


Evolutionary dynamics and functional characterization of Jasmonate ZIM-domain (JAZ) genes across *Camellia sinensis* pan-genome

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Abstract

Jasmonate ZIM-domain (JAZ) proteins regulate critical processes in plants, including growth, development, secondary metabolism, and responses to biotic and abiotic stresses. Previous studies primarily focused on single reference genomes, neglecting gene presence-absence variations (PAV) across populations. Investigating the JAZ gene family at the pan-genomic scale is thus essential to fully understand its evolutionary and functional dynamics in tea plants. Here, 22 high-quality *Camellia sinensis* genomes were analyzed, and 21 JAZs exhibiting substantial presence-absence variability were identified. These included two core genes (present in all 22 genomes), three near-core genes (present in 20–21 genomes), ten dispensable genes (present in 2–19 genomes), and six private genes (unique to single genomes). Phylogenetic analysis categorized these JAZs into five distinct groups, aligning with the *AtJAZ* family. Selection pressure analysis revealed positive selection ($K_a/K_s > 1$) acting on *CsJAZ1*, *CsJAZ8*, and *CsJAZ9*, suggesting adaptive roles during tea domestication. Structural variants (SVs) significantly impacted gene expression and structural integrity; notably, *CsJAZ4*, *CsJAZ9*, and *CsJAZ12* exhibited differential expression when affected by SVs. RNA-seq analysis across four tissues from the 22 tea plant cultivars showed consistently high expression of *CsJAZ1*, *CsJAZ2*, *CsJAZ6*, *CsJAZ9*, *CsJAZ13*, and *CsJAZ14*, highlighting their potential fundamental roles. This study elucidates the JAZ gene family's evolutionary complexity and functional versatility within the tea plant pan-genome. These findings provide valuable insights for future research into *CsJAZ* functions and serve as a model for pan-genomic analyses of gene families in other plant species.

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Introduction

Jasmonates (JAs) are a class of lipid-derived phytohormones that play essential roles in plant growth, development, stress responses, and secondary metabolism regulation^[1]. The JA signaling pathway modulates plant physiological processes through a cascade of molecular interactions, with JAZ (Jasmonate ZIM-domain) proteins acting as key repressors^[2,3]. In the absence of JA signals, JAZ proteins interact with transcription factors such as MYC2, suppressing the expression of downstream genes^[3]. Upon JA perception, JAZ proteins undergo ubiquitination and degradation via the 26S proteasome pathway, releasing MYC2 and other transcription factors to activate gene expression^[4].

JAZ proteins belong to the larger Threonine-Isoleucine-Phenylalanine-Tyrosine (TIFY) superfamily, which also includes the TIFY, PPD, and ZML subfamilies^[5,6]. JAZ proteins are characterized by two conserved domains: the ZIM domain and the Jas domain. The ZIM domain contains a conserved TIFY motif (TIF[F/Y]XG), essential for forming protein dimers and interacting with transcription factors such as MYC2^[7]. The Jas domain, located at the protein's C-terminal end, has a conserved sequence (SLX2FX2KRX2RXSPY) critical for transcription factor binding^[8–10]. Additionally, the TIFY domain interacts with the NINJA protein, collectively repressing JA signaling^[11].

Gene family size and subfamily conservation differences among species are valuable indicators of plant evolutionary histories and environmental adaptations. Although copy number variations (CNVs) and gene presence/absence variants (PAVs) are common findings in pan-genomic studies, most genome-wide analyses of

gene families remain restricted to single reference genomes^[12]. Such approaches overlook population-level genetic diversity, including gene PAVs and CNVs. Recent pan-genomic studies in plants have demonstrated that these variations are widespread, categorizing genes into core (strictly conserved across all individuals) and variable (non-essential, absent in some individuals), classifications considered biologically meaningful. Nevertheless, comprehensive pan-genomic analyses of specific gene families, such as JAZ, remain rare.

Tea, sourced from *Camellia sinensis*, is one of the most widely consumed non-alcoholic beverages worldwide, conferring significant economic, health, and cultural value^[13]. The distinctive quality and bioactive properties of tea are largely attributed to specialized metabolites such as polyphenols and caffeine. Recent studies have shown that jasmonic acid signaling, mediated by the JAZ gene family, plays a central role in regulating the biosynthesis of these key compounds, with jasmonic acid treatments markedly enhancing tea polyphenol and caffeine content by inducing the expression of specific genes^[14,15]. Furthermore, members of the *CsJAZ* family display dynamic expression patterns in response to various hormonal signals (e.g., jasmonic acid, abscisic acid, gibberellin) and environmental stresses (e.g., drought, salt), highlighting their importance in tea plant growth and adaptation^[16]. Despite these advances, current understanding of JAZ gene family evolution, diversity, and function in tea plants remains limited. Notably, traditional analyses based on a single reference genome often overlook gene presence-absence variations (PAVs) present across diverse genetic backgrounds. Therefore, a systematic pan-genome analysis

is essential to comprehensively characterize the JAZ gene family in tea, address existing knowledge gaps, and elucidate their roles in shaping tea quality and environmental resilience.

In this study, a pan-genome-level analysis of the JAZ gene family was conducted using 22 published high-quality tea genomes. The identified JAZs were categorized into core (present in all tea plant cultivars), near-core (present in all but one or two cultivars), dispensable (present in two to twenty cultivars), and private (present only in a single variety) groups based on their distribution. Additionally, structural variations (SVs) and their impacts on gene structure, conserved domains, and protein structure were assessed. Using multi-tissue RNA-seq data, this study further explored the effects of these variations on gene expression to elucidate their evolutionary dynamics and functional significance.

