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Genome-wide analysis and expression profiling of the polyamine oxidase gene family in *Solanum tuberosum* L.

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Abstract

Background Polyamine oxidase (PAO) is a crucial enzyme involved in the breakdown of polyamines (PAs) in plants. It not only regulates the levels of PAs, but also plays a role in the oxidative decomposition of PAs and the release of stress-related signals, contributing to the plant's response and resistance to various adversities. While there have been numerous studies on the response of PAO to stress in other crops, there is a lack of research on this topic in potatoes, a major food crop.

Results In this study, we aimed to explore the biological function of the *StPAO* gene in potato growth and development, as well as its expression patterns under stress. Using bioinformatics methods, we identified 14 *StPAO* genes in the potato genome. Protein sequence comparisons revealed a high similarity between the PAO proteins of potato and *Arabidopsis*. Chromosomal mapping and gene structure analysis showed that the *StPAO* genes were not evenly distributed on the chromosome and all contained an *amino-oxidase* domain. Furthermore, analysis of the promoters of these genes revealed the presence of abiotic and stress-related *cis*-acting elements, indicating their potential role in responding to different stresses. To investigate the expression patterns of these genes under stress, we used qRT-PCR to study their response to high temperature, drought, and ABA stress. Our results showed that *StPAO6* and *StPAO10* were significantly up-regulated under high temperature stress, indicating that they were involved in the process of potato resistance to high temperatures. Similarly, *StPAO1*, *StPAO3*, and *StPAO4* were significantly up-regulated under drought stress, indicating their potential role in potatoes' responses to drought. After ABA treatment, the expression levels of *StPAO4*, *StPAO5*, *StPAO7*, and *StPAO14* were significantly up-regulated, suggesting their involvement in chemical defense mechanisms. Interestingly, the expression of *StPAO11–13* was inhibited by all three stresses.

Conclusions In conclusion, our study highlights the multifunctional nature of the *StPAO* gene family in potatoes, which plays a crucial role in coping with various stresses. This research deepens our understanding of the potato *StPAO* gene family and provides a reference for future studies on its function. It also serves as a theoretical basis for breeding stress-resistant potato varieties in the future.

Keywords Potato, PAO, Stress, Evolution, Expression

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Background

Polyamines (PAs) are low-molecular-weight aliphatic nitrogen-containing substances with high biological activity produced during the metabolism of living organisms. The most common PAs are putrescine (Put), spermidine (Spd), and spermine (Spm) [1]. Numerous studies have demonstrated the wide involvement of PAs in various stages of plant growth, development, and the adaptation process to external stress [2], such as rooting [3], seed germination [4], pollen tube growth [5], fruit development and maturation [6], senescence [7], and stress response [8]. The enzyme responsible for the oxidative degradation of PAs is polyamine oxidase (PAO). PAOs were first found in the exoplasm of maize (*Zea mays*). They are 53-kDa monosomic glycoproteins that rely on fatty acid desaturase (FAD) for their function. *PAO* genes have been identified in several plants, including *Arabidopsis thaliana* [9], rice (*Oryza sativa*) [10], peach (*Prunus persica*) [11], tomato (*Solanum lycopersicum*) [12], apple (*Malus pumila*), cucumber (*Cucumis sativus*) [13], and sweet orange (*Citrus sinensis*) [14].

Plants can be affected by abiotic stresses during growth and development, resulting in reduced crop yields [15–17]. The homeostasis of polyamines in the cell is attributed to the regulation of PA biosynthesis and catabolism. Under unfavorable conditions, the overaccumulation of PA needs to be balanced by increased levels of PAO proteins. PAO can catalyze the oxidative decomposition of PAs, producing H_2O_2 [16, 18]. This H_2O_2 can then trigger downstream signaling molecules in response to stress [19]. For example, in a study on barley (*Hordeum vulgare* L.) seedlings treated with spermidine and subjected to a water deficit, an increase in polyamine content and improved antioxidant enzyme activities were observed, allowing for a more effective response to drought stress [20]. In maize, overexpression of *ZmPAO6* has been shown to enhance heat tolerance by regulating polyamine catabolism in transgenic *A. thaliana*, suggesting a potential role for *ZmPAO6* in improving heat tolerance [21]. Additionally, abscisic acid has been found to modulate PAs metabolism in response to environmental stress [22]. A study on tea tree plants showed that exogenous ABA treatment resulted in changes in the expression of *CsPAO* genes, with all but one responding to stress in the roots [23]. This is an important indicator of a plant's stress tolerance [24].

Potato (*S. tuberosum* L.) tuber is one of the most important food crops for human consumption around the world, second only to rice and wheat [25]. Although relevant studies have shown that *PAO* genes exhibit corresponding responses to biological and abiotic stresses, the potato *StPAO* gene family has hitherto lacked in-depth research. Therefore, this study aims to analyze and identify 14 different *StPAO* genes in the potato *PAO* gene family and adopt bioinformatics analysis methods to investigate their physicochemical properties, phylogenetic relationships, gene structure, chromosomal location, conserved motifs, *cis*-acting elements, protein interaction networks, synteny analysis, gene expression, and qRT-PCR analysis. It provides a research basis for further elucidating the functions of the potato *PAO* gene family and new insights into revealing potential candidate genes associated with potato stress response.

Methods

Plant materials preparation organ

The experimental material was the potato variety Desiree, provided by the College of Agriculture at Northwest A&F University. The experiment was conducted in the State Key Laboratory of Crop Stress Biology in Dry Areas of Northwest University of Agriculture and Forestry Science and Technology (34°14′ -34°20′ N, 107°59′ -108°08′ E). Potato seedlings were cultured using plant tissue culture, using Murashige and Skoog (MS) liquid medium with a pH of 5.9, containing 2% sucrose and 0.05% MES (2-Morpholinoethanesulfonic acid). The study period is from November to December 2023. Place the liquid medium containing potato plantlets in a culture box with 22 °C, 16 h of light (10,000 Lx), 8 h of darkness, 70% relative humidity, and a three-week incubation period, and then perform the following treatments: Place the plantlets in a high-temperature environment of 38 °C for 6 h, transfer them to a nutrient solution containing 20% polyethylene glycol (PEG4000) for 24 h, soak the plantlets in a nutrient solution containing 200 mM NaCl for 24 h, and soak the plantlets in a 2% MS nutrient solution, then add 100 μM abscisic acid (ABA) for 3 h, and set up a control group. Finally, RNA was extracted from the roots of potato plants in the control and treatment groups. Three biological replicates were set up for each treatment to improve the accuracy of the experimental results [26].

Identification of the PAO gene family in desiree potato

The protein sequences of the *PAO* gene family identified in the *Arabidopsis* genome database (https://www.Arabidopsis.org/index.jsp (accessed on 29 September 2023)) were used as query sequences to search the potato genome database(http://solanaceae.plantbiology.msu.edu/blast.shtml (accessed on 29 September 2023)) through local Blastp to obtain the sequence information of the potato homologous *StPAO* gene family members (Table A1). The *PAO* gene family domain (PF01593) model file was downloaded from the Pfam database (http://pfam.xfam.org/ (accessed on 30 September 2023)), and potato protein sequences containing PAO domains were screened using SPDE2.0 and HAMMER3.0 software. Finally, the candidate protein was submitted to the SMART website (http://smart.embl-heidelberg.de/

(accessed on September 30, 2023)). The *amino-oxidase* domain was selected as the identification standard. To determine the correctness of the results. Using an exPAsy website (https://web.exPAsy.org/protparam/ (accessed on 7 October 2023)) and combined with the potato genome database information of all PAOs in the potato protein sequence forecast and analysis on the physical and chemical properties [27].

Multiple sequence alignment and phylogenetic tree construction

Utilizing the Jalview software, the potato and *A. thaliana* PAO protein sequences were subjected to multiple sequence alignments in order to determine their structural domains and conservative residues. The ClustalW algorithm was applied to compare the potato PAO family with *A. thaliana*, *Z. mays*, *O. sativa*, and *S. lycopersicum*; the MEGA11.0 software was utilized for the construction of the phylogenetic tree; the Neighbor-Joining method (NJ) was adopted; and the Poisson model was selected. This analysis involved 1000 bootstrap tests [28].

