

Functional Genomics in Tea: Pathways and Mechanisms Underlying Key Traits

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Abstract Recent years, the research on functional genomics of tea trees has accelerated, with the release of high-quality genomes, pan genomes, and the maturity of multi omics technologies being key driving forces behind it. Many key traits, such as the synthesis of flavor compounds (catechins, theanine, terpenes, etc.) and stress resistance (cold resistance, drought resistance), their corresponding core genes, regulatory pathways, and even hidden structural variations, are being gradually uncovered. This study mainly focuses on several typical methods, including transcriptome analysis, gene silencing, metabolome integration, QTL mapping, GWAS to explore their practical applications in functional gene analysis. By combining representative varieties such as Longjing 43 and Zikui, the association pathways between gene expression, copy number variation, and specific phenotypes were further demonstrated. This study not only explains the mechanism of trait formation, but provides support for molecular breeding and quality improvement of tea trees.

Keywords Tea tree; Functional genomics; Multi omics integration; Molecular breeding; Quality traits; Anti stress mechanism

1 Introduction

Tea (*Camellia sinensis*), one of the most widely consumed beverages in the world, with a unique flavor, health benefits and economic value. The initial sequencing of the tea tree genome revealed its large genome size, high proportion of repetitive sequences, and complex evolutionary history, including genome-wide replication events, and large-scale expansion of gene families related to secondary metabolism (Xia et al., 2017; Wei et al., 2018; Xia et al., 2020a; Tariq et al., 2024). Later, researchers constructed pan-genome and reference genome assemblies of various tea tree varieties, identified and annotated core genes, optional genes, structural variations, and allelic diversity related to important traits (Chen et al., 2023). These resources have also facilitated the development of molecular markers, and databases, such as the tea tree information archive, providing support for comparative analysis and functional studies (Xia et al., 2019; 2020b).

Functional genomics methods, including transcriptomics, gene co expression network analysis, gene silencing techniques, and multi omics integration strategies, have played an important role in studying the association between annotated genes and phenotypic traits (Tai et al., 2018; Kong et al., 2022; Li et al., 2022a). These studies identified candidate genes and regulatory modules involved in the biosynthesis, stress response, and developmental processes of key metabolites (e.g., catechins, theanine, and caffeine), providing mechanistic explanations for understanding tea plant trait variations (Qiu et al., 2020; Fang et al., 2021).

Functional genomics has revealed the complex regulatory mechanisms of gene expression, and metabolic networks in tea plants, clarifying how transcription factors, epigenetic modifications and gene co-expression modules synergistically regulate the synthesis of quality-related metabolites, and responses to environmental stress (Tai et al., 2018; Wang et al., 2018; Shen et al., 2019; Krishnatreya et al., 2021). Through the analysis of integrated transcriptomic, metabolomic and epigenomic data, researchers further deepened their understanding of these networks and their roles in tea quality and adaptability (Han et al., 2024).

The combination of functional genomics with genome assisted breeding strategies, such as genome-wide association analysis (GWAS), marker assisted selection, and QTL mapping, accelerates the identification process

of allele variations, and molecular markers associated with desirable traits (Xu et al., 2018; Chen et al., 2023). These advances are driving efficient and precise breeding of tea tree varieties, improving their quality, yield, and stress resistance (Koech et al., 2019; Yamashita et al., 2020).

This study explores the latest advances in functional genomics of tea plants, based on the molecular mechanisms, and regulatory pathways of key agronomic, and quality traits. By integrating the research results of genomics, transcriptomics, and metabolomics in recent years, we hope to summarize existing achievements, identify current knowledge gaps, and propose research directions for the future application of functional genomics in tea tree improvement.

2 Key Technologies in Tea Functional Genomics

2.1 Transcriptome sequencing and gene expression profiling

RNA sequencing (RNA-Seq) is a fundamental tool for studying gene expression in tea plants and can be used to identify differentially expressed genes and alternative splicing events in different tissues and developmental stages. Full-length transcript analysis using long-read sequencing technology further improved the gene model and revealed transcript diversity, which is important for functional annotation and trait association studies (Xia et al., 2019; 2020b).

