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Genome-wide identification and characterization of the UDP-glycosyltransferase gene family in passion fruit (*Passiflora edulis*)

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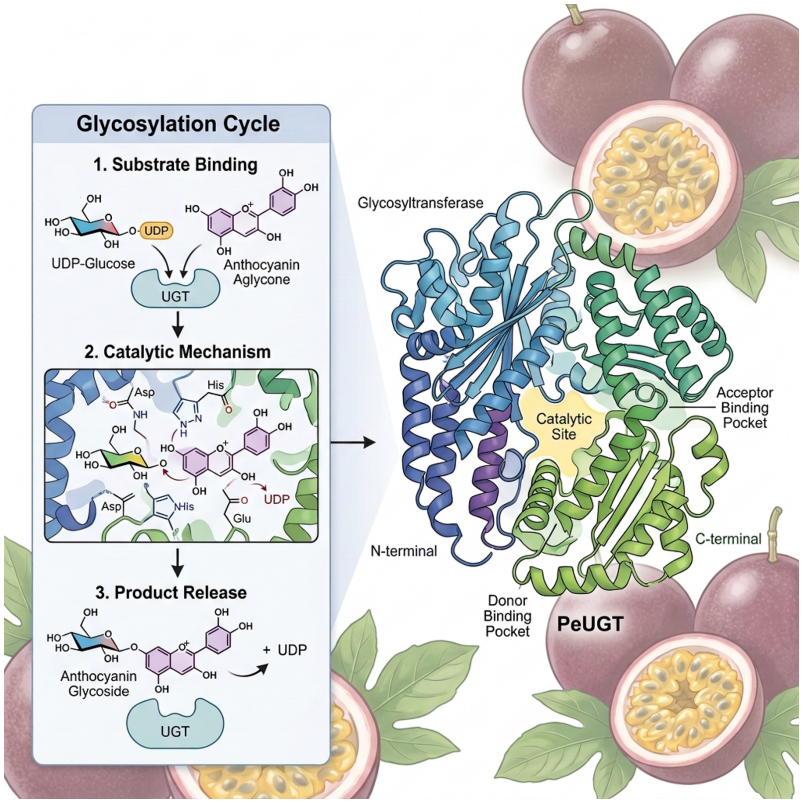
In Brief

A total of 149 *PeUGT* genes were identified in the passion fruit genome, and tandem and segmental duplications were the main driving forces for the expansion of this family. Functional analysis indicated that they were closely related to flavonoid biosynthesis, especially anthocyanin metabolism. During fruit development and maturation, three anthocyanin synthesis-related genes (*PeUGT10*, *PeUGT17*, and *PeUGT38*) showed specific expression trends, and the transcription factors that might regulate these genes were predicted.

Graphical abstract



Highlights

- A total of 149 *PeUGT* genes were identified for the first time in the passion fruit genome.
- *PeUGT* is closely related to hormone signal transduction and stress response, and is significantly enriched in the biosynthetic pathway of flavonoids (e.g., anthocyanin).
- During the four stages of fruit ripening, the *PeUGT* gene shows a dynamic expression pattern and plays a regulatory role.
- Three key anthocyanin-related genes (*PeUGT10*, *PeUGT17*, and *PeUGT38*) and their potential regulatory transcription factors were identified.

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Genome-wide identification and characterization of the UDP-glycosyltransferase gene family in passion fruit (*Passiflora edulis*)

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Abstract

Glycosylation, catalyzed by UDP-glycosyltransferases (UGTs), is a pivotal modification enhancing the solubility, stability, and diversity of plant metabolites, influencing growth, development, and stress responses. Passion fruit (*Passiflora edulis*) is an economically important fruit crop renowned for its rich flavor and health-promoting metabolites, particularly flavonoids. However, a comprehensive understanding of the *UGT* gene family underlying its metabolic diversity remains limited. In this study, we performed a genome-wide analysis and identified 149 *PeUGT* genes in the passion fruit genome. Phylogenetic analysis clustered these genes into 11 distinct subfamilies, revealing high evolutionary conservation. Structural analyses demonstrated conserved exon-intron architectures and motifs within subfamilies, with the PSPG-box signature present in all members. Chromosomal mapping revealed an uneven distribution across nine chromosomes, and duplication event analysis suggested that tandem and segmental duplications were the primary drivers of family expansion. Promoter *cis*-element analysis identified an abundance of motifs related to stress, hormone signaling, and development. Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) enrichment highlighted associations with flavonoid biosynthesis, particularly anthocyanin metabolism. Expression profiling across four fruit developmental stages revealed dynamic patterns, with 14 genes up-regulated and 23 down-regulated during ripening. Notably, three key anthocyanin-related genes—*PeUGT10*, *PeUGT17*, and *PeUGT38*—showed contrasting expression trajectories. Subsequent co-expression network analysis identified potential transcription factors (e.g., G2-like, MYB, WRKY) regulating these genes. Our findings provide a foundational resource for the functional characterization of *PeUGT*-mediated glycosylation in passion fruit and offer prime candidate targets for molecular breeding aimed at improving fruit quality traits, such as color and nutritional value.

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Introduction

Glycosylation is a critical post-synthetic modification of plant secondary metabolites, significantly enhancing their solubility, stability, transportability, and structural diversity[1]. This modification plays a pivotal role in plant growth, development, and responses to both biotic and abiotic stresses[2]. Flavonoids—including flavonols, isoflavones, flavones, and anthocyanins—represent a major class of plant secondary metabolites that predominantly exist as glycoside conjugates. These glycosylation reactions are catalyzed by UDP-glycosyltransferases (UGTs), which transfer glycosyl moieties from activated donor molecules to specific acceptor substrates such as sugars and lipids[3,4].

The UGT family constitutes the predominant group within the CAZy glycosyltransferase family GT1 across the plant kingdom[5]. Structurally, plant UGTs exhibit a complex N-terminal domain responsible for substrate recognition and binding, enabling the accommodation of diverse substrates[6]. The C-terminal region harbors a highly conserved PSPG-box motif (Plant Secondary Product Glycosyltransferase box), which is essential for glycosyltransferase catalytic activity[7]. This 44-amino acid signature sequence is invariant across all characterized plant UGTs[8]. Owing to this conserved structural architecture, UGT gene families have been systematically identified and annotated in numerous plant species, including *Arabidopsis thaliana*[9], rice (*Oryza sativa*)[10], apple (*Malus domestica*)[11], potato (*Solanum tuberosum*)[12], and tea (*Camellia sinensis*)[13].

Furthermore, emerging evidence indicates that numerous glycosyltransferase genes are implicated in fruit growth, development, and responses to abiotic stress. During sweet cherry (*Prunus avium*) fruit development, *PavUGT48* mediates the glycosylation of cyanidin and other anthocyanidins, thereby promoting anthocyanin accumulation and fruit coloration—playing a pivotal role in fruit ripening and quality formation[14]. In citrus, *CitUGT72AZ4* participates in the regulation of flavonoid metabolism by catalyzing the 4-O-glycosylation of flavonols, thereby modulating the biosynthesis of citrus flavonoid glycosides during fruit development[15]. Additionally, *UGT* genes contribute to enhanced plant stress tolerance through the accumulation of protective glycosides. For instance, apple *MdUGT88F1* regulates phloridzin biosynthesis and is involved in disease resistance[16], while tea plant *CsUGT78A14* and *CsUGT91Q2* modulate cold tolerance by regulating the synthesis of flavonoid and terpenoid glycosides[17]. Nevertheless, functional characterization of *UGT* genes remains predominantly confined to model plants and a limited number of economically important crops, leaving the biological functions of UGTs in many non-model plants largely unexplored.