Chromosomal location analysis and gene structure

Download potato gene location information from the gff3 file of the potato genome database (http://solanaceae.plantbiology.msu.edu/ (accessed on 29 September 2023)). Potato *PAO* genes of chromosome distribution through TBtools software analysis and mapping [29]. Download the potato *PAO* gene exon and intron distribution storage file from the potato genome database website, and use TBtools software to draw a gene structure diagram.

Cis-acting elements analysis and conserved motif identification

MEME website (http://meme-suite.org/ (accessed on 16 October 2023)) was used to analyze the conserved motifs of potato PAO protein [30], and SPDE2.0 software was used to map the motifs. To study *cis*-acting elements in the promoter region of the potato PAO, we used TBtools to extract the 2000 bp sequence of the 5 'end of the *StPAO* gene. And submit it to the PlantCARE website (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/ (accessed on 19 October 2023)) to find the *cis*-acting elements on the promoter. Finally, the filtered results were classified and statistically analyzed, and the distribution map of *cis*-acting elements in the promoter region was drawn using SPDE2.0 software.

Analysis of PAO protein interaction in potato

We uploaded the fourteen PAO proteins of potatoes to the STRING website (https://cn.string-db.org/ (accessed on 28 October 2023)), selected *A. thaliana* as the model plant, and determined the fourteen protein sequences corresponding to proteins in *A. thaliana* to construct the protein interaction network. The results were calculated by Microsoft Excel and plotted by Cytoscape 3.10.0 software.

Interspecific collinearity analysis and gene ontology annotation of the PAO gene in potato

Downloaded from the potato and *A. thaliana* genome databases of two kinds of plant DNA and a gff3 file using TBtools software, rendering the potato and *A. thaliana PAO* gene collinearity map. The Gene Ontology (GO) analysis of the potato PAO protein was performed using the David website [44] (https://david.ncifcrf.gov/ (accessed on 31 October 2023)).

Organ expression and stress treatment expression analysis of the potato PAO genes

We downloaded the fragments per kilobase million (FPKM) values of potato *PAO* gene family fragments from the PGSC database (http://solanaceae.plantbiology.msu.edu/dm_v6_1_download.shtml/ (accessed on 7 October 2023)), deleted genes with FPKM values less than one, calculated Log2 values, and drew a heatmap [31].

RNA isolation and qRT-PCR analysis

Total RNA was extracted from potatoes using the rnassimple Total RNA Extraction reagent (TIANGEN, Beijing, China, DP419) according to the manufacturer's instructions, followed by the PerfectStart Uni RT&qPCR kit ((TRAN, Beijing, China, China,)). AUQ-01-V2) for reverse transcription. Specific potato *PAO* gene primers for quantitative real-time PCR (qRT-PCR) were designed using Primer Premier 6 software and National Center for Biotechnology Information (NCBI). The results were standardized using the *ef1α* gene (Table A4), setting up three repeats of the technique. Using the SuperReal PreMix Color (SYBR Green) reagent, the Q7 real-time PCR system performed the qRT-PCR process under the following thermal cycling conditions: initial activation at 95 °C for 15 min, followed by 40 cycles at 95 °C for 10 s, 56 °C for 20 s, and 72 °C for 20 s. Relative expression was calculated using the comparative $2^{-\Delta\Delta CT}$ method [32].

Results

Identification of members of PAO gene family in potato

The protein sequences of the *Arabidopsis PAO* gene family were searched by Blastp in the potato genome database, and 14 potato protein sequences were selected. At the same time, we used SPDE2.0 software and the *PAO* gene domain (PF01593) to screen and obtain 59 candidate genes of potato PAO. Combined with the results of the two screening methods, 14 *PAO* genes were finally identified in the potato genome according to the identification standard a*mino-oxidase* domain (Table 1). To

Table 1 The PAO genes in potatoes (*S. Tuberosum* L.) and the properties of the deduced proteins

Gene[1]	Gene ID[1]	Chromosome Location (bp)[1]	ORF Length (bp)[1]	No. of Exons[1]	Protein[2]			Instability index	GRAVY
					Length (aa)	MW (kDa)	pI		
StPAO1	Soltu.DM.01G027080.1	chr01:66817448.66824124 (-)	1488	10	495	55.79	5.27	39.16	-0.30
StPAO2	Soltu.DM.03G002990.1	chr03:2850583.2856310 (-)	1437	10	478	52.88	5.59	34.21	-0.09
StPAO3	Soltu.DM.12G023960.1	chr12:53808228.53814160 (-)	1467	10	488	53.90	5.32	34.26	-0.10
StPAO4	Soltu.DM.07G014310.1	chr07:43813155.43819483 (+)	1536	12	511	57.05	5.71	36.23	-0.15
StPAO5	Soltu.DM.02G020890.1	chr02:35011968.35017045 (-)	1488	10	495	54.66	5.74	35.56	-0.14
StPAO6	Soltu.DM.10G012870.1	chr10:37224196.37227129 (-)	2439	1	812	89.11	5.8	48.36	-0.16
StPAO7	Soltu.DM.07G024810.1	chr07:54598857.54601482 (+)	2280	2	759	83.92	8.13	45.17	-0.21
StPAO8	Soltu.DM.04G036220.1	chr04:67442350.67454873 (-)	6240	8	2079	227.50	5.47	45.52	-0.43
StPAO9	Soltu.DM.05G026290.1	chr05:54432969.54435054 (-)	1479	2	492	53.78	6.28	26.97	0.02
StPAO10	Soltu.DM.11G004390.1	chr11:4408787.4414867 (+)	2991	6	966	108.16	6.97	41.21	-0.24
StPAO11	Soltu.DM.05G013880.1	chr05:21192310.21194290 (-)	1563	1	520	57.75	5.58	38.43	-0.23
StPAO12	Soltu.DM.07G011640.1	chr07:37238642.37240410 (+)	1563	1	520	57.95	5.08	41.01	-0.21
StPAO13	Soltu.DM.03G016020.1	chr03:39956106.39957921 (+)	1623	1	540	60.09	5.31	35.11	-0.21
StPAO14	Soltu.DM.12G025820.1	chr12:55807961.55810060 (+)	2100	1	699	77.69	4.53	35.5	-0.54

1 Gene information was retrieved from the S. tuberosum v6.1 genome annotation (http://solanaceae.plantbiology.msu.edu/dm_v6_1_download.shtml(accessed on 7 October 2023))

2 Protein profile information from the exPASy–ProtParam tool (https://web.exPAsy.org/protparam/(accessed on 7 October 2023))

verify the correctness of the results, we used the SMART website and the NCBI CDD (https://www.ncbi.nlm.nih.gov/Structure/cdd/cdd.shtml) website to further confirm the gene domains.

Table 1 presents the results of *PAO* gene and protein sequence studies in potatoes: gene name, gene ID, chromosome location, open reading frame (ORF) length, exon number, protein length, molecular weight (kDa), pI value (isoelectric point), subcellular localization prediction, instability coefficient, and average hydrophilic coefficient of 14 *PAO* genes. The ORF size of the *StPAO* protein ranges from 1437 bp to 6240 bp. The length of the protein is 478–2079 amino acids, the molecular weight is 52.88–227.50 kDa, and the predicted pI value is 4.53–8.13, of which only *StPAO7* is a basic protein (pI>7), and the other 13 are acidic proteins (pI<7). The instability coefficient ranged from 26.97 to 48.36, among which *StPAO6*, *StPAO7*, *StPAO8*, *StPAO10*, and *StPAO12* were unstable proteins (instability coefficient>40). The *StPAO9* protein is a hydrophobic protein, and other proteins are hydrophilic (mean hydrophilic coefficient<0).

Phylogenetic analysis of PAO gene family in potato

According to the results of protein sequence comparison between the potato *PAO* gene family and the *Arabidopsis PAO* gene family (Fig. 1), the gene sequences of the two are highly identical, and the blue from light to dark indicates 60%, 80%, and 100% sequence identity, respectively. The peroxisome targeting signal (PTS1) is a C-terminal tripeptide composed of a common sequence (S/A/C)(K/R/H)(L/M) [33]. The SRM sequences of *StPAO2*, *StPAO3*, and *StPAO5* at the C-terminal of the potato protein sequence were consistent with those of *AtPAO2* SRL, *AtPAO3*, and *AtPAO4* in *A. thaliana*, indicating that they may all target the peroxisome. The positions in human MAO-A and MAO-B involved in covalent binding to the isoxazole ring of FAD through cysteine residues are represented by the symbol # [34].