Materials and methods

Identification of the CsJAZ family

The 22 tea plant genomes were obtained from a study by Chen et al.^[12]. *Arabidopsis thaliana* JAZ protein sequences from *A. thaliana* were downloaded from the Arabidopsis Information Resource (TAIR, www.arabidopsis.org, accessed on 10 June 2023). The hidden Markov model (HMM) profiles of the tify domain (PF06200) and Jas_{motif} (PF09425) were retrieved from the Pfam database (www.ebi.ac.uk/interpro/entry/pfam, accessed on 10 June 2023). JAZ domains were searched using HMMER 3.3.2, with an E-value threshold of < 1e-5^[17,18]. A BLASTP search was performed using 12 AtJAZ protein sequences against 22 tea plant genomes to identify JAZs in tea plants. The candidate genes were screened out further through BLAST and HMMER double screening to identify CsJAZ family members. The identified sequences of candidate genes were further verified for the presence of conserved domains using the NCBI Conserved Domain Database (www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi, accessed on 28 July 2023) and SMART (<http://smart.embl-heidelberg.de>, accessed on 28 July 2023). Finally, proteins containing the tify domain and Jas_{motif} were considered JAZ members. CsJAZs were categorized into core genes (present on all tea cultivar genomes), near-core genes (> 90%), dispensable genes (5%–90%), and private genes (< 5%) following the direction of Sun et al.^[19]. The predicted isoelectric points (pI) and molecular weight (MW) of the CsJAZs were predicted using the tool from the ExPasy website (<https://web.expasy.org/protparam>).

Phylogenetic analysis and presence/absence variation of the CsJAZ family

The protein sequences of the JAZs from *Arabidopsis* and *C. sinensis* were used for phylogenetic analysis. Multiple sequence alignments were performed using MAFFT v7.490^[20], and the maximum likelihood method (ML) phylogenetic tree was constructed using RAXML software^[21]. Finally, the ML phylogenetic tree was uploaded to the iTOL (<https://itol.embl.de>) online website for optimization^[22]. Using RScript and the R package *heatmap*, heatmaps were used to describe the presence/absence of each JAZ in 22 accessions^[23].

Ka/Ks calculation of the CsJAZs family

The amino acid sequence and CDS coding sequence of CsJAZs were downloaded from (www.tea-pangenome.cn/download)^[16], and the CDS sequence of AtJAZs was downloaded from (www.arabidopsis.org). The CDS sequence of AtJAZ was used as a reference to compare with 22 tea plant cultivars. JAZ by diamond, data processing, and calculation of synonymous substitution rates (Ks) values were performed using the WGD program, and visualization was performed using the R packages *ggribes* and *ggplot2* to plot peak ridge maps^[24]. The CsJAZs protein sequence was compared

with the reference genomic protein sequence ('Mingke 1' [MK1]) in both directions by BLAST, and TBtools calculated the Ka/Ks values of CsJAZs^[25]. Finally, the heat map was plotted using the R package *heatmap*.

Analysis of the gene structure, conserved and structural domains of TPS under the influence of SV of CsJAZs

Multiple sequence comparisons of CsJAZs were performed using MUSCLE to obtain the position of SVs in each species, and the results were visualized using the R package *ggmsa*. The conserved motif analysis of CsJAZs sequences was performed using the MEME program^[26]. The parameters were set as follows: the number of occurrences of each functional domain in each sequence was variable, and the maximum number of motifs was set to ten. The gene structure and conserved motifs of CsJAZ family members were visualized using the TBtools subroutine 'Gene Structure Viewer' using the files generated in the previous step and the GFF file^[25].

Analysis of protein tertiary structure of JAZs under the influence of SV

The SV-containing CsJAZs protein sequences were uploaded to the Interpro database (www.ebi.ac.uk/interpro/search/sequence) to obtain structural domain information. To further analyze the three-dimensional structural changes under the influence of SV, via the AlphaFold2 online tool <https://colab.research.google.com/github/sokrypton/ColabFold/blob/main/AlphaFold2.ipynb>) to analyze the 3D structure of CsJAZs^[27]. The sequences with pLDDT scores greater than 90 were considered to be approximations of the true structure, and the sequences with pLDDT > 90 were extracted using an in-house Perl script and finally visualized by PyMOL.

RNA-seq data analysis

RNA-seq data for tea plants were obtained from Chen et al.^[12]. After quality control of the raw data using fastp software, all clean reads were mapped to the *C. sinensis* genome using hisat2 software with default parameters. Gene expression levels were quantified by calculating transcripts per million (TPM) values using featureCount. The CsJAZs expression in different tissues was visualized using the R package *heatmap* with log₁₀ (TPM + 1).

Results

Pan-genome-wide identification of CsJAZs

A pan-genome-wide analysis was performed to identify JAZ family members across 22 tea plant genomes using BLASTP searches and conserved domain validations (Pfam, CDD, and SMART). A total of 21 CsJAZs were identified and classified as two core genes (present in all 22 genomes), three near-core genes (present in 20–21 genomes), ten dispensable genes (present in 2–19 genomes), and six private genes (unique to single genomes) (Supplementary Table S1). The predicted CsJAZs ranged from 137 to 451 amino acids in length (mean: 292 residues), with molecular weights varying from 15.6 to 48.2 kDa (mean: 31.3 kDa) and isoelectric points (pI) between 4.66 and 10.57 (mean: 8.56) (Supplementary Table S2). Based on comparisons with JAZs protein structure in *A. thaliana* (AtJAZs) classification^[5], CsJAZs were assigned to five groups: group I and III contained a single member each, group II had two members, group IV comprised four members, and group V was the largest, with thirteen members (Fig. 1a). Notably, six private genes (CsJAZ16–CsJAZ21) were uniquely detected in single tea plant cultivars (*C. sinensis* var. *assamica* (CSA) 'Guihong 3' [GH3], 'Yinghong 9' [YH9], *C. sinensis* var. *sinensis* (CSS) 'Jiaming 1' [JM1], 'Longjing 43' [LJ43], and 'Zhuyeqi' [ZYQ]), suggesting potential contributions to cultivar-specific traits (Fig. 1b).