Transcriptome analysis at different tissues and developmental stages, revealed the spatiotemporal expression regulatory patterns of genes, which related to key metabolic pathways (such as polyphenol and caffeine biosynthesis) (Xia et al., 2019; Li et al., 2022b), provides important clues for understanding how gene expression patterns affect trait variation and quality formation in tea plants.

2.2 Gene editing and functional validation

Although the technology for achieving stable genetic editing in tea plants with CRISPR/Cas9, is still under development, virus-induced gene silencing (VIGS) technology, has been successfully established and can serve as a rapid and efficient functional verification method. VIGS can achieve specific silencing of target genes. For example, the silencing of the caffeine synthase gene *CsTCS1* reduces the caffeine content in tea plants, and verifies the function of this gene *in vivo* (Li et al., 2022a).

The transient gene expression system, provides a practical alternative for tea plant functional genomics research, enabling gene overexpression, silencing and promoter function analysis without the need to establish a stable transformation system (Mohajer et al., 2022).

2.3 Multi-omics integration

The multi-omics integration strategy combines genomic, transcriptomic and metabolomic data, which can comprehensively analyze the molecular mechanisms behind key traits. This integration helps to establish the mapping relationship from genotype to phenotype, identify candidate genes, and pathways involved in metabolite synthesis and stress response (Xia et al., 2019; 2020b; Li et al., 2022b).

With the help of multi-omics datasets, researchers can reconstruct the gene regulatory network that regulates important agronomic traits and quality traits (Xia et al., 2020b). These networks, help identify key regulatory factors and their interactions, providing a theoretical basis and technical support for trait mining and precise tea tree breeding.

3 Functional Genomics of Tea Quality Traits

3.1 Pathways regulating catechin biosynthesis

Catechins, the major polyphenolic compounds in tea, play a key role in tea's flavor and health benefits. Their synthesis occurs primarily through the flavonoid metabolic pathway. Genes encoding enzymes such as chalcone synthase (CHS), anthocyanidin reductase (ANR), leucocyanidin reductase (LAR), and flavonoid 3'5'-hydroxylase (F3'5'H) play a central role in this metabolic pathway. Studies have shown that, functional allelic variation in the F3'5'H gene determines the ratio of dihydroxy to trihydroxy catechins, and that specific single-nucleotide

polymorphisms (SNPs) can explain phenotypic differences in catechin content (Jin et al., 2016). QTL mapping and genome-wide association studies (GWAS) have also identified candidate genes, and molecular markers associated with catechin biosynthesis, providing theoretical support for molecular marker-based breeding of high-quality tea varieties (Koech et al., 2018; 2019; Yamashita et al., 2020).

Transcription factors such as the MYB, bHLH, and WRKY families regulate the expression of genes involved in catechin synthesis, exhibiting tissue-specific and developmental stage-specific regulation, thereby controlling catechin accumulation (Maritim et al., 2020; Parmar et al., 2022). Environmental factors such as drought and temperature regulate catechin content by influencing gene expression. Transcriptome and QTL studies have revealed associations between stress-responsive genes and catechin levels (Koech et al., 2019; Maritim et al., 2020).

3.2 Regulation of theanine accumulation

Theanine is an amino acid unique to tea leaves, whose synthesis primarily relies on the synergistic action of theanine synthase (TS), glutamine synthase (GS), and glutamate dehydrogenase (GDH). The expansion and functional divergence of the GS gene family are closely associated with the high theanine content in tea leaves (Wei et al., 2018). Transcriptome and genomic studies have shown that the regulation of theanine synthesis involves the expansion of related gene families and includes tea-specific regulatory mechanisms, such as unique gene variants and specific expression patterns. These characteristics lead to significant differences in theanine metabolism between tea plants and their closely related species (Wei et al., 2018; Xia et al., 2020b).

Wei et al. (2018) identified a tea plant gene, *CsTSI*, through phylogenetic analysis, that is highly homologous to bacterial GSI-type glutamine synthases. Tissue expression analysis revealed that it is highly expressed in roots, consistent with the tissue distribution of theanine. The researchers constructed a *CsTSI* overexpression line in *Arabidopsis thaliana* and confirmed its ability to synthesize theanine through ethylamine precursor feeding experiments, clarifying its functional role in theanine biosynthesis (Figure 1).

