



Transcriptomic Insights into Stress Physiology and Metabolic Adaptation in *Cinnamomum* Species

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Abstract: The genus *Cinnamomum* comprises ecologically, and economically important plant species widely recognized for their medicinal and aromatic properties, largely attributed to their rich secondary metabolite content. These species are frequently exposed to diverse environmental stressors that necessitate coordinated molecular responses to maintain physiological stability and metabolic balance. In this study, publicly available RNA-Seq datasets were analyzed to investigate stress-associated transcriptional responses in *Cinnamomum verum* and *C. camphora*. Differential expression analysis revealed extensive transcriptome reprogramming between control and stress-treated samples, indicating large-scale regulatory adjustments under stress conditions. Multivariate analyses demonstrated clear separation of samples according to treatment, supporting distinct stress-responsive expression patterns. Functional annotation and enrichment analyses showed that differentially expressed genes were predominantly involved in stress-responsive signaling pathways, defense mechanisms, and secondary metabolite biosynthesis, including phenylpropanoid, flavonoid, and terpenoid pathways. The coordinated activation of these pathways highlights the central role of specialized metabolism in stress adaptation and chemical defense. Overall, this study provides transcriptome-based insights into stress physiology and metabolic regulation in *Cinnamomum* species and demonstrates the applicability of RNA-Seq approaches for elucidating stress-responsive molecular networks in non-model woody plants.

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1. Introduction

Cinnamomum species, members of the Lauraceae family, are widely valued for their medicinal, aromatic, and commercial importance, largely due to their rich repertoire of secondary metabolites. These compounds, including phenylpropanoids, terpenoids, and flavonoids, contribute to diverse biological activities such as antimicrobial, antioxidant, anti-inflammatory, and anticancer effects (Ranasinghe et al., 2013; Sharifi-Rad et al., 2021). The pronounced phytochemical diversity of *Cinnamomum* species underpins their significance in pharmaceutical and food-related applications and highlights the need for detailed molecular investigations to elucidate the regulatory mechanisms governing metabolite biosynthesis (López et al., 2005; Jayaprakasha et al., 2011; Shari et al., 2025).

Plants are frequently exposed to environmental stressors such as drought, salinity, temperature extremes, and pathogen pressure, which impose significant constraints on growth and productivity. To cope with these challenges, plants have evolved complex physiological and molecular mechanisms that maintain cellular homeostasis and ensure survival. Central to these adaptive responses is the regulation of gene expression, which coordinates stress perception, signal transduction, defense responses, and the production of stress-related secondary metabolites (Zhu, 2016). Consequently, stress-induced transcriptional reprogramming often leads to large-scale shifts in both primary and specialized metabolic pathways.

RNA sequencing (RNA-Seq) has emerged as a powerful and widely adopted approach for capturing genome-wide transcriptional responses to environmental stress. This technology enables high-resolution analysis of transcriptome dynamics and has proven particularly valuable for non-model and woody plant species, where genomic resources are often limited (Wang et al., 2009; Love et al., 2014). Integration of RNA-Seq data with functional annotation frameworks such as Gene Ontology and KEGG pathway analysis facilitates systematic interpretation of differentially expressed genes and their roles in stress physiology and metabolic adaptation (Ashburner et al., 2000; Kanehisa and Goto, 2000).

In this context, the present study employs a transcriptome-based approach to investigate stress-responsive gene expression dynamics in *Cinnamomum verum* and *C. camphora*. Differential expression analysis was conducted to identify genes exhibiting significant transcriptional changes under stress conditions, followed by functional annotation to elucidate their involvement in key biological processes, including phenylpropanoid biosynthesis, MAPK signaling, and plant–pathogen interaction pathways. By elucidating the molecular basis of stress adaptation, this study aims to advance our understanding of how *Cinnamomum* species modulate physiological and metabolic processes in response to environmental challenges and to provide a foundation for future molecular breeding and bioengineering efforts targeting stress resilience in these economically important plants (Zhao et al., 2022).

2. Materials and Methods

2.1. RNA-Seq dataset and quality assessment

Publicly available RNA-Seq datasets of *Cinnamomum verum* (BioProject: PRJNA559058) and *C. camphora* (BioProject: PRJNA913600) were retrieved from the NCBI Sequence Read Archive (SRA). Each dataset comprised three biological replicates representing control and stress-treated conditions, with samples derived from bark tissue in *C. verum* and mature leaf tissue in *C. camphora*, as reported in the original studies.

Raw sequencing reads were initially assessed for quality using FastQC (Andrews, 2010), including evaluation of per-base sequence quality, GC content, read length distribution, and potential adapter contamination. Adapter trimming and quality filtering were performed using Trimmomatic (Bolger et al., 2014). Illumina adapter sequences were removed, and low-quality bases were trimmed using a sliding window approach. Reads with an average Phred quality score below 20 and reads shorter than 50 bp after trimming were discarded. Only high-quality reads passing all quality control criteria were retained for subsequent transcriptomic analyses.

Although detailed RNA extraction protocols were not fully described in the original studies, the overall sequencing quality metrics and post-filtering read characteristics indicated that the datasets were suitable for downstream differential expression and functional enrichment analyses.

2.2. Transcriptome mapping and gene expression analysis

Following quality filtering, high-quality reads were used for transcriptome-based expression analysis. Transcript quantification was performed using publicly available reference transcriptomes corresponding to *Cinnamomum verum* and *C. camphora*, obtained from the NCBI database.

Given the non-model status of *Cinnamomum* species and the absence of fully annotated reference genomes, a transcriptome-based strategy was adopted as an appropriate and widely accepted approach for RNA-Seq expression analysis in these species. Quality-filtered reads were quantified against the reference transcriptomes using Salmon, a lightweight and alignment-free method for transcript abundance estimation (Patro et al., 2017). Transcript-level abundance estimates were imported into R and summarized to gene-level count matrices using the tximport framework to ensure

compatibility with downstream differential expression analysis. Differential gene expression analysis between control and stress-treated samples was performed using DESeq2 (Love et al., 2014). Gene-level counts were normalized to account for differences in sequencing depth and dispersion, and statistical significance was assessed using adjusted p -values based on the Benjamini–Hochberg correction. Genes with an adjusted p -value < 0.05 and an absolute $\log_2$ fold change greater than 1 were considered significantly differentially expressed.

2.3. Functional annotation

Functional annotation of differentially expressed genes (DEGs) was conducted using eggNOG-mapper v2, which enables orthology assignment and functional classification based on evolutionary relationships (Cantalapiedra et al., 2021). Gene Ontology (GO) terms and KEGG Orthology (KO) identifiers obtained from eggNOG-mapper outputs were used for functional categorization and pathway analysis. KEGG pathway mapping was performed using KEGG Mapper to identify metabolic and signaling pathways associated with stress responses and secondary metabolite biosynthesis (Kanehisa et al., 2023).

2.4. Visualization

All statistical analyses and visualizations were performed using R (version 4.3.0). Principal component analysis (PCA) was applied to normalized gene expression data to explore global transcriptional patterns. Heatmaps of selected DEGs were generated using the ComplexHeatmap package, while volcano plots, GO term barplots, and KEGG pathway summaries were created using appropriate R-based visualization tools.