Passiflora edulis Sims is a perennial evergreen climbing vine indigenous to tropical regions of South America and represents the most extensively cultivated species within the Passiflora genus[18]. Passion fruit juice is nutritionally rich, containing substantial amounts of sugars, organic acids, amino acids, vitamins, and flavonoids[19]. Notably, flavonoids exhibit potent biological activities, including anti-carcinogenic, antioxidant, and anti-inflammatory properties, conferring significant health benefits. In recent years, the release of the chromosome-scale passion fruit genome has catalyzed increasing research interest in the biosynthetic pathways

and genetic underpinnings of its specialized metabolites[20]. Previous studies have demonstrated that heterologous overexpression of *PeMYB114* in tobacco enhances flavonoid accumulation[21]; *PeLOX4* expression elevates lipoxygenase activity, thereby promoting volatile ester biosynthesis and intensifying fruit aroma[22]; and *PeCWINV5* overexpression augments soluble sugar accumulation[23], *PeWRKY20* regulates the production of malic acid and volatile compounds by inhibiting the expression of *PeMDH1*[24]. However, systematic investigation of the *UGT* gene family in passion fruit remains scarce. Therefore, comprehensive characterization of the *PeUGT* family holds substantial significance for elucidating glycosylation-mediated metabolic regulation in this economically important fruit crop.

In this study, we conducted a genome-wide analysis of the *UGT* gene family in *Passiflora edulis* based on the published chromosome-scale genome, identifying a total of 149 *UGT* genes. We systematically characterized these genes through comprehensive analyses of phylogenetic relationships, gene structure, conserved motifs, chromosomal distribution, gene duplication events, promoter cis-acting elements, KEGG and GO functional annotations, and expression patterns across fruit developmental stages. This genome-wide investigation provides a valuable foundation for the functional characterization of UGT-mediated glycosylation in passion fruit secondary metabolism.

Materials and methods

Identification of the *UGT* gene family in passion fruit

The *Passiflora edulis* genome sequence was retrieved from previously published studies. A total of 73 *Arabidopsis thaliana* UGT protein sequences were downloaded from the TAIR database (https://arabidopsis.org/). These sequences were employed as queries for BLASTP searches against the passion fruit genome, with stringent filtering criteria of E-value < 1e-10 and sequence identity > 50%[25]. Concurrently, the UDP-glucosyltransferase domain (PF00201) was retrieved from the Pfam database, and Hidden Markov Model (HMM) searches were performed using default parameters to identify putative UGT proteins in *P. edulis*. Candidate genes identified by both BLASTP and HMM approaches were merged as the preliminary *PeUGT* family members. Subsequently, the Conserved Domain Database (CDD; https://ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi) was employed to verify the presence of the characteristic UGT domain, thereby determining the final set of *PeUGT* family members.

Phylogenetic analysis of the *PeUGT* gene family

Phylogenetic analysis was performed using PeUGT and selected UGT amino acid sequences from *Arabidopsis thaliana* and other representative plant species. A neighbor-joining (NJ) phylogenetic tree was constructed using MEGA 12 software with 1,000 bootstrap replicates. Subsequently, the resulting tree was visualized using iTOL (https://itol.embl.de)[26].

Chromosome distribution and collinearity analysis of the *PeUGT* gene family

The chromosomal locations of *PeUGT* genes were determined based on genome annotation files and visualized using MapChart[27]. Intraspecific collinearity analysis of the *PeUGT* gene family and interspecific synteny analysis between *Passiflora edulis*, tomato (*Solanum lycopersicum*)[28], and *Arabidopsis thaliana* were performed using MCScanX[29], with the results visualized using TBtools[30].

Gene structure and conserved motif analysis of the *PeUGT* gene family

Gene structure analysis of *PeUGT* genes was performed using the GSDS online tool (https://gsds.gao-lab.org) based on genome annotation data[31]. Additionally, conserved motifs in PeUGT protein sequences were predicted using MEME (Multiple Em for Motif Elicitation) with a maximum motif number of 10 and default parameters for all other settings.

Prediction of cis-elements in *PeUGT* gene family promoters

For each *PeUGT* gene, the 2,000 bp sequence upstream of the translation start codon was extracted from the *Passiflora edulis* genome as the putative promoter region. These sequences were submitted to PlantCARE (https://bioinformatics.psb.ugent.be/webtools/plantcare/html) for cis-acting regulatory element identification[32]. The predicted elements were subsequently filtered, statistically analyzed, and visualized.

GO annotation and KEGG enrichment analysis of *PeUGT* gene family

To perform Gene Ontology (GO) annotation and Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway enrichment analysis of the *PeUGT* gene family, functional annotation of all Passion fruit protein-coding genes was first conducted using eggNOG-mapper[33]. Subsequently, GO term mapping and KEGG pathway enrichment analysis specific to *PeUGT* genes were performed using TBtools[30], with the results visualized accordingly.

Analysis of expression levels during fruit development and maturation of the *PeUGT* gene family

Passion fruit peel samples were collected at four developmental stages: 18 d after flowering (S1), 28 d after flowering (S2), 41 d after flowering (S3), and 58 d after flowering (S4). S1 (18 d after flowering, the young fruit stage) is mainly characterized by cell division; S2 (28 d after flowering, the fruit expansion stage) features a significant accumulation of water and sugar; S3 (41 d after flowering, the coloring stage) is marked by the degradation of chlorophyll, the synthesis of anthocyanins and carotenoids, and a substantial accumulation of organic acids (primarily citric acid); S4 (58 d after flowering, the mature stage) sees the content of soluble sugar reach its peak and a large release of volatile aroma substances. All samples were immediately frozen in liquid nitrogen and stored at −80 °C prior to RNA extraction. Total RNA isolation and transcriptome sequencing were performed by Haikou Heliyuan Biotechnology Co., Ltd. (Haikou, China). Three biological replicates were collected for each developmental stage.

Construction of the transcriptional regulatory network of the *PeUGT* gene

To construct the putative transcriptional regulatory network, the FIMO (Find Individual Motif Occurrences) program was first used to scan the promoter sequences of candidate genes to identify

potential transcription factors that could bind to the promoter region of the *PeUGT* gene[34]. Subsequently, the prediction results were integrated with the weighted gene co-expression network analysis (WGCNA) based on the transcriptome data of four ripening stages of passion fruit using TBtools[30]. Finally, the transcription factors that could bind to the promoter region of the *PeUGT* gene and were in the same co-expression module as the *PeUGT* gene in the WGCNA were screened as candidate regulatory factors.

Results

Identification and sequence analysis of the *PeUGT* genes

BLASTP alignment against AtUGT sequences combined with HMM domain searches identified 149 PeUGT-encoding genes in the passion fruit genome. These genes were designated *PeUGT1* to *PeUGT149* based on chromosomal order. The encoded proteins exhibited substantial physicochemical diversity, with lengths ranging from 177 amino acids (PeUGT122) to 931 amino acids (PeUGT56), molecular masses of 20.2 kDa (PeUGT122) to 105.3 kDa (PeUGT56), theoretical isoelectric points (pI) spanning 4.71 (PeUGT98) to 8.93 (PeUGT42), instability indices of 27.76 (PeUGT22) to 54.20 (PeUGT16), aliphatic indices of 72.15 (PeUGT122) to 114.89 (PeUGT35), and grand averages of hydropathicity (GRAVY) from −0.442 (PeUGT122) to 0.352 (PeUGT35) (Supplementary Table S1), indicating varying degrees of hydrophilicity. These parameters collectively highlight significant hydrophilicity variations across the 149 UGT proteins in passion fruit.