3.3 Aroma biosynthesis networks

Tea aroma is composed of a complex network of volatile compounds, dominated by monoterpenes and fatty acid derivatives. Genes encoding enzymes such as terpene synthase (TPS), and lipoxygenase (LOX) are highly expressed in tea varieties with distinctive aroma characteristics (Maritim et al., 2020).

The TPS gene family is responsible for the synthesis of monoterpenes, while the LOX pathway produces fatty acid-derived volatiles. Transcriptome analysis and protein-protein interaction studies have revealed that, the coordinated regulation of these pathways, and identified several key candidate genes, providing potential targets for future improvements in tea aroma traits (Maritim et al., 2020; Parmar et al., 2022).

4 Functional Genomics of Stress Resistance Traits

4.1 Cold and drought resistance pathways

The abscisic acid (ABA) signaling pathway plays a core role in tea plants' response to abiotic stress. The PYL gene family encodes ABA receptors, and its members are upregulated under drought and low-temperature stress. Some specific genes (like *CSS0047272.1*) respond in both drought and pathogen infection, indicating signal crossover between abiotic and biological stress pathways (An et al., 2023).

Transcription factor families, such as HD-Zip and BZR1, showed stress-responsive expression under cold, drought and salt stress, suggesting their involvement in ABA and other plant hormone-mediated response pathways (Shen et al., 2019; Li et al., 2023a). The expression levels of MYB transcription factors, especially *CsMYB45*, *CsMYB46* and *CsMYB105*, increased under low temperature and methyl jasmonate treatment, regulating the cold resistance of tea plants through the jasmonic acid signaling pathway (Han et al., 2022).

The superoxide dismutase (*SOD*) gene plays a key role in eliminating ROS accumulated, during low temperatures and drought stress. Most *CsSOD* genes are induced under low-temperature stress, while *CsCSD* genes mainly

respond to drought stress. Regulatory mirnas, like *csn-miR398a-3p-1* can regulate *SOD* gene expression, providing a layer of regulation of the post-transcriptional regulatory mechanism (Zhou et al., 2019). Glutathione transferase (GSTs) and MATE, were also upregulated under abiotic stress, which contributed to ROS detoxification and maintaining osmotic pressure balance (Cao et al., 2022; Xie et al., 2024).