To identify the evolutionary relationships between potato PAO proteins, sequences of PAO proteins from several different species, including: *A. thaliana*, *Z. mays*, *O. sativa*, and *S. lycopersicum*, were collected (Table A1). The NJ tree was constructed using the MEGA 11.0 software, and phylogenetic analysis was performed. As shown in Fig. 2, the evolutionary tree was modified using the online tool iTOL (https://itol.embl.de/itol.cgi).

Chromosomal location and gene structure of potato PAO gene family

The results showed that the 14 potato *PAO* genes were scattered on chromosomes 1, 2, 3, 4, 5, 7, 10, 11, and 12, with one *PAO* gene on chromosomes 1, 2, 4, 10, and 11, and two *PAO* genes on chromosomes 3, 5, and 12. There are three *PAO* genes on chromosome 7 (Fig. 3a). In addition, *StPAO4*, *StPAO6*, and *StPAO11* are located in chromosome regions with high gene density. *StPAO2*, *StPAO7*, *StPAO8*, *StPAO9*, *StPAO10*, and *StPAO14* are located near the ends of chromosomes, suggesting that these genes may be involved in the maintenance of cell activity and chromosome stability.

The analysis of the *PAO* gene structure indicates that (Fig. 3b), *StPAO1*, *StPAO2*, *StPAO3*, and *StPAO5* all contain ten exons, while *StPAO6*, *StPAO11*, *StPAO12*, *StPAO13*, and *StPAO14* each contain one exon, and *StPAO10*, *StPAO8*, and *StPAO4* contain six, eight and twelve exons, respectively. Most introns in the *PAO* gene

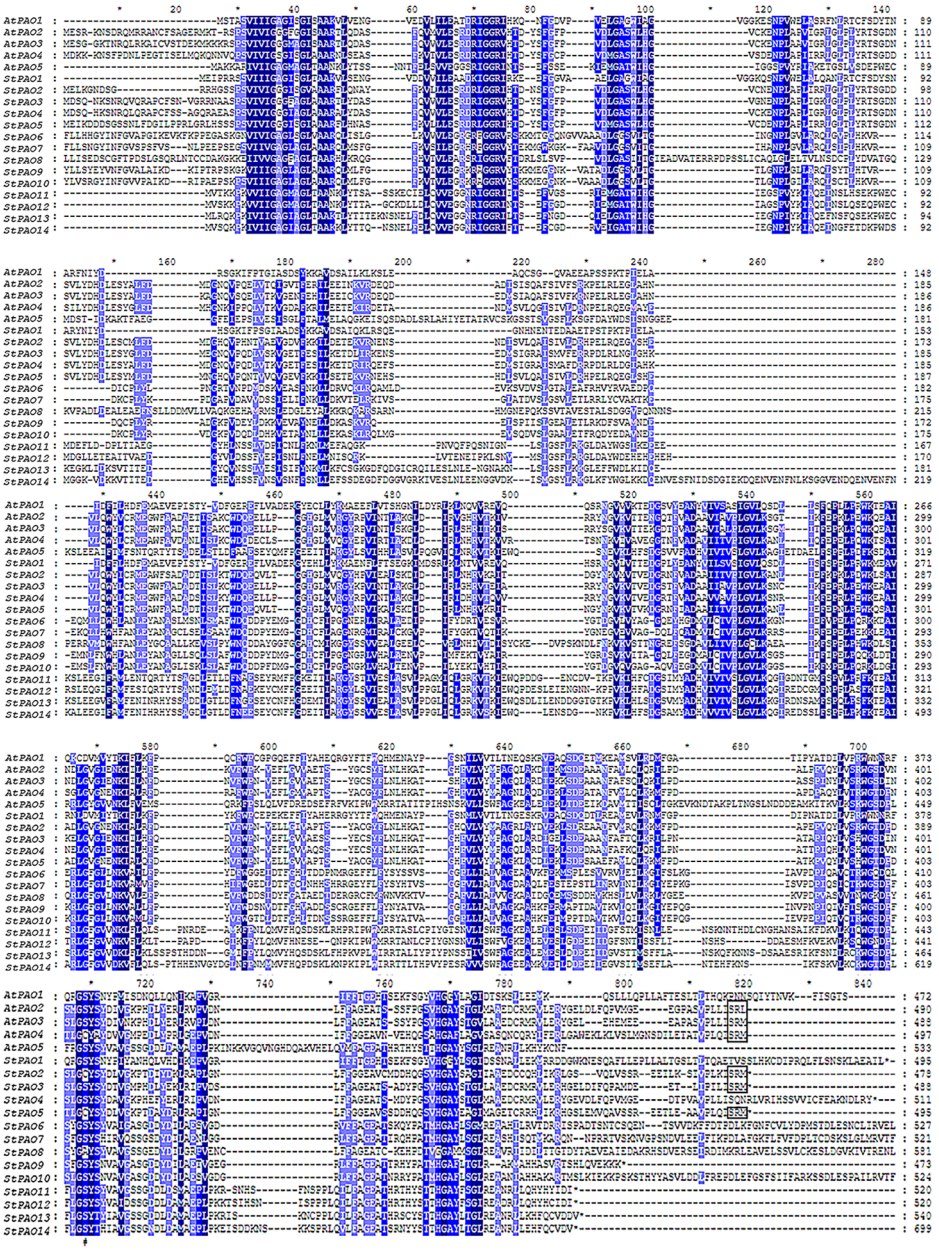

Fig. 1 Multiple sequence comparison of potato PAO protein and *Arabidopsis* PAO protein. Using MAFFT with default values for alignment, the conserved domain of the sequence is marked in blue, the darker the region, the more conserved. The numbering of amino acid residues is shown on the right. with black boxes indicating the peroxisome targeting signals in potato and *A. thaliana*

family have nine introns. As a result, the structural differences between members of the *StPAO* gene family are not significant, suggesting that only a few members have diverged.

Conserved motif identification

In order to further explore the conservation of the potato PAO protein sequence and the differences in potato protein motif composition, and explore the potential regulatory mechanism of the *StPAO* gene in response to abiotic stress in potatoes, we utilized MEME technology to analyze the conserved motifs of the potato PAO protein sequence and finally identified 26 conserved motifs (Fig. 4a, Table 2). The motif analysis results showed that the gene structures of the potato PAO family were not completely consistent, but all contained the *amino-oxidase* domain (Fig. 4a). *StPAO2* and *StPAO5* contain 13 identical conserved motifs, *StPAO3* and *StPAO4* contain 14 identical conserved motifs, and *StPAO6*, *StPAO7*, and *StPAO10* contain 16 identical conserved motifs. *StPAO11*, *StPAO12*, *StPAO13*, and *StPAO14* contain 16 identical conserved motifs. All *StPAO* genes