PeUGT phylogenetic analysis

To elucidate evolutionary relationships among PeUGT family members, full-length protein sequences from 73 *Arabidopsis thaliana* AtUGTs and 149 passion fruit PeUGTs were analyzed using BLASTP and multiple sequence alignment tools. Neighbor-Joining phylogenetic reconstruction generated a robust tree (Fig. 1) demonstrating that PeUGT members clustered into 11 distinct subfamilies, exhibiting significant size heterogeneity. Comparative analysis revealed that intra-subfamily sequences shared high pairwise identity between Arabidopsis and passion fruit, suggesting strong purifying selection and functional conservation. Notably, subfamilies IV, X, and XI contain only passion fruit UGT proteins. Subfamily V has also undergone significant expansion in passion fruit. These findings establish that while core UGT functions are evolutionarily conserved, subfamily-specific diversification reflects adaptation to distinct ecological niches.

Chromosome localization and collinearity analysis of the *PeUGT* gene

To elucidate the genomic distribution of *PeUGT* genes, chromosomal mapping was performed. Among the 149 identified *PeUGT* genes, 147 were mapped to nine passion fruit chromosomes, while two remained on unassembled scaffolds (Fig. 2). Chromosomal

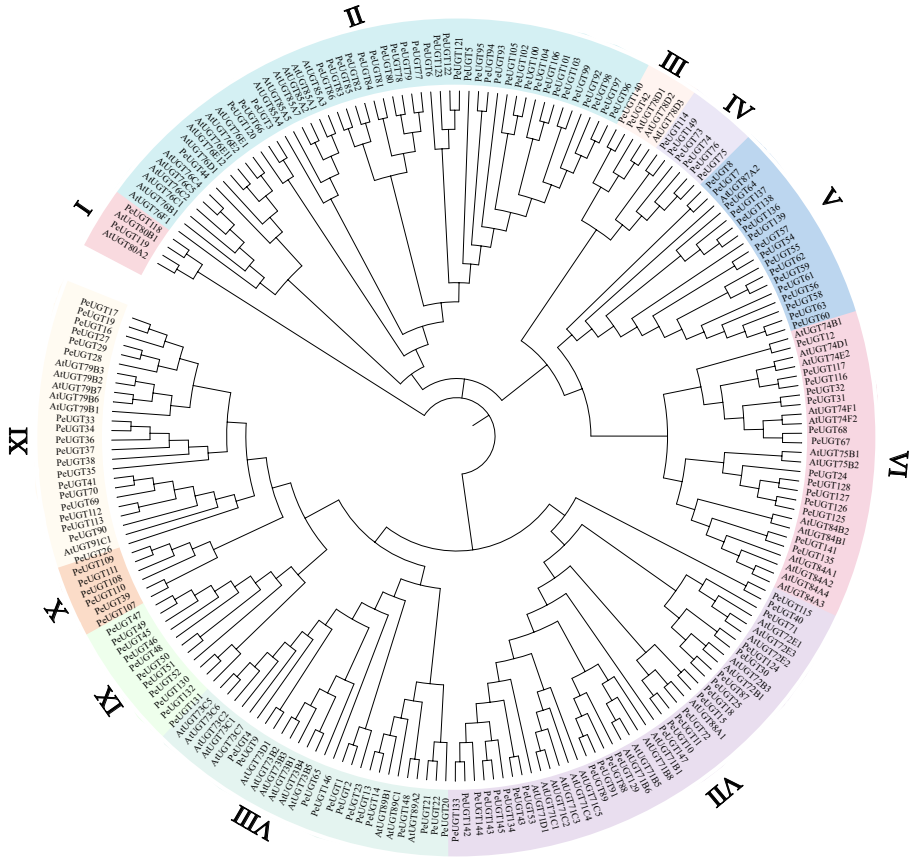

Fig. 1 Phylogenetic analysis of UGT proteins in Arabidopsis and passion fruit. Using the neighbor-joining (NJ) method implemented in MEGA12 software, a phylogenetic tree was constructed using 73 AtUGT proteins from Arabidopsis and 149 PeUGT proteins from passion fruit. Different subfamilies are represented by different colors.

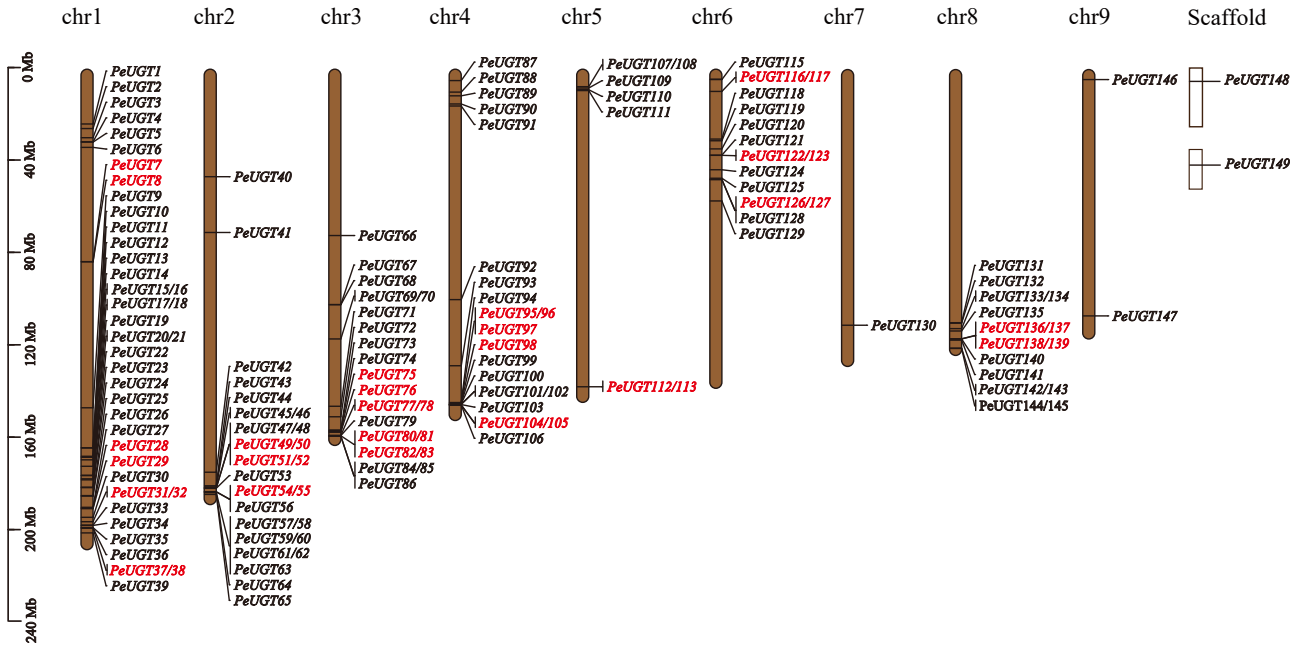

Fig. 2 Chromosome distribution and tandem repeat analysis of the *PeUGT* gene. Each line represents a chromosome, with duplicated gene pairs highlighted in red. The approximate location of each *PeUGT* gene on each chromosome is indicated.

density analysis revealed significant variation, with chromosome 1 harboring the highest gene density (39 *PeUGTs*), followed by chromosomes 2 (26), 3 (21), and 4 (20). Subsequent chromosomes exhibited progressively lower densities, ranging from one to 16 genes per chromosome (chromosomes 5–9).