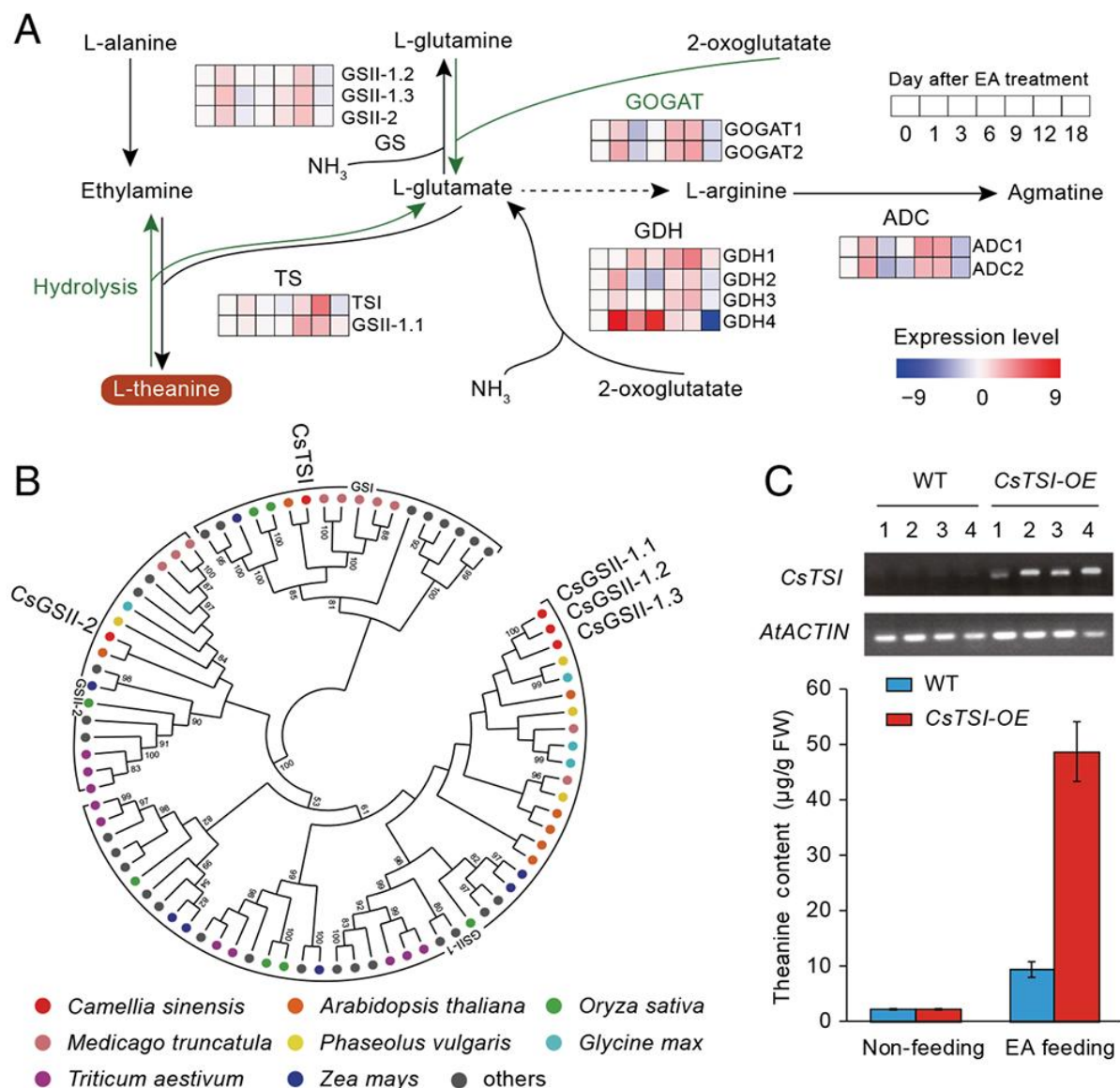


Figure 1 Key genes involved in the theanine biosynthesis pathway. (A) The proposed pathway for theanine biosynthesis and expression of key genes upon precursor ethylamine feeding. TS, GS, GOGAT, GDH, and ADC represent genes encoding theanine synthetase, glutamine synthetase, glutamate synthetase, glutamate dehydrogenase, and arginine decarboxylase, respectively. Tea seedlings grown hydroponically were fed ethylamine chloride for different numbers of days before being sampled for amino acid profiling and transcriptome analyses. (B) Phylogenetic tree of tea TS and GS candidate genes and the available GS genes from prokaryotes, fungi, and plants. The tea TS candidate gene (*CsTSI*) shows high similarity to known GSI-type genes, and other GS candidate genes exhibit high homology with previously reported GSII-type genes in plants. (C) Assay of theanine synthesis activity of *CsTSI* in *Arabidopsis* seedlings. The candidate tea TS gene (*CsTSI*) that shows high similarity to known GSI-type genes was cloned into a binary vector and overexpressed in *Arabidopsis* driven by a 35S promoter. *CsTSI*-OE indicates *CsTSI*-overexpression lines, while WT represents wild type (control). Seedlings were fed with or without 10 mM EA chloride solution (with water as control) for 3 d. Theanine synthesized by the seedlings was extracted and measured. Data are expressed as means \pm SD from at least three independent transgenic lines with replicate experiments. FW, fresh weight (Adopted from Wei et al., 2018)

4.2 Biotic stress responses

Transcriptomic analysis revealed that when tea plants are infected by fungal diseases, a large number of defense-related genes are activated, including those involved in MAPK signal transduction, receptor kinase activity, and cell wall structure regulation. Genes containing the NB-ARC domain, were significantly enriched and positively correlated with both cold resistance and disease resistance traits, suggesting that these defense mechanisms may be shared (Hazra et al., 2023; Li et al., 2025). The *PYL* gene was also expressed in response after insect feeding, further supporting its role in biological stress (An et al., 2023).

The flavonoid synthesis pathway is significantly enriched in the cold and disease resistance of tea plants, among which secondary metabolites play a role as key defense compounds. Under stress conditions, GSTs and other enzymes involved in secondary metabolism, were differentially expressed, enhancing the resistance of plants to pathogenic bacteria (Cao et al., 2022; Hazra et al., 2023; Li et al., 2025).