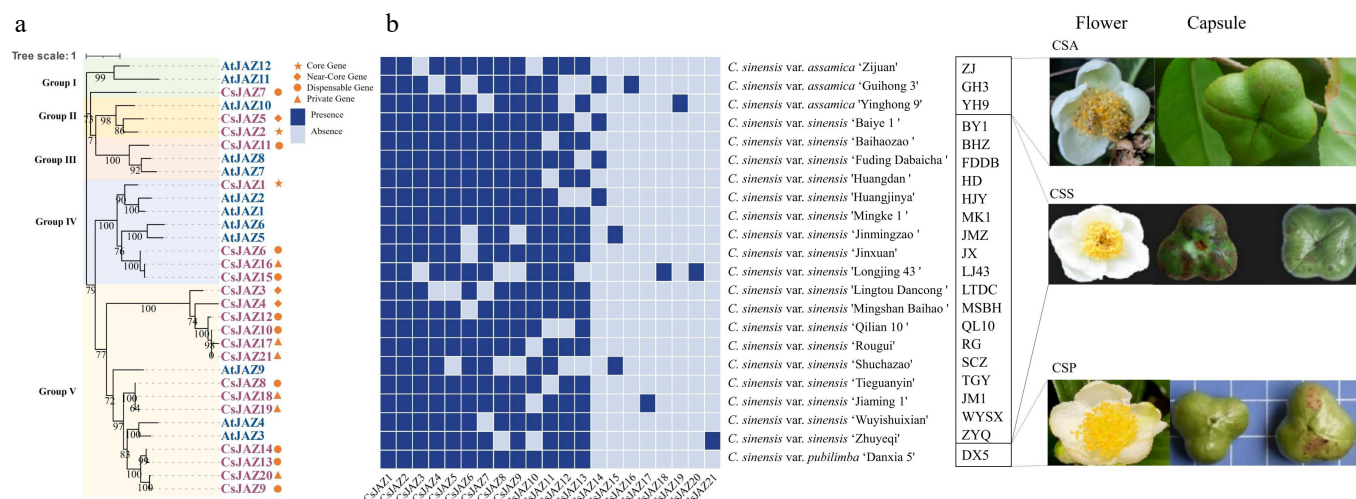


Fig. 1 (a) Phylogenetic tree of JAZ gene family in tea plant and *Arabidopsis*. (b) Heatmap of the presence and absence of 21 JAZs in 22 tea plant cultivars.

Selection pressures acting on CsJAZs

To understand the selective pressures influencing *CsJAZs* evolution, the synonymous substitution rate (K_s) and the ratio of non-synonymous to synonymous substitutions (K_a/K_s) were analyzed across 22 tea plant cultivars. K_s distribution revealed two distinct peaks across all cultivars, indicating two recent gene duplication events specific to the JAZ family (Fig. 2a). Cultivars 'Baihaozao' (BHZ) and 'Huangdan' (HD) exhibited smaller K_s values for the most recent duplication event, suggesting these duplications occurred more recently. Additionally, 15 cultivars—*C. sinensis* var. *sinensis* 'Baiye 1' (BY1), 'BHZ', 'HD', 'Lingtou Dancong' (LTDC), 'Huangjinya' (HJY), 'MK1', 'Fuding Dabaicha' (FDDB), 'Jinxuan' (JX), 'Longjing 43' (LJ43), 'Mingshan Baihao' (MSBH), 'Rougui' (RG), 'Zhuyeqi' (ZYQ), 'Shuchazao' (SCZ), 'Tieguanyin' (TGY), and 'JM1'—had notably shorter intervals between the two duplication peaks compared to the remaining seven cultivars. Further, most *CsJAZs* exhibited K_a/K_s ratios below 1.0, indicating that they are likely subject to purifying selection, which maintains sequence conservation by removing deleterious mutations. In contrast, *CsJAZ1* (in 'FDDB' and 'MSBH'), *CsJAZ8* (in 'YH9', *C. sinensis* var. *pubilimba* 'Danxia 5' [DX5], 'BY1', 'JM1', 'LJ43', and *C. sinensis* var. *sinensis* 'Qilan 10' [QL10]), and *CsJAZ9* (in 'JM1' and 'LJ43')—displayed K_a/K_s values greater than 1.0, which may suggest either positive selection or relaxed selective constraints during tea domestication. To further assess these signals, PAML

branch-site model analyses were performed on *CsJAZ1*, *CsJAZ8*, and *CsJAZ9*. However, these analyses did not yield significant likelihood ratio test statistics nor identify any codons under positive selection using BEB analysis. Thus, robust evidence for adaptive evolution in these genes was not obtained from the branch-site model analysis (Fig. 2b; Supplementary Table S3).

SVs influence different *CsJAZ* gene structures and expression

Three SV-affected genes were examined: *CsJAZ4*, *CsJAZ9*, and *CsJAZ12*, comparing their sequences across representative tea plant varieties (CSS, CSA, var. *pubilimba*) (Figs 3, 4; Supplementary Figs S1–S3). *CsJAZ4* exhibited a 77-bp insertion in cultivars 'Zijuan' (ZJ), 'DX5', and 'MK1' relative to the reference cultivar 'FDDB', resulting in significant expression changes in 'ZJ' (Fig. 3b). *CsJAZ9* had a 315-bp deletion in 'ZJ', 'JX', and 'MK1' relative to 'DX5', correlating with elevated expression in 'DX5' (Fig. 3c). *CsJAZ12* showed deletions of 86 and 58 bp in 'LTDC', 'DX5', and 'MK1' relative to 'ZJ', leading to higher expression in 'ZJ' compared to deletion cultivars (Fig. 3d). These findings underscore that SVs significantly impact gene expression patterns of *CsJAZ9* and *CsJAZ12*.

Compared to the reference cultivar 'FDDB', *CsJAZ4* contained a 77-bp insertion in cultivars 'ZJ', 'DX5', and 'MK1', coinciding with significant differences in gene expression levels in 'ZJ' and 'MK1' relative to 'FDDB' (Fig. 4a). Similarly, *CsJAZ9* exhibited a 315-bp