Syntenic analysis identified 20 tandem and 11 segmental duplication events within the *PeUGT* family, suggesting both intrachromosomal and interchromosomal expansion mechanisms (Fig. 3a). Comparative genomics revealed 21 *PeUGT* genes with collinear relationships to *AtUGT* genes and 26 with *Solanum lycopersicum SlUGTs* (Fig. 3b). Notably, 12 *PeUGT* genes demonstrated dual synteny with both *AtUGT* and *SlUGT* orthologs, indicating functional conservation across evolutionarily divergent species.

Conservative motif and gene structure analysis of the *PeUGT* gene

MEME analysis identified ten conserved motifs across the PeUGT proteins, exhibiting high conservation among members. Motif 7 was exclusively present in subfamily II, while a core set of motifs (4, 9, 10, 2, 8, 1, 3, and 5) was distributed across nearly all PeUGT members. Notably, motifs 1 and 3 corresponded to the canonical PSPG-box signature. Members containing PSPG-box exhibit strict conservation in the C-terminus region, but show significant differences in the N-terminus region, consistent with observations from other plant species such as apples[11] and blueberries[35] (Fig. 4). In addition, other typical domains—including GTB (motifs 2, 5, and 9), YjiC (motif 4), and GT1 (motifs 3, 6, and 8)—were identified across all

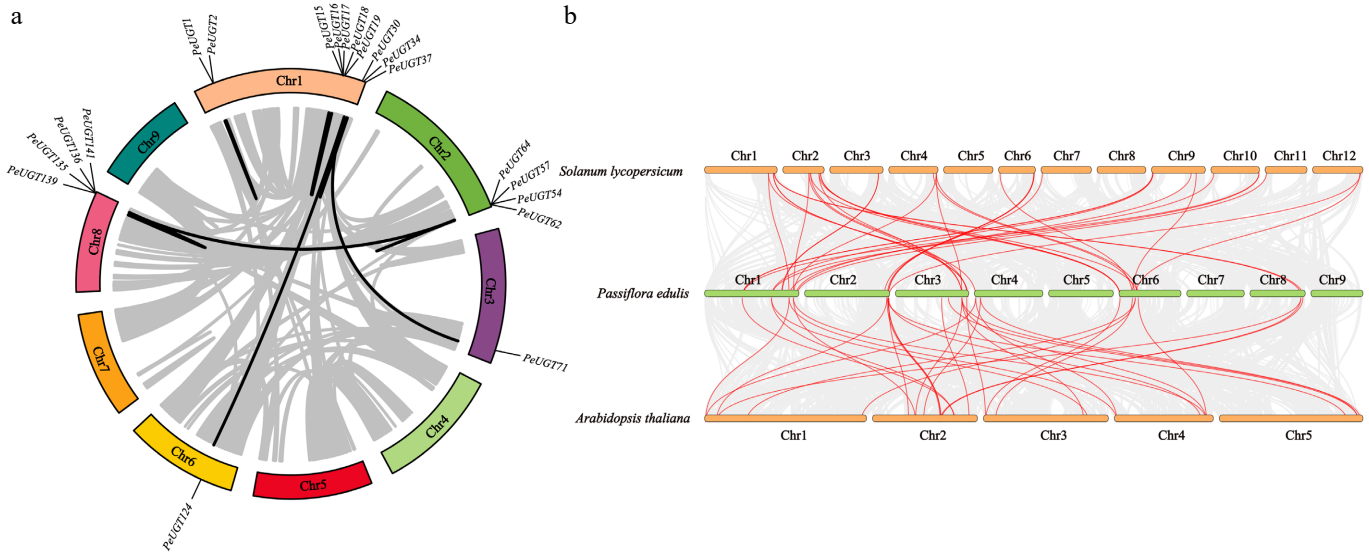

Fig. 3 Analysis of intraspecific and interspecific collinearity of *UGT* genes. (a) Intraspecific collinearity analysis of the *PeUGT* gene in passion fruit. (b) Collinearity analysis of *UGT* genes in passion fruit, *Arabidopsis thaliana*, and tomato.