4.3 Epigenetic regulation of stress responses

Although research on the methylation and histone modification of tea plants under stress conditions is currently insufficient, the expansion and structural variation of gene families related to stress resistance suggest that epigenetic mechanisms may play an important role in regulating stress responsive genes (Tong et al., 2024; Tariq et al., 2024).

Regulatory RNAs, especially miRNAs and long chain non coding RNAs (lncRNAs), are important post transcriptional regulators in stress response. MiRNAs such as *csn-miR398aa-3p-1* and *csn-miR166* target *SOD* and *HD Zip III* genes, respectively, to regulate tolerance to drought and cold stress (Qian et al., 2023; Li et al., 2025). The *csn-miR171b-3p_2-CsSCL6-4* module can promote the expression of drought tolerance related genes. LncRNAs can also interact with transcription factors and miRNAs, participating in the regulation of response responses to salt and drought stress (Cao et al., 2015). By integrating RNA Seq and small RNA sequencing (sRNA Seq) data, researchers have identified a large number of miRNA mRNA regulators involved in response to low temperature, freezing, and drought stress (Wang et al., 2022; Xu et al., 2023).

5 Case Studies in Functional Genomics of Tea

5.1 Functional gene discovery in Longjing 43

Longjing 43 is a widely cultivated high-quality green tea variety, and its outstanding aroma characteristics have long attracted attention. In recent years, researchers have discovered through high-quality reference genome assembly and pan-genome analysis that genes related to terpene synthesis in Longjing 43 and other dominant varieties have been amplified. This amplification is usually achieved through tandem duplication and the formation of gene clusters (Xia et al., 2020a; Chen et al., 2023) (Figure 2). Transcriptome analysis indicated that, the expression of these aroma-related genes, especially those involved in the monoterpene and sesquiterpene synthesis pathways, was elevated in young leaves and buds, which are the main raw materials of high-end tea products (Xu et al., 2018; Xia et al., 2020a). These results emphasize the significance of gene copy number variations and tissue-specific expression in the formation of the unique aroma of Longjing 43.

Genome-wide association studies (GWAS) and SNP variation studies conducted in Longjing 43 also revealed a strong correlation between allelic differences and the accumulation of key flavor metabolites (such as catechins, theanine, caffeine) (Yamashita et al., 2020; Fang et al., 2021; Chen et al., 2023). e.g., SNP loci in genes encoding flavonoid biosyntheses (*FLS*, *UGT*, *MYB*, *WD40*, etc.), and their transporter genes have been shown to be significantly associated with catechin content and overall tea quality (Xu et al., 2018; Fang et al., 2021). Currently, these genetic markers are being used to guide the genome-assisted breeding of Longjing 43 and related varieties, enhancing superior traits.

5.2 Regulatory network modeling in purple tea

Purple tea varieties (like Zijuan and Zikui), have a distinct purple appearance and potential health benefits due to their high content of anthocyanins. Pan-genome and transcriptome studies have found that anthocyanin

synthesis-related genes in purple tea, especially anthocyanin synthase (ANS), have copy number variations and functional variations, and these changes are the key factors determining the purple phenotype (Maritim et al., 2021; Cai et al., 2022; Tariq et al., 2024). Modeling of the regulatory network further revealed that, the co-expression modules composed of structural genes (e.g., PAL, 4CL, F3'H, DFR, UFGT), and transcription factors (such as MYB, bHLH, NAC, WRKY), play a synergistic role in anthocyanin synthesis and accumulation (Maritim et al., 2021; Cai et al., 2022).