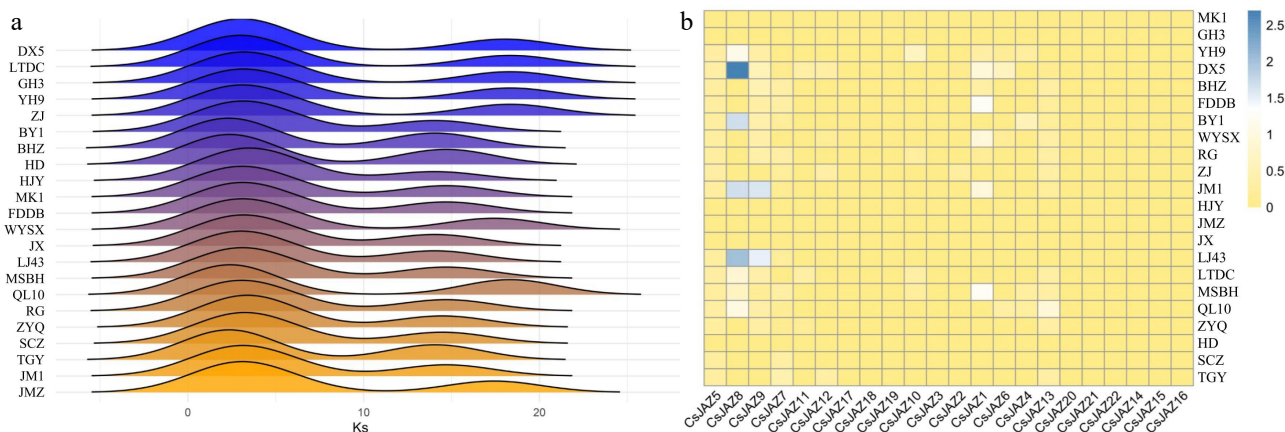


Fig. 2 K_a/K_s values of *CsJAZ*. (a) Distribution of K_s values of *CsJAZ* in 22 tea plant cultivars. (b) Heatmap of the frequency of occurrence of different tea plant cultivars at each JAZ.

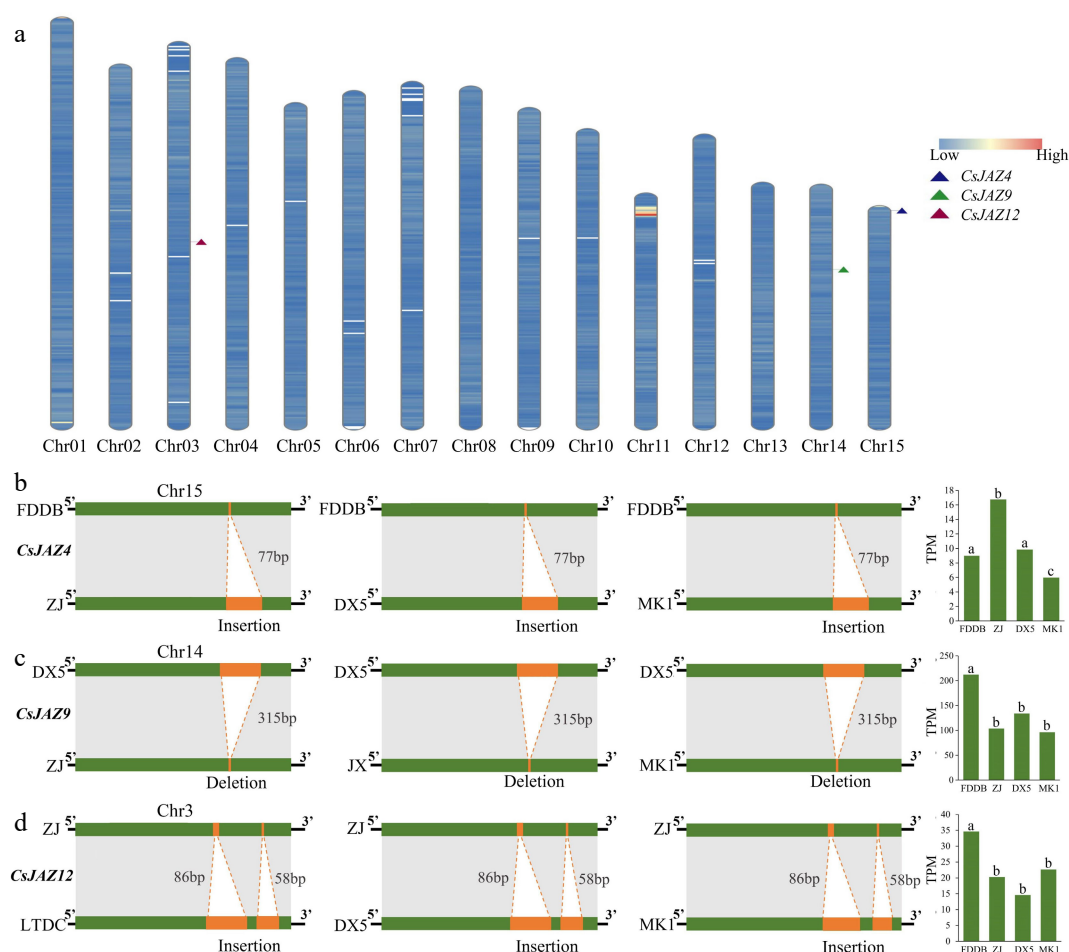


Fig. 3 Effect of SVs on genes. (a) Location of genes on chromosomes, using the 'MK1' genome as a template. (b) Effect of SV insertion and deletion on *CsJAZ4* and significant effect of SVs on the expression of JAZ4 in different tea plant cultivars. (c) Effect of SV insertion and deletion on *CsJAZ9* and significant effect of SVs on the expression of JAZ9 in different tea plant cultivars. (d) Effect of SV insertion and deletion on *CsJAZ12* and significant effect of SVs on the expression of JAZ12 in different tea plant cultivars. The bar graph shows the TPM expression matrix of tea plant leaves.

deletion in 'ZJ', 'JX', and 'MK1' compared to the reference 'DX5', potentially explaining its higher expression in 'DX5' (Fig. 4b). For *CsJAZ12*, deletions of 86 and 58 bp occurred in 'LTDC', 'DX5', and 'MK1' compared to the reference 'ZJ', correlating with elevated expression observed in 'ZJ' (Fig. 4c). Together, these results indicate that structural variations substantially shape expression patterns of these *CsJAZs*.

Effects of SVs on *CsJAZ* protein structure

To assess how SVs influence protein conformation, the three-dimensional structures of *CsJAZ4*, *CsJAZ9*, and *CsJAZ12* were predicted (using cultivar 'MK1' as reference) with AlphaFold2. This method assigns each amino acid residue a confidence score (pLDDT: 0–100), with values above 90 indicating highly reliable structural predictions. Regions scoring above 90 overlapped substantially with conserved functional domains (Fig. 5). Specifically, *CsJAZ4* and *CsJAZ12* each contained the conserved CCT, ZnF-GATA, and Tify domains, whereas *CsJAZ9* included the conserved Tify and Jas-motif domains. The presence of these intact core domains suggests that, despite SV-induced sequence alterations, the key structural features of these *CsJAZs* are likely maintained, though their functional integrity requires further experimental validation.