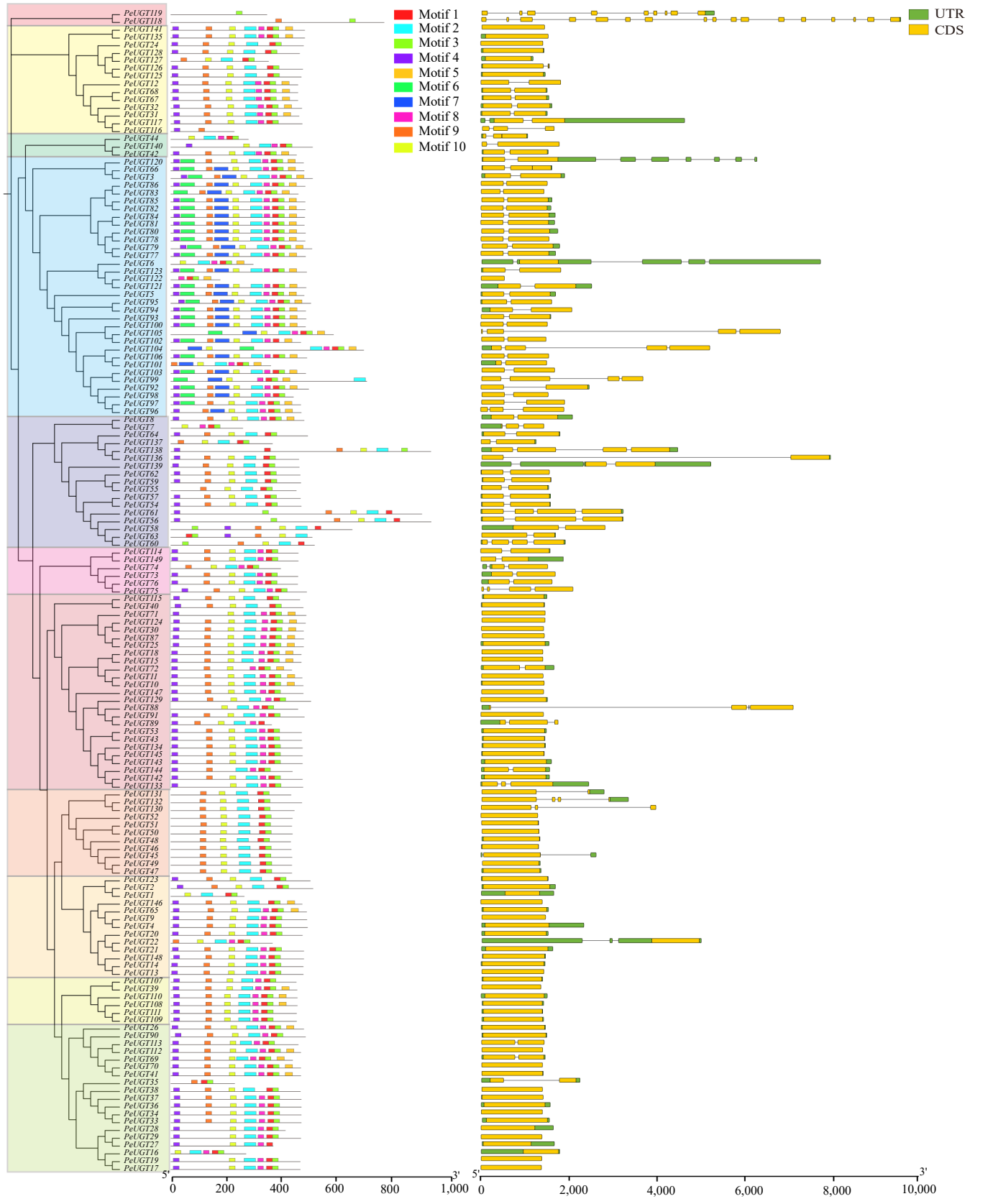

Fig. 4 Analysis of PeUGT conserved motifs and gene structure. PeUGT conservative motifs are sorted according to different subfamilies, with different colors representing different subfamilies in the evolutionary tree. There are a total of ten motifs, each represented by a colored box, and non-conservative regions represented by black lines. In the *PeUGT* gene structure analysis, CDS is represented by yellow boxes, UTR is represented by green boxes, and introns are represented by black lines.

PeUGT members, despite each being annotated in only one member. These differential domain distributions likely contribute to functional diversification within the PeUGT family.

Investigation of intron-exon architectures revealed *PeUGT* genes ranged from 1 to 17 exons (median: nine exons) and 0 to 16 introns (median: five introns). Subfamily I exhibited the highest structural complexity (9–17 exons, 8–16 introns), whereas subfamilies II–V predominantly contained three or more introns, whereas the remaining subfamilies displayed less intron content, potentially attributable to shorter sequence lengths or evolutionary loss of intron-rich domains (Fig. 4).

Analysis of cis acting-elements of the *PeUGT* gene

Analysis of the 2 kb upstream promoter regions of *PeUGT* genes identified 4,271 predicted cis-regulatory elements, categorized into three functional classes: phytohormone responsiveness, plant growth and development, and stress response. Stress-responsive elements demonstrated significant enrichment, including 325 anaerobic induction elements, 64 defense and stress-responsive elements, 163 drought-inducible elements, 339 light-responsive elements, and 165 low-temperature-responsive elements. This pronounced bias toward stress-related motifs aligns with the proposed role of *UGTs* in abiotic stress mitigation, suggesting their evolutionary adaptation to environmental perturbations.

A total of 1,793 cis-regulatory elements associated with six phytohormone response pathways were identified, including 726 abscisic acid-responsive elements, 130 auxin-responsive elements, 102 gibberellin-responsive elements, 515 methyl jasmonate-responsive elements, and 156 salicylic acid-responsive elements. This substantial enrichment of hormone-responsive elements indicates that phytohormones play pivotal roles in regulating *PeUGT* gene expression (Fig. 5).

Additionally, the *PeUGT* promoter regions contained 532 cis-acting elements associated with growth and developmental processes, including 30 circadian rhythm control elements, 25 endosperm expression elements, and 56 zein metabolism regulatory elements. The diversity of these regulatory elements suggests that *PeUGT* genes participate in a broad spectrum of physiological processes during passion fruit development.

PeUGT gene GO and KEGG enrichment analysis

To elucidate the functional roles of *PeUGT* genes in passion fruit developmental biology, Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) enrichment analyses were performed. PeUGT proteins demonstrated predominantly catalytic activity, with primary functional annotations in metabolic processes, biological regulation, and developmental processes. The most significantly enriched biological process categories included cellular metabolite biosynthesis, anthocyanin-containing compound metabolism, and secondary metabolic pathways. Notably, the majority of *PeUGT* members were annotated to specific metabolic pathways, including biosynthesis of secondary metabolites, and terpenoid and polyketide metabolism (Fig. 6). These findings suggest that *PeUGT* genes likely participate in biotic and abiotic stress responses, as well as plant growth and development, through the regulation of secondary metabolite glycosylation.

Analysis of expression patterns of *PeUGT* gene during developmental stages

RNA sequencing (RNA-seq) analysis was performed to elucidate the spatiotemporal expression dynamics of *PeUGT* genes in passion fruit peel across four post-flowering developmental stages: S1–S4. Quantitative transcriptomic profiling revealed distinct temporal expression patterns, with 36 *PeUGTs* exhibiting peak expression at S1, 47 at S2, 27 at S3, and 24 at S4. Notably, the highest aggregate expression level occurred during S2, whereas the lowest was observed at S4, suggesting a developmental phase-dependent regulatory mechanism (Fig. 7).

Members of the tandemly duplicated gene family exhibit highly coordinated expression patterns across four developmental stages. Specifically, *PeUGT75/76* shows significantly high expression in stages S1 and S3, but is significantly downregulated in stages S2 and S4; *PeUGT122/123* expression gradually increases with development, reaching a peak in stage S2 and then showing a decreasing trend. These expression profile characteristics suggest that tandemly duplicated genes may have functional redundancy and cooperatively regulate specific biological processes throughout the entire developmental cycle (Fig. 7).

Construction of transcriptional regulatory network for the *PeUGT* gene

Our integrated analysis of functional enrichment and developmental expression dynamics revealed that *PeUGT* genes associated with anthocyanin biosynthesis exhibited distinct stage-specific expression patterns. *PeUGT10* and *PeUGT17* displayed significant upregulation during early development stages, peaking at S2, followed by progressive downregulation. Conversely, *PeUGT38* exhibited sustained upregulation across all developmental stages, achieving maximum at S4 (Fig. 7).

To elucidate the transcriptional regulatory architecture, we performed comprehensive co-expression network analysis coupled with FIMO-based motif enrichment. This identified 28, 2, and 20 candidate transcription factors (TFs) regulating *PeUGT10*, *PeUGT17*, and *PeUGT38*, respectively. The candidate TF families for *PeUGT10* included ARF, bHLH, bZIP, C2H2, Dof, EIL, ERF, G2-like, GATA, HD-ZIP, HSF, MIKC_MADS, MYB, WOX, and WRKY; *PeUGT17* candidate regulators comprised G2-like and HD-ZIP family members; while *PeUGT38* candidate TFs encompassed ARF, BBR-BPC, bZIP, C2H2, Dof, G2-like, MIKC_MADS, MYB, NAC, and WRKY (Fig. 8). These findings establish key regulatory targets for investigating the transcriptional control of anthocyanin-related *PeUGT* genes during passion fruit ripening.

Discussion

In this study, we conducted a comprehensive genome-wide identification and characterization of the *UGT* gene family in *Passiflora edulis*, including phylogenetic relationships, gene structure, conserved motifs, chromosomal distribution, duplication events, intraspecific and interspecific synteny, promoter cis-regulatory element analysis, developmental expression patterns, and functional enrichment analyses (GO and KEGG). A total of 149 *PeUGT* genes were identified and clustered into 11 subfamilies. Comparative analysis revealed that the *PeUGT* family size was comparable to that of other plant species, including Arabidopsis (120 members)[9], maize (147)[36], wheat (179)[6], citrus (145)[37], and upland cotton (174)[38].