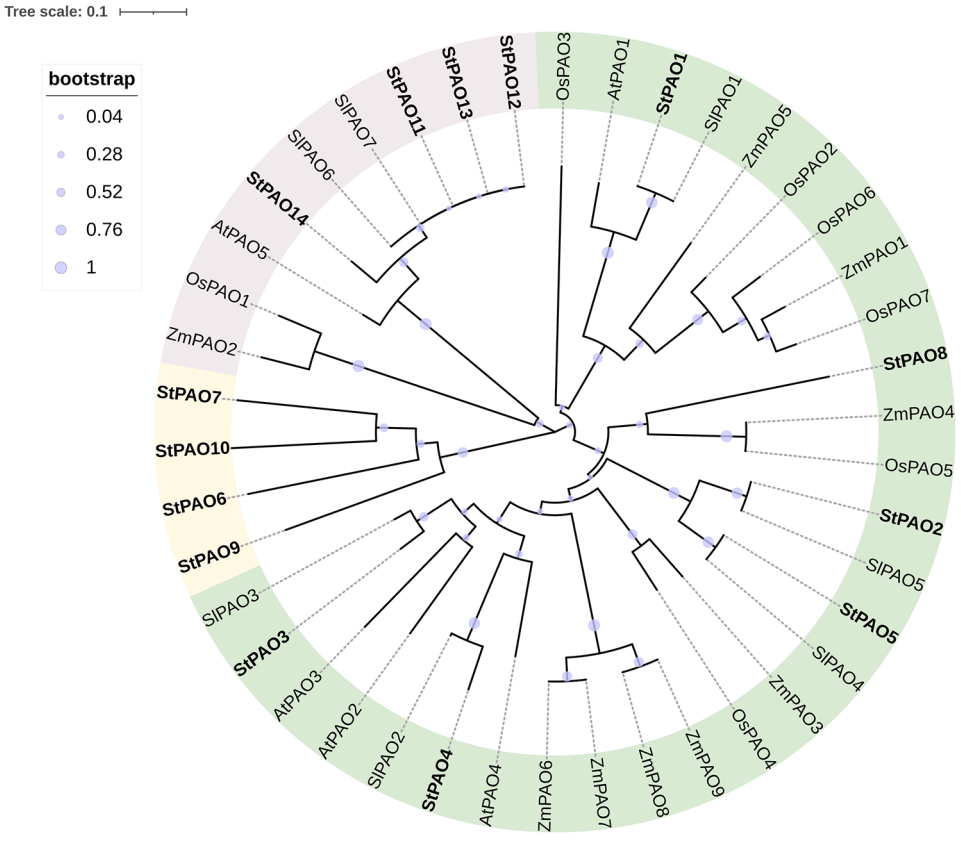

Fig. 2 Phylogenetic analysis of plant PAO proteins. Conserved PAO proteins from *S. tuberosum*, *A. thaliana*, *Z. mays*, *O. sativa*, *and S. lycopersicum* were aligned using the ClustalW function of MEGA11. The phylogenetic tree (1000 replicates) was constructed by NJ method and bootstrapping analysis

contain motif1, motif2, and motif6, and their distribution sequence is the same, from the 5 'end to the 3' end, motif6→motif2→motif1, respectively (Fig. 4b).

Cis-acting elements analysis

The response of the *StPAO* gene to abiotic stress was further studied by using the analysis of *cis*-acting elements. The 2000 bp sequence upstream of the translation start site of each gene was analyzed. According to the function of *cis*-acting elements, we screened sixteen *cis*-acting elements related to plant growth and development, hormone response, and environmental stress response (Fig. 5). According to the analysis results, *StPAO2*, *StPAO7*, and *StPAO12* contain the most *cis*-acting elements, while *StPAO3* and *StPAO4* contain at least two *cis*-acting elements. The stress response components include a low-temperature response (LTR), drought response (MBS), light response (G-box, G-Box, I-box), anaerobic induction (ARE), and stress defense response (TC-rich repeats). Hormone response elements include abscisic acid (ABRE), methyl jasmonate (CGTCA-motif), gibberellin (TATC-box, P-box), ethylene (ERE), auxin (TGA-element), and salicylic acid (TCA-element). Growth and development response elements are meristem expression regulation (CAT-box) and cirCADian regulation (cirCADian), respectively. The most significant number of active elements in the *StPAO* gene is ABRE with forty-one and light response (G-box, G-Box, I-box) with fifty, indicating that these genes may be participating in the plant's light response and responding to hormones such as abscisic acid. Meristem expression regulation (CAT-box) responds only in the *StPAO1* gene. The analysis of *cis*-acting elements revealed that the *StPAO* gene is closely related to abiotic stress, growth and development, and hormones in plants.

Potato PAO protein interaction analysis

A. thaliana was used as the species model to predict the *PAO* gene regulatory network and protein-protein interaction network in potatoes using the STRING protein database. The results (Fig. 6) showed that MHK10.21, F27M3.9, T4C9.130, and F23N1450 were most significantly associated with PAO proteins, all of which were amine-oxidases. Amine-oxidase is a major enzyme in biological amine metabolism and is considered a biological regulator, especially for cell growth and differentiation [35]. SPDSYN1, SPDSYN2, and SPMS belong to the spermine synthetase family. Spermine is a type of polyamine that exists widely in various organisms [36], and PAO is an enzyme involved in the oxidative degradation

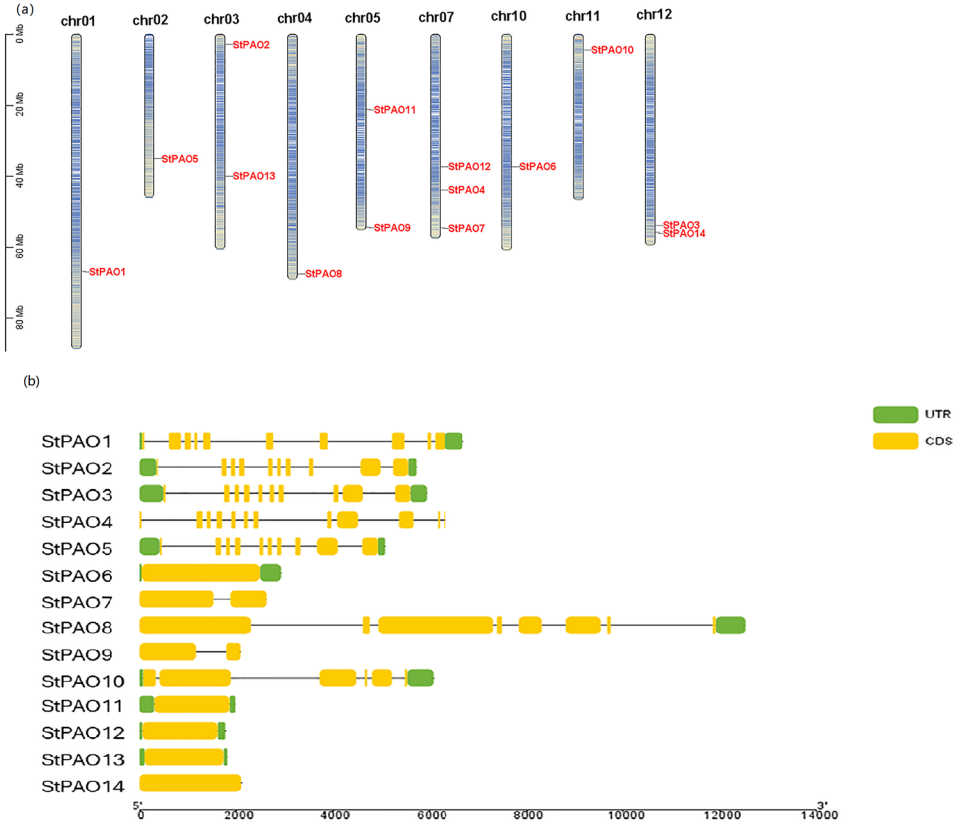

Fig. 3 (**a**)Chromosomal distribution of the potato *PAO* genes. Blue lines on chromosomes indicate gene density. (**b**) Gene structure of *PAO* genes in potato. The yellow bar indicates the coding sequence (CDS), the line indicates the intron, and the green bar indicates the untranslated region (UTRs)

of polyamines. LDL1, LDL2, and LDL3 are homologs of lysine-specific histone demethylase (LSD), which contain Swi3p, Rsc8p, Moira (Swirm), and amine-oxidase (AO) structures [37], and play a partially redundant role with flowering regulatory genes (FLD). Polyamines are metabolized by copper-containing amine oxidase (CuAO) and FAD-dependent PAO [38] (See Fig 7).

Collinear analysis of PAO gene in potato and A. Thaliana

The results of gene collinearity analysis showed that the *PAO* gene of potato and *Arabidopsis* have some homologous evolutionary relationship, and may have similar functions and play an important role in potato and *Arabidopsis*. In the results of collinear analysis, AT3G10390.3, a paralogous homolog of the *Arabidopsis PAO* gene family, was found. It is a plant homolog encoding mammalian histone deacetylase complex containing the SWIRM domain, which plays a key role in regulating the reproductive ability of *Arabidopsis* buds and leading to different developmental stage transitions [39]. Among them, three pairs of homologous genes were collinear: *AtPAO4* and *StPAO5*, AT3G10390.3 and *StPAO10*, and *AtPAO5* and *StPAO10*. In addition, there is no collinearity between *StPAO1*, *StPAO2*, *StPAO3*, *StPAO4*, *StPAO6*, *StPAO7*, *StPAO8*, *StPAO9*, *StPAO11*, *StPAO12* and *StPAO13* genes. These genes may be specific to potato evolution.