3. Results

3.1. RNA-Seq data quality overview

Quality control analysis confirmed high base quality scores and consistent GC content across all samples. After trimming, all datasets retained sufficient read depth and quality for transcriptomic analysis.

3.2. Differential gene expression

A total of 15116 differentially expressed genes were identified between control and stress-treated samples.

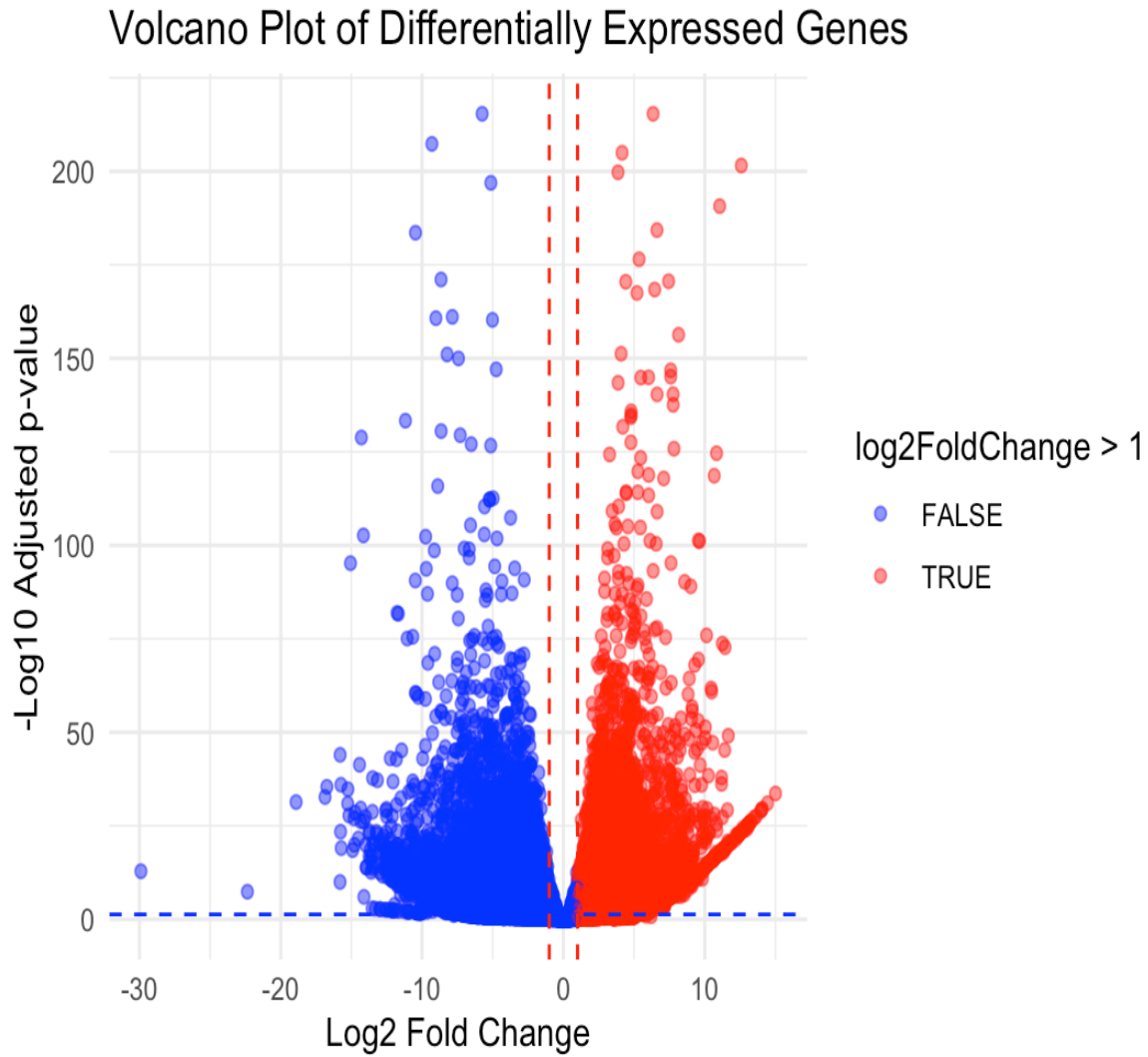
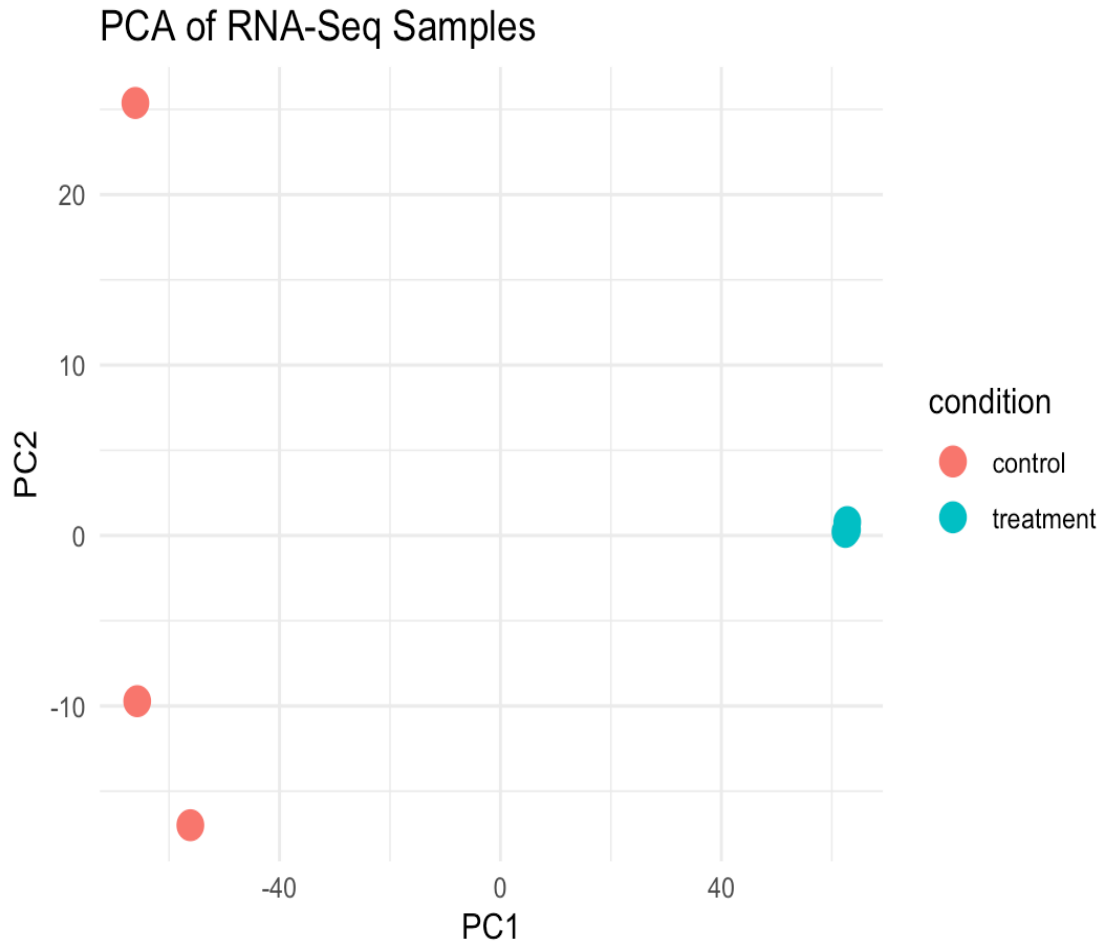


Figure 1. Volcano plot of differentially expressed genes (DEGs).