Phylogenetic and structural analyses demonstrated substantial conservation within *PeUGT* subfamilies, with members of the same clade exhibiting identical or highly similar exon-intron architectures. This pattern is consistent with previous findings in tomato[28] and blueberry[35], underscoring the evolutionary conservation of *UGT* family organization across diverse plant taxa. Conserved motif

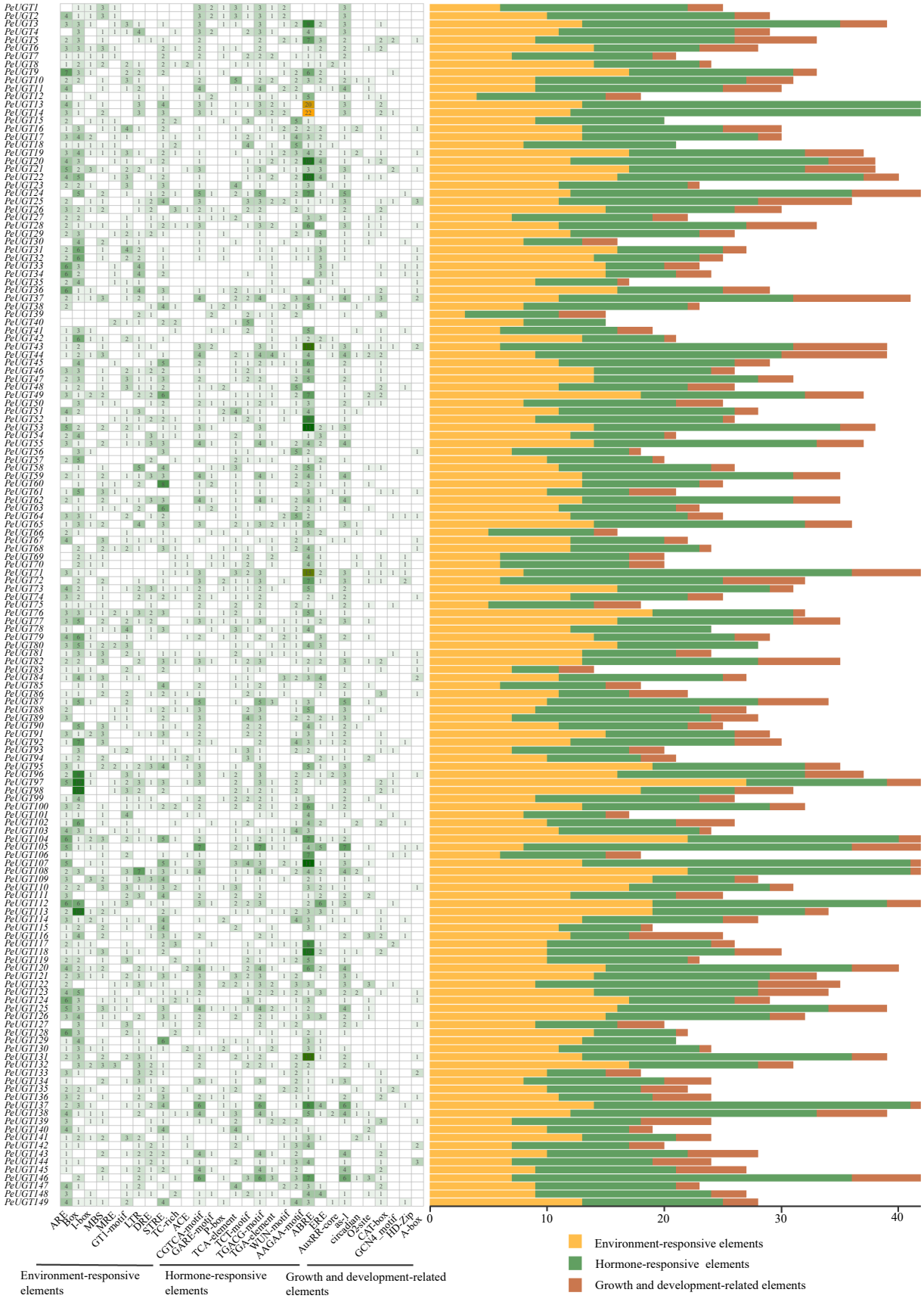

Fig. 5 Identification of cis-regulatory elements in the *PeUGT* gene promoter. The left figure shows the number of each type of cis-regulatory element present in each gene promoter region, while the right figure shows the number of elements belonging to plant hormone response, plant growth and development, and stress responsiveness within each genome promoter.

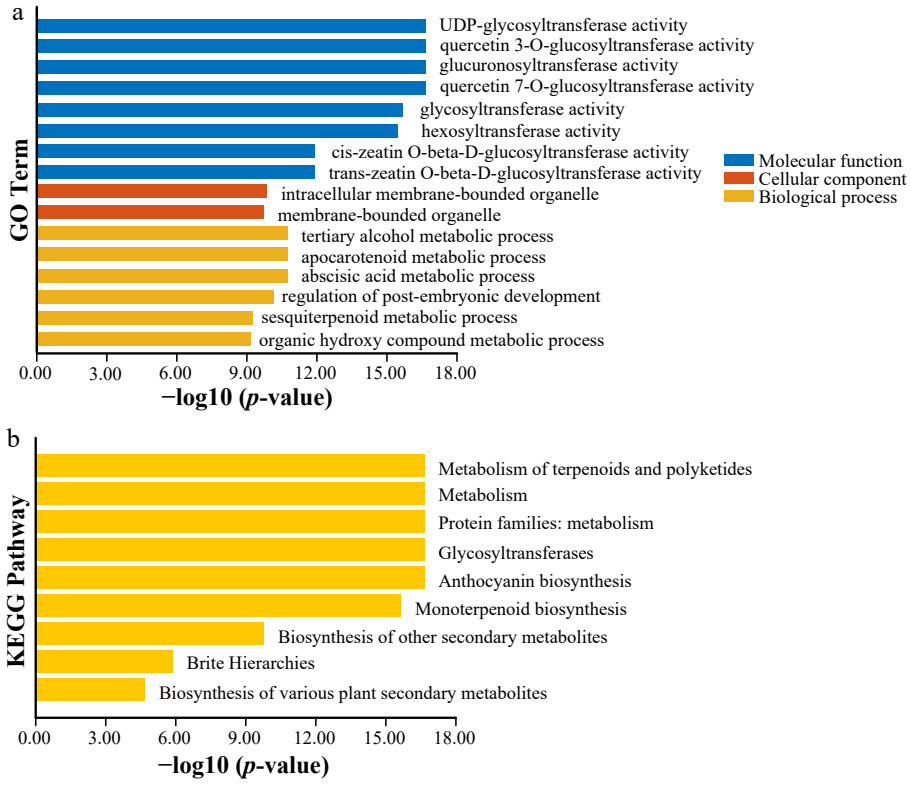

Fig. 6 GO and KEGG enrichment analysis of the *PeUGT* gene. (a) GO analysis of the *PeUGT* gene. GO classification of cellular components, molecular functions, and biological processes has been determined. (b) Annotation of the KEGG pathway of the *PeUGT* gene.

analysis confirmed that motifs 1 and 3 constitute the characteristic PSPG-box signature present in all *PeUGT* members. Notably, genes containing the PSPG-box exhibited high conservation in the C-terminal region and significant variability in the N-terminal region, the latter being responsible for substrate specificity. These findings align with established evidence that the PSPG-box directly interacts with sugar donors, thereby modulating glycosylation activity and substrate specificity[39]. Analysis of the 2 kb upstream region of the *PeUGT* gene identified three categories of cis-regulatory elements associated with plant hormone responses, growth and development, and stress responses. Notably, hormone-responsive elements were found to be particularly critical. In rice, hormones such as strigolactones (SLs) can directly regulate the biosynthesis of flavonoid and terpenoid phytoalexins through the *WRKY45* transcription factor, thereby coordinating the balance between plant growth and defense metabolism. This suggests that *PeUGT* may participate in flavonoid glycosylation modifications under hormone-mediated regulatory signaling[40].