Organ expression and stress treatment expression analysis of the potato PAO genes

To study the expression of the *StPAO* gene in potato growth, development, and stress response, the RNA-seq data of the *StPAO* gene in different organs and under various stresses were searched on the potato genome database website and TBtools was used to make a heat map. The expression of the *StPAO* gene in sepals, leaves, roots, shoots, callus, stolons, tubers, flowers, petioles, petals, stamens, and carpel organs were counted (Fig. 8, Table A2). And the expression of genes in salt, heat, mannitol, ABA, IAA, GA3, BAP, BABA, BTH, and *Phytophthora infestans* (Fig. 9, Table A3).

The results of *PAO* gene expression in potato organs showed that *StPAO3*, *StPAO4*, and *StPAO5* were highly expressed in all the tested organs, and the expression of *StPAO4* reached its peak in carpels, followed by the significant expression in stamens. *StPAO3* has the highest expression in flowers and *StPAO5* has the highest expression in petals, these three genes may play a key regulatory role in potato growth and development. In contrast, *StPAO9* and *StPAO14* were not expressed in all tested

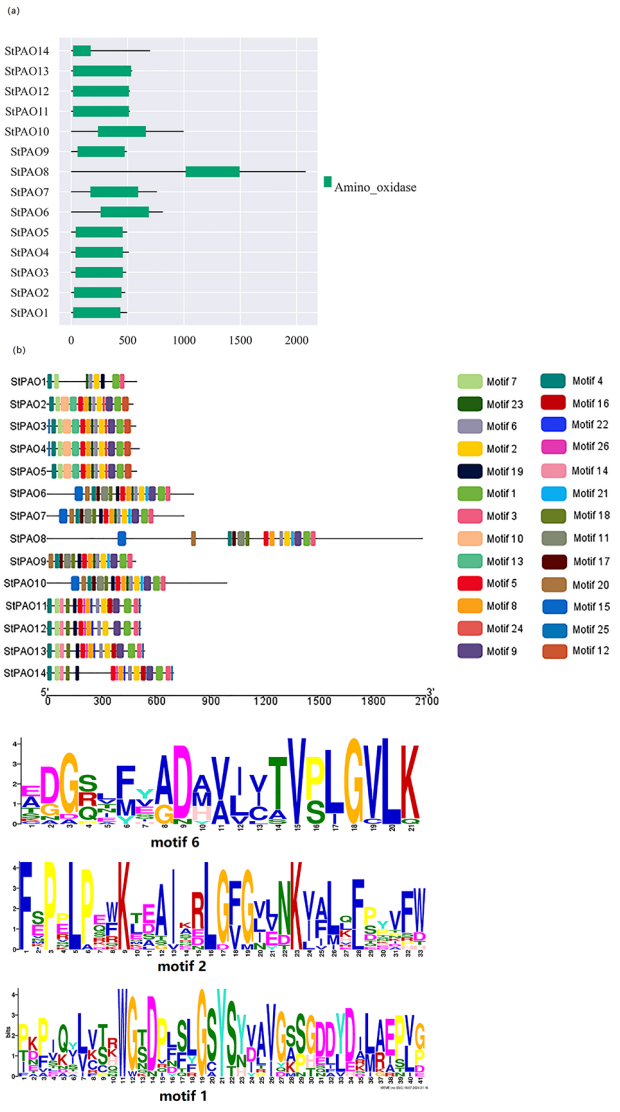

Fig. 4 (**a**)The conserved motif of the potato PAO proteins. Different colors indicate different motifs. **b** shared motif structure of *StPAO*

organs, and the expression levels of *StPAO11*, *StPAO12*, and *StPAO13* were extremely low, indicating that these genes did not play a significant role in potato growth and development. In addition, the expression results of the potato *PAO* gene under different stress treatments showed that except *StPAO2*, *StPAO11*, *StPAO12*, *StPAO13*, and *StPAO14*, other genes were up-regulated, and *StPAO9* had no obvious response to stress. Other genes respond to ABA, IAA, GA3, BAP, BABA, and *P. infestans*.

Expression analysis of StPAO genes in different treatments

Based on the above analysis, to further study the response of the potato *PAO* gene to various abiotic stresses, potato materials were treated with high temperature, drought, and abscisic acid. The expression level of the *StPAO* gene was quantitatively analyzed by qRT-PCR (Fig. 10). It was found that the potato *PAO* gene family responded to all three types of stress treatments, and there was a significant difference in the expression of different genes.

Figure 10 (a) displays the relative expression levels of 14 potato *PAO* genes at a high temperature of 38 °C, compared to untreated plants, roughly consistent with the expression levels indicated by RNA-seq data. With the exception of non-significant and significant down-regulation of *StPAO1* and *StPAO11-14* respectively, and no notable response from *StPAO9* to stress, the remaining genes were significantly up-regulated. *StPAO6* and *StPAO10* were significantly up-regulated, up 31.27 times and 8.65 times, respectively, while *StPAO11* and *StPAO12* were most significantly down-regulated, down 0.65 times and 0.57 times, respectively.

Figure 10 (b) illustrates the relative expression levels of fourteen genes under drought conditions compared to untreated plants, which generally align with the expression levels from RNA-seq data. Except for the down-regulation of *StPAO8-12* and a non-significant up-regulation of *StPAO14* by 1.25-fold, all other genes were up-regulated. The most significantly up-regulated gene was

Table 2 List of the conserved motifs of the *StPAO* proteins

Motif	Length	Amino Acid Sequence
Motif1	41	PKPIQVLVTRWGSDPLSLGSYSYVAVGSSGDDY-DILAEPVG
Motif2	33	FSPELPEWKTEAIKRLGFGVLNKVALKFPYVFW
Motif3	28	RLFFAGEATHRQYPATTHGAYLSGLREA
Motif4	25	SKPSVIIIGAGJAGLAAARQLYTAG
Motif5	29	VLNWHLANLEYAFAALLDNISLKYWDQDD
Motif6	21	ADGSLFYADAVJVTVPLGVLK
Motif7	27	BRIGGRIHTDEFFGDPVELGASWJHGV
Motif8	29	FPGDHCLIAGGYSPVIEALAKVLPIRLIH
Motif9	41	FLNYPKVTGSPVLVALVAGKAALDFEKLSDEEAIDGVLTIL
Motif10	50	CNENPLAPLIGRLGLPLYRTSGDNSVLYDHDLESYMLFD-MDGNQVPQDLV
Motif11	41	KVAAADLGGSVLTGTLGNPLGVLARQLSIPLHKVRDKCPLY
Motif12	38	FGGGEVTSDDHPGSVHGAYSAGJMAAEDCRMRLJERHG
Motif13	41	VGEVFEKILKETDKIRNENSEDMSIGRAISIVFDRRPDLRQ
Motif14	24	EGNPIYKIAQEINSFQSEKPWECM
Motif15	48	FPVDSLTEEEIEAGVVSZIGGIEQANYIVVRNHILAKWREN-VSVWLTK
Motif16	29	MKFPNLQMVFHQSDSKLKHPKIPLWIRRT
Motif17	21	FKVTVLEGRKRPGGRVYTKKM
Motif18	22	EDGYPVBSSLDEKIENLFNKLL
Motif19	22	ISJGSFLRKGLKAYWDAKEDEE
Motif20	27	CENLVDSAYNFLLSHGYINFGVAPAIK
Motif21	18	DTFGHLTDDSSSRGEFFL
Motif22	11	LGRKVTKIEWQ
Motif23	15	RVKEIRYGYBGVKVT
Motif24	15	NVEFLGVVAPSSYEC
Motif25	11	NRLLQHYHCID
Motif26	11	TLDFNAESEYC