This large number of DEGs reflects extensive transcriptional reprogramming, consistent with genome-wide stress responses reported in woody and non-model plant species. Such extensive differential expression is consistent with severe stress-induced transcriptome remodeling and has been reported in non-model woody species lacking fully curated reference genomes.

3.3. Principal component analysis and heatmap clustering

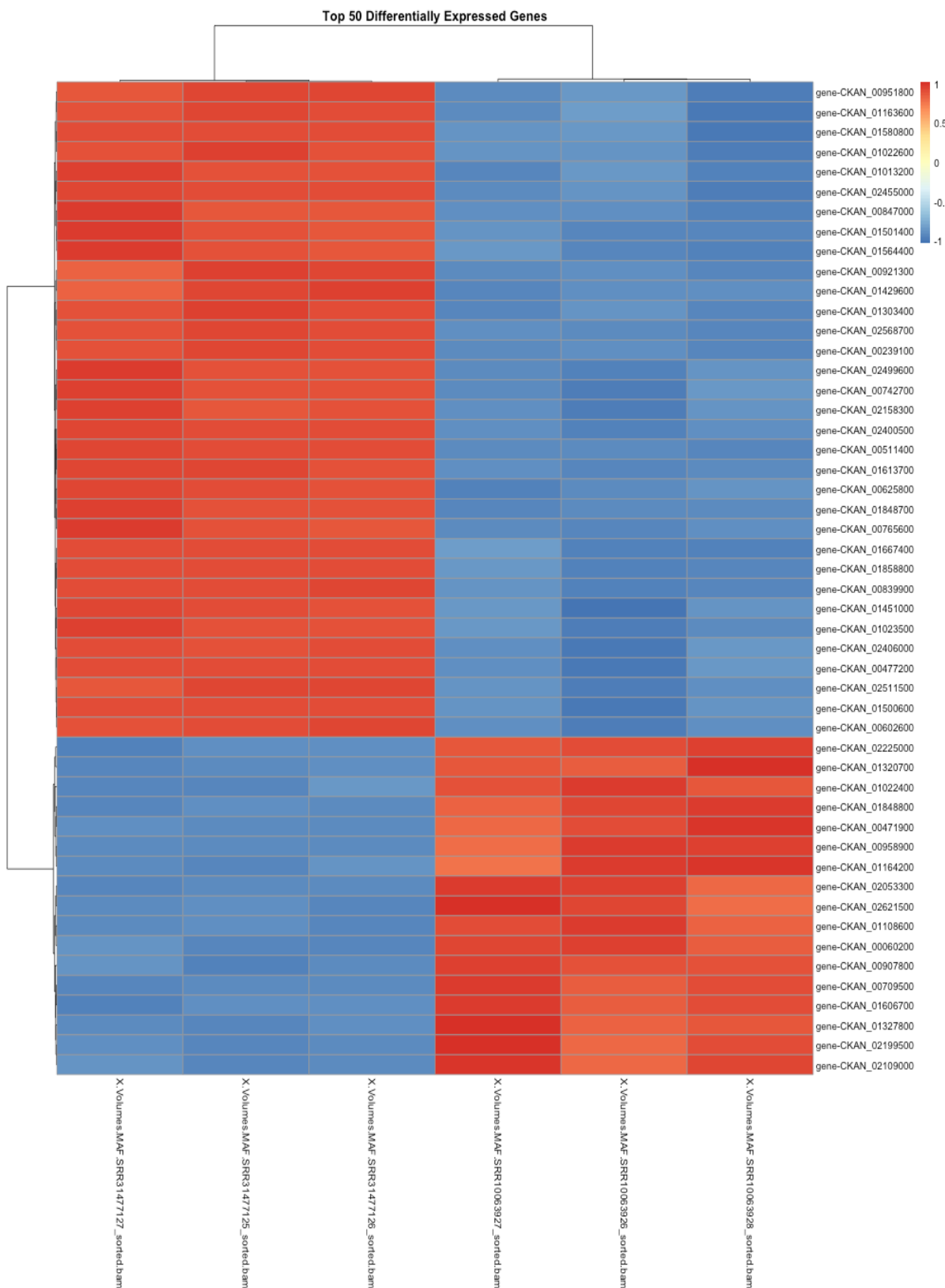
Principal component analysis revealed clear separation between control and stress-treated samples.



Principal component analysis (PCA) was performed using normalized gene expression values to examine global transcriptional patterns under control and stress conditions. The PCA plot shows clear separation between control and stress-treated samples along the principal components, indicating distinct stress-responsive transcriptional profiles. PC1 and PC2 explain 99.9998% and 0.0002% of the total variance, respectively, reflecting a dominant axis of transcriptional variation associated with stress treatment rather than species-specific differences.

Figure 2. Principal component analysis (PCA) of RNA-Seq samples.

PC1 accounted for 99.9998% of the total variance, indicating a dominant axis of stress-associated transcriptional change, while PC2 explained 0.0002% of the variance. Heatmap clustering of the top differentially expressed genes showed coherent grouping of replicates and condition-specific expression patterns.



Gene expression profiles across samples show clustering of upregulated (red) and downregulated (blue) DEGs.

Figure 3. Heatmap of the top 50 differentially expressed genes.