GO and KEGG enrichment analyses revealed that ten *PeUGT* genes were associated with anthocyanin biosynthesis pathways, consistent with established roles of *UGTs* in flavonoid glycosylation across plant species. In Arabidopsis, *UGT79B* subfamily members (*UGT79B1*, *UGT79B2*, and *UGT79B3*) catalyze anthocyanin modifications, with distinct substrate specificities: *UGT79B1* preferentially recognizes 3-O-glucosylated anthocyanins and flavonols, whereas *UGT79B2* and *UGT79B3* favor anthocyanidin aglycones over 3-O-glucosylated substrates. Their expression is directly regulated by *CBF1*[41]. The first plant *UGT* gene identified, maize (*Zea mays*) UDP-glucose: flavonoid 3-O-glucosyltransferase BRONZE1, is endosperm-specific and responsible for seed pigmentation through flavonoid 3-O-glycosylation[42]. Additionally, quercetin glucosyltransferase activity has been extensively characterized: Arabidopsis *UGT78D* subfamily members (*UGT78D1*, *UGT78D2*, and *UGT78D3*) glycosylate flavonoids with varying specificities - *UGT78D2* catalyzes glucose transfer to cyanidin[43], kaempferol, and quercetin, while *UGT78D1* and *UGT78D3* specifically modify flavonol glycosides[44]. The second maize flavonol glycosyltransferase, *UFGT2*, exhibits high catalytic efficiency toward kaempferol and quercetin and enhances abiotic stress tolerance[45]. These findings suggest that passion fruit *PeUGT* genes enriched in anthocyanin-related pathways may fulfill analogous biochemical functions, providing a foundation for subsequent functional characterization.

Furthermore, we investigated developmental expression dynamics across fruit ripening stages. Fourteen *PeUGT* genes exhibited progressively increasing expression, including *PeUGT13*, *14*, *24*, *38*, *39*, *63*, *71*, *72*, *87*, *90*, *116*, *135*, *138* and *140*; conversely, 23 genes displayed declining expression patterns, comprising *PeUGT3*, *11*, *19*, *25*, *30*, *33*, *40*, *64*, *73*, *82*, *89*, *91*, *93*, *94*, *104*, *110*, *112*, *114*, *130*, *131*, *133*, *134*, and *136*. Notably, three anthocyanin-associated genes—*PeUGT10, PeUGT17*, and *PeUGT38*—exhibited contrasting trajectories (decreasing vs increasing), prompting transcriptional regulatory network analysis. This identified 28, 2, and 20 candidate transcription factors (TFs) potentially regulating *PeUGT10*, *17*, and *38*, respectively. *PeUGT10* candidates encompassed ARF, bHLH, bZIP, C2H2, Dof, EIL, ERF, G2-like, GATA, HD-ZIP, HSF, MIKC_MADS, MYB, WOX, and WRKY families; *PeUGT17* candidates comprised G2-like and HD-ZIP; while *PeUGT38* candidates included ARF, BBR-BPC, bZIP, C2H2, Dof, G2-like, MIKC_MADS, MYB, NAC, and WRKY.

Strikingly, all three gene sets shared G2-like TFs, members of the GARP superfamily implicated in chloroplast development, chlorophyll biosynthesis, and abiotic stress responses. Arabidopsis *GLK2* positively regulates high-light-induced anthocyanin accumulation, establishing a molecular link between light signaling and anthocyanin biosynthesis[46]. In cotton, *GhBLH2* antagonizes

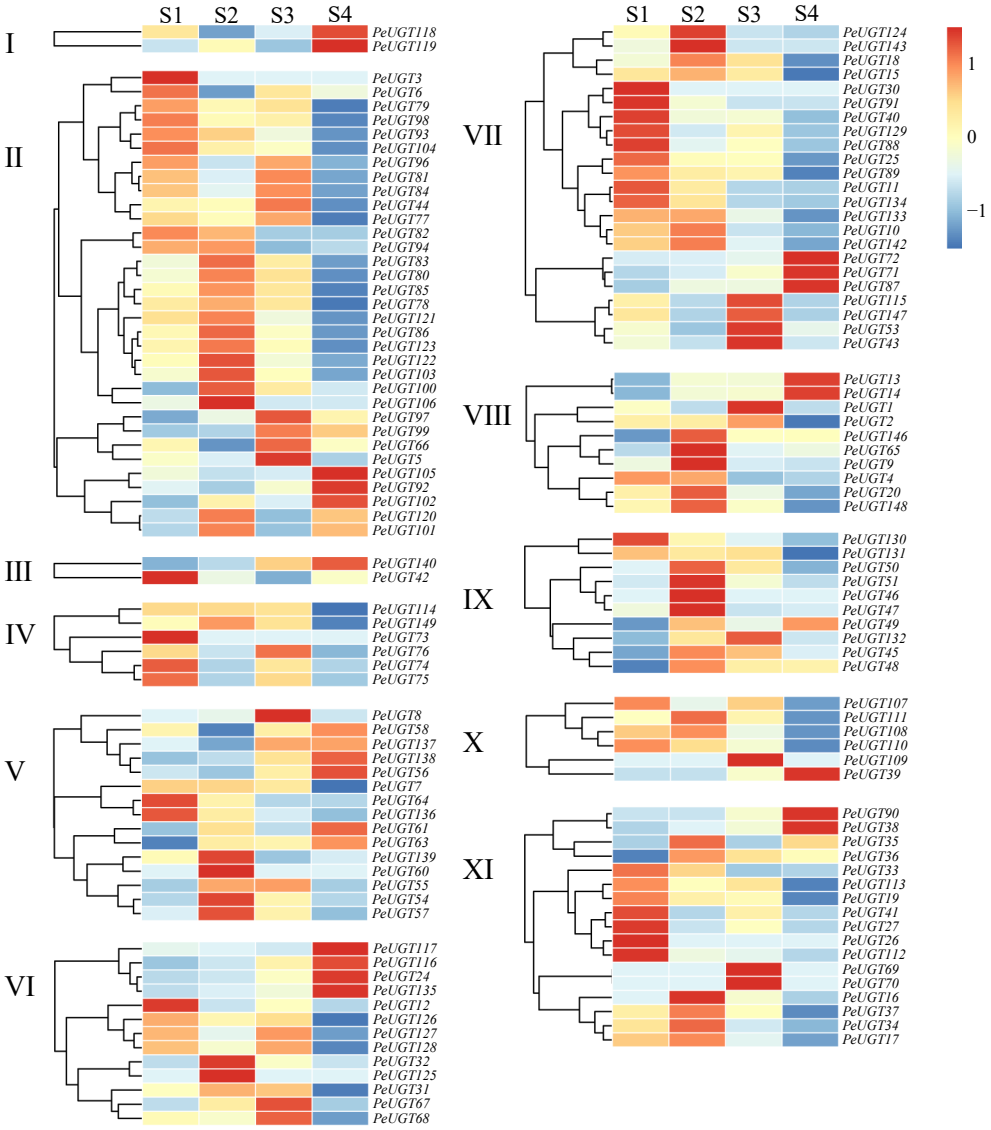

Fig. 7 Analysis of *PeUGT* gene expression pattern during the developmental stage of passion fruit. Different subfamilies of *PeUGT* are clustered separately, with S1 representing 18 d after flowering, S2 representing 28 d after flowering, S3 representing 41 d after flowering, and S4 representing 58 d after flowering. Gene expression levels are represented as TPM (Transcripts Per Million) values and subjected to Z-score normalization (row-wise scaling). The color gradient indicates the deviation from the mean expression level: red denotes higher-than-average expression (Z-score > 0), while blue denotes lower-than-average expression (Z-score < 0).