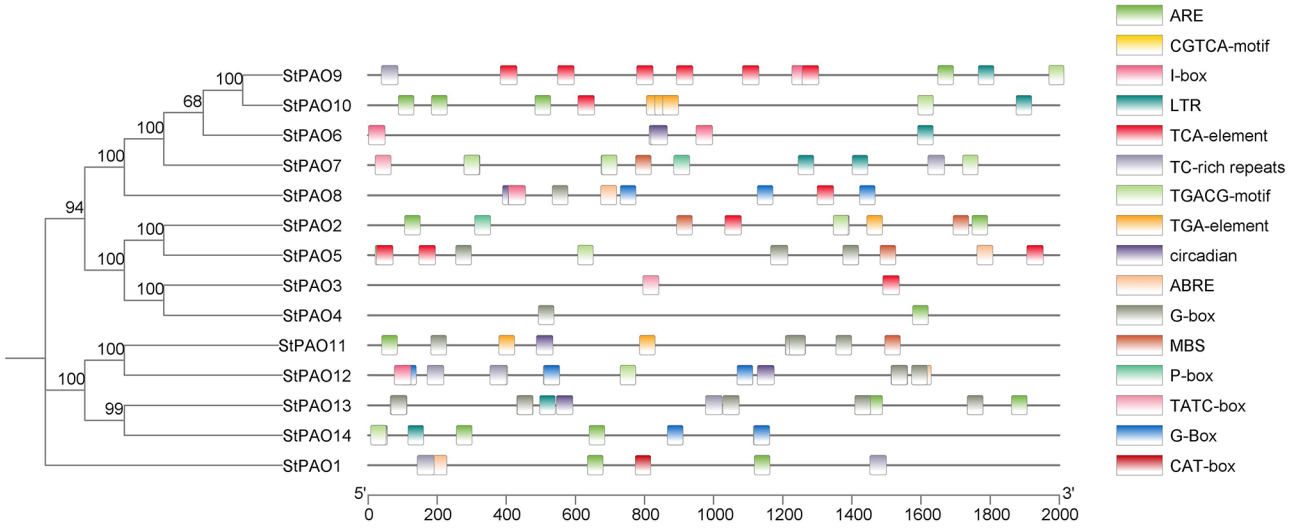

Fig. 5 The *cis*-acting element within the 2000 bp upstream sequence of the potato *StPAO* gene. This study used the database PlantCARE to predict the motif

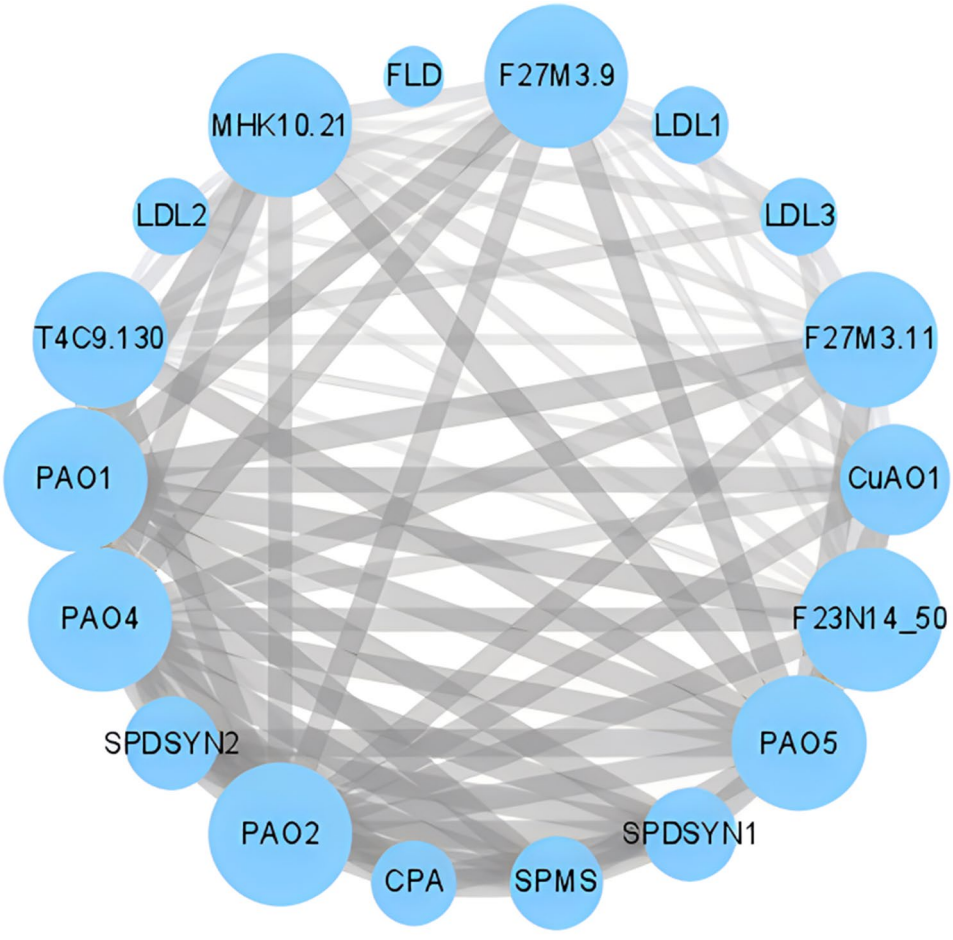

Fig. 6 Functional network prediction of *StPAO* interacting proteins. The size of the circle indicates how often the protein appears (the larger the area, the higher the frequency). The thickness of the line segment between proteins indicates the overall score of the degree of correlation between the two proteins (the thicker the line segment, the higher the correlation)

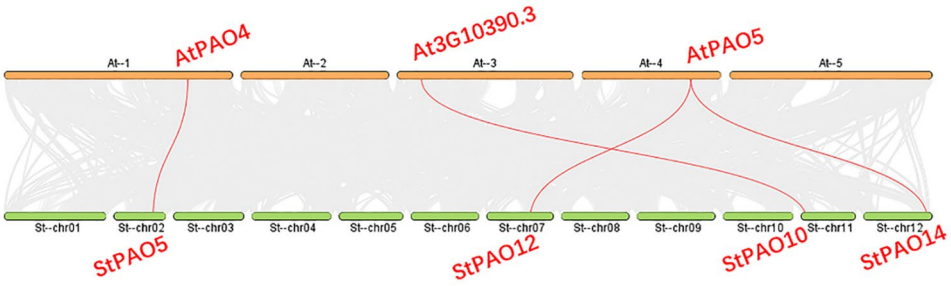

Fig. 7 Collinearity analysis of *PAO* genes in potato and *Arabidopsis*. Gray line: collinear region between potato and *Arabidopsis* genomes. Red line: represents homo-linear *PAO* gene pairs between potato and *Arabidopsis*

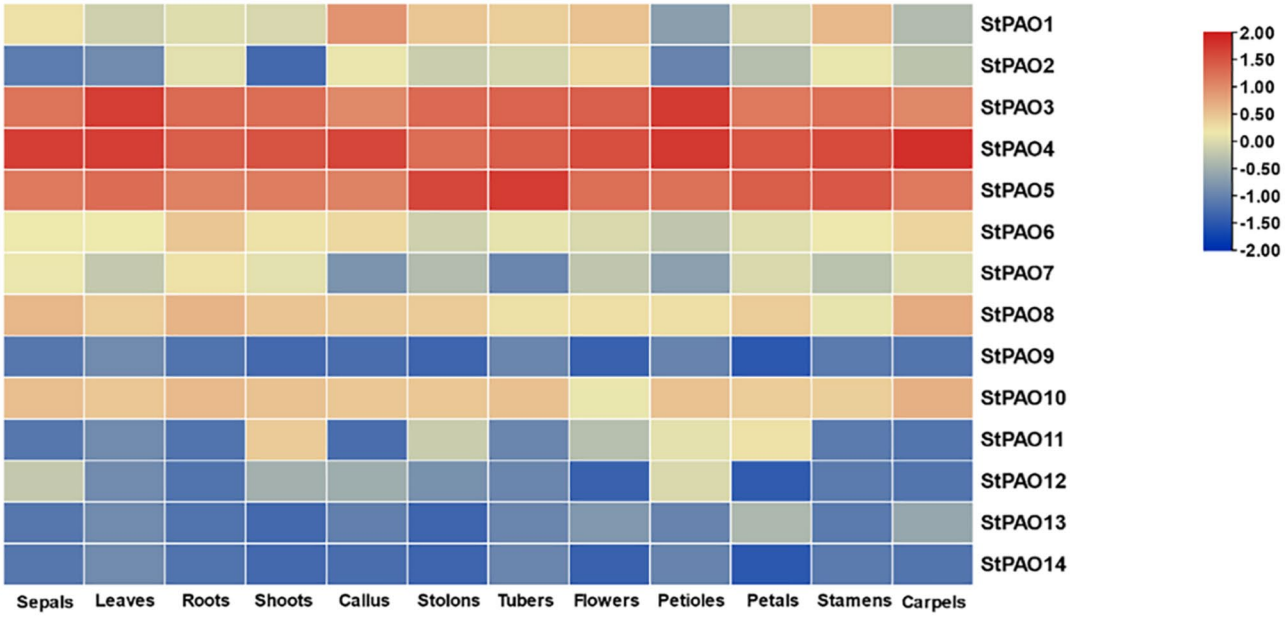

Fig. 8 The heatmap shows the expression of the *StPAO* gene in the organs or callus tissues including the sepals、leaves、roots、shoots、callus、stolons、tubers、flowers、petioles、 petals、stamens and carpels. Red indicates high relative gene expression, whereas blue indicates low relative gene expression

StPAO4, which increased by 8.26-fold. In contrast, the most significantly down-regulated gene was *StPAO11*, which decreased to 0.12-fold from its original level.