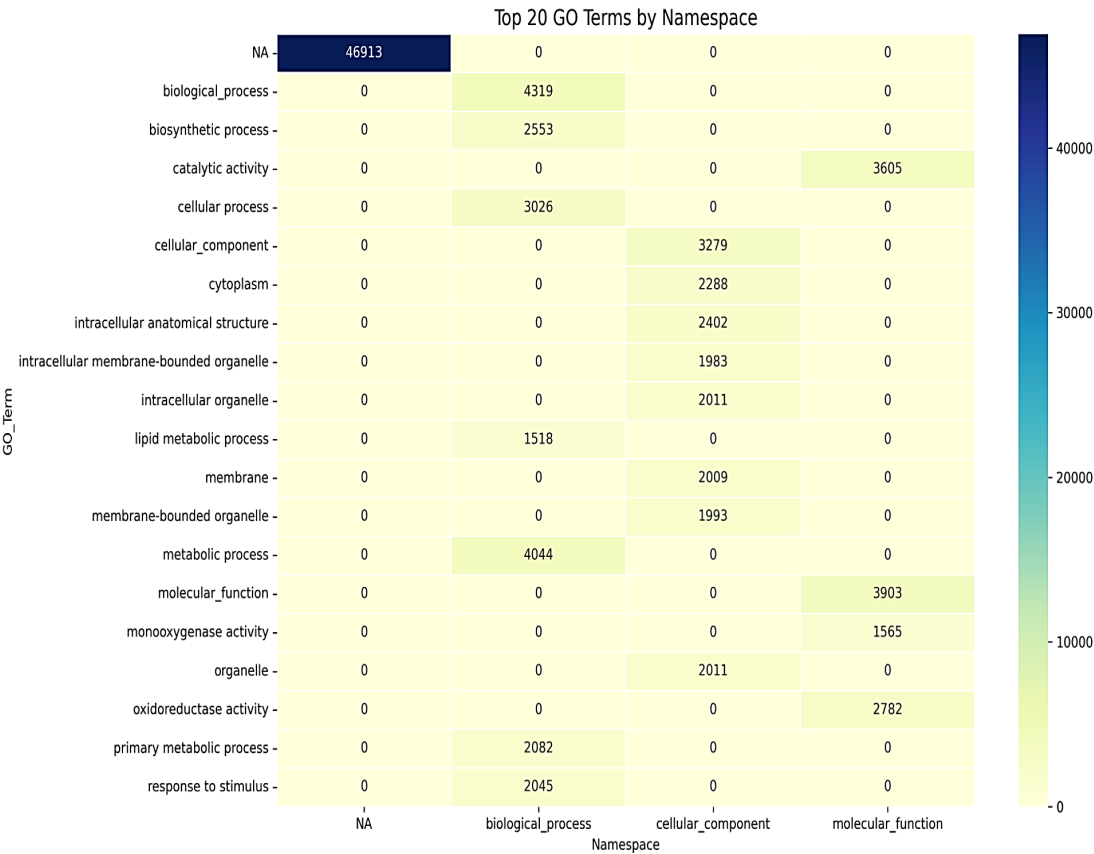
Table 1. Representative differentially expressed genes associated with stress response and secondary metabolism

Gene ID	Seed Ortholog	Description	KEGG KO	KEGG Pathway	PFAM
29584-33185_17	3988.XP_002540303.1	Cytochrome P450	ko:K09588, ko:K09590	map00905, map01100, map01110	p450
29584-33185_23	GSMUA_Achr3P08890_001	Cytochrome P450 family protein	ko:K09587, ko:K09588, ko:K09590	map00905, map01100, map01110	p450
29584-33185_25	XP_008233747.1	Cytochrome P450	ko:K09588, ko:K09590	map00905, map01100, map01110	p450
29584-33185_27	Gorai.011G286100.1	Cytochrome P450 family protein	ko:K09588, ko:K09590	map00905, map01100, map01110	p450
29584-33185_28	A0A087GK63	Cytochrome P450 family protein	ko:K12637	map00905, map01100, map01110	p450
29584-33185_31	XP_008233747.1	Cytochrome P450	ko:K09588, ko:K09590	map00905, map01100, map01110	p450
29584-33185_32	XP_010031233.1	Cytochrome P450 family protein	ko:K09588, ko:K09590	map00905, map01100, map01110	p450
31322-31577_2	XP_008233747.1	Cytochrome P450	ko:K09588, ko:K09590	map00905, map01100, map01110	p450
31722-31872_1	GSMUA_Achr3P08890_001	Cytochrome P450 family protein	ko:K09587, ko:K09588, ko:K09590	map00905, map01100, map01110	p450
32660-33185_7	XP_002540303.1	Cytochrome P450	ko:K09588, ko:K09590	map00905, map01100, map01110	p450
119394- 139575_125	XP_008361413.1	Oxidoreductase activity	—	—	2OG-FeII_Oxy, DIOX_N
430247-440504_1	VIT_08s0007g02980.t01	GMC oxidoreductase	—	—	GMC_oxred_N

This table presents annotation information for representative significantly differentially expressed genes associated with stress response and secondary metabolite biosynthesis, identified through differential expression analysis and eggNOG-mapper annotation. Corresponding KEGG Orthology (KO) identifiers, associated metabolic pathways, and PFAM domain annotations are provided.

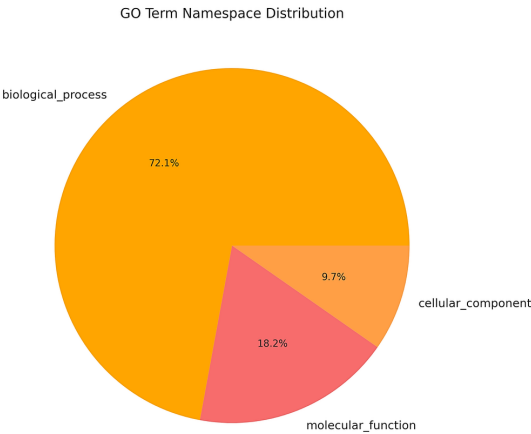
4. Discussion

Transcriptome-wide analyses revealed extensive reprogramming of gene expression in *Cinnamomum* species in response to environmental stress, highlighting coordinated regulation of stress-responsive signaling pathways and secondary metabolite biosynthesis. The high frequency of enriched biological process (BP) terms identified through Gene Ontology (GO) analysis underscores the dynamic modulation of metabolic, biosynthetic, and defense-related processes under stress conditions.



Most frequently enriched GO terms from biological process, molecular function, and cellular component domains are visualized.

Figure 4. Distribution of the top 20 GO terms across categories.