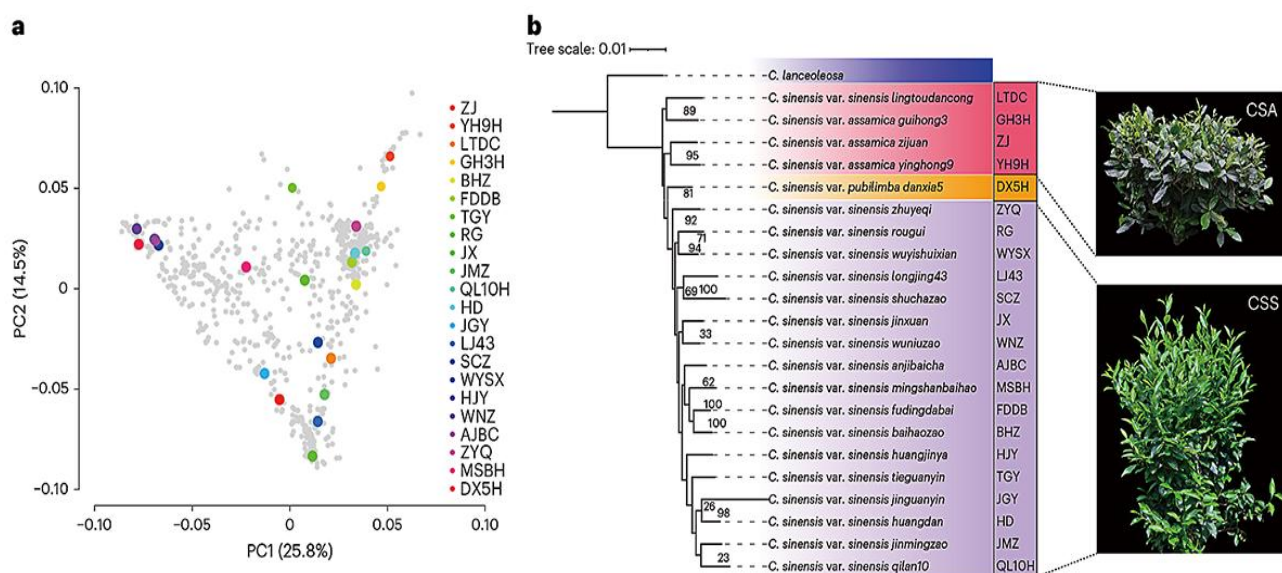


Figure 2 A total of 22 representative cultivars of tea plant were selected for the pangenome analysis. a, The 736 resequenced tea genomes were subjected to principal component analysis to reveal their genetic diversity. The coloured dots indicate the cultivars chosen for pangenome analysis, which collectively represent the broad genetic diversity of *C. sinensis* species. PC, principal component. b, Phylogenetic analysis of the 22 representative tea cultivars was conducted on the basis of 1,063 single-copy genes, with *C. lanceoleosa* as an outgroup. The selected cultivars are highlighted with different colours: CSA samples have a red background, CSP is indicated by yellow and CSS samples are represented by light blue. On the right, the images illustrate the morphological differences between CSA and CSS. The numbers on the branches represent the bootstrap values supported, with higher values indicating stronger bootstrap support (Adopted from Chen et al., 2023)

Taking the new variety of purple bud tea "Zikui" (ZK) as an example, Cai et al. (2022) revealed the molecular mechanism of its purple leaf formation through the integration of metabolome and transcriptome analysis. The research found that the accumulation of anthocyanins in the leaves of the purple sunflower reached its peak (4.97 mg/g) at 15 days, significantly higher than that of the green control variety N61. The relative abundance of the three main anthocyanins - cyanidin 3-O-glucoside, cyanidin 3-O-galactoside and cyanidin 3-O-glucoside - was the highest (Figure 3).

Further analysis indicated that the high expression of CsMYB90, and its targeted genes F3'H and ANS was closely related to the enrichment of the above-mentioned anthocyanins, clarifying the molecular association between transcription factor regulation and metabolite accumulation (Cai et al., 2022). These findings provide a theoretical basis, and practical targets for the molecular breeding and metabolic engineering of anthocyanin-enriched tea tree varieties.

6 Prospects of Functional Genomics in Tea Breeding

6.1 Trait-associated markers and genomic selection

With the development of pan genome construction, and high-throughput sequencing technology, researchers are able to identify functional SNPs and haplotypes, associated with key traits of tea trees, such as flavor, stress resistance, and leaf color. These variations were discovered through genome-wide association analysis (GWAS),

and resequencing of diverse germplasm, laying the foundation for deciphering the genetic basis of complex traits and developing trait specific molecular markers (Wang et al., 2020; Chen et al., 2023; Tariq et al., 2024).