Figure 10 (c) presents the comparative expression levels of 14 genes in response to ABA treatment compared to untreated plants. *StPAO10* exhibited no significant alteration under ABA stress, while *StPAO4*, *StPAO5*, *StPAO7*, and *StPAO14* were up-regulated by factors of 1.50, 6.41, 2.83, and 2.97 respectively. Conversely, other genes displayed down-regulation with a decrease of approximately 0.27 for *StPAO2* and 0.33 for *StPAO11* respectively under ABA treatment conditions.

Discussion

The dynamic balance of PAs in plant bodies is well regulated by biosynthesis and catabolism, playing an important role in the normal growth and development of plants and their response to stress [40]. PAO is encoded by a small number of gene families [14]. So far, an increasing number of plant *PAO* genes have been analyzed and identified. For example, five genes encoding *PAO* in *Arabidopsis*, six *PAO* genes in *Kandelia obovata* [41], seven *PAO* genes in rice, seven *PAO* genes in tomato, six putative *PAO* genes in sweet orange, and six *PAO* genes in pepper (*Capsicum annuum L.*) have been identified. This indicates that the number of PAO family members varies among different plants.

In this study, 14 genes encoding *PAO* were screened and identified in potatoes. Phylogenetic analysis of PAO proteins in potatoes, dicotyledonous plants, and monocotyledonous plants showed that these 14 PAO proteins were evenly distributed in four subfamilies, which was consistent with the classification of lychee and sweet orange [14]. The majority of the potato PAO protein family is acidic and hydrophilic (Table 1), which is crucial for regulating cellular functions and serves as a marker

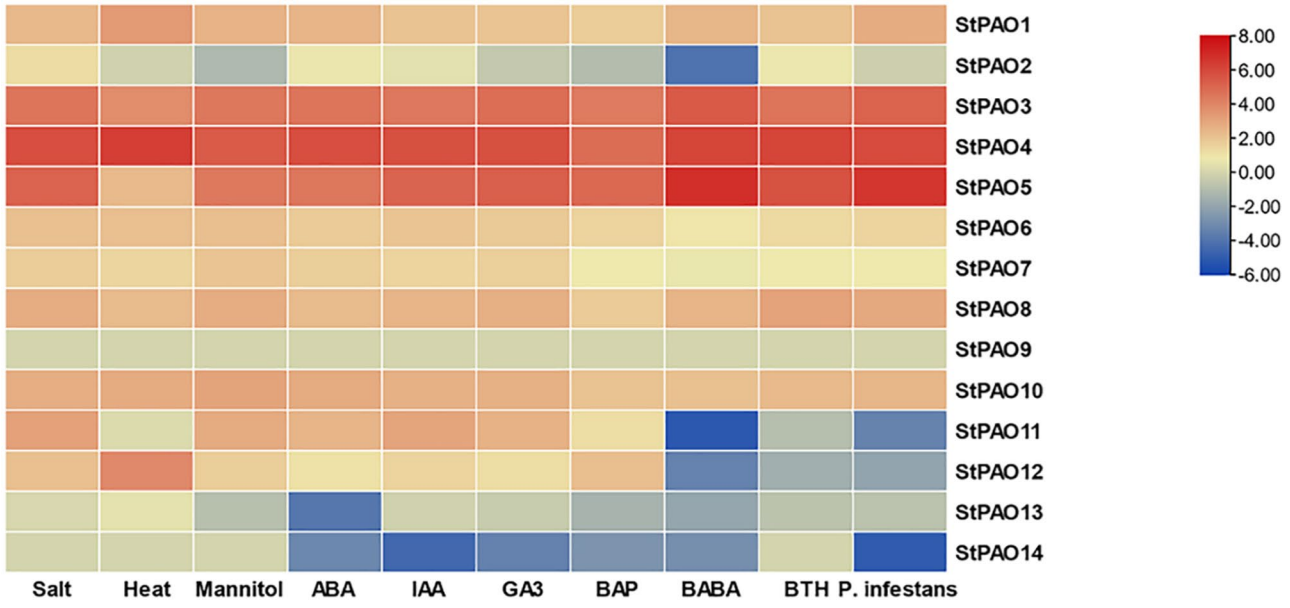

Fig. 9 Heatmap of the expression profile of the potato *PAO* genes under 10 different biotic or abiotic stresses. Biotic stresses included β-aminobutyric acid (BABA), benzothiadiazole (BTH), and *P. infestans*; abiotic stresses included heat, mannitol, and salt; other stress responses were mainly induced by the following four plant hormones: abscisic acid (ABA), 6-benzyl amino purine (BAP), gibberellic acid (GA3), and auxin (IAA). Red indicates gene upregulation, while blue indicates gene down-regulation

for diagnosing human diseases [42]. *StPAO2*, *StPAO3*, and *StPAO5* of the potato family contain putative peroxisome-targeting signals that are consistent with those found in *AtPAO2*-4 in *Arabidopsis* [9], *OsPAO4* in rice [10], *SlPAO2-5* in tomato [12], and *ZmPAO3*, *ZmPAO4*, *ZmPAO6*, and *ZmPAO9* in maize [21]. This suggests that potatoes may also be localized to the peroxisome [43]. The evolutionary analysis shows highly conserved homology between potatoes' PAO proteins and those of other plants, indicating similar functions. *StPAO1-5* and *StPAO8* consist of eight exons, similar to *Arabidopsis AtPAO2-4*, which all contain eight highly conserved introns belonging to the first subfamily. The analyses within the same subfamily exhibited similar patterns, indicating comparable functions. It is noteworthy that *Arabidopsis AtPAO5* lacks introns and consists of only one exon, while the *ZmPAO2* gene also lacks introns in its gene structure. Similarly, *SlPAO6* and *SlPAO7* in tomato are also intron-less genes [44], which aligns with the intron/exon organization of *StPAO11–14* (Fig. 4) in the potato family. This demonstrates the research value of the screened genes.

The potato *PAO* genes were located on nine chromosomes, unevenly distributed by chromosomal localization and conserved motif analysis. Unlike other crops, no tandem duplication genes were found. All 14 genes contained the *amino-oxidase* structural domain, consistent with the results of sequence analyses of the newly defined PAO subfamily [45]. *StPAO* core structural domains are highly conserved. RNA-seq data from the potato gene bank and qRT-PCR were further used to explore the expression of the *StPAO* gene in different parts of the plant and under different stresses. This coincided with the predicted function of the *cis*-acting element, containing *cis*-acting elements on the promoter region related to abiotic stress and hormone response, correlating with plant growth and development and gene expression under adverse conditions [46]. PAO can be expressed in various organs, but the expression of different genes is significantly different, and their levels also vary under different stresses. In this study, *StPAO3*, *StPAO4* and *StPAO5* are highly expressed in all organs, consistent with results in rice and tea trees [23]. Gene expression levels differ under high or low temperature conditions; wheat shows significant expression under both low and high temperature conditions [47]. Similarly, *MdPAO2* is upregulated when apples are subjected to low-temperature stress [48]. Tomato *SlPAO4* may play an important role during the flowering and fruit ripening stages; *SlPAO2-5* are expressed in response to both cold and heat [44]. Additionally, *SlPAOs* respond to abiotic stresses such as drought, injury, and salinity.