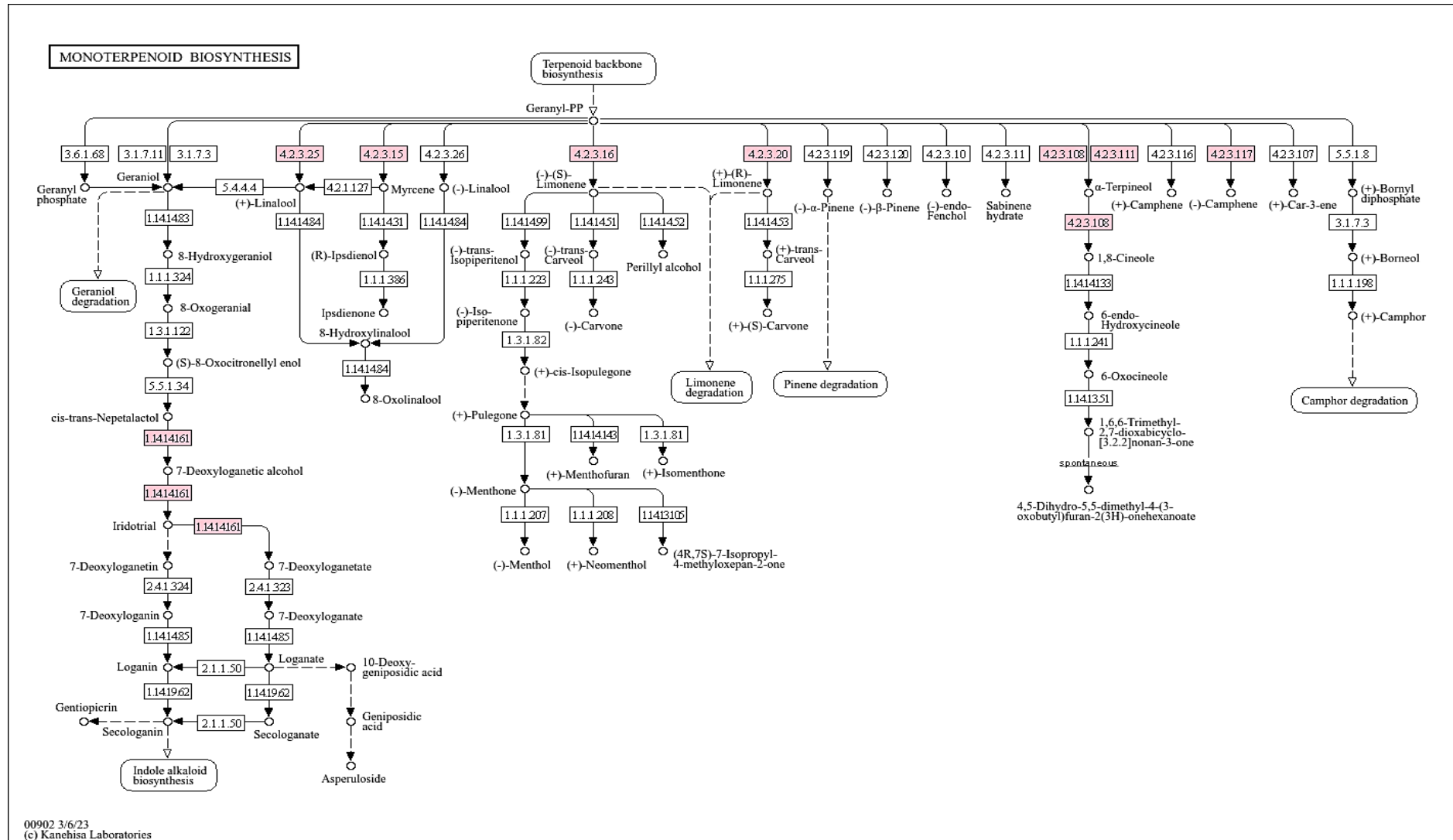


Proportional distribution of GO terms across biological process (BP), molecular function (MF), and cellular component (CC) domains among DEGs.

Figure 5. Pie chart of GO annotation categories.

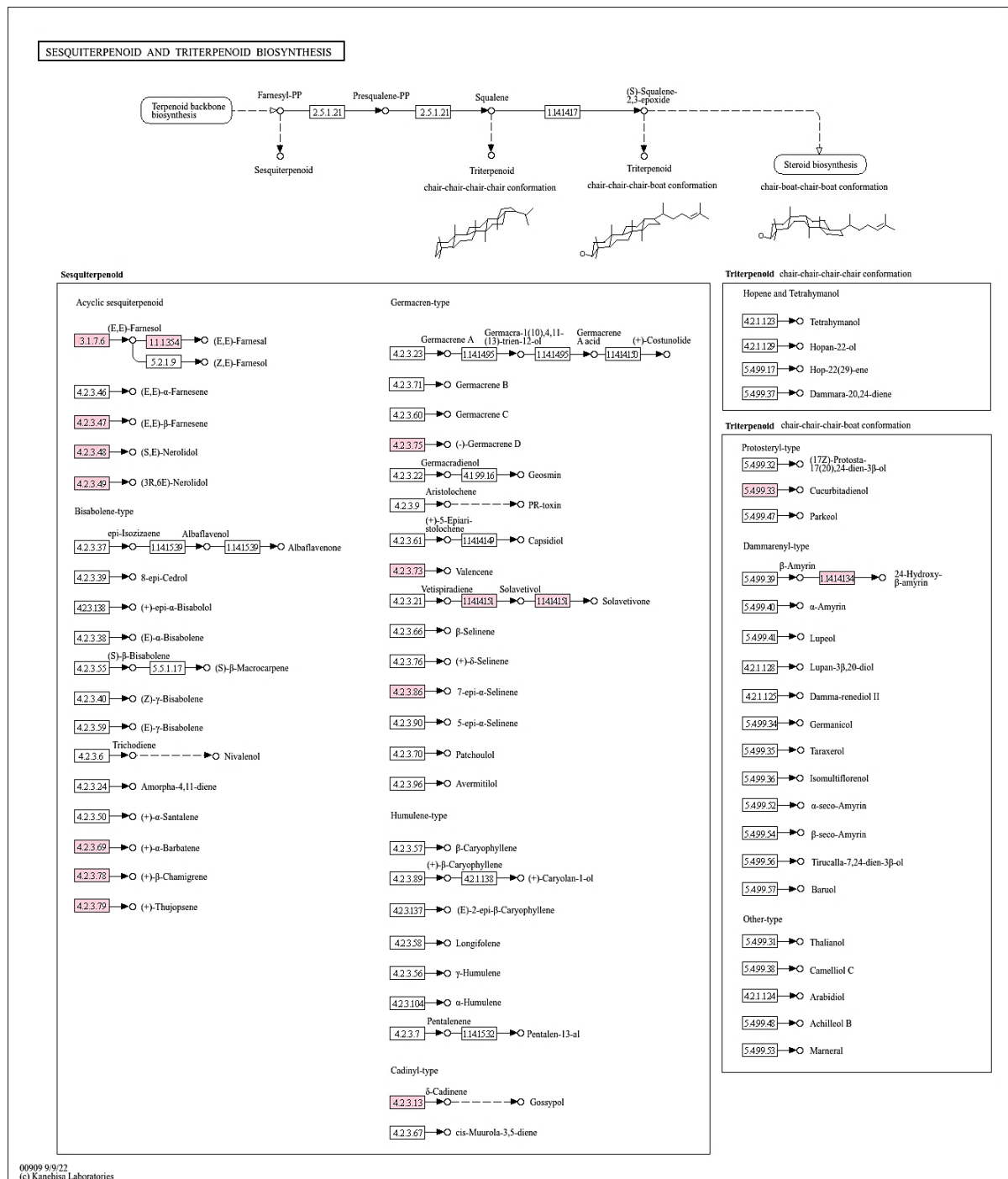
In particular, the enrichment of oxidoreductase and hydrolase activities suggests enhanced redox regulation and detoxification mechanisms, which are essential for mitigating oxidative damage and maintaining cellular homeostasis during stress exposure (Zhu, 2016).

The results of KEGG pathway enrichment analysis further support these observations, revealing substantial activation of secondary metabolite biosynthetic pathways, including phenylpropanoid, flavonoid, and terpenoid metabolism.



Differentially expressed genes associated with monoterpene production—compounds relevant to aroma and essential oils—are visualized.

Figure 6. KEGG pathway for monoterpene biosynthesis.



Genes linked to the production of medically relevant secondary metabolites are highlighted.

Figure 7. KEGG pathway of sesquiterpenoid and triterpenoid biosynthesis.

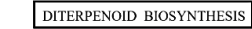
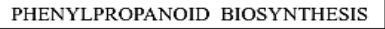


Figure 8. KEGG pathway for diterpenoid biosynthesis.