Transcriptome analyses and evolutionary patterns of *CsJAZs*

Transcriptome sequencing data were analyzed across four tissues (flower, root, stem, leaf) in 22 tea plant cultivars to characterize gene

expression. Expression analysis confirmed the transcription of over half of the identified *CsJAZs* in at least one tissue (Fig. 6a), supporting the accuracy of our pan-genome predictions. Clustering analyses grouped genes according to their expression profiles: genes highly expressed in all tissues, genes uniformly low or absent across tissues, and genes lacking expression, specifically in flowers, formed distinct clusters. Among the most consistently expressed genes were *CsJAZ1*, *CsJAZ2*, *CsJAZ6*, *CsJAZ9*, *CsJAZ13*, and *CsJAZ14*, highlighting their potential roles as core regulatory genes across diverse tissues.

A comparative analysis of gene expression patterns against phylogenetic relationships among the 22 tea plant cultivars revealed clear patterns of transcriptomic divergence. Cultivars clustered into three distinct phylogenetic branches: 'GH3' formed a distinct lineage; 'JM1', 'HJY', 'FDDB', 'WYSX', 'JX', 'BY1', 'SCZ', 'ZYQ', and 'JMZ' grouped closely; 'YH9', 'LTDC', 'HD', 'TGY', 'LJ43', 'ZJ', 'BHZ', 'MK1', 'DX5', 'RG', 'MSBH', and 'QL10' comprised a separate lineage (Fig. 6b). By aligning transcriptomic data clusters with these phylogenetic relationships, evolutionary divergence was visualized in expression patterns, demonstrating how pan-genomic and transcriptomic data integration elucidates the evolutionary dynamics of gene families.

Discussion

Integrating pan-genomic and transcriptomic approaches offers a robust framework for unraveling gene family evolution and

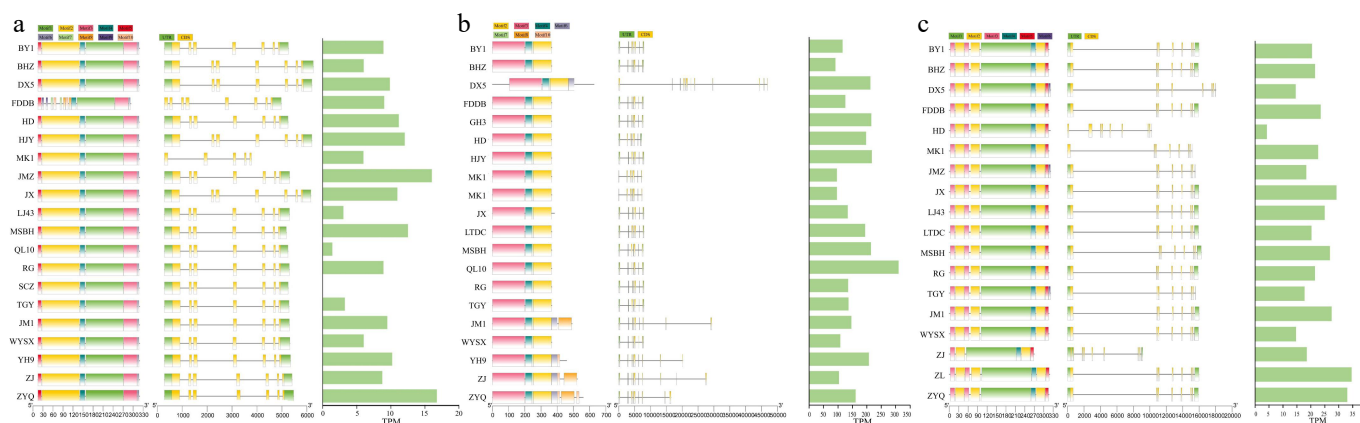


Fig. 4 Gene structure and TPM values in 22 tea plant genomes. (a) Gene structure and TPM values of *CsJAZ4* in 22 tea plant genomes. (b) Gene structure and TPM values of *CsJAZ9* in 22 tea plant genomes. (c) Gene structure and TPM values of *CsJAZ12* in 22 tea plant genomes. TPM values represent transcript abundance in leaf tissue, which was used as a representative condition for assessing expression variation across accessions, where 'QL10' and 'SCZ' are mixed tissues (containing leaves).

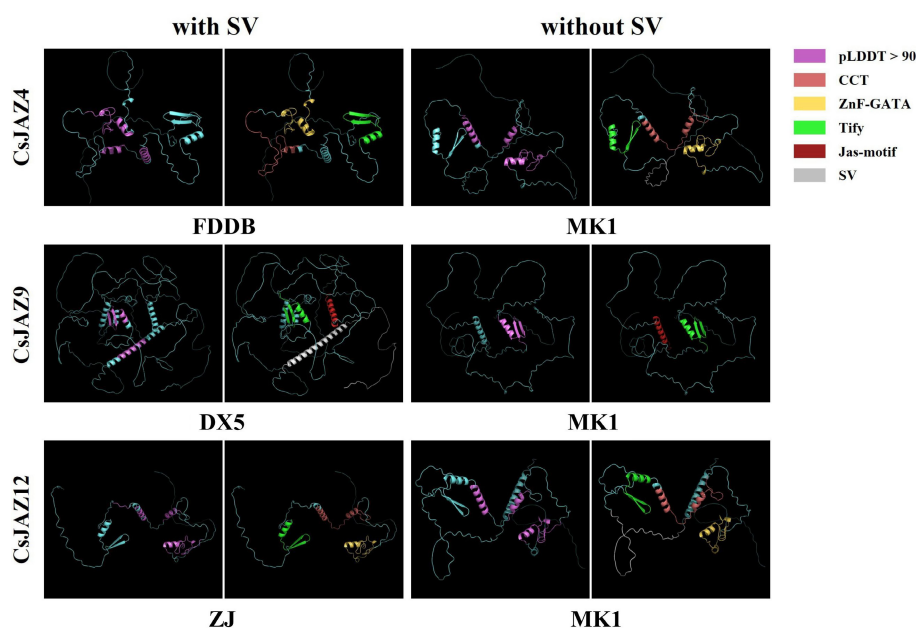


Fig. 5 Protein tertiary structure of JAZs under the influence of SV. Purple represents pLDDT > 90 indicating that the residue has a very high model confidence; pink represents the CCT motif, yellow represents the ZnF-GATA, green represents the Tify domain, red represents the Jas-motif domain, grey represents SV, and blue represents the amino acid sequence.

functional diversity beyond traditional single-genome analyses^[28,29]. This approach enhances our understanding of gene function, evolutionary dynamics, and cultivar-specific traits, providing a model for future genomic investigations in tea and other plant species.