In this study, we observed that high temperatures resulted in up- or down-regulation of *StPAO* genes. Among them, *StPAO6* showed the most significant upregulation, by 31.27-fold, indicating its potential involvement in high temperature stress and the subsequent synthesis and accumulation of polyamines, leading to improved tolerance [49]. Drought stress has a substantial impact on plant growth and survival, resulting in reduced

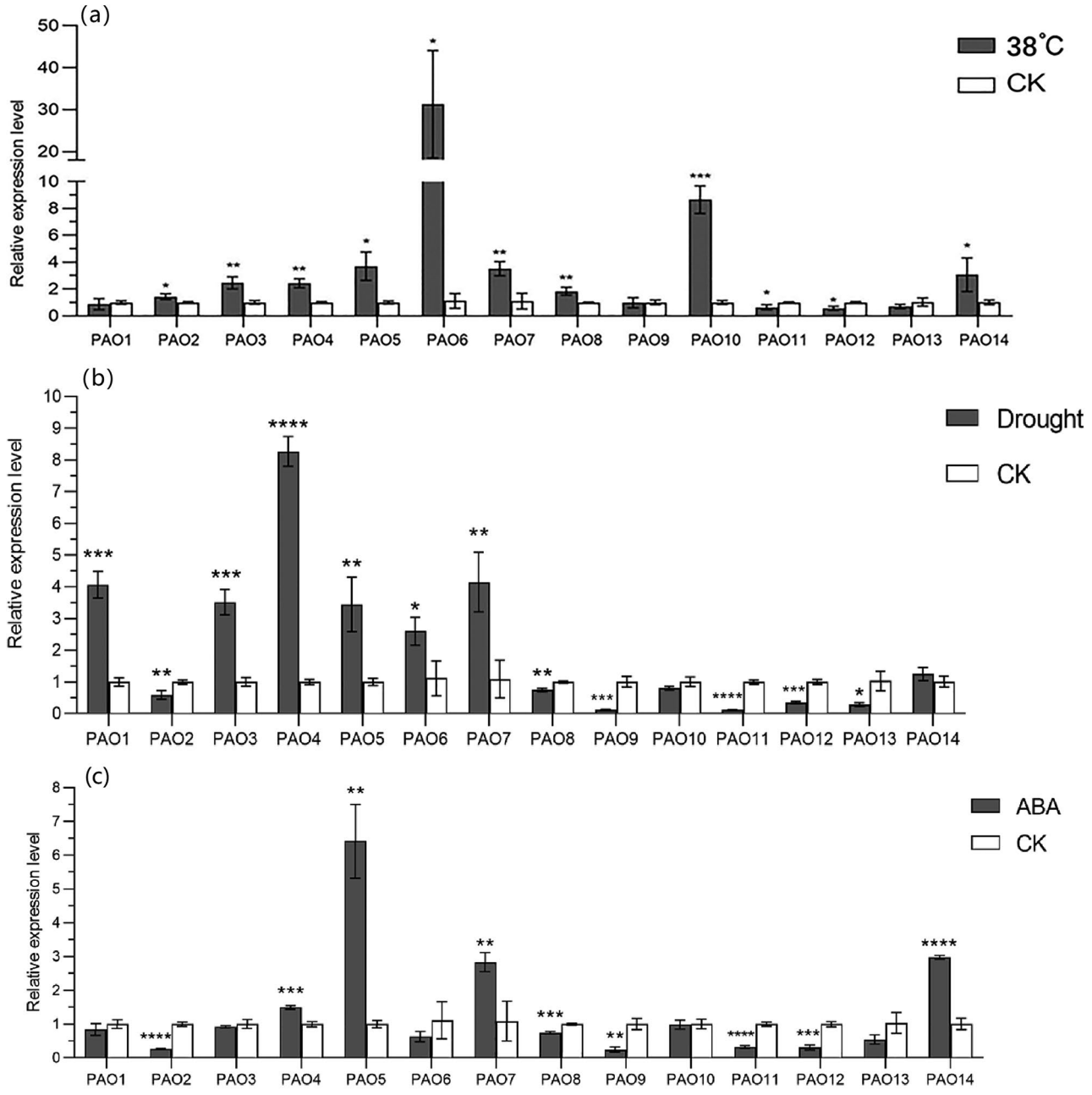

Fig. 10 Relative expression levels of the *PAO* gene family in response to abiotic stress and hormone induction. Figure (**a**) shows the relative expression level at 38 °C. Figure (**b**) shows the relative expression level under drought treatment. Figure (**c**) shows the relative expression level under ABA treatment. (p value of * t test < 0.05, p value of ** t test < 0.01, p value of *** t test < 0.001, p value of **** t test < 0.0001)

crop productivity [50]. In our investigation, potato plants were subjected to drought treatment to assess the expression of *PAO* genes under drought conditions. Our analysis revealed that the expression levels of *StPAO1* and *StPAO3*-7 were up-regulated under drought stress, suggesting their potential role in defending against adversity caused by drought in potatoes. However, prolonged exposure of tobacco plants to stressful conditions disrupts PA homeostasis [51], leading to a notable increase in PAO activity and H_2O_2 production, which induces intracellular PAs accumulation. This ultimately results in an excessive generation of reactive oxygen species (ROS) and plant death [52, 53]. Abscisic acid (ABA) acts as a signaling molecule in plant stress response [54], adapting to environmental stress by regulating the production of H_2O_2 [22], and plays a crucial role in the response of plants to abiotic stress. The analysis of the *PAO* gene family in tea trees showed that the roots and leaves of tea

trees had different tolerance to ABA stress, promoted the synthesis of PA, and activated the expression of the *CsPAO* gene [23]. Sweet orange *CsPAO4* is rapidly and significantly up-regulated by the ABA hormone. Our findings also indicated that after treatment with ABA, the expression levels of *StPAO4*, *StPAO5*, *StPAO7*, and *StPAO1*4 were significantly up-regulated. This suggests that ABA may act as a signal for regulating H_2O_2 production and initiating a stress response [55]. The experimental results confirmed that both abiotic stresses and phytohormones can regulate the expression of most *PAO* genes. Furthermore, differences were found in the responses of all *StPAO* genes to heat, drought, and ABA; all of these differences were favorable. However, further studies are required to investigate the response mechanism of the potato *StPAO* gene to stress and the variations in gene expression.

Conclusions

In this study, we identified 14 *StPAO* genes in potatoes for the first time. They were unevenly distributed on nine chromosomes, and all contained the same *amino-oxidase* domain. Phylogenetic tree analysis revealed a close relationship between the potato PAO protein sequence and the *Arabidopsis* PAO protein sequence. Additionally, peroxisome targeting signals were found in *StPAO2*, *StPAO3*, and *StPAO5* of the potato PAO family, indicating that the gene may be located in the peroxisome. *Cis*-acting element analysis showed that most *StPAOs* participated in the defense response to hormones and adverse environment. Further qRT-PCR analysis demonstrated that the expression of *StPAO* was either up-regulated or down-regulated under stress conditions such as high temperature, drought, and ABA. This confirms the important role of the potato in regulating high temperature, drought, and hormones, and further supports the idea that PAO is a multifunctional gene family that can respond to various stresses. The genome-wide identification of the *StPAO* gene family in potatoes provides a more comprehensive understanding of its diversity. This study serves as an important theoretical basis for further research on the regulatory mechanism of *StPAO* genes in potato growth and development, as well as their response to abiotic stress.

Abbreviations

Pas	Polyamines
PAO	Polyamine Oxidase
qRT-PCR	Quantitative real time polymerase chain reaction
ABA	Abscisic acid
PUT	Putrescine
CAD	Cadaverine
SPM	Spermine
FAD	Flavine adenosine dinucleotide
ETH	Ethephon
MS	Murashige and Skoog
MES	2-morpholine ethane sulfonic acid
MW	Molecular weight
PI	Theoretical isoelectric point

Supplementary Information

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Supplementary Material 1

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Author contributions

Conceptualization, X.M. and Y.C.; software, X.M. and S.W.; formal analysis, S.C., X.W. and Y.W.; resources, X.M. and S.W.; data curation, X.M. and S.W.; writing—original draft preparation, X.M.; writing—review and editing, Y.C. All authors have read and agreed to the published version of the manuscript.

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Data availability

All data generated or analysed during this study are included in this published article [and its supplementary information files。 Protein sequence datasets for the crops in this study are available in the NCBI database [https://ftp.ncbi.nlm.nih.gov/genomes/refseq/plant/].

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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