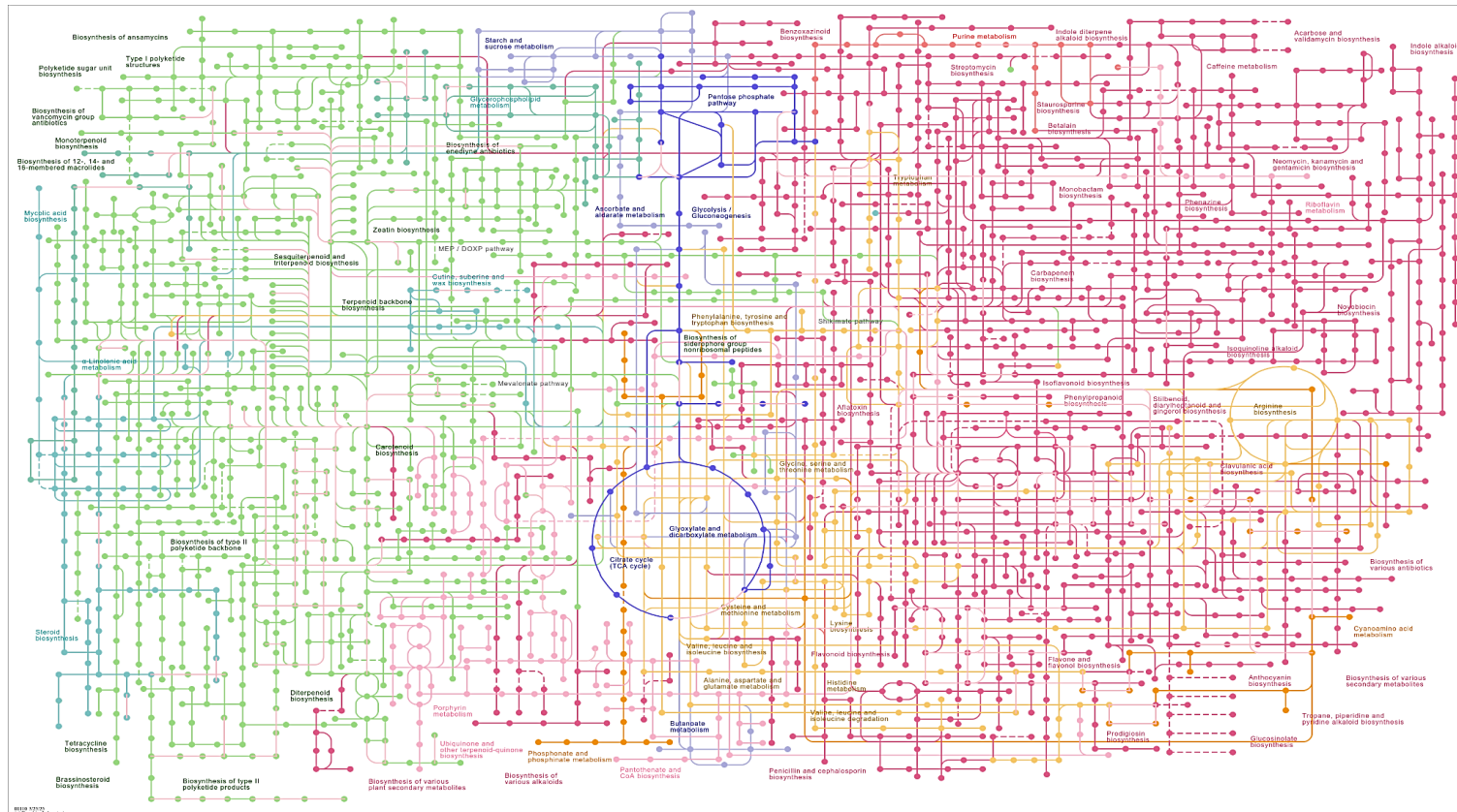


Genes involved in synthesizing lignin and phenolic compounds are annotated, reflecting their role in plant defense and structure.

Figure 9. KEGG pathway for phenylpropanoid biosynthesis.

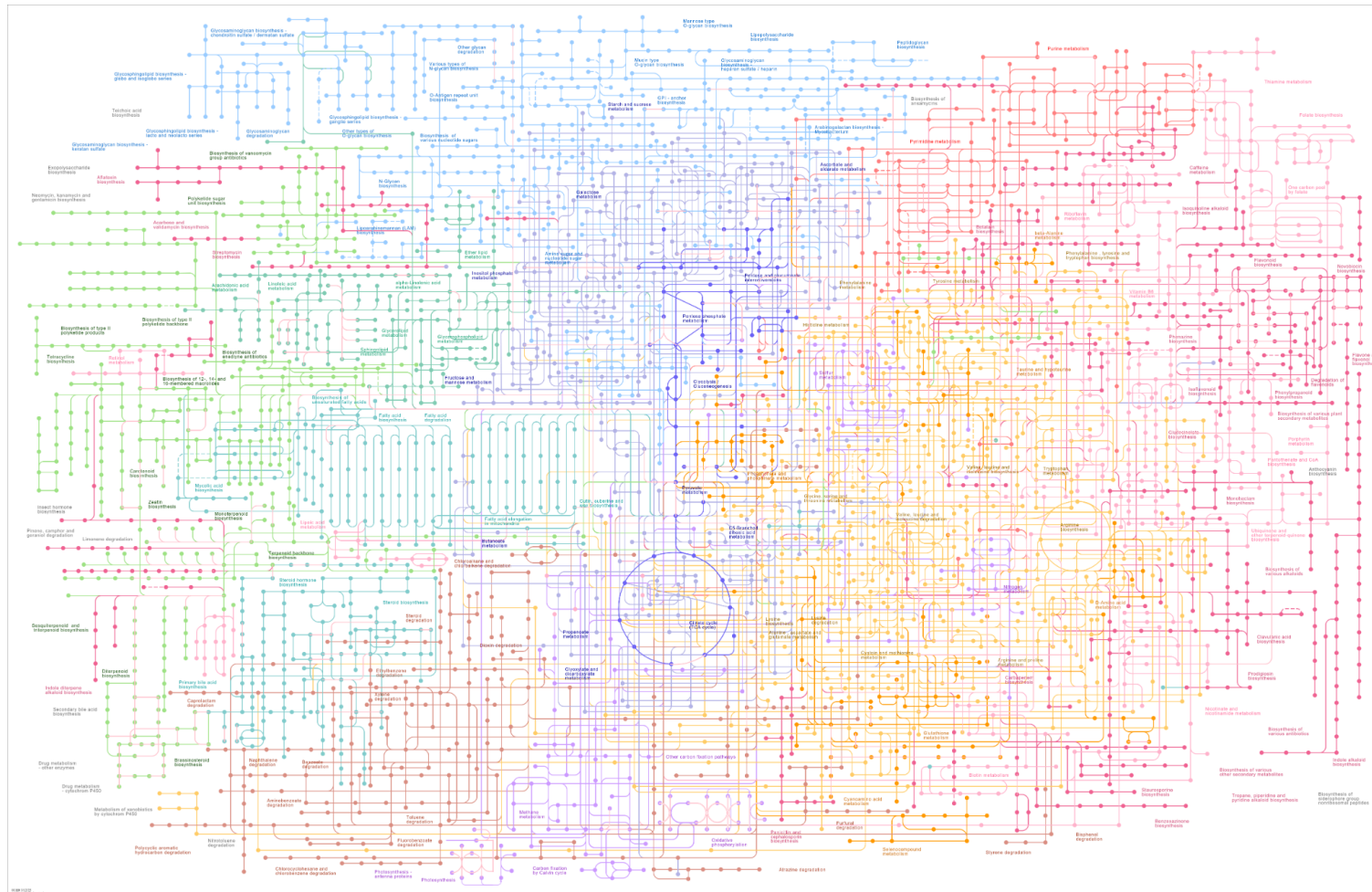


Figure 10. KEGG pathway of flavonoid biosynthesis.