JAZ proteins play crucial roles in plant development, flowering, stress responses, and plant-pathogen interactions^[5,30]. Studies in *A. thaliana* revealed that *AtJAZ1* positively regulates flowering time and seed traits, whereas *AtJAZ4* influences hypocotyl and petiole elongation by repressing auxin- and cytokinin-associated regulators^[31,32]. Additionally, overexpression of *AtJAZ8*, *AtJAZ9*, or *AtJAZ13* reduces jasmonate sensitivity, thus affecting root growth^[33]. While JAZ family members have been extensively characterized in model plants, investigations based solely on a single reference genome often fail to capture a species' full genetic diversity and complexity^[34,35].

Here, a pan-genomic approach was leveraged, analyzing 22 high-quality tea plant genomes to understand the JAZ family^[12] comprehensively. 21 *CsJAZs* were identified, categorizing them into core

(present in all cultivars), near-core, dispensable, and private (unique to specific cultivars) groups. Core genes likely fulfill essential biological roles, while private genes (*CsJAZ16*–*CsJAZ21*), identified exclusively in cultivars such as 'JM1', 'LJ43', 'YH9', and 'ZYQ', potentially underpin cultivar-specific traits. Notably, *CsJAZ3*, *CsJAZ4*, *CsJAZ10*, *CsJAZ12*, *CsJAZ17*, and *CsJAZ21* cluster closely in the phylogeny and display mutually exclusive presence-absence patterns across cultivars (Fig. 1b), suggesting functional redundancy. The mutually exclusive distribution may ensure the maintenance of critical JAZ-mediated functions despite gene loss in individual genomes^[29].

Evolutionary analysis based on *Ks* and *Ka/Ks* ratios indicated distinct selective pressures across *CsJAZ* family members. Two recent duplication events were evident from the *Ks* distributions, with particularly recent duplications in cultivars 'BHZ' and 'HD'. Most *CsJAZs* exhibited *Ka/Ks* ratios below 1.0, indicating pervasive purifying selection and evolutionary constraints that likely preserve essential gene functions. In contrast, *CsJAZ1* (in 'FDD8' and 'MSBH'), *CsJAZ8* (in 'YH9', 'DX5', 'BY1', 'JM1', 'LJ43', and 'QL10'), and *CsJAZ9* (in