Molecular marker assisted selection (MAS) and genomic selection (GS), are profoundly changing the breeding methods of tea plants, improving the accuracy of selection and shortening the breeding cycle. Especially genome selection can achieve higher genetic gain and cost-effectiveness, even under limited resource conditions. The integration of MAS and GS enables breeder to objectively select quality, and stress resistance traits at an early stage, thereby accelerating the cultivation of superior varieties (Yamashita et al., 2020; Lubanga et al., 2021; 2023).

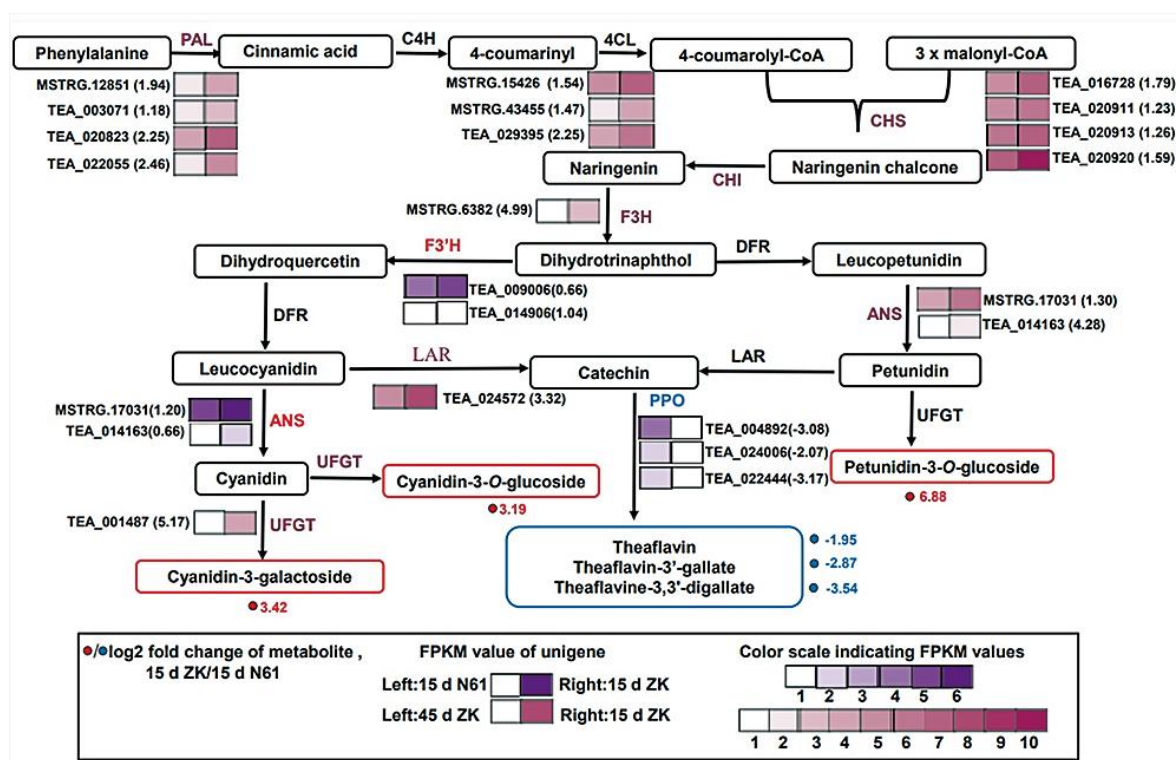


Figure 3 Transcriptional profiling of genes involved in the phenylpropane and flavonoid biosynthesis pathways in Zikui (ZK) and N61 tea cultivars. Grids with a purple color scale from light to dark represent fragments per kilobase of exon per million fragments mapped (FPKM) values of 0–10, 10–20, 20–40, 40–80, 80–160, and 160–320. Grids with a red color scale from light to dark represent FPKM values of 0–10, 10–20, 20–40, 40–80, 80–160, 160–320, 320–640, 640–1280, 1280–2560, and more than 2560. PAL, phenylalanine ammonia-lyase; C4H, cinnamic acid 4-hydroxylase; 4CL, 4-coumarate CoA ligase; CHS, chalcone synthase; CHI, chalcone isomerase; F3H, flavanone 3-hydroxylase; F3'H, flavonoid 3'-hydroxylase; DFR, dihydroflavonol 4-reductase; ANS, anthocyanin synthase; UFGT, UDP glucose-flavonoid 3-O-glucosyl-transferase; LAR, leucocyanidin reductase (Adopted from Cai et al., 2022)