GhGLK1-mediated salt tolerance by interacting with its activation domain[47]. Metabolites may also vary among different varieties[48], In passion fruit, differential *FLS* enzyme activities between YPF-p and PPF-p may alter the competitive dynamics with *F3'H*, *DFR*, and *F3'5'H*, consequently leading to distinct anthocyanin synthesis patterns between the two varieties[49]. We hypothesize that passion fruit G2-like TFs may directly activate anthocyanin glycosyltransferase genes (*PeUGT10*, *PeUGT17*, and *PeUGT38*) to promote pigment synthesis and stability, or alternatively, interact with environmental signaling pathways (light, temperature) to coordinate fruit development.

Conclusions

In this study, we identified 149 *PeUGT* genes in *Passiflora edulis* and systematically characterized them through integrated phylogenetic, structural, chromosomal, syntenic, and functional analyses. Three candidate genes, *PeUGT10*, *PeUGT17*, and *PeUGT38,* were prioritized as potential regulators of anthocyanin biosynthesis during fruit development based on their phylogenetic affiliations, conserved domain architectures, chromosomal locations, duplication histories, promoter cis-regulatory element profiles, developmental expression patterns, and pathway enrichment signatures. Co-expression analysis and candidate transcription factor screening revealed distinct yet overlapping regulatory networks for these genes, with G2-like TFs emerging as shared hub regulators. This comprehensive characterization of the *PeUGT* family establishes a transcriptional regulatory framework for key anthocyanin glycosylation genes, implicating G2-like transcription factors as central nodes integrating developmental and environmental signals. These findings advance the mechanistic understanding of anthocyanin biosynthesis in passion fruit and provide candidate gene targets and regulatory hubs for marker-assisted breeding and genome editing-directed improvement of fruit color traits.

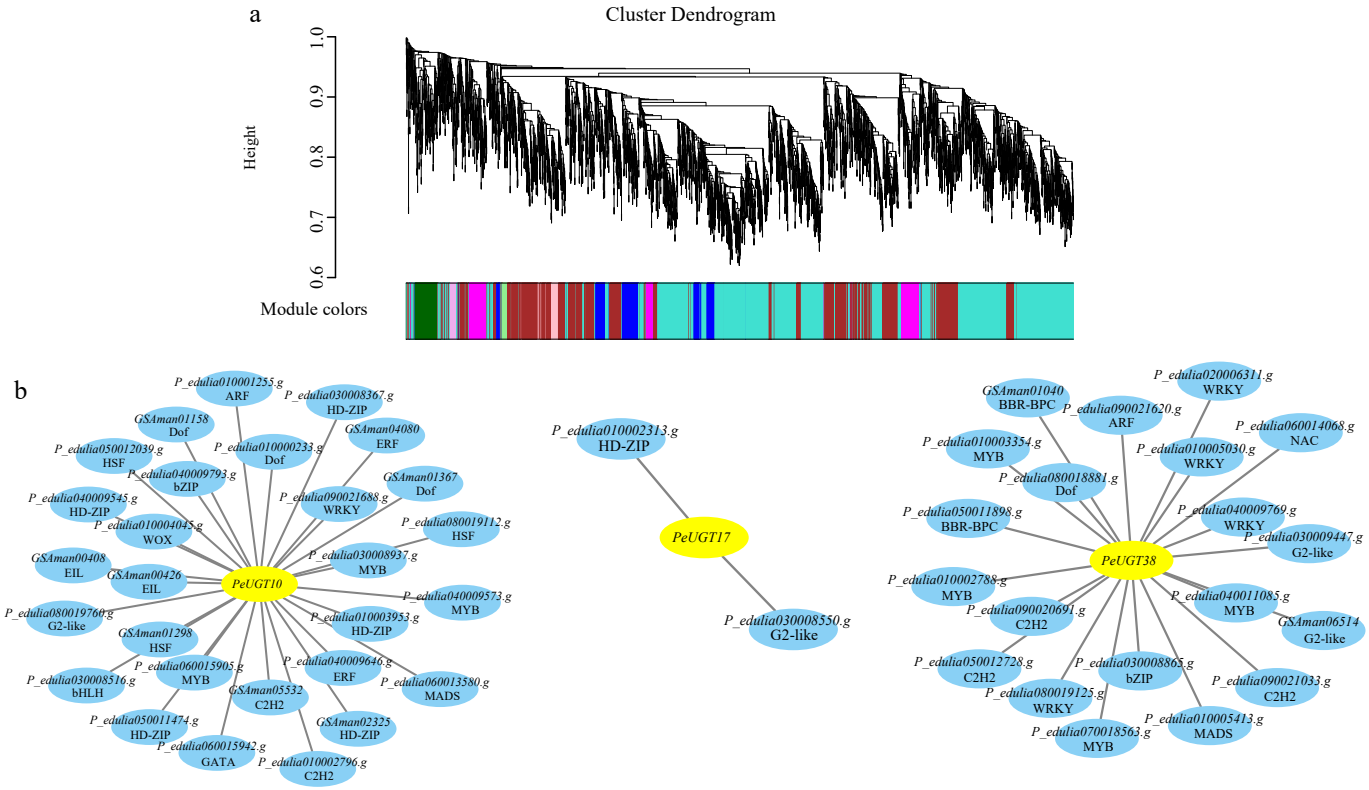

Fig. 8 Potential transcriptional regulatory networks of *PeUGT10*, *PeUGT17*, and *PeUGT38*. (a) Identify gene co-expression modules through WGCNA. (b) Identifying transcription factors with potential regulatory relationships with *PeUGT10*, *PeUGT17*, and *PeUGT38* through integration of co-expression and FIMO analysis. The first row in the circle in the figure is the gene number, and the second row is the corresponding transcription factor family.

Ethical statements

During the preparation of this work, the author used Stork (version: 2026, date of use: March 12, 2026) to enhance the images of the graphical abstract. The author reviewed and edited all content generated with the assistance of these tools, verified its accuracy, and takes full responsibility for the integrity and originality of the final manuscript. This work represents the author's own intellectual contribution, and no artificial intelligence tool is regarded as an author.

Author contributions

The authors confirm contribution to the paper as follows: study conception and design: Fang C; data collection: Wang L, Peng J, Luo L; analysis and interpretation of results: Wang L, Luo L; draft manuscript preparation: Fang C, Wang L, Luo L. All authors reviewed the results and approved the final version of the manuscript.

Data availability

Data will be made available on request. RNA sequence data that support the findings of this study have been deposited under SRA Bio-Project accession number CRA038695.

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Conflict of interest

The authors declare that they have no conflict of interest.

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