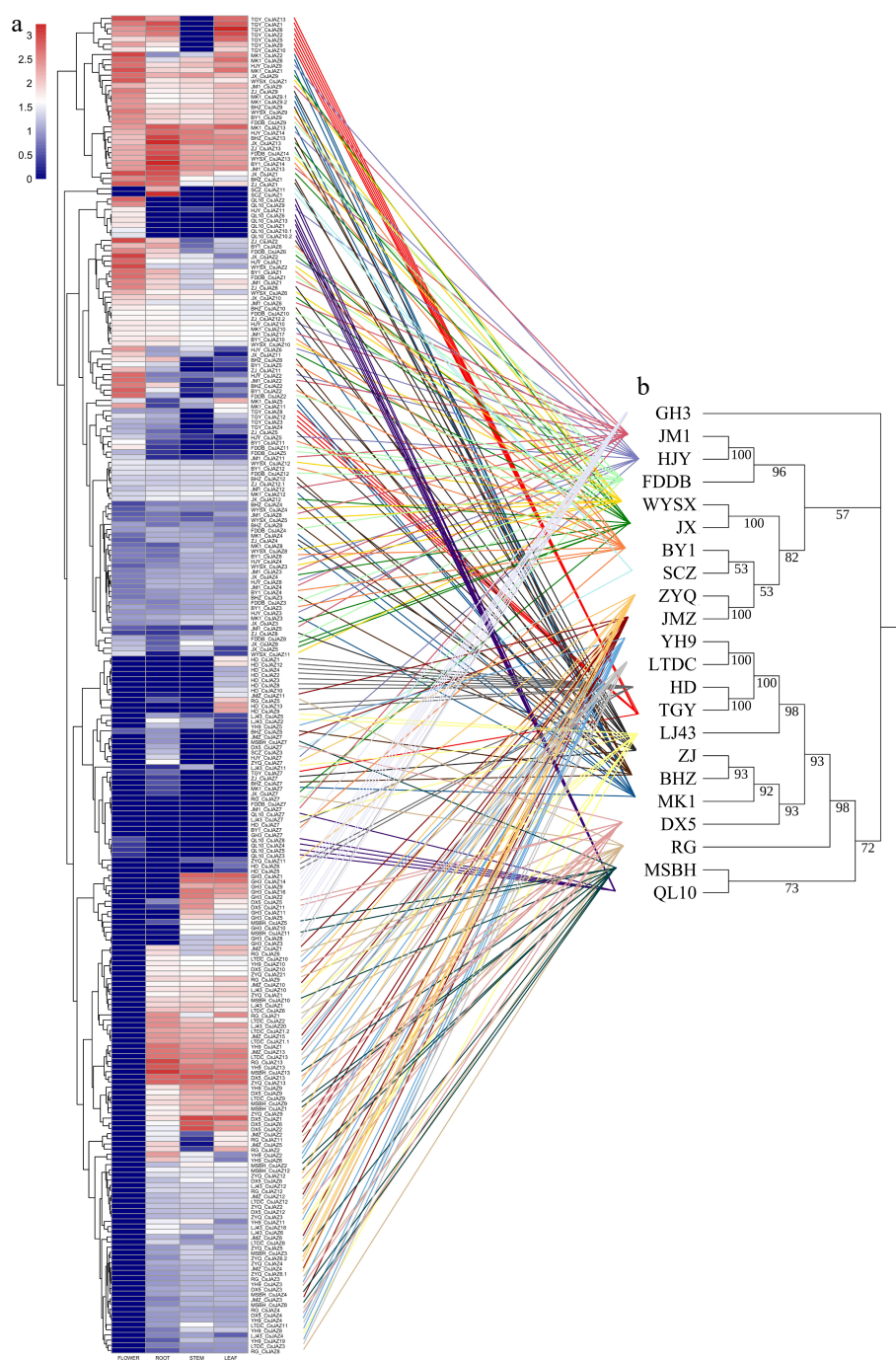


Fig. 6 (a) The heatmap of expression profile clustering in the pangenome of *CsJAZs* from 22 tea plant cultivars in four tissues (flower, root, stem, leaf). (b) Species phylogeny tree. Gene expression values were normalized using $\log_{10}(\text{TPM} + 1)$ transformation. Comparison of gene expression clustered branching plots (left tree) with species phylogenies (right tree) via connecting lines (different species highlighted in different colors).

'JM1' and 'LJ43') showed Ka/Ks ratios greater than 1.0, which may reflect either episodes of positive selection or relaxed functional constraints. However, further branch-site model analyses using PAML did not yield significant likelihood ratio tests or identify any codons under positive selection, suggesting that the elevated Ka/Ks values may not robustly support adaptive evolution in these gene lineages. These findings highlight the complexity and potential limitations of inferring positive selection from Ka/Ks ratios alone, especially in gene families subject to recent duplication and structural variation.

SVs, including insertions and deletions, significantly impacted *CsJAZ* structures and expression patterns. For instance, SVs within

CsJAZ4, *CsJAZ9*, and *CsJAZ12* altered their expression levels across cultivars. Such SV-induced modifications can also result in loss or alteration of functional domains, complicating traditional bioinformatics identification. Nevertheless, genes with these altered sequences may retain critical biological functions. Similar phenomena have been documented in other tea genes: structural variants in *GluRS* disrupt domains involved in chlorophyll synthesis pathways, affecting leaf coloration^[12], and insertion of LTR/Gypsy elements upstream of *CsMYB114* correlates strongly with anthocyanin-related leaf pigmentation^[12,36,37]. Thus, SVs are crucial in shaping cultivar-specific phenotypic diversity.

Transcriptome analyses across multiple tissues revealed stable expression of core *CsJAZs* (*CsJAZ1* and *CsJAZ2*), underscoring their fundamental roles. Several *CsJAZs* showed tissue-specific or cultivar-specific expression patterns, likely reflecting adaptive specialization, such as stress responses. Previous studies indicated that *CsJAZ3*, *CsJAZ5*, *CsJAZ6*, *CsJAZ8*, and *CsJAZ12* positively regulate the ICE-CBF/DREB1 pathway in response to cold stress^[34]. Our comparative analyses between phylogenetic relationships and gene expression patterns further illustrated that closely related tea plant cultivars share similar transcriptional profiles, highlighting conserved expression patterns linked to evolutionary history.

Conclusions

This study conducted a comprehensive pan-genome analysis of the JAZ family across 22 high-quality tea plant genomes, identifying 21 *CsJAZs* categorized as two core, three near-core, ten dispensable, and six private genes. These genes are clustered into five groups based on comparisons with the *Arabidopsis* JAZ classification. Evolutionary analyses revealed that *CsJAZ1*, *CsJAZ8*, and *CsJAZ9* underwent positive selection during tea domestication, as indicated by elevated *Ka/Ks* values (> 1). SVs significantly influenced gene structure, conserved protein domains, and expression patterns, particularly for *CsJAZ4*, *CsJAZ9*, and *CsJAZ12*. Transcriptome analyses across multiple tissues demonstrated consistently high expression for *CsJAZ1*, *CsJAZ2*, *CsJAZ6*, *CsJAZ9*, *CsJAZ13*, and *CsJAZ14*, highlighting their functional importance across tea plant cultivars. Collectively, these findings enhance our understanding of the evolutionary dynamics and functional diversity of the JAZ family, providing valuable genomic resources and insights for future genetic improvement and stress adaptation studies in tea plants.

Author contributions

The authors confirm their contributions to the paper as follows: study conception and design, and manuscript editing and revision: Niu S, Xiong B; data analysis: Xiong B, Yang Y, Li Q; figures and manuscript constructing: Yang Y; experiments performing: Li Q; materials providing and facilities testing: Niu S; manuscript writing: Xiong B. All authors reviewed the results and approved the final version of the manuscript.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Conflict of interest

The authors declare that they have no conflict of interest.