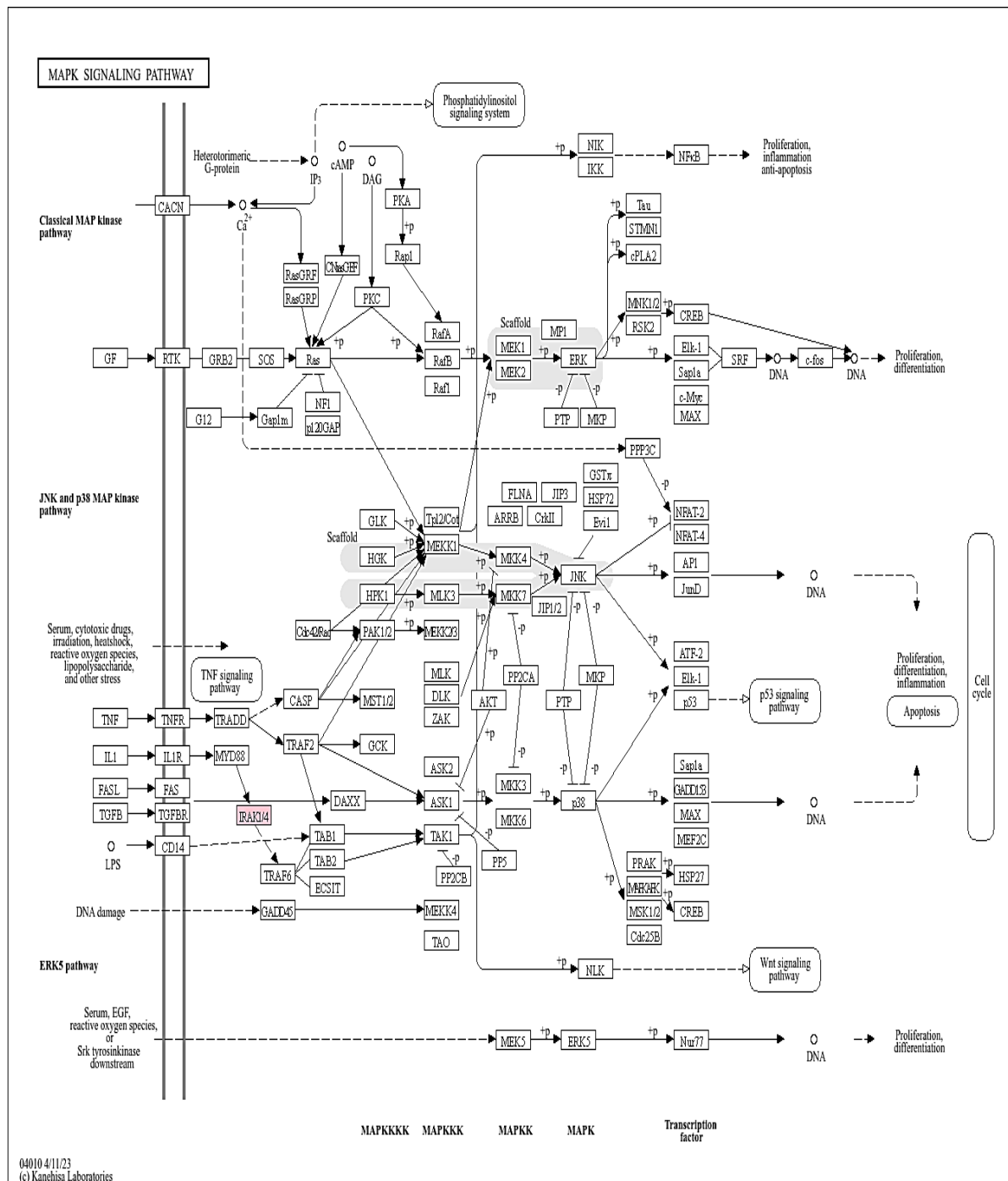
Comprehensive visualization of DEGs mapped to diverse secondary metabolic routes, including terpenoid, alkaloid, and flavonoid biosynthesis.

Figure 11. KEGG overview of secondary metabolite biosynthesis.



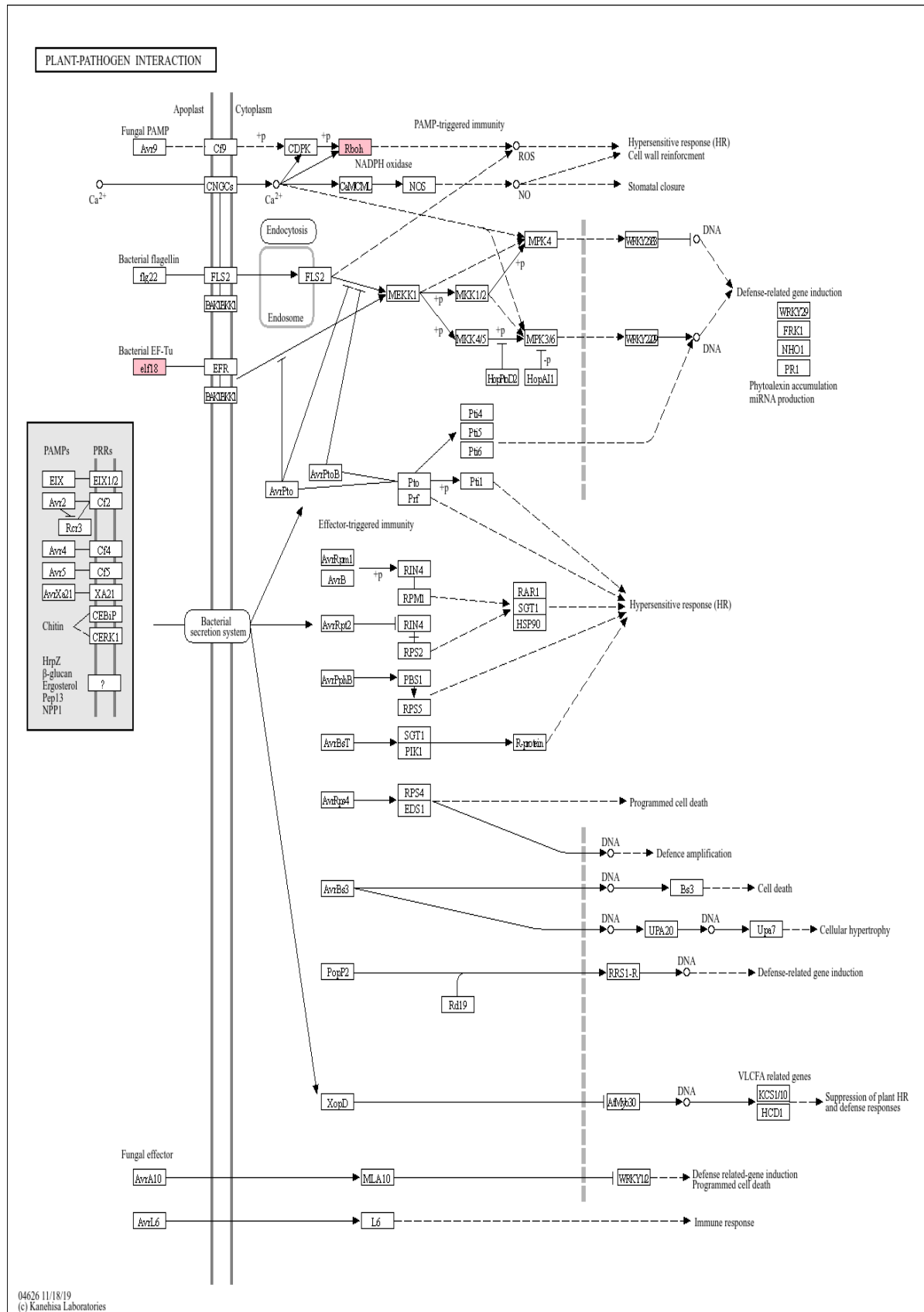
Genes are differentially expressed and mapped to general metabolic processes, such as carbohydrate and energy metabolism.

Figure 12. KEGG map of primary metabolic pathways.



Genes enriched in MAPK signaling, a key stress-responsive pathway, are shown based on KO annotations of DEGs. Pathway mapping highlights genes involved in intracellular signaling and defense.

Figure 13. KEGG representation of the MAPK signaling pathway in *Cinnamomum* species.



Differential expressions in genes related to immune signaling and pathogen recognition indicates enhanced stress response mechanisms.

Figure 14. KEGG pathway map of plant-pathogen interaction.

These pathways are well known for their roles in structural reinforcement, antioxidative defense, and chemical protection against environmental challenges. Increased transcriptional activity within these pathways likely reflects an adaptive strategy that enables *Cinnamomum* species to balance growth, defense, and metabolic demands under adverse conditions. Similar transcriptome-based studies have demonstrated that stress-induced activation of specialized metabolism represents a key molecular component of plant stress tolerance and ecological adaptation (Zhao et al., 2022).

In addition to metabolic pathways, the significant enrichment of MAPK signaling and plant–pathogen interaction pathways highlights the integration of biotic and abiotic stress responses within interconnected transcriptional networks.

MAPK cascades function as central hubs for stress signal transduction, coordinating downstream transcriptional responses that regulate defense-related genes and metabolic pathways. The concurrent activation of plant–pathogen interaction pathways suggests that *Cinnamomum* species employ overlapping molecular strategies to cope with diverse stressors, reflecting a multifaceted and cohesive stress-response architecture.

The identification of differentially expressed genes associated with these pathways provides a valuable foundation for understanding the molecular mechanisms underlying stress adaptation and secondary metabolism in *Cinnamomum* species. Notably, the enrichment of gene families involved in detoxification, redox balance, and specialized metabolite biosynthesis supports the notion that transcriptomic reprogramming plays a central role in enabling physiological flexibility under fluctuating environmental conditions. Such coordinated gene regulation contributes to phenotypic plasticity, allowing plants to dynamically adjust their metabolic and defensive strategies in response to stress.

Importantly, this study demonstrates the feasibility of obtaining high-resolution functional genomic insights in non-model plant species that lack fully annotated reference genomes. The integration of RNA-Seq data with functional annotation frameworks such as GO and KEGG enables systematic interpretation of complex transcriptomic responses, even in species with limited genomic resources (Wang et al., 2009; Ashburner et al., 2000; Kanehisa and Goto, 2000; Love et al., 2014). Collectively, these findings highlight the utility of transcriptome-based approaches for advancing our understanding of plant stress physiology and metabolic adaptation in economically and ecologically important non-model species.

Conclusion

This study provides a comprehensive transcriptomic assessment of stress adaptation and metabolic regulation in *Cinnamomum verum* and *C. camphora* using publicly available RNA-Seq data. Functional enrichment analyses based on Gene Ontology and KEGG pathways revealed substantial activation of secondary metabolite biosynthetic routes, including phenylpropanoid, flavonoid, and terpenoid pathways, which are closely associated with chemical defense and stress tolerance. The coordinated regulation of these pathways underscores the capacity of *Cinnamomum* species to initiate effective molecular defense mechanisms while maintaining metabolic balance under adverse environmental conditions.

The findings contribute to fundamental plant stress biology by demonstrating how large-scale transcriptome reprogramming supports phenotypic plasticity in *Cinnamomum* species. Such plasticity enables flexible adjustment of metabolic and defense-related processes in response to fluctuating environmental stressors. The observed enhancement of secondary metabolism further highlights the potential of these species to produce bioactive compounds of pharmaceutical and ecological relevance under stress conditions.

Importantly, the identification of stress-responsive and metabolism-related genes provides a valuable genetic resource for future functional and comparative studies. These transcriptome-derived insights may support downstream applications such as molecular breeding strategies, functional characterization of candidate genes, and metabolic engineering aimed at improving stress resilience in *Cinnamomum* and other non-model plant species.

Finally, this study demonstrates the feasibility of conducting high-resolution functional genomic analyses in plant species lacking fully annotated reference genomes. The integration of RNA-Seq data with functional annotation frameworks offers a robust and transferable approach for investigating stress

physiology and genetic adaptability in non-model and woody plants, thereby broadening the scope of transcriptome-based research in plant science.

Ethical Statement

Ethical approval is not required for this study because the research is based solely on publicly available RNA-Seq datasets and does not involve any experiments on humans, animals, or endangered plant species.

Conflict of Interest

The authors declare that there are no conflicts of interest.

Artificial Intelligence Declaration

The author declares that generative artificial intelligence tools were used during the preparation of this manuscript for text drafting, language editing, and refinement. Specifically, ChatGPT (OpenAI, GPT-5.2) was used to assist with language correction, structural organization, and improvement of scientific clarity. All scientific interpretations, analyses, and conclusions were critically reviewed and verified by the author. The author assumes full responsibility for the accuracy, integrity, and scientific validity of all content generated with the assistance of these tools.

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Author Contributions

M.A.F. conceived the study, performed all data analyses, interpreted the results, and prepared the manuscript. G.G. contributed to minor editorial assistance and general support during the manuscript preparation process. Both authors read and approved the final version of the manuscript.

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