Image caption: The figure shows the expression profiles of anthocyanin biosynthesis-related genes in the leaves of ZK and N61 at 15 and 45 days. The results indicate that key structural genes such as F3'H, ANS, and UFGT were significantly upregulated in ZK at 15 days, with expression levels higher than those at 45 days and in N61 at the same stage. This suggests that Zikui activates the anthocyanin biosynthetic pathway during the critical period of purple leaf formation, and the upregulation of structural genes is the main driving force behind anthocyanin accumulation (Adapted from Cai et al., 2022)

6.2 Functional gene mining and synthetic biology

Functional genomics techniques, like QTL mapping, GWAS, and pan genomic analysis, have provided strong support for key gene mining of important agronomic and quality traits (Chen et al., 2023; Tariq et al., 2024). With resources, researchers can identify and validate key candidate genes, achieving targeted improvement of traits.

Emerging synthetic biology tools, such as heterologous gene expression and metabolic engineering, are providing new avenues for improving tea quality and resistance. Functional validation by expressing candidate genes in model plants, as well as restructuring the synthesis of specific compounds, through metabolic pathway engineering, can help rapidly translate genomic discoveries into practical breeding outcomes (Zhang et al., 2020; Wang et al., 2023).

6.3 Challenges and future directions

The main challenge still faced at present is how to establish an effective connection between gene functions and complex quantitative traits, which are often controlled by multiple genes and significantly influenced by environmental factors. To solve this difficult problem, it is necessary to integrate multi-omics data, high-resolution positioning technology and functional verification methods, so as to achieve precise regulation of the target trait (Wang et al., 2023).

In the future, tea tree breeding will move towards the construction of an intelligent platform, integrating genomics, phenomics and bioinformatics, making full use of big data, machine learning and advanced molecular techniques to promote the development of sustainable breeding strategies and cultivate new tea tree varieties with high yield, stress resistance and high quality (Xia et al., 2020b; Li et al., 2023b).

7 Concluding Remarks

Over the past two decades, the research progress in tea plant functional genomics has been quite rapid. Technically, the construction of high-quality reference genomes, and pan-genomes has indeed played a key role. Especially behind core traits such as flavor, stress resistance and leaf color, researchers have identified a number of key genes and allelic variations. Meanwhile, the integration of multi-omics data, such as transcriptomics, metabolomics, and epigenomics, has also enabled us to gain a deeper understanding of the formation of tea tree quality and the mechanism of environmental adaptation.

Further, some changes at the genetic structure level, such as the expansion of gene families, tandem repeats and large-scale structural variations, have been confirmed to be closely related to the formation of the diversity of tea plant traits, especially in the synthesis of secondary metabolites and responses to stress. For instance, SNPS in the flavonoid synthesis pathway, have been associated with quality traits such as catechins. The discovery of structural differences, like presence/absence variations (PAVs), has also helped us better understand the genetic basis of tea plants in terms of cold resistance, disease resistance and flavor characteristics, providing a fundamental support for subsequent molecular breeding.

But, to truly implement these research results, there are still many practical problems to be faced. Although functional genomics has been continuously integrated with breeding techniques such as molecular marker-assisted selection, genomic selection and gene editing, it is still not easy to precisely match complex traits. Nowadays, there is still room for breakthroughs in data sharing, cross-platform integration and practical transformation. Tasks such as establishing a complete database and a bioinformatics tool platform, though not conspicuous, are indispensable parts of promoting intelligent breeding.

How to link the functions of key genes with actual agronomic traits and rapidly transform, and apply them in the breeding system still relies on the coordination of multi-disciplinary collaboration, high-throughput phenotypic technology and gene function verification. Tea plant functional genomics research is at a critical stage of transition from "information accumulation" to "precision application," promising to provide more solid theoretical and technical support for improving tea quality, enhancing environmental adaptability, and accelerating the development of new varieties.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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