ussuriensis*, where endogenous (MeJA) can specifically induce a significant upregulation of *PuHox52* during AR formation. Plants overexpressing *PuHox52* exhibit significant changes in the number and length of AR, a significant increase in root biomass, and an earlier rooting time of 1–2 days compared to the wild-type, thus confirming the role of overexpression in promoting AR formation. In addition, studies have shown that the higher the enzyme activity in plants, the stronger the resistance of cuttings, which is beneficial for the growth of AR and accelerates their occurrence time [40]. In this study, the enzyme activities (SOD and POD) of transgenic *P. domestica* and *A. thaliana PpSAT1* were significantly higher than those of wild-type plants, indicating that the AR growth of transgenic plants is better than that of wild-type. In summary, SAT may promote AR formation by altering the rooting parameters and oxidase parameters.

Conclusions

In this study, transcriptome screening was employed to screen serine acetyltransferase (SAT) in the cysteine metabolic pathway associated with AR formation, and characterized the members of this gene family from the peach genome. A total of 4 members were identified, classified into 3 subgroups and located on two different chromosomes. *Cis*-element analysis revealed that the primary responses included photomorphogenesis, MeJA signaling, auxin response, and salicylic acid signaling. The qRT-PCR results showed that the *PpSAT1* gene was highly expressed during the process of AR formation. In view of this, *PpSAT1* was cloned for functional validation. The results showed that overexpression of *PpSAT1* could increase various root parameters (root length, root volume, root surface area, and root tip numbers) as well as POD and SOD activities. In addition, overexpression of *PpSAT1* gene was found to significantly increase root length and enzyme activity in *A. thaliana*, suggesting that may have a similar function in *A. thaliana* as *P. domestica*. In summary, our results preliminarily confirmed that *PpSAT1* plays an active role in promoting AR formation. In the future, further research will be conducted to reveal the molecular mechanism by which this gene promotes AR growth in *P. persica*, providing a theoretical basis for the breeding of excellent varieties of *P. persica* trees.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40538-025-00759-1.

Supplementary Material 1: Fig. S1. Expression analysis of P. persica SAT family genes in AR formation. qRT-PCR was used to investigate the expression levels of each PpSAT gene. To calculate the relative expression level, the expression of each gene under control treatment was set as 1. The reference gene used in qRT-PCR was actin. Vertical bars represent the standard errors of the means (three replicates). Lowercase letters indicate the difference in the expression level of *P. persica* SAT family genes at different time points in AR formation ($P < 0.05$).

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Author contributions
LH and HW designed the research. LH and YY performed the experiments. FZ performed the data analysis. LH and XZ prepared the figures and tables. LH wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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Availability of data and materials
No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate
We all declare that manuscript reporting studies do not involve any human participants, human data, or human tissue. Therefore, it is not applicable. Experimental research and field studies on plants (either cultivated or wild), including the collection of plant material, must comply with relevant institutional, national, and international guidelines and legislation. No permission is required. Plants material was purchased.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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