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References

1. Wasternack C, Hause B. 2013. Jasmonates: biosynthesis, perception, signal transduction and action in plant stress response, growth and development. An update to the 2007 review in *Annals of Botany*. *Annals of Botany* 111:1021–58
2. Chini A, Fonseca S, Fernández G, Adie B, Chico JM, et al. 2007. The JAZ family of repressors is the missing link in jasmonate signalling. *Nature* 448(7154):666–71
3. Thines B, Katsir L, Melotto M, Niu Y, Mandaokar A, et al. 2007. JAZ repressor proteins are targets of the SCF^{COI1} complex during jasmonate signalling. *Nature* 448(7154):661–65
4. Das S, Goswami M, Yadav RNS, Baruah AM, Bandyopadhyay T. 2024. Methyl jasmonate alters expression of enzymes and metabolites of terpenoid biosynthesis in tea cell culture. *Plant Cell, Tissue and Organ Culture (PCTOC)* 159:25
5. Song H, Duan Z, Wang Z, Li Y, Wang Y, et al. 2022. Genome-wide identification, expression pattern and subcellular localization analysis of the JAZ gene family in *Toona ciliata*. *Industrial Crops and Products* 178:114582
6. Ju L, Jing Y, Shi P, Liu J, Chen J, et al. 2019. JAZ proteins modulate seed germination through interaction with ABI5 in bread wheat and *Arabidopsis*. *New Phytologist* 223(1):246–60
7. Vanholme B, Grunewald W, Bateman A, Kohchi T, Gheysen G. 2007. The tify family previously known as ZIM. *Trends in Plant Science* 12(6):239–44
8. Yan Y, Stolz S, Chételat A, Reymond P, Pagni M, et al. 2007. A downstream mediator in the growth repression limb of the jasmonate pathway. *The Plant Cell* 19(8):2470–83
9. Sheard LB, Tan X, Mao H, Withers J, Ben-Nissan G, et al. 2010. Jasmonate perception by inositol-phosphate-potentiated COI1–JAZ co-receptor. *Nature* 468(7322):400–5
10. Zhou SL, Zhang JX, Jiang S, Lu Y, Huang YS, et al. 2024. Genome-wide identification of JAZ gene family in sugarcane and function analysis of *ScJAZ1/2* in drought stress response and flowering regulation. *Plant Physiology and Biochemistry* 210:108577
11. Geerinck J, Pauwels L, De Jaeger G, Goossens A. 2010. Dissection of the one-MegaDalton JAZ1 protein complex. *Plant Signaling & Behavior* 5(8):1039–41
12. Chen S, Wang P, Kong W, Chai K, Zhang S, et al. 2023. Gene mining and genomics-assisted breeding empowered by the pangenome of tea plant. *Camellia sinensis*. *Nature Plants* 9:1986–99
13. Xia EH, Zhang HB, Sheng J, Li K, Zhang QJ, et al. 2017. The tea tree genome provides insights into tea flavor and independent evolution of caffeine biosynthesis. *Molecular Plant* 10(6):866–77
14. Shen J, Zou Z, Xing H, Duan Y, Zhu X, et al. 2020. Genome-wide analysis reveals stress and hormone responsive patterns of JAZ family genes in *Camellia Sinensis*. *International Journal of Molecular Sciences* 21(7):2433
15. Shen Y, Wang J, Si X, Liang X, Zheng Z, et al. 2025. Revealing the molecular mechanism of biosynthesis and transcriptional regulation of PAs, caffeine and linalool globally under simulative stress in coffee plants. *International Journal of Biological Macromolecules* 310:143103
16. Li C, Xu M, Cai X, Han Z, Si J, et al. 2022. Jasmonate signaling pathway modulates plant defense, growth, and their trade-offs. *International Journal of Molecular Sciences* 23(7):3945
17. Finn RD, Bateman A, Clements J, Coghill P, Eberhardt RY, et al. 2014. Pfam: the protein families database. *Nucleic Acids Research* 42(D1):D222–D230
18. Johnson LS, Eddy SR, Portugaly E. 2010. Hidden Markov model speed heuristic and iterative HMM search procedure. *BMC Bioinformatics* 11:431
19. Sun Y, Xiao W, Wang QN, Wang J, Kong XD, et al. 2023. Multiple variation patterns of terpene synthases in 26 maize genomes. *BMC Genomics* 24(1):46

20. Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30:772–80
21. Stamatakis A. 2014. RAXML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30(9):1312–13
22. Letunic I, Bork P. 2016. Interactive tree of life (iTOL) v3: an online tool for the display and annotation of phylogenetic and other trees. *Nucleic Acids Research* 44(W1):W242–W245
23. Gu Z, Eils R, Schlesner M. 2016. Complex heatmaps reveal patterns and correlations in multidimensional genomic data. *Bioinformatics* 32:2847–49
24. Zwaenepoel A, Van de Peer Y. 2019. wgd—simple command line tools for the analysis of ancient whole-genome duplications. *Bioinformatics* 35(12):2153–55
25. Chen C, Chen H, Zhang Y, Thomas HR, Frank MH, et al. 2020. TBtools: an integrative toolkit developed for interactive analyses of big biological data. *Molecular Plant* 13(8):1194–202
26. Bailey TL, Boden M, Buske FA, Frith M, Grant CE, et al. 2009. MEME SUITE: tools for motif discovery and searching. *Nucleic Acids Research* 37:W202–W208
27. Jumper J, Evans R, Pritzel A, Green T, Figurnov M, et al. 2021. Highly accurate protein structure prediction with AlphaFold. *Nature* 596(7873):583–89
28. Xuan X, Su S, Tan J, Guo H, Jiao Y, et al. 2024. Genome-wide identification, characterization, and expression pattern analysis of the JAZ gene family in Moso bamboo during rapid shoot development. *Advances in Bamboo Science* 7:100083
29. Huang H, Gao H, Liu B, Qi T, Tong J, et al. 2017. *Arabidopsis* MYB24 regulates jasmonate-mediated stamen development. *Frontiers in Plant Science* 8:1525
30. Navarro A, Barton NH. 2003. Chromosomal speciation and molecular divergence—accelerated evolution in rearranged chromosomes. *Science* 300(5617):321–24
31. Kazan K, Manners JM. 2012. JAZ repressors and the orchestration of phytohormone crosstalk. *Trends in Plant Science* 17(1):22–31
32. de los Angeles Miccono M, Yang HW, DeMott L, Melotto M. 2023. Review: losing JAZ4 for growth and defense. *Plant Science* 335:111816
33. Han X, Kui M, He K, Yang M, Du J, et al. 2023. Jasmonate-regulated root growth inhibition and root hair elongation. *Journal of Experimental Botany* 74(4):1176–85
34. Zheng Y, Chen X, Wang P, Sun Y, Yue C, et al. 2020. Genome-wide and expression pattern analysis of JAZ family involved in stress responses and postharvest processing treatments in *Camellia sinensis*. *Scientific Reports* 10(1):2792
35. Tong C, Jia Y, Hu H, Zeng Z, Chapman B, et al. 2025. Pangenome and pantranscriptome as the new reference for gene-family characterization: a case study of basic helix-loop-helix (*bHLH*) genes in barley. *Plant Communications* 6(1):101190
36. Schön A, Krupp G, Gough S, Berry-Lowe S, Kannangara CG, et al. 1986. The RNA required in the first step of chlorophyll biosynthesis is a chloroplast glutamate tRNA. *Nature* 322(6076):281–84
37. Wei K, Wang L, Zhang Y, Ruan L, Li H, et al. 2019. A coupled role for *CsMYB75* and *CsGSTF1* in anthocyanin hyperaccumulation in purple tea. *The Plant Journal* 97(5):825